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SYSTEMATIC EMBRYOLOGY OF THE ANISOPHYLLEACEAE[1]

HIROSHI TOBE[2] AND PETER H. RAVEN[3]

ABSTRACT

An embryological study of Anisophylleaceae, which comprise *Anisophyllea, Combretocarpus, Poga,* and *Polygonanthus,* and which have traditionally most often been referred as a tribe or subfamily to Rhizophoraceae, is presented as a contribution to the clarification of the systematic position of the family and the evolutionary interrelationships of its constituent genera. The gametic chromosome number of *Combretocarpus* is reported as $n = 8$, that of the other three genera as $n = 7$. Embryologically Anisophylleaceae are diversified and show differences from genus to genus, but they are clearly distinct from Rhizophoraceae in having their combination of consistent character states, including persistent nucellar tissue at least until early stages of seed development, thin two cell-layered inner integument (*Poga* and *Polygonanthus*), and exalbuminous seeds. In contrast to Rhizophoraceae, Anisophylleaceae agree almost completely with Myrtales in their embryological features of the order. Embryological evidence therefore supports the recognition of Anisophylleaceae as a distinct family and, with support from other lines of evidence, suggests a Myrtalean affinity for the family. Proposed assignments of Anisophylleaceae to Rosales or to Cornales are not supported. An analysis of similarities in character states in the four genera suggests that the ancestral Anisophylleaceae diverged into two main branches: one leading to *Anisophyllea* and *Combretocarpus,* and the other leading to *Poga* and *Polygonanthus. Combretocarpus,* with which *Anisophyllea* shares a few synapomorphies, is most specialized within the family in having many apomorphies. In contrast, *Poga* and *Polygonanthus* share many plesiomorphies, most of which are also common to *Anisophyllea.*

Anisophylleaceae, as defined here, consists of four genera and 34 species, *Anisophyllea* (30 spp.), *Combretocarpus* (1 sp.), *Poga* (1 sp.), and *Polygonanthus* (2 spp.) (Airy Shaw, 1973; Cronquist, 1981, 1983). In contrast with the stable assignment of three other genera, various authors have referred *Polygonanthus* to Euphorbiaceae (Ducke, 1932, 1933; Kuhlmann, 1940), Olacaceae (Croizat, 1939), Saxifragaceae (Baehni & Dansereau, 1939), or to its own family, Polygonanthaceae (Croizat, 1943). Despite these, there is little doubt, on the basis of morphological and wood anatom-

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TABLE 1. Studied taxa and collections.

Taxa	Collections
Anisophyllea disticha (Jack.) Baill.	Singapore. Bukit Timah Nature Reserve. *Sidek Bin Kiah & Tan Yam Leong s.n. in 1984,* no voucher. Singapore. Botanic Garden, Singapore. *Sidek Bin Kiah s.n. in 1984,* no voucher; *Mohd Shah s.n. in 1984,* no voucher. Malaysia. Maxwell Hill, Perak. *B. C. Stone 15403,* (KLU, MO). Brunei. *A. M. Juncosa s.n. in 1981,* no voucher.
Anisophyllea sp.	Cameroon. *D. W. Thomas 3494,* (MO).
Combretocarpus rotundatus (Miq.) Dans.	Malaysia. Kuching, Sarawak. *P. Chai s.n. in 1981, 1983, and 1985,* no voucher. Brunei. *A. M. Juncosa s.n. in 1983,* no voucher.
Poga oleosa Pierre	Cameroon. Korup Natl. Park. *D. W. Thomas 2273,* (MO). Nigeria. Awi, Akamkpa. *J. O. Ariwaodo s.n. in 1983,* (FHI 99607).
Polygonanthus amazonicus Ducke	Brazil. Along the Rio Paca, Amazonas. *J. Zarucchi 3138, 3184,* (US).

ical evidence, that *Polygonanthus* fits well in Anisophylleaceae, together with the three other genera that have traditionally been placed there (see Kuhlmann, 1944; Pires & Rodrigues, 1971; Van Vliet, 1976). Of the four genera of this family, *Anisophyllea* is relatively widely distributed in tropical Africa and Asia, also occurring in tropical South America; *Combretocarpus* is restricted to West Malaysia, *Poga* to tropical West Africa; and *Polygonanthus* to the Amazon Basin of Brazil (Pires & Rodrigues, 1971).

The relationships of Anisophylleaceae have been controversial. A traditional view, and the one most widely accepted, is that Anisophylleaceae have close affinities with Rhizophoraceae, and they often have been considered a tribe or subfamily within a broadly conceived Rhizophoraceae (Bentham & Hooker, 1865; Baillon, 1877; Schimper, 1893; Melchior, 1964; Pires & Rodrigues, 1971; Geh & Keng, 1974; Van Vliet, 1976; Takhtajan, 1980). Even when they have been treated as a distinct family, Anisophylleaceae have generally been considered closely related to Rhizophoraceae (Ridley, 1922; Corner, 1940). The resulting family, Rhizophoraceae sensu lato, has traditionally been placed in the Myrtales (Bentham & Hooker, 1865; Schimper, 1893; Melchior, 1964; Takhtajan, 1980), but Thorne (1983) placed Rhizophoraceae (composed of two subfamilies: Rhizophoroideae and Anisophylleoideae) in the Cornales.

Recently, however, Cronquist (1981, 1983) concluded that Anisophylleaceae were not closely related to Rhizophoraceae and assigned them to Rosales (Rosidae) and Rhizophoraceae sensu stricto to its own order, Rhizophorales (Rosidae). Dahlgren (1983), who also denied any close relationships between Anisophylleaceae and Rhizophoraceae, placed Anisophylleaceae in Cornales (Corniflorae) and Rhizophoraceae in its own order, Rhizophorales (Myrtiflorae; see also Dahlgren & Thorne, 1984).

In the light of these diverse opinions, we have attempted to determine whether Anisophylleaceae are actually closely related to Rhizophoraceae sensu stricto or not, or whether they might even be grouped together as one family. If the two groups are not closely related, what are their respective affinities?

Anisophylleaceae have been studied to a very limited extent, particularly regarding their anatomical characteristics. Their wood anatomy, however, has been studied relatively intensively (Marco, 1935; Geh & Keng, 1974; Van Vliet, 1976). Based on a comparison of the wood anatomy of the two groups, Van Vliet (1976) supported a broad definition of Rhizophoraceae including Anisophylleaceae. In contrast, Behnke (1984), basing his conclusions on the features of their sieve-tube plastids, suggested Anisophylleaceae were quite distinct from Rhizophoraceae sensu stricto. He found that both *Anisophyllea* and *Combretocarpus* have S-type plastids (containing starch grains only) in contrast to the P-type plastids (containing protein) that are characteristic of Rhizophoraceae sensu stricto. Another interesting distinction between the two groups, which has been known for some time, is that all four genera of Anisophylleaceae are aluminum accumulators; whereas the genera of Rhizophoraceae sensu stricto are not (Chenery, 1948; Kukachka & Miller, 1980). Although embryological information has been extremely useful in suggesting relationships at this level (see Tobe &

Raven, 1983), almost no information is available on Anisophylleaceae. The only published data on ovule morphology (of "*Anisophylleia zeylanica*") is that of Karsten (1891) nearly 100 years ago; however, most of these observations seem to be incorrect, as we shall discuss subsequently. Vaughan (1970) described the mature seed coat structure of *Poga,* providing a drawing; Geh and Keng (1974) reported on the endosperm in the seeds of *Anisophyllea* and *Combretocarpus.* Except for these fragments of information, apparently nothing has been reported about the embryological features of Anisophylleaceae.

In this paper, we present an overall study of the embryology of Anisophylleaceae, which is intended to provide information bearing on their relationships and systematic position. We have studied *Anisophyllea* and *Combretocarpus* in detail, and *Poga* and *Polygonanthus* to a lesser degree. Important features have been noted for all genera and are presented here.

MATERIALS AND METHODS

All four genera, *Anisophyllea, Combretocarpus, Poga,* and *Polygonanthus,* were investigated in this study. The species we studied are listed in Table 1 together with their voucher information. Flower buds and fruits in all stages of development were collected and fixed in FAA (5 parts stock formalin; 5 parts glacial acetic acid; 90 parts 70% ethanol); however, female buds of *Poga oleosa* and fruits of *Polygonanthus amazonicus* were not available. Herbarium material of *Anisophyllea* and *Combretocarpus* was studied to supplement our observations of fruits and seeds.

Preparations of microtome sections for observation were made following standard paraffin techniques. After dehydration through a tertiary-butyl alcohol series, the samples were embedded in Paraplast with 56–58°C mp. Flower buds of *Anisophyllea disticha* and fruits of *Poga oleosa* were too hard to be sectioned without being softened initially. Therefore, after these structures were trimmed to expose their tissues, the embedded samples attached to blocks were soaked in a mixture of a 10 : 3 : 90 glycerol : 10% Aerosol OT : water (Schmid & Turner, 1977) for at least several days at 20–25°C and then sectioned. Serial sections 6–10 μm thick were stained with Heidenhain's hematoxylin, safranin, and fast-green FCF and were mounted in Entellan. Mature seed coats of *Anisophyllea* sp. (*D. W. Thomas 3494,* MO) and *Poga oleosa,* which were too thick and hard to be sectioned by standard paraffin techniques, were embedded in a JB-4 plastic and stained with 0.1% Toluidine Blue.

In order to count the number of cells in mature pollen, we attempted to use safranin-staining of the grains (Tobe & Raven, 1984). We failed to obtain any staining of the pollen nuclei, however, probably because a thick exine hinders the infiltration of dye. Consequently, we counted the number of cells in the pollen using microtome-sectioned pollen grains. The expressions we have used for the frequency of different shapes of microspore tetrads follow those of Schmid (1982).

OBSERVATIONS

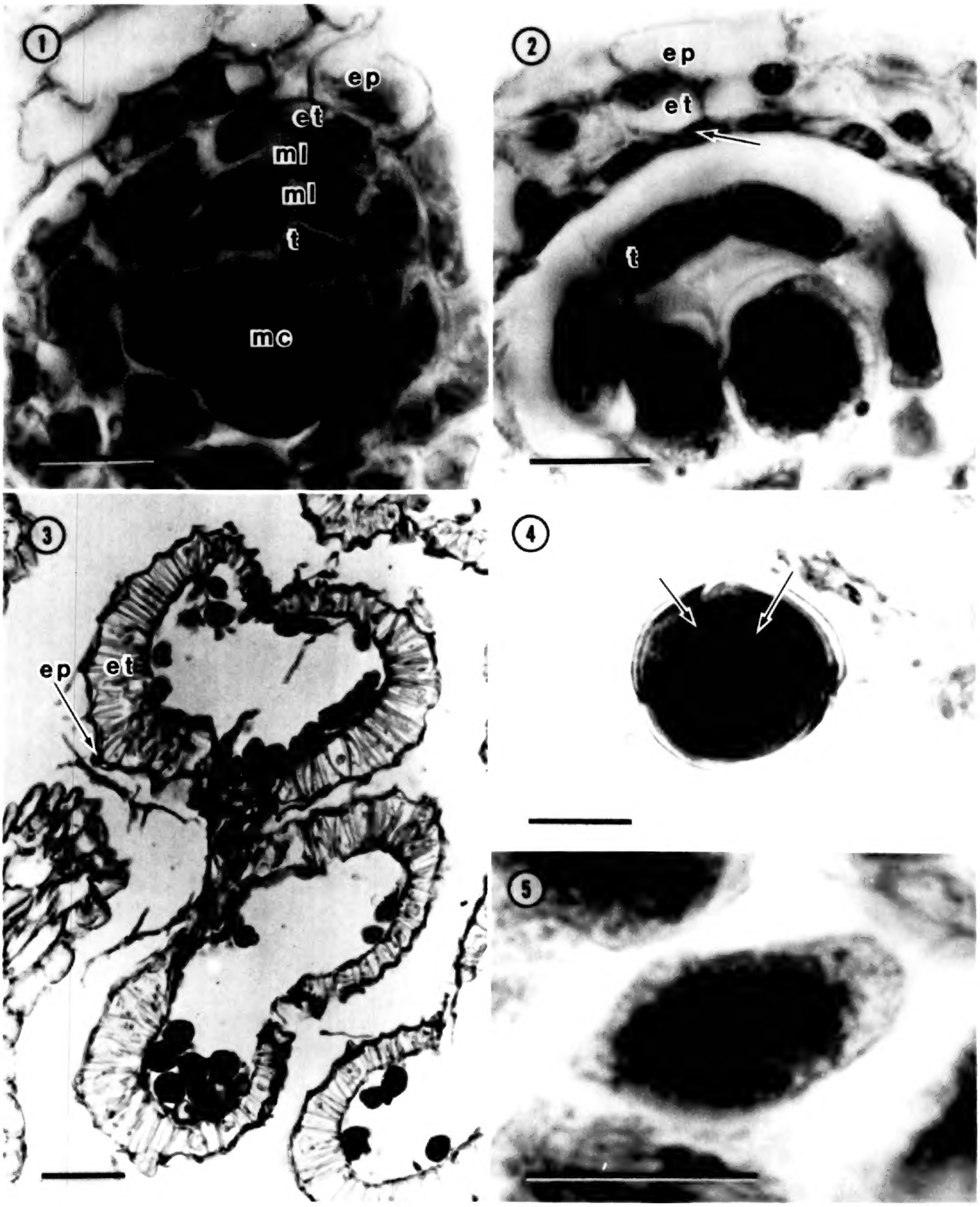
ANISOPHYLLEA R. BR.

The embryological characteristics were basically the same in the two species studied, one from Africa and one from Asia. The features reported in the following descriptions were found to be common to both species, unless particular comments are given.

Anther and microspores. The anther is tetrasporangiate. The wall prior to maturation comprises basically five cell layers: an epidermis, an endothecium, two middle layers, and a tapetum (Fig. 1); the wall formation therefore conforms to be the Basic type (Davis, 1966: 10). The anther wall, however, often has only one middle layer, which shares a histogenetic origin with the tapetum. The tapetum is glandular (Fig. 2). At one point in their development, the cells of the tapetum become 2-nucleate, but subsequently the two nuclei fuse with each other. During maturation, the middle layer(s) degenerate and the epidermal cells are stretched tangentially while the cells of the endothecium become more or less enlarged (Fig. 2). Eventually, the endothecium develops fibrous thickenings. Although the epidermis persists, it is often collapsed on the endothecium (Fig. 3). Anther dehiscence takes place by longitudinal slits (Fig. 3). The connective tissue between the two microsporangia of each theca is completely disorganized before an anther dehisces (Fig. 3).

Meiosis in a microspore mother cell is accompanied by simultaneous cytokinesis, and the resultant microspore tetrads, on the basis of 50 selected tetrads (of *Anisophyllea disticha*), are "usually" (92%) tetrahedral, "very occasionally" (6%) decussate, and "rarely" (2%) isobilateral. The pollen grains are two-celled at the time of shedding (Fig. 4).

Chromosomes. Since pollen mother cells between the telophase of meiosis I and the meta-



FIGURES 1–5. *Anisophyllea*.—1, 2, 4, 5. *A. disticha*.—3. *A.* sp. (*D. W. Thomas 3494,* MO).—1. Transverse section (TS) of a young anther showing the five cell-layered wall structure. Bar = 10 μm.—2. TS of an older anther with degenerating middle layers (arrow). Bar = 10 μm.—3. TS of a developed anther. Its wall consists of the fibrous endothecium and the epidermis. Bar = 50 μm.—4. Two-celled mature pollen at the time of shedding. Arrows indicate nuclei of the two cells. Bar = 10 μm.—5. Chromosomes of a pollen mother cell at a stage between telophase I and metaphase II. $n = 7$. Bar = 10 μm. ep, epidermis; et, endothecium; ml, middle layer; t, tapetum; mc, microspore mother cell.

phase of meiosis II were fixed by chance and included in microtome sections, we were able to count the chromosome number of *Anisophyllea* for the first time: *A. disticha* has $n = 7$ (Fig. 5).

Megagametophyte and nucellus. The ovule is anatropous. A single archesporial cell differentiates beneath the apical dermal layer of the nucellus (Fig. 6). The archesporial cell divides periclinally into two: the upper primary parietal cell and the lower sporogenous cell (Fig. 7). The primary parietal cell divides periclinally, and its derivatives further divide anticlinally and periclinally, forming parietal tissue with three to five layers above the embryo sac. The sporogenous cell develops into a megaspore mother cell and undergoes meiosis, giving rise to a linear tetrad of megaspores. A triad of megaspores may also be formed by suppression of the second, mitotic division on the micropylar side. In the megaspore tetrad (or triad), the chalazal megaspore functions (Fig. 8). A functional megaspore develops successively into a 2- (Fig. 9), 4- (Fig. 10), and 8-nucleate embryo sac (Fig. 11). Thus the mode of the embryo sac formation is of the *Polygonum* type. The synergids are slightly hooked (Fig. 12). The three antipodal cells are ephemeral, degenerating before fertilization. The two polar nuclei fuse into a single central nucleus, which is positioned near the egg apparatus (Fig. 13). Consequently an organized mature embryo sac has only five nuclei or cells: an egg cell, two synergids, and two polar nuclei (as a single central nucleus; Figs. 12, 13).

During megasporogenesis and megagametogenesis, apical epidermal cells of the nucellus divide periclinally, and their daughter cells also repeat periclinal divisions. As a result, a four to six cell-layered nucellar cap is formed above the embryo sac (Fig. 14); Karsten (1891) also illustrated such a nucellar growth in "*Anisophylleia zeylanica.*" The nucellar cap and the other nucellar tissue, both of which enclose the embryo sac, persist into younger stages of fruit development (Figs. 11, 14, 17). There is no case in which the nucellar tissue degenerates before fertilization so that the embryo sac directly borders on the integument.

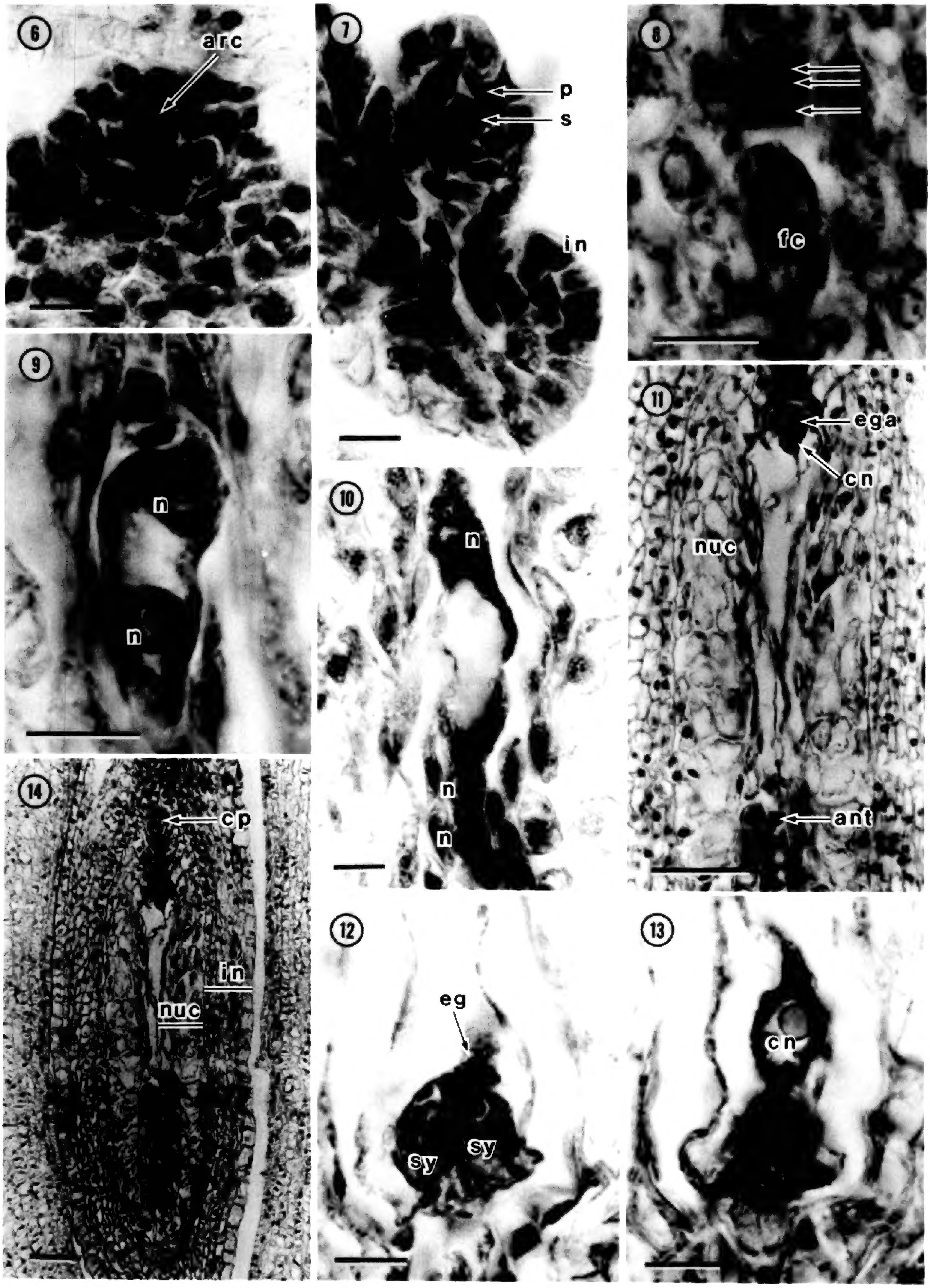
Integument. The ovule has a single integument (Figs. 7, 15), although Karsten (1891) described the ovule of "*Anisophylleia zeylanica*" as having two integuments. Judging from the drawing he published, it seems very probable that Karsten misunderstood a persistent, lateral nucellar tissue surrounding the embryo sac as the inner integument and the (only) true integument as the outer integument.

A micropyle is always formed by the integument, excepting one very unusual case in which the integument did not grow beyond the nucellar apex (Fig. 16). In this respect as well, Karsten (1891) seems to have erred: he considered the persistent, lateral nucellar tissue to be the inner integument, which he concluded did not enclose the nucellar apex. In fact, Karsten concluded that a micropyle is not formed in "*Anisophylleia zeylanica.*" Referring to Karsten's drawing of ovules and descriptions, we also mistakenly characterized the ovule of *Anisophyllea* not only as being bitegmic but also as having a nucellar beak (which actually was the well-developed persistent nucellar cap; see Tobe & Raven, 1983).

The integument is about five to seven cells thick in *Anisophyllea disticha* (Fig. 15) and about four to five cells thick in *A.* sp. (Fig. 17). The thickness of the integument is not different from one part of ovule to another, and therefore the cross section of the ovule is nearly circular (Fig. 17). A raphe bundle ramifies oblique-laterally toward the chalazal end (Fig. 18). Therefore in cross section the ovule or fruit has four to five vascular bundles at the peripheral part of the integument of testa (Fig. 19).

Throughout the development of the ovule or fruit, the integument or seed coat is thickened by secondary multiplication. However, the innermost cell layer never differentiates toward the so-called endothelium.

Fertilization, endosperm, and embryo. Despite their multiovular condition in *Anisophyllea* (usually four and rarely three ovules per ovary), fruits were always one-seeded. Fertilization is porogamous. Endosperm formation is of the Nuclear type (Fig. 20). Because of incompleteness of our fruit sample, we could not confirm whether or not wall formation takes place in free endosperm nuclei. Hand-sectioned mature seeds of the two species we studied lacked endosperm (Fig. 21). Concerning the presence of endosperm in seeds, Hou (1958) described that in *Anisophyllea disticha* seeds consist of a solid body, of which the main part is formed by a thick, hard albumen. Geh and Keng (1974) stated that in *Anisophyllea disticha*, the entire undifferentiated embryo is embedded in endosperm; consequently, they characterized the seed of Anisophylleae (*Anisophyllea* and *Combretocarpus*) as albuminous. Based on results of our observations, however, it seems that what Hou thought



FIGURES 6–14. *Anisophyllea.*—6, 7, 9–13. *A. disticha.*—8. *A.* sp. (*D. W. Thomas 3494,* MO).—6. Longitudinal section (LS) of an ovular primordium with the 1-celled archesporium. Bar = 10 μm.—7. LS of a young ovule with the primary parietal cell. Bar = 10 μm.—8. LS of a young ovule with the functional megaspore. Arrows above the functional megaspore indicate three degenerating megaspores. Bar = 10 μm.—9. LS of an ovule at the 2-nucleate embryo sac stage. Bar = 10 μm.—10. LS of an older ovule at the 4-nucleate embryo sac stage. One of the two nuclei at the micropylar side appears in the next section. Bar = 10 μm.—11. LS of a nearly

to be the thick, hard albumen was actually the embryo itself, and that the seed that Geh and Keng observed was too young to confirm the endosperm condition.

Although we did not pursue the whole process of embryogenesis either, the development of proembryos and embryos seems to proceed normally (Fig. 20). In embryos of the two species we studied, which were dissected from mature fruits, we could not observe differentiation of the cotyledons. Geh and Keng (1974), however, reported two protuberances on the apical part of the embryo in *Anisophyllea disticha,* which they interpreted as two cotyledons. We conclude that the cotyledons of *Anisophyllea* either develop incompletely or are essentially absent in *Anisophyllea.* No hypostase is differentiated after fertilization.

Mature seed and seed coat. The mature seed is narrowly cylindrical, 13.0–13.5 mm long and 3.8–4.0 mm thick in *Anisophyllea disticha,* whereas it is ovoid or elliptical in outline, 13.0–13.8 mm long and 6.0–6.4 mm thick in *A.* sp. (Fig. 21). In the young seed, the seed coat appears to be constructed of a thick, massive tissue, with the outer epidermis specialized and tanniferous (Fig. 22). In the mature seed, the seed coat is formed both of a conspicuous outer epidermis and a multiple inner layer about 25–30 cells thick (Fig. 23). The cells of the outer epidermis are thick-walled and cuboid, whereas those of the underlying multiple inner layer are also thick-walled but extremely stretched tangentially.

COMBRETOCARPUS HOOK F.

Anther and microspores. The anther is tetrasporangiate. The wall prior to maturation comprises five cell layers: an epidermis, endothecium, two middle layers, and a tapetum (Fig. 24). Wall formation conforms to the Basic type. During maturation, the cells of the epidermis are somewhat enlarged and become tanniferous; the cells of the endothecium are also enlarged; the middle layers degenerate (Fig. 25). The tapetum is glandular, and its cells become 2-nucleate. The two nuclei in a tapetal cell later are fused with each other. Thus the mature anther wall is composed of the persistent but somewhat collapsed epidermis and the fibrous endothecium (Fig. 26). By the time of anther dehiscence, the connective tissue between two microsporangia of each teca degenerates completely. After dehiscence by longitudinal slits, the anther wall is remarkably reflexed (Fig. 27).

Meiosis in the microspore mother cells is accompanied by simultaneous cytokinesis. The shape of the resultant tetrads, on the basis of the examination of 50 selected tetrads, is "usually" (78%) tetrahedral, "occasionally" (14%) decussate, and "very occasionally" (8%) isobilateral. The pollen grains are two-celled at the time of shedding (Fig. 28).

Chromosomes. Pollen mother cells at the metaphase of meiosis I happened to be fixed and appeared in microtome sections. On the basis of those sections, we observed the chromosomes of *Combretocarpus* for the first time and determined $n = 8$ (Fig. 29). Size differences seem to be present among those eight chromosomes.

Megagametophyte and nucellus. The ovule is anatropous and crassinucellate. The archesporium is nearly always 1-celled (Fig. 30). A multicellular archesporium may very rarely differentiate—an ovule or young fruit containing twin embryo sacs was very rarely observed (Fig. 38). The archesporial cell divides periclinally into two: the upper primary parietal cell and the lower sporogenous cell. The primary parietal cell may or may not divide further periclinally; if it does so, a two cell-layered parietal tissue is formed. The sporogenous cell develops into a megaspore mother cell (Fig. 31). After enlarging in volume, the megaspore mother cell undergoes meiosis. After meiosis I, however, the subsequent mitosis in each megaspore of the dyad is not accompanied by cytokinesis. As a result, both the micropylar and the chalazal megaspore of the dyad become 2-nucleate (Fig. 32). The chalazal megaspore is functional. Then, while the micropylar megaspore degenerates, the two nuclei in the

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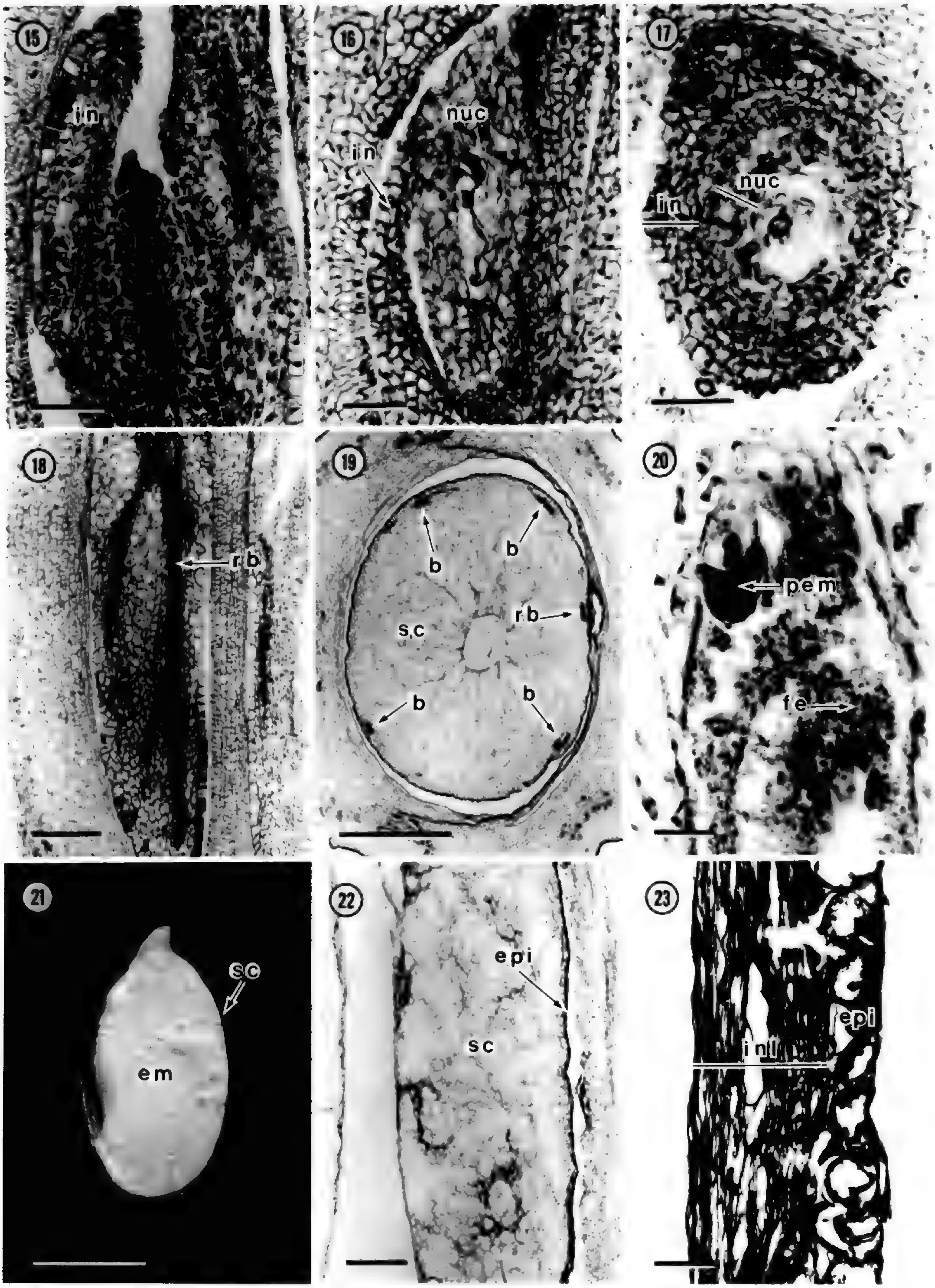
mature ovule at the 8-nucleate embryo sac stage. Of the eight nuclei, two polar nuclei are fused into a single central nucleus, and three antipodal cells are degenerating. Bar = 50 μm.—12, 13. Two serial LSs of a part of the mature ovule showing the egg apparatus and the central nucleus. Bars = 10 μm.—14. Same as Figure 11, but at a lower magnification. Note that the nucellar tissue is persistent and that no cell layer of the integument shows differentiation into an endothelium. Bar = 50 μm. arc, archesporial cell; p, primary parietal cell; s, sporogenous cell; fc, functional megaspore; n, nucleus of the embryo sac; eg, egg cell; ega, egg apparatus; cn, central nucleus; ant, antipodal cell; sy, synergid; nuc, nucellar tissue; in, integument; cp, nucellar cap.



FIGURES 15–23. *Anisophyllea*.—15, 18–20, 22. *A. disticha*.—16, 17, 21, 23. *A.* sp. (*D. W. Thomas 3494*, MO).—15. Longitudinal section (LS) of a young ovule. Note that the ovule is unitegmic. Bar = 50 μm.—16. LS of an unusual mature ovule lacking a micropyle. Bar = 50 μm.—17. Transverse section (TS) of a mature ovule. Bar = 50 μm.—18. LS of a mature ovule tangentially cut through a raphe showing the ramification of a raphe bundle. Bar = 100 μm.—19. TS of a young seed. Note that the thick seed coat contains several vascular bundles at the peripheral part. Bar = 1 mm.—20. LS of a young seed containing a proembryo and free endosperm

functional chalazal megaspore separate from each other: one moves toward the micropylar end, while the other moves toward the chalazal end (Fig. 33). Each nucleus divides successively to form a 4- and an 8-nucleate sac (Fig. 34). Thus the embryo sac formation conforms to the bisporic *Allium* type. The synergids are slightly hooked, and the antipodals are ephemeral, disappearing before fertilization. Two polar nuclei do not fuse with each other until fertilization takes place; they are positioned near the egg apparatus. A mature embryo sac just before fertilization is composed of five nuclei or cells: an egg cell, two synergids, and two polar nuclei.

Embryo sacs characteristically accumulate an abundance of starch grains (Fig. 35). The starch grains, which begin to accumulate from the 2-nucleate embryo sac stage, are most abundant in the 8-nucleate embryo sac stage but disappear after fertilization.

During megasporogenesis and megagametogenesis, the nucellar tissue does not show any particular differentiation and persists at least until the earliest fruit stages (Figs. 36, 38). Apical dermal cells of the nucellus do divide periclinally (Fig. 37), and their daughter cells also repeat periclinal divisions, thus forming a nucellar cap four to six cell layers thick above the embryo sac (Fig. 36).

Integument. The ovule is unitegmic (Figs. 31, 36). The growing integument is about four or five cells thick (Figs. 36; see also Fig. 38). No difference in thickness exists between the different parts of the ovule. Therefore, except for the raphe, the cross section of ovule is nearly circular (Fig. 38). The integument is not vascularized. Neither secondary multiplication of the integument nor differentiation of the innermost cell layer into a so-called endothelium occur.

The integument elongates beyond the nucellar apex and forms a micropyle (Fig. 36).

Fertilization, endosperm, and embryo. The fruits are always one-seeded. Fertilization is porogamous. After fertilization, the fruit elongates remarkably (Fig. 39). Endosperm formation is of the Nuclear type (Fig. 40). In the early stages, free endosperm nuclei are located around the proembryo (Fig. 40) and at the peripheral region of the embryo sac (Fig. 43). Because of incompleteness of our fruit sample, we could not observe to what degree an amount of endosperm increases later. The mature seeds lack endosperm (Figs. 41, 42). We did not investigate embryogenesis in detail but can state, on the basis of our observations of a few microtome-sectioned proembryos, that it proceeds normally (Fig. 40).

Within the mature fruit of *Combretocarpus*, the embryo is elongate and nearly circular in cross section (Figs. 41, 42). The embryo is dicotyledonous with two small cotyledons and a long hypocotyl (Fig. 41).

The hypostase is not differentiated even after fertilization.

Mature seed and seed coat. The mature seed is linear, 9.5–10.4 mm long and 1.2–1.3 mm thick; it contains several vascular bundles in the raphe (Fig. 42), which are derived by ramification from a raphe bundle. These bundles are restricted to the raphe, never entering the integument or testa.

In the young seed, the seed coat is composed of a tanniferous outer epidermis and a multiple inner layer, which degenerates (Fig. 43). Eventually, in the mature seed, the seed coat comprises only the outer epidermis, which is formed of pigmented, cuboid cells (Fig. 44).

POGA PIERRE

Anther and microspores. The anther is tetrasporangiate. The wall prior to maturation comprises five cell layers: an epidermis, endothecium, two middle layers, and a tapetum (Fig. 45). Wall formation conforms to the Basic type. During maturation, cells of the epidermis as well as of the endothecium enlarge, while the middle layers degenerate (Fig. 46). The tapetum is glandular, and its cells become 2-nucleate (Fig. 46). The two nuclei in a tapetal cell are not fused with each other. The mature anther wall is composed of the persistent epidermis and the endothecium. The epidermis is tanniferous, and the endothecium develops fibrous thickenings (Fig. 47). The anther dehisces by longitudinal slits. By the time of dehiscence, the connective tissue between two

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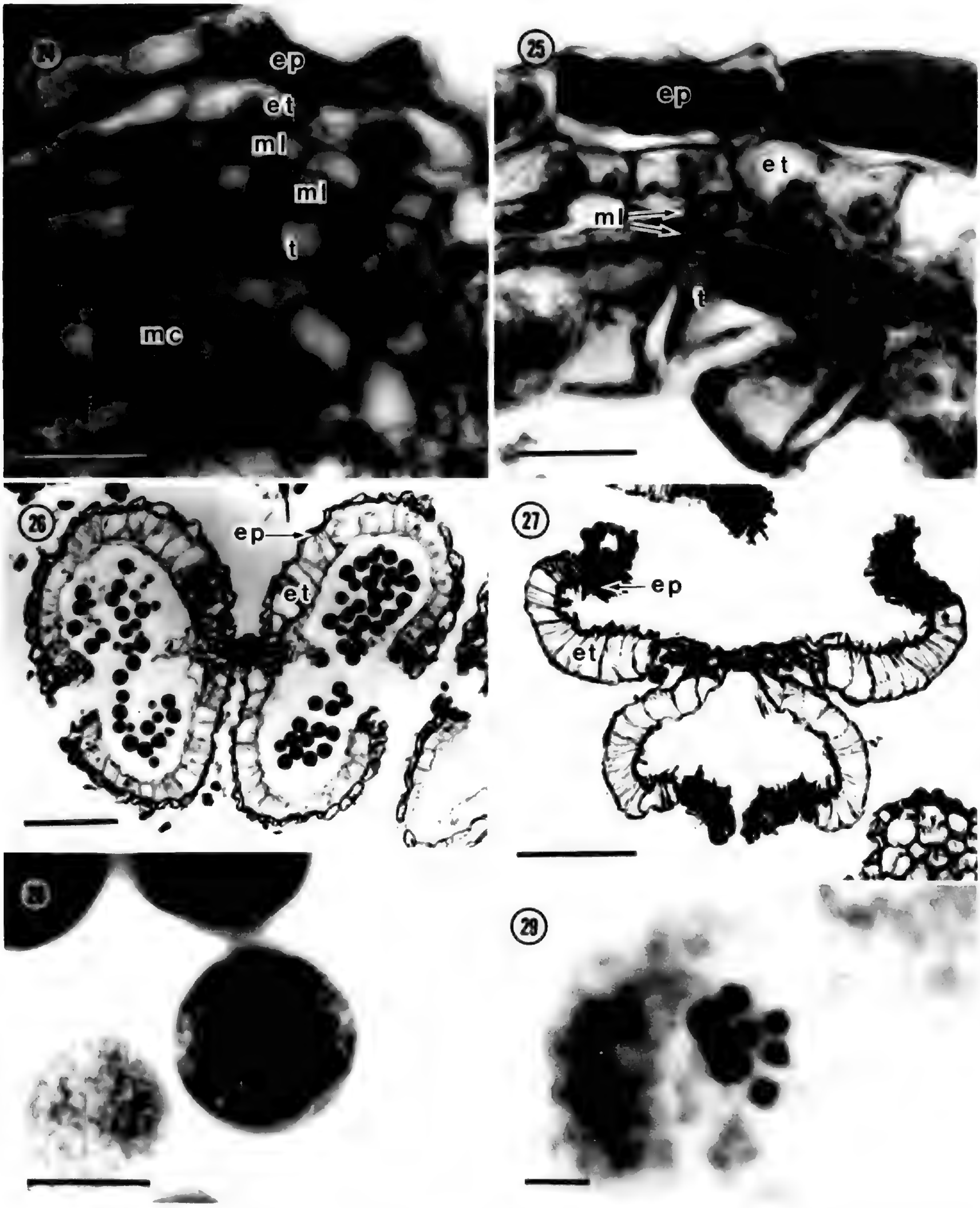
nuclei. Bar = 20 μm.—21. Longitudinal hand-section of a mature seed. Note that the mature seed is exalbuminous. Bar = 5 mm.—22. LS of a young seed showing a thick seed coat. Bar = 200 μm.—23. LS of a mature seed coat that is formed by both the multiple inner layer and the conspicuous outer epidermis. Bar = 40 μm. in, integument; nuc, nucellar tissue; rb, raphe bundle; b, vascular bundle; pem, proembryo; fe, free endosperm nucleus; em, embryo; sc, seed coat; epi, epidermis of seed coat; inl, multiple inner layer.



FIGURES 24–29. *Combretocarpus rotundatus.*—24. Transverse section (TS) of a young anther showing the five cell-layered wall structure. Bar = 10 μm.—25. TS of an older anther with degenerating middle layers. Bar = 10 μm.—26. TS of an anther at the time of dehiscence. Its wall comprises the fibrous endothecium and the epidermis. Bar = 50 μm.—27. TS of an older anther than that shown in Figure 26. The anther wall is remarkably reflexed. Bar = 50 μm.—28. Two-celled mature pollen at the time of shedding. Bar = 10 μm.—29. Chromosomes of pollen mother cell at metaphase I. $n = 8$. Bar = 2 μm. ep, epidermis; et, endothecium; ml, middle layer; t, tapetum; mc, microspore mother cell.

microsporangia of each theca degenerates completely.

Meiosis in the microspore mother cell is accompanied by simultaneous cytokinesis. The shape of the resultant tetrads, on the basis of the examination of 50 selected tetrads are "usually" (86%) tetrahedral, "occasionally" (12%) decussate, and "rarely" (2%) isobilateral. The pollen grains are 2-celled at the time of shedding (Fig. 48).

Chromosomes. Using serially sectioned pollen mother cells that were fixed at the later prophase of meiosis I, we observed the chromosomes of *Poga* for the first time and determined the chromosome number $n = 7$ (Figs. 49–51).

Nucellus and integuments. Although female flowers were not available, we confirmed by using mature ovules and very young fruits that the nucellar tissue enclosing the embryo sac persists at least until the early stages of fruit development (Figs. 52, 54). No hypostase is differentiated even after fertilization.

The ovule is bitegmic, i.e., possessing the outer and the inner integument (Fig. 52). The outer integument is originally about four or five cells thick, and the inner integument two cells thick (Fig. 53). The cells of the outer epidermis of the outer integument, which later become those of the outermost layer of the exotesta, are conspicuously enlarged into cuboid cells. The raphe bundle ramifies and vascularizes the outer integument. In a cross section of a young fruit, six to eight vascular bundles in addition to several raphe bundles are observed in the testa (Fig. 54).

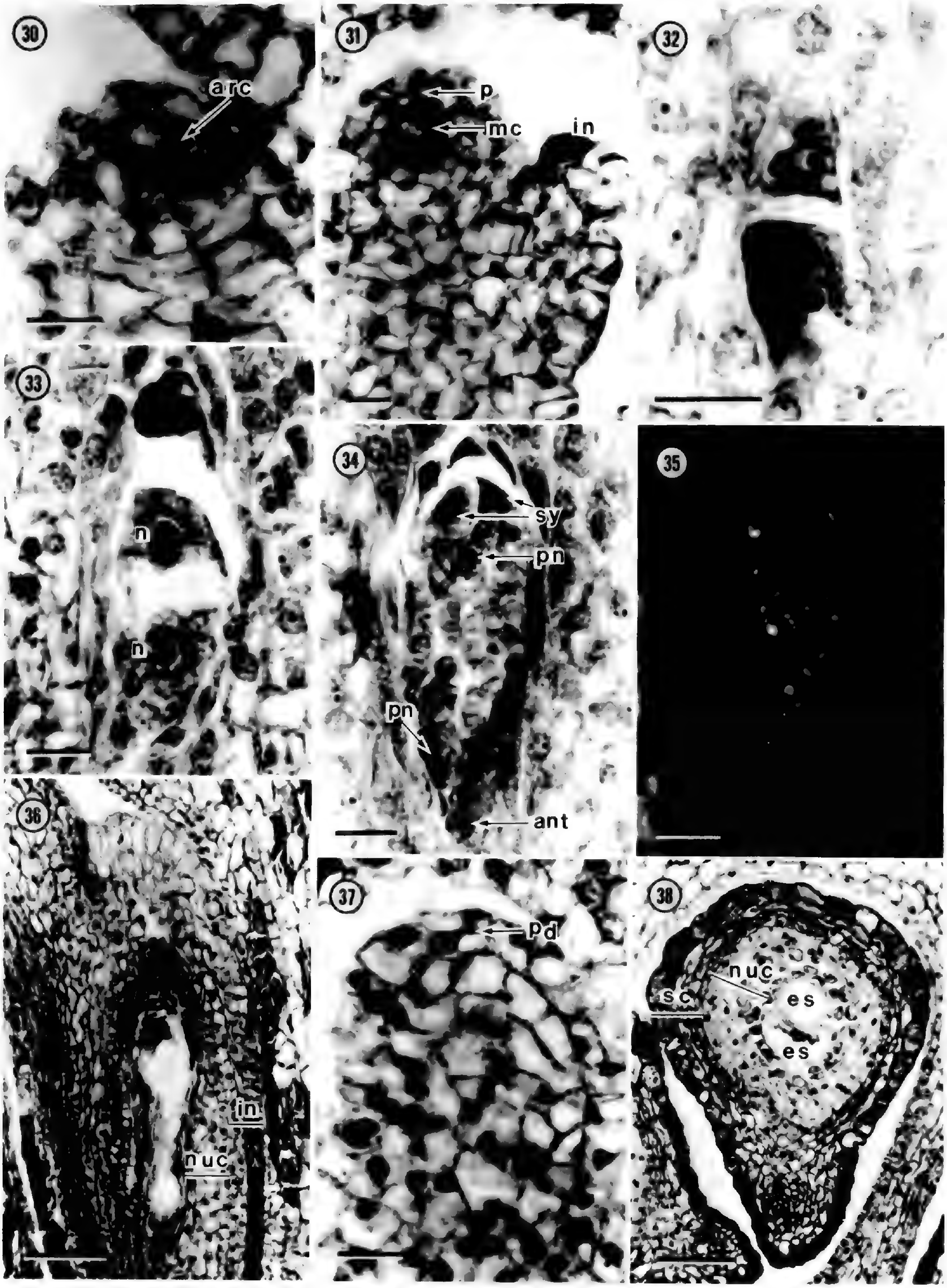
The micropyle is formed by both integuments (Fig. 52).

Endosperm and embryo. We could not observe either the mode of endosperm formation or embryogenesis. But we can say at least that the mature seed completely lacks endosperm (Figs. 55, 56) as Vaughan (1970) described, and that the embryo does not have cotyledons. Concerning the cotyledons, Vaughan (1970) mentioned that they are fused. However, judging from the resemblance in exomorphology of the embryo with *Anisophyllea,* it seems that *Poga* also lacks cotyledons from the beginning.

Mature seed and seed coat. The fruits are always one-seeded. The mature seed is 20.0–22.5 mm long and 12.0–13.5 mm thick, is ovoid and slightly suppressed toward the raphe-antiraphe direction, and has a thick, dark brown seed coat (Figs. 55, 56).

In the young seed, the seed coat is composed only of a thick testa and lacks a tegmen. It seems that, during the process of seed development, the inner integument or tegmen is crushed, while the outer integument or testa increases in thickness by secondary multiplication. Within the young testa, a differentiation into a multiple outer layer and a multiple inner layer can be observed (Fig. 57). The multiple outer layer is about 8 cells thick and has cells that are more or less enlarged. In contrast, the multiple inner layer is 7–10 cells thick, with the cells stretched tangentially (Fig. 57). The structure of the mature seed coat basically does not differ from that of the young seed coat. In the mature seed coat, however, the walls of the constituent cells are thickened, and the multiple inner layer occupies nearly one-third of the whole thickness of the testa, with the multiple outer layer occupying the remaining two-thirds (Fig. 58). Because our microtome sections of the seed coat were not very good, we could not examine the details of cell structure. Vaughan (1970), however, gave a drawing of the anatomical structure of the testa, which consists of an inner layer that is about 12 cells thick and an outer layer about six or seven cells thick. Referring to Vaughan (1970), Corner (1976) described the outer epidermis of the multiple outer layer as composed of cuboid cells with slightly thickened, lignified walls, and the other cells of the multiple outer layer as thin-walled.

The mature seed coat structure of *Poga,* which is bitegmic, seems comparable with that of *Anisophyllea,* which is unitegmic. In both genera, the mature seed coat contains a similar (probably identical) multiple inner layer, which is characteristically composed of tangentially stretched cells with thick walls. The only evident difference between the mature seed coat structure of *Poga* and that of *Anisophyllea* lies in thickness of the outer layer, i.e., about six or seven cells thick in *Poga* (see Vaughan, 1970) and one cell thick (outer epidermis only) in *Anisophyllea.* In other words, the seed coat of *Anisophyllea,* like that of *Poga,* may also be constructed principally of the "testa" (or "outer integument"), which of course is not differentiated in the single integument of *Anisophyllea.* Therefore the seed of unitegmic *Anisophyllea* and even of unitegmic *Combretocarpus* (with a mature seed coat consisting only of the outer epidermis) may be regarded as testal, and the seed of bitegmic *Poga* can also be defined in this way.



Figures 30–38. *Combretocarpus rotundatus.*—30. Longitudinal section (LS) of an ovule with the 1-celled archesporium. Bar = 10 μm.—31. LS of a young ovule with the primary parietal cell and the megaspore mother cell. Note that the ovule has only a single integument. Bar = 10 μm.—32. LS of a young ovule with the megaspore dyad. Note that each megaspore has two nuclei. Bar = 10 μm.—3. LS of an ovule at the 2-nucleate embryo sac stage. Bar = 10 μm.—34. LS of a nearly mature ovule at the 8-nucleate embryo sac stage. Bar = 10 μm.—35.

POLYGONANTHUS DUCKE

Anther and microspores. The anther is basically tetrasporangiate. The microsporogenous tissue, however, is occasionally transversely divided by a septum composed of tapetal cells (Fig. 59). Although we could not determine the modes of anther wall formation, the wall prior to maturation comprises five cell layers: an epidermis, endothecium, two middle layers, and a tapetum. During maturation, the middle layers degenerate, while the cells of both the epidermis and the endothecium become enlarged (Fig. 59). The tapetum is glandular, and its cells become 2-nucleate before degeneration (Fig. 60). The two nuclei in a tapetal cell do not fuse with each other. Eventually the mature anther wall is composed of a persistent epidermis, whose cells are somewhat collapsed in places, and a fibrous endothecium (Fig. 61). The connective tissue between two microsporangia of each theca degenerates completely before the anthers dehisce.

Meiosis in the microspore mother cells is accompanied by simultaneous cytokinesis. The pollen grains are 2-celled at the time of shedding (Fig. 62).

Chromosomes. Using serially sectioned microspore mother cells that were fixed at the late prophase of meiosis I, the chromosomes of *Polygonanthus* were observed for the first time. Throughout, at examination and reconfirmation in many cells, we determined the chromosome number of *P. amazonicus* as $n = 7$ (Figs. 63–65).

Megagametophyte and nucellus. Although our observations are fragmentary, we were able to observe some aspects of the process of megasporogenesis and megagametogenesis in *Polygonanthus*. The ovule is anatropous and crassinucellate. At least one parietal cell is cut off above the megaspore mother cell (Figs. 66, 67). Although the mode of embryo sac formation was not determined, the 2-nucleate embryo sac of *Polygonanthus amazonicus* differs in aspect from that of *Combretocarpus rotundatus* (which develops a bisporic *Allium* type embryo sac) (Fig. 68; compare with Fig. 33). The accumulation of starch grains in the embryo sac, which is characteristic of *Combretocarpus*, does not occur in *Polygonanthus amazonicus*. The antipodal cells are probably ephemeral, because they are absent in the organized mature embryo sacs (Fig. 69).

The nucellar tissue enclosing the embryo sac is persistent until at least the stage of fertilization (Fig. 69). Periclinal divisions occur in the apical dermal cells of the nucellus. Therefore the nucellar cap is probably formed by derivatives of the apical dermal cells.

Integuments. The ovule is bitegmic, i.e., it has both an outer and an inner integument (Fig. 66). The outer integument is initially about five cells thick, but later becomes seven to nine or more cells thick because of secondary multiplication (Fig. 66). The inner integument, in contrast, is two cells thick (Fig. 67). In the later stages, the inner integument becomes very much less conspicuous, while the outer integument increases in thickness (Fig. 69). Although we could not observe any stages of the development of the seed coat, it seems very unlikely that the inner integument or tegmen contributes to its structure when mature. The raphe bundle ramifies throughout the outer integument, which is therefore vascularized. In cross section, seven or eight bundles in addition to several raphe bundles are observed (Fig. 70).

The micropyle is formed by both integuments (Fig. 69).

DISCUSSION

Our own results on the embryology and chromosome numbers of Anisophylleaceae, together with some data on ovule and seed morphology published earlier (Karsten, 1891; Vaughan, 1970; Geh & Keng, 1974), are presented in Table 2. On this basis, we summarize the embryological features of Anisophylleaceae as follows.

Anther tetrasporangiate, but occasionally polysporangiate because of insertion of tapetal septa (*Polygonanthus*); anther wall with five cell

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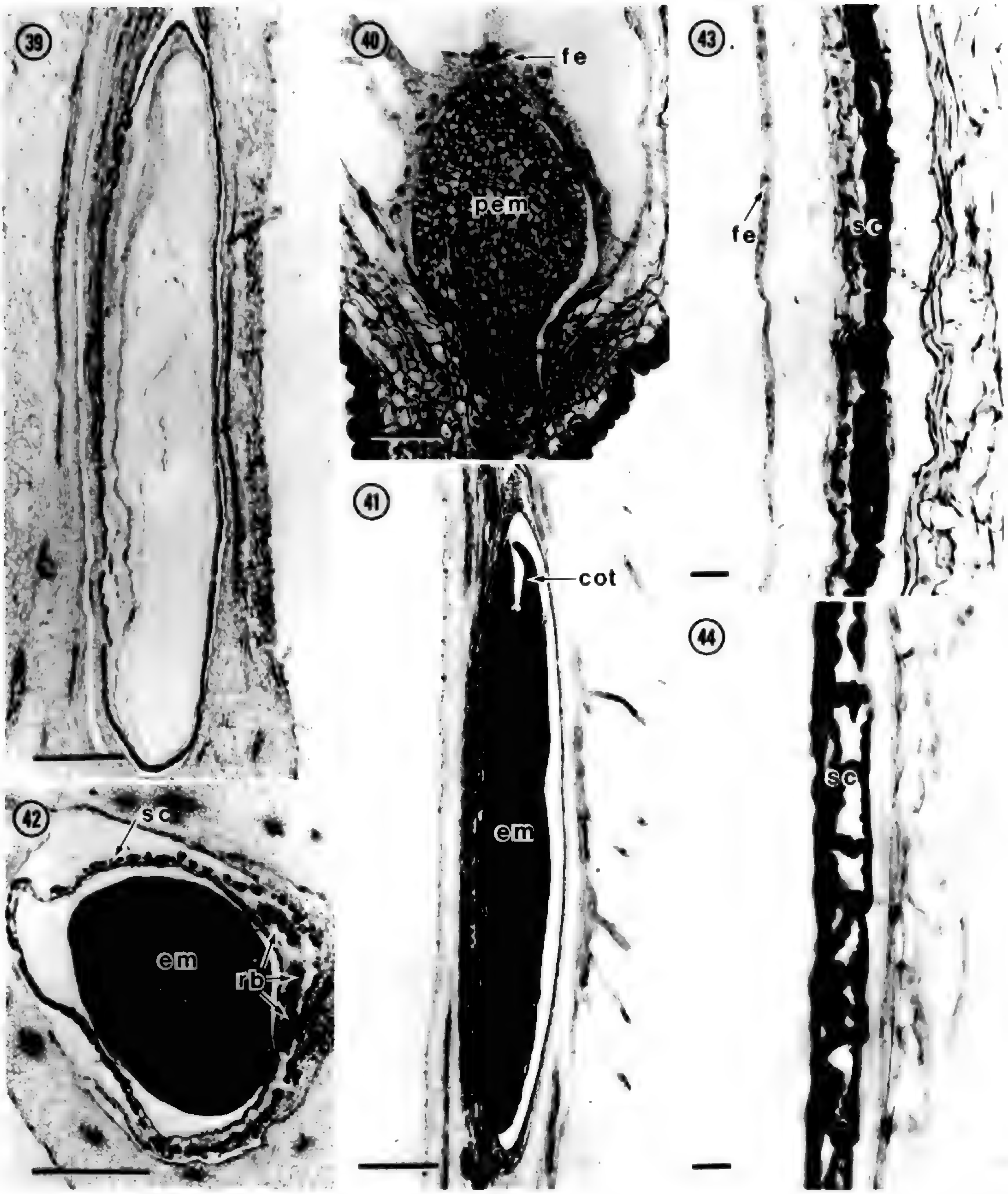
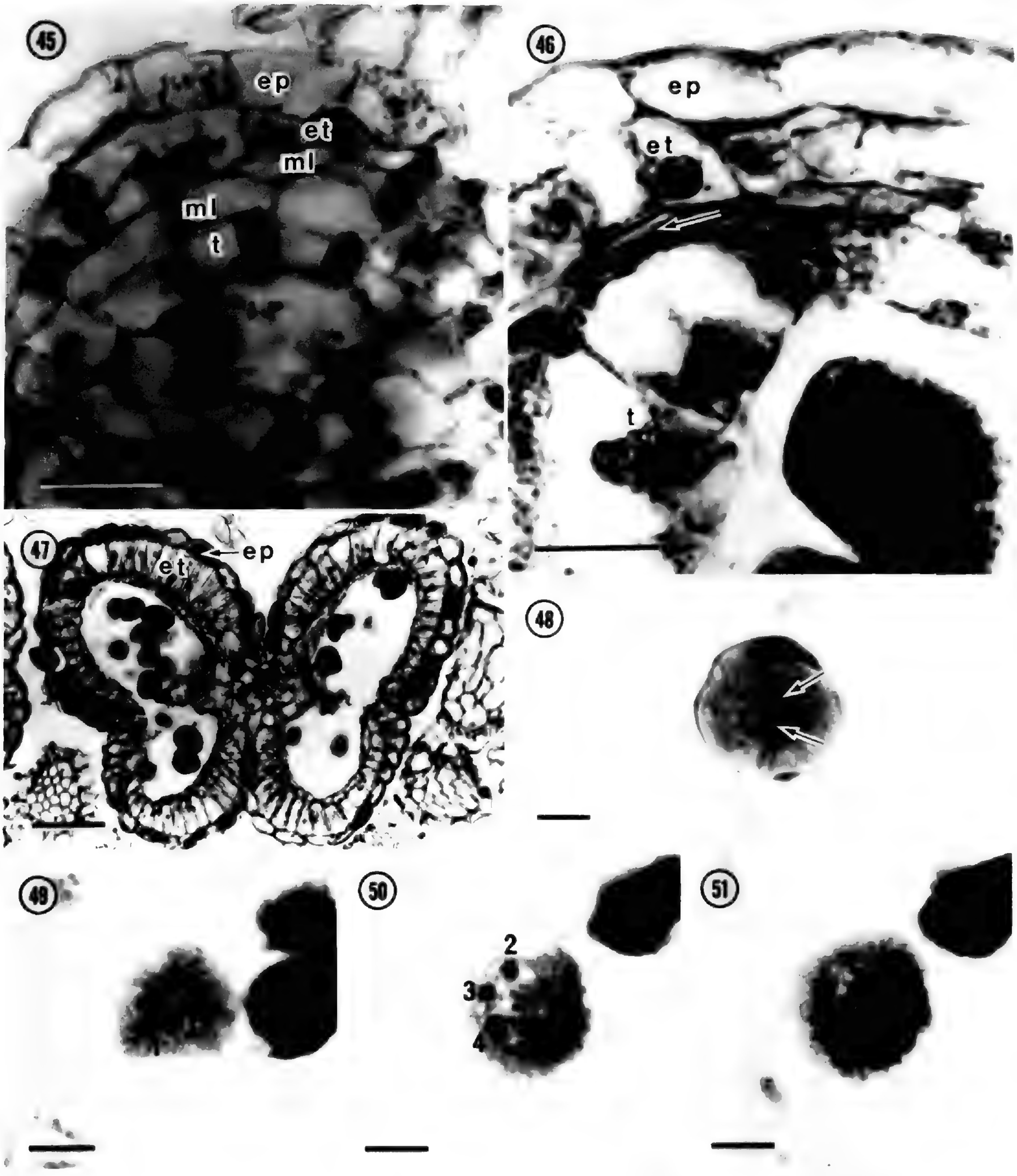
Polarized view of the same as that shown in Figure 34, showing a conspicuous accumulation of starch grains in the embryo sac. Bar = 10 μm.—36. LS of a mature ovule with an organized embryo sac. Note that the nucellar tissue is persistent. Bar = 50 μm.—37. LS of a young ovule nearly at the megaspore dyad stage showing periclinal divisions occurring in apical epidermal cells of the nucellus. Bar = 10 μm.—38. Transverse section of a young seed with twin embryo sacs. Bar = 50 μm. arc, archesporial cell; p, primary parietal cell; mc, megaspore mother cell; in, integument; n, nucleus of the embryo sac; sy, synergid; pn, polar nucleus; ant, antipodal cell; nuc, nucellar tissue; pd, periclinal cell division; sc, seed coat; es, embryo sac.



FIGURES 39–44. *Combretocarpus rotundatus.*—39. Longitudinal section (LS) of a remarkably elongated young fruit. Bar = 500 μm.—40. LS of a proembryo with free endosperm nuclei surrounding it. Bar = 50 μm.—41. LS of a mature seed with a cotyledonous embryo. Note that the mature seed is exalbuminous. Bar = 1 mm.—42. Transverse section of a mature seed with several vascular bundles at the raphe. Bar = 500 μm.—43. LS of a young seed coat. Bar = 10 μm.—44. LS of a mature seed coat. Bar = 10 μm. pem, proembryo; fe, free endosperm nucellus; cot, cotyledon; em, embryo; sc, seed coat; rb, raphe bundle.

layers, its formation of the Basic type; anther epidermis persistent, consisting of more or less collapsed cells; endothecium persistent and developing fibrous thickenings; middle layers ephemeral; tapetum glandular, its cells 2-nucleate; the two nuclei in each tapetal cell eventually fused in *Anisophyllea* and *Combretocarpus,* but not in *Poga* and *Polygonanthus.*

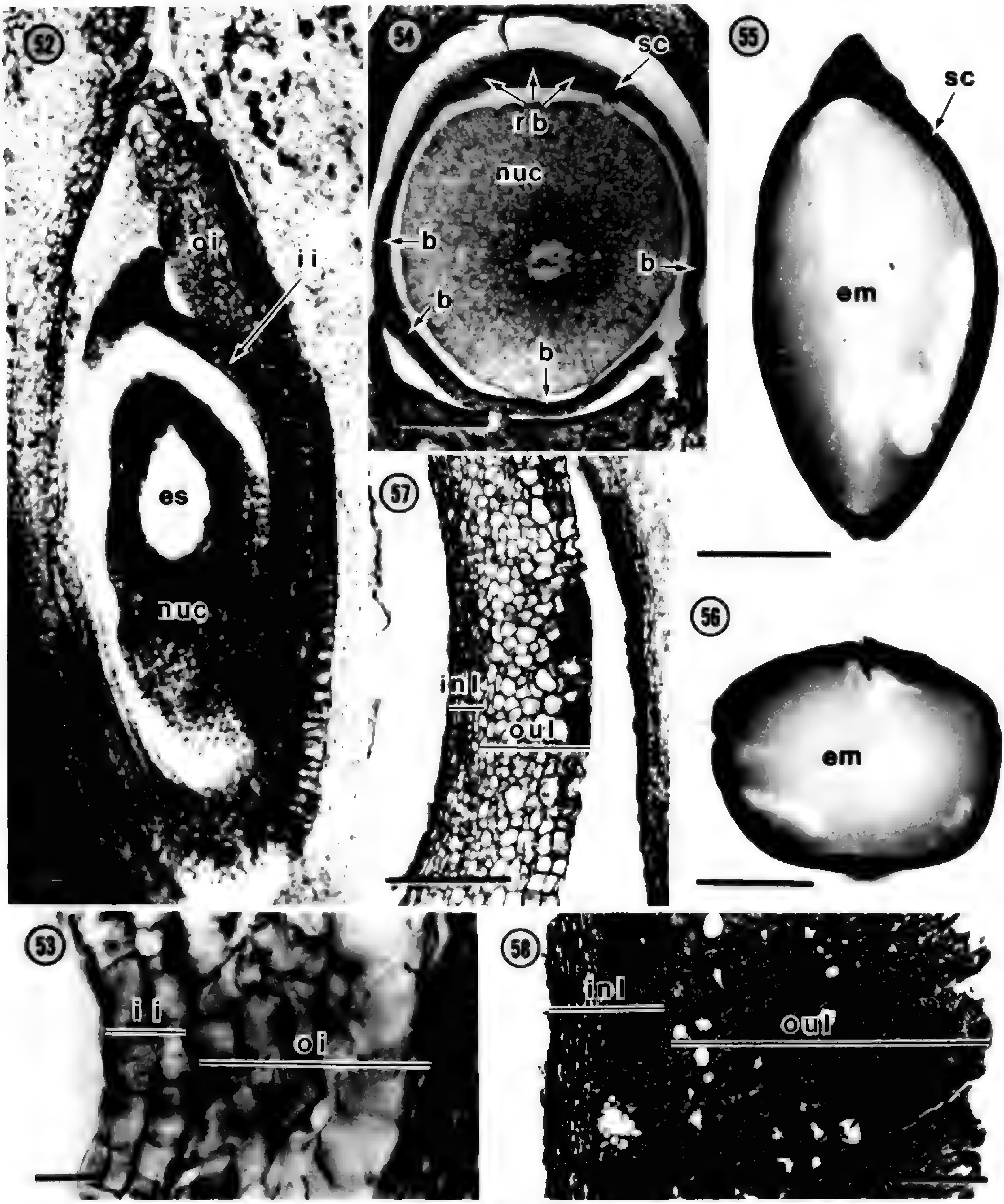


FIGURES 45–51. *Poga oleosa.*—45. Transverse section (TS) of a young anther showing the wall structure with five cell layers. Bar = 10 μm.—46. TS of an older anther with degenerating middle layers (arrow). Bar = 10 μm.—47. TS of a nearly mature anther. Its wall consists of the fibrous endothecium and the epidermis. Bar = 100 μm.—48. Two-celled mature pollen at the time of shedding. Arrows indicate nuclei of the two cells. Bar = 10 μm.—49–51. Three serial sections of pollen mother cell at the late prophase I showing chromosomes of n = 7. Seven chromosomes are numbered 1 to 7. Bars = 10 μm. ep, epidermis; et, endothecium; ml, middle layer; t, tapetum.

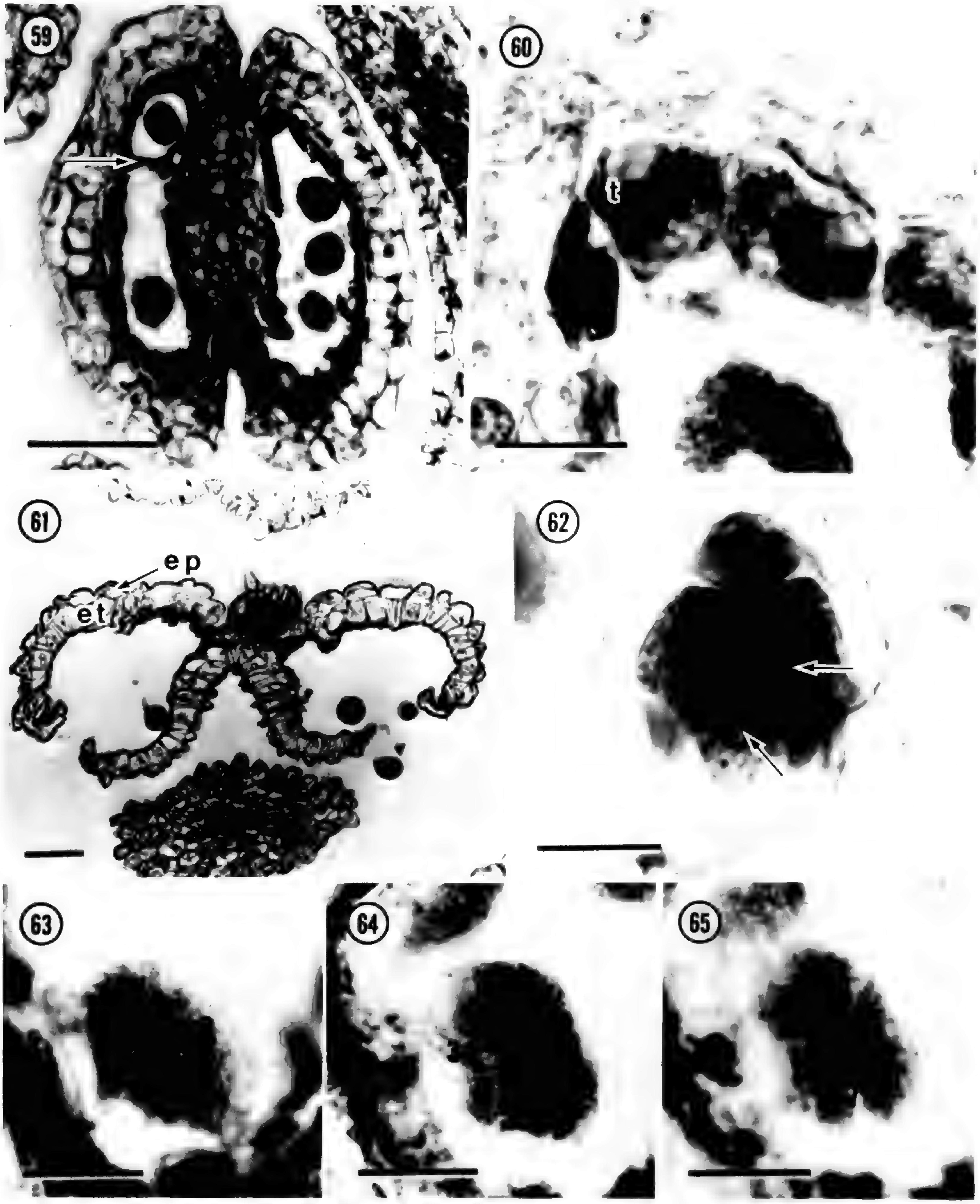
Cytokinesis in the microspore mother cells simultaneous; microspore tetrads tetrahedral, decussate, or isobilateral; pollen grains 2-celled when shed.

Gametic chromosome number $n = 8$ in *Combretocarpus*, $n = 7$ in *Anisophyllea*, *Poga*, and *Polygonanthus*.

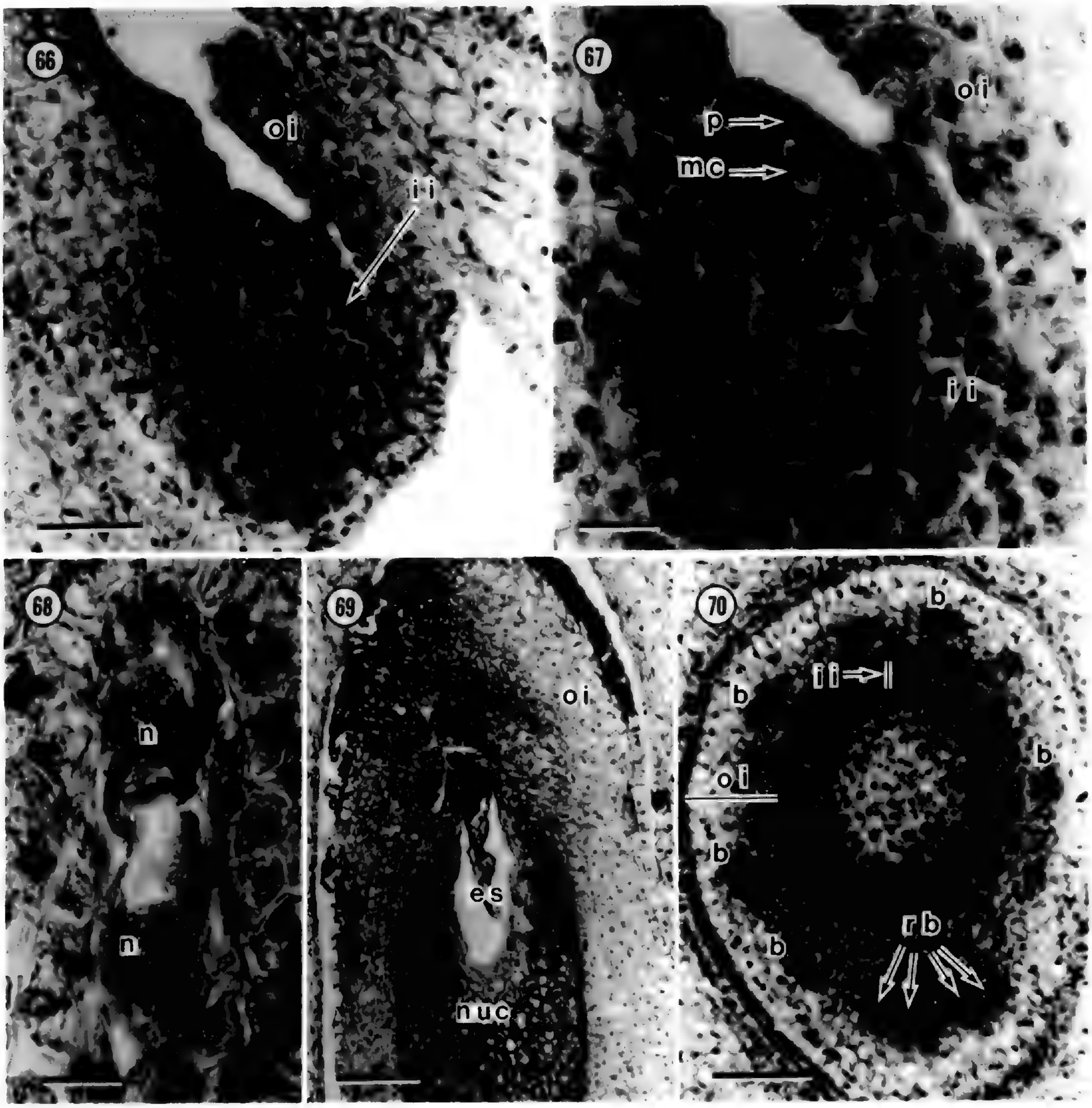
Ovule anatropous and crassinucellate; arche-



FIGURES 52–58. *Poga oleosa*. — 52. Longitudinal section (LS) of a mature ovule. Note that the ovule is bitegmic and has a persistent nucellar tissue. Bar = 100 μm. — 53. Transverse section (TS) of a mature ovule showing the inner integument, with two cell layers, and the outer integument, with four cell layers. Bar = 10 μm. — 54. TS of a young seed showing the vascularized seed coat. Bar = 500 μm. — 55. Longitudinal hand-section of the mature seed. Note that the mature seed is exalbuminous. Bar = 5 mm. — 56. Transverse hand-section of the mature seed. Bar = 5 mm. — 57. TS of a young seed coat. Note that there is no tegmen and that the testa is differentiating into the multiple inner layer and the multiple outer layer. Bar = 100 μm. — 58. LS of a mature seed coat. Bar = 100 μm. ii, inner integument; oi, outer integument; es, embryo sac; nuc, nucellar tissue; rb, raphe bundle; b, vascular bundle; sc, seed coat; em, embryo; inl, multiple inner layer; oul, multiple outer layer.



FIGURES 59–65. *Polygonanthus amazonicus.*—59. Longitudinal section of a developed anther. Arrow indicates the tapetal septum dividing a microsporangium. Bar = 50 µm.—60. Transverse section of a young anther. Bar = 10 µm.—61. TS of a mature anther at the time of dehiscence. Its wall consists of the fibrous endothecium and the epidermis. Bar = 50 µm.—62. Two-celled mature pollen at the time of shedding. Arrows indicate nuclei of the two cells. Bar = 10 µm.—63–65. Three serial sections of pollen mother cell at late prophase I showing chromosomes of $n = 7$. Seven chromosomes are numbered 1 to 7. Bars = 10 µm. t, tapetum; ep, epidermis; et, endothecium.



FIGURES 66–70. *Polygonanthus amazonicus*.—66. Longitudinal section (LS) of a young ovule. Note that the ovule is bitegmic. Bar = 50 μm.—67. Same as that shown in Figure 66, but shown at higher magnification. Note that the inner integument is two cells thick. Bar = 20 μm.—68. LS of an ovule at the 2-nucleate embryo sac stage. Bar = 10 μm.—69. LS of a mature ovule. Note that the nucellar tissue is persistent. Bar = 50 μm.—70. Transverse section of a young ovule showing that the outer integument has vascular bundles. ii, inner integument; oi, outer integument; p, primary parietal cell; mc, megaspore mother cell; n, nucleus of the embryo sac; es, embryo sac; nuc, nucellar tissue; rb, raphe bundle; b, vascular bundle.

sporium 1-celled, cutting off a primary parietal cell; embryo sac formation of the *Polygonum* type (*Anisophyllea*) or the *Allium* type (*Combretocarpus*); synergids slightly hooked; antipodals ephemeral; polar nuclei fused before fertilization (*Anisophyllea*) or not fused (*Combretocarpus*). Nucellar tissue not degenerating at least until the early stages of seed development; apical dermal nucellar cells dividing periclinally, forming a nucellar cap, chalaza without a hypostase.

Ovule unitegmic (*Anisophyllea* and *Combretocarpus*) or bitegmic (*Poga* and *Polygonanthus*); in bitegmic ovules, the inner integument two cells thick and the outer integument thicker; outer integument vascularized due to ramification of raphe bundles, but not vascularized in *Combre-*

tocarpus; micropyle formed by either the one integument or both integuments, depending on whether one or two integuments are present.

Fertilization porogamous; endosperm formation of the Nuclear type; seed exalbuminous; mode of embryogenesis not determined; embryo (potentially) dicotyledonous with a long hypocotyl, having either small cotyledons (*Combretocarpus*) or rudimentary and/or no cotyledons (*Anisophyllea* and *Poga*). Seed coat testal (*Poga*) or logically testal (*Anisophyllea* and *Combretocarpus*); mature seed coat formed by the outer epidermis alone (*Combretocarpus*), both the outer epidermis and the multiple inner layer (*Anisophyllea*), or both the multiple outer layer and the multiple inner layer (*Poga*).

RELATIONSHIPS WITH RHIZOPHORACEAE

Although, as shown in Table 2, some of the embryological features of Anisophylleaceae are diverse, the family is consistent enough in most such characteristics to allow a more critical comparison with Rhizophoraceae than has hitherto been possible. In summary, these two families share only a few embryological features. They do agree, for example, in having a crassinucellate, bitegmic ovule and the Nuclear type of endosperm formation; but a combination of these and other shared features is widespread among many other unrelated families of the angiosperms as well.

In contrast, Anisophylleaceae differ from Rhizophoraceae in some important embryological features. First of all, in Anisophylleaceae the nucellar tissue persists until at least the early stages of seed development, whereas in Rhizophoraceae the nucellar tissue is ephemeral, disappearing completely by the time of fertilization (see Karsten, 1891, for *Rhizophora, Ceriops, Bruguiera,* and *Carallia*; Cook, 1907, for *Rhizophora*; Carey, 1934, for *Rhizophora*; Mauritzon, 1939, for *Gynotroches*; Juncosa, 1984a, 1984b, for *Bruguiera* and *Cassipourea*). Therefore in Rhizophoraceae the embryo sac borders directly on the inner integument.

Secondly, in Anisophylleaceae (*Poga* and *Polygonanthus*) the inner integument is characteristically two cells thick, whereas in Rhizophoraceae it is much thicker. Indeed, an inner integument with four to eight layers has been illustrated by Karsten (1891) for *Bruguiera, Ceriops,* and *Carallia,* by Carey (1934) for *Rhizophora,* and by Mauritzon (1939) for *Bruguiera* and *Gynotroches.* Juncosa (1984a, 1984b) described the inner integument of *Bruguiera exaristata* as initially being about 10 cells thick and that of *Cassipourea elliptica* as being about five to eight cells thick. In addition, a specialization of the innermost cell layer of the inner integument into an endothelium has been reported in some inland genera of Rhizophoraceae, including *Carallia* (Karsten, 1891), *Gynotroches* (Mauritzon, 1939), and *Cassipourea* (Juncosa, 1984a). An endothelium is never formed in Anisophylleaceae.

Thirdly, the mature seed is exalbuminous in Anisophylleaceae, but albuminous in Rhizophoraceae. The presence of abundant endosperm in mature seeds has been reported for *Rhizophora* (Cook, 1907; Carey, 1934; Juncosa, 1982), *Ceriops* (Carey, 1934), and *Cassipourea* (Juncosa, 1984a).

Some critical differences in embryo and seed coat morphology might also be added for distinguishing Anisophylleaceae from Rhizophoraceae (see Corner, 1976). However, studies on those characters in Rhizophoraceae are still too limited to allow this. Further studies on the embryology of Rhizophoraceae, including embryo and seed coat morphology, are needed to clarify the differences between this family and Anisophylleaceae.

To sum up, despite insufficient information on the embryology of Rhizophoraceae, the available data indicate that Anisophylleaceae differ significantly from them. If Anisophylleaceae were included as a tribe or subfamily, Rhizophoraceae sensu lato would be defined very broadly. With the support of exclusive occurrence of the nature of aluminum accumulation (Chenery, 1948; Kukachka & Miller, 1980); alternate, exstipulate leaves; three or four free styles (Geh & Keng, 1974); and S-type sieve-element plastids (Behnke, 1984) in Anisophylleaceae, the embryological evidence now available strongly suggests that Anisophylleaceae and Rhizophoraceae are not closely related and warrants regarding Anisophylleaceae as a distinct family.

SYSTEMATIC POSITION OF ANISOPHYLLEACEAE

Cronquist (1981, 1983) has proposed assigning Anisophylleaceae to Rosales. Within Rosales, Anisophylleaceae were referred to the suborder Grossularineae, which includes six other families (Hydrangeaceae, Columelliaceae, Grossulariaceae, Greyiaceae, Bruniaceae, and Alseuosmiaceae). Of these, only Grossulariaceae have been

TABLE 2. Embryological and chromosomal data of Anisophylleaceae.

Character	*Anisophyllea*	*Combretocarpus*	*Poga*	*Polygonanthus*
Anther and microspores:				
Number of sporangia	4	4	4	4, sporangium occasionally divided by tapetal septa
Anther wall development	Basic type	Basic type	Basic type	?
Anther epidermis	Persistent	Persistent	Persistent	Persistent
Endothecium	Fibrous	Fibrous	Fibrous	Fibrous
Tapetum	Glandular	Glandular	Glandular	Glandular
Number of tapetal nuclei	2	2	2	2
Tapetal nuclear fusion	Occur	Occur	Not occur	Not occur
Cytokinesis in meiosis	Simultaneous	Simultaneous	Simultaneous	Simultaneous
Shape of microspore tetrad	Usually tetrahedral, very occasionally decussate, rarely isobilateral	Usually tetrahedral, occasionally decussate, very occasionally isobilateral	Usually tetrahedral, occasionally decussate, rarely isobilateral	?
Mature pollen	2-celled	2-celled	2-celled	2-celled
Chromosomes:				
Base number	$x = 7$	$x = 8$	$x = 7$	$x = 7$
Megagametophyte and nucellus:				
Ovule curvature	Anatropous	Anatropous	Anatropous	Anatropous
Nature of nucellus	Crassinucellate	Crassinucellate	Crassinucellate	Crassinucellate
Archesporium	1-celled	Nearly always 1-celled, very rarely 2-celled	?	?
Thickness of parietal tissue	3–5 cell-layered	1–2 cell-layered	?	?
Shape of megaspore tetrad	Linear	Linear	?	?
Functional megaspore	Chalazal cell	Chalazal cell	?	?
Pattern of embryo sac formation	*Polygonum* type	*Allium* type	?	?
Synergids	Slightly hooked	Slightly hooked	?	?
Antipodal cells	Ephemeral	Ephemeral	?	Probably ephemeral
Number of nuclei or 5 cells in mature embryo sac	5	5	?	5
Accumulation of starch grains in embryo sac	Not occur	Occur	?	Not occur
Nucellar tissue	Persistent	Persistent	Persistent	Persistent
Nucellar cap	Formed	Formed	?	Probably formed
Hypostase	Not formed	Not formed	Not formed	Not formed
Integuments:				
Number of integuments	1	1	2	2
Thickness of integuments when bitegmic	—	—	i.i. 2 cell-layered; o.i. 4–5 cell-layered	i.i. 2 cell-layered; o.i. about 5 cell-layered

TABLE 2. Continued.

Character	*Anisophyllea*	*Combretocarpus*	*Poga*	*Polygonanthus*
Vasculature	Present	Absent	Present	Present
Micropyle formation	By the only integument	By the only integument	By both integuments	By both integuments
Differentiation of endothelium	Not occur	Not occur	Not occur	Not occur
Fertilization, endosperm, and embryo:				
Path of pollen tube	Porogamous	Porogamous	?	?
Endosperm formation	Nuclear type	Nuclear type	?	?
Endosperm in mature seed	Absent	Absent	Absent	?
Embryogenesis	?	?	?	?
Embryo in mature seed	Cotyledonous or not cotyledonous	Cotyledonous	Not cotyledonous	?
Size of cotyledons when present	Very small (rudimentary)	Small	—	?
Mature seed and seed coat:				
Shape of seed	Narrow–cylindrical (*A. disticha*); ovoid or elliptical (*A.* sp.)	Linear	Ovoid and slightly suppressed toward raphe-antiraphe direction	?
Size of seed	13.0–13.6 mm long and 3.8–4.0 mm diam. (*A. disticha*); 13.0–13.8 mm long and 6.0–6.4 mm diam (*A.* sp.)	9.5–10.4 mm long and 1.2–1.3 mm diam.	20.5–22.5 mm long, 12.0–13.5 mm wide	?
Tegmen	—	—	Ephemeral	?
Whole thickness of seed coat (SC)	26–31 cell-layered	1 cell-layer	17–20 cell-layered	?
Thickness of inner layer of SC	25–30 cell-layered	—	7–10 cell-layered	?
Thickness of outer layer of SC	1 cell-layer	1 cell-layer	About 10 cell-layered	?

i.i., inner integument; o.i., outer integument.

relatively well studied embryologically, whereas the others have been studied little or not at all in this respect. Anisophylleaceae differ from all Grossularineae in having exalbuminous seeds (Cronquist, 1981). On the other hand, Anisophylleaceae resemble Grossulariaceae (principally *Ribes,* from which most data are available) in nearly all features of anther and microspore development; in their anatropous, bitegmic, and crassinucellate ovule; *Polygonum*-type embryo sac; ephemeral antipodal cells; inner integument with two cell layers (see Davis, 1966; Corner, 1976; Cronquist, 1981, for data on Grossulariaceae). However, Anisophylleaceae differ from Grossulariaceae in several embryological features. For example, the tapetal cell is basically 2-nucleate in Anisophylleaceae, but multinucleate in Grossulariaceae; the integument is vascularized in Anisophylleaceae, but not vascularized in Grossulariaceae; endosperm formation is of the Nuclear type in Anisophylleaceae, but of the Cellular or the Helobial type in Grossulariaceae; the tegmen is ephemeral in Anisophylleaceae (*Poga*), but persists in Grossulariaceae; the seeds are non-arillate in Anisophylleaceae, but arillate in Grossulariaceae (see Netolitzky, 1926; Davis, 1966; Corner, 1976, for data on Grossulariaceae). Therefore it seems that available embryological evidence neither supports nor denies a close relationship between Anisophylleaceae and Grossularineae (Rosales).

In contrast, Dahlgren (1983) placed Anisophylleaceae in the Cornales, which comprise 27 families including Hydrangeaceae (and five families whose position is uncertain; see also Dahlgren & Thorne, 1984). Of 27 families, nine have either not been studied embryologically, or have been studied only to a very limited degree. Of the 18 remaining families, nearly all share a unitegmic ovule, ephemeral nucellar tissue, endothelium, Cellular type of endosperm formation, and albuminous seed. The Cornales thus seem to be very well defined by a combination of those shared embryological features. Anisophylleaceae, which lack any of those characteristic embryological features of the Cornales (almost certainly unitegmic ovule in *Anisophyllea* and *Combretocarpus*), seem clearly distinct from the Cornalean families and do not belong in that order.

We would rather suggest Myrtalean affinities for Anisophylleaceae. Embryologically, Anisophylleaceae agree almost completely with Myrtales, and in fact share the eight ordinal embryological features (see Tobe & Raven, 1983, 1984): 1) anther tapetum glandular, 2) ovule crassinucellate, 3) inner integument two cells thick, 4) micropyle formed by both integuments, 5) antipodal cells ephemeral, 6) endosperm formation—Nuclear type, 7) seed exalbuminous, and 8) mature pollen 2-celled. One might point out a fusion of tapetal nuclei (in *Combretocarpus* and *Anisophyllea*), formation of the nucellar cap, and testal seed as features distinguishing Anisophylleaceae from Myrtales. However, nuclear fusion in the tapetal cells is undoubtedly a secondary characteristsic that evolved in two genera of Anisophylleaceae. Indeed *Poga* and *Polygonanthus*, both of which have many primitive features, as will be discussed later, have unfused tapetal nuclei. The nucellar cap, which is formed by derivatives of the apical nucellar dermal cells, is commonly observed in Combretaceae (Myrtales; Venkateswarlu & Rao, 1972). A seed coat lacking a tegmen is frequent in Melastomataceae (Myrtales; Corner, 1976). Anisophylleaceae may differ from Myrtales in having embryos with reduced or rudimentary cotyledons and a long hypocotyl. Such an embryo morphology seems to result in hypogeal germination, which is reported in at least *Anisophyllea disticha* (Geh & Keng, 1974). The peculiar embryo morphology and germination habit may suggest a specialized position of Anisophylleaceae. However, embryos devoid of cotyledons are recorded in many unrelated families, a majority of them growing in ecologically specialized habitats (Natesh & Rau, 1984, review). Study of embryogenesis and organogenesis in seeds through germination seems to be needed for the elucidation of the ecological significance of such specialized embryos in Anisophylleaceae. Except for the difference in embryo morphology, there seems to be essentially a perfect correspondence in embryological features between Anisophylleaceae and Myrtales.

Viewing other reproductive and vegetative character states, Anisophylleaceae lack both the intraxylary phloem and the vestured pits, which are regarded as characteristic features defining the Myrtales (Van Vliet, 1976; Van Vliet & Baas, 1984; Dahlgren & Thorne, 1984). However, the occurrence of S-type sieve-element plastids in *Anisophyllea* and *Combretocarpus*, in contrast with the P-type plastids in Rhizophoraceae, agrees with Myrtales (Behnke, 1982, 1984). Tricolporate pollen morphology in Anisophylleaceae (as well as in Rhizophoraceae) is of the basic type found in the Myrtales (Erdtman, 1966; see also Dahlgren & Thorne, 1984). Aluminum accumulation characteristic of Anisophylleaceae (unknown in Rhizophoraceae) is known to occur in Crypteroniaceae and Melastomataceae of Myrtales (Chenery, 1948; Kukachka & Miller, 1980).

Thus, considering a considerable number of coincidences (in reproductive anatomy) in contrast with a limited number of differences (in wood anatomy), in conjunction with support by sieve-element plastid type, palynology, and aluminum accumulation, it seems that Anisophylleaceae are closely related to Myrtales. Depending on how we interpret the lack of intraxylary phloem and vestured pits in Anisophylleaceae, it might even be justifiable to place Anisophylleaceae in the Myrtales. According to Van Vliet and Baas (1984), the combined occurrence of intraxylary phloem and vestured pits is very restricted in the dicotyledons; in fact, except for the Myrtales, this combination is found only in part of the Gentianales, Thymelaeales, Polygalales, and Polygonales. Outside these orders, either one of these features (but not both) sporadically occurs in many different groups of dicotyledons (see Van Vliet & Baas, 1985: 784, fig. 1). Only a few orders are characterized by consistent possession of one or both of those two wood anatomical features.Therefore it does not seem that the lack of intraxylary phloem and vestured pits in Anisophylleaceae necessarily precludes a possibility of close affinity with Myrtales. Based on total evidence now available, we would suggest that Anisophylleaceae be placed near Myrtales. Perhaps Anisophylleaceae represent one of the groups that diverged from a common ancestral stock with Myrtales and then spread widely. The position of Anisophylleaceae will be evaluated better as the Rosiflorae or the Rosales, which are considered phylogenetically basic in position with respect to Myrtales, are understood better embryologically.

Interrelationships and Evolution of the Genera

Because of many shared embryological features, as shown in Table 2, as well as of shared vegetative and some other shared reproductive features (see also Geh & Keng, 1974; Van Vliet, 1976), there is no doubt that *Anisophyllea, Combretocarpus, Poga,* and *Polygonanthus* are monophyletic. Despite the lack of data about several features in *Poga* and *Polygonanthus,* the available embryological data are now enough to allow us to compare all four genera.

Of these, *Combretocarpus* is the most distinct. It has a gametic chromosome number of $n = 8$, *Allium* type embryo sac, nonvascularized integument, starch grains in the embryo sac, cotyledonous embryo, and thin mature seed coat one cell layer thick. In contrast, *Anisophyllea, Poga,* and *Polygonanthus* have a chromosome number of $x = 7$, *Polygonum* type embryo sac (unknown in *Poga* and *Polygonanthus*), vascularized integument, no starch grains in the embryo sac, noncotyledonous embryo (unknown in *Polygonanthus*), and thick mature seed coat (unknown in *Polygonanthus*). *Combretocarpus* agrees with *Anisophyllea* only in having fused tapetal nuclei and a unitegmic ovule. On the contrary, *Anisophyllea* differs from *Poga* and *Polygonanthus* in sharing neither bitegmic ovules nor distinct tapetal nuclei as well as in not sharing a multiple outer layer in the mature seed coat (though uncertain in *Polygonanthus*). *Polygonanthus* differs from *Poga* only in its occasionally divided microsporogenous tissue. Except for this, there is no essential difference between *Poga* and *Polygonanthus,* as far as the data available are concerned.

In order to clarify phylogenetic interrelationships of the genera, it seems necessary to evaluate each of the characters showing differences between them. Therefore, as an attempt, we evaluated embryological character states of Anisophylleaceae following Eldredge and Cracraft (1980) as regards principles of analyzing methods of character state similarities (i.e., synapomorphies or symplesiomorphies). Of the embryological features, the *Polygonum* type embryo sac formation (*Anisophyllea*) that is characteristic of a majority of the dicotyledons (Davis, 1966) is undoubtedly primitive to the *Allium* type manner (*Combretocarpus*), and also bitegmy (*Poga* and *Polygonanthus*) is primitive to the unitegmy (*Anisophyllea* and *Combretocarpus*; Bouman, 1984).

Concerning the vasculature of the integument, there is no consensus regarding whether or not the vascularized integument represents an archaic condition. Bouman (1984) suggested that there seems to be a general relation between the size of ovules or seeds and the degree of vascularization. As far as Anisophylleaceae are concerned, the vascularized integument or testa (*Anisophyllea, Poga,* and *Polygonanthus*) is probably primitive (symplesiomorphous) compared to the nonvascularized one (*Combretocarpus*). *Combretocarpus* has multiple vascular bundles in the raphe of the mature seed (see Fig. 42). This vascular condition in *Combretocarpus* is probably derived from the condition seen in the three other genera by suppression of vascular extension into the integument, because *Combretocarpus* has the thin integument that eventually becomes the one cell-layered seed coat at maturity. In this connection, the thick mature seed coat or testa is probably primitive (symplesiomorphous) to the thin, one cell-layered mature seed coat. Compared with *Poga, Anisophyllea* lacks a hypodermal tissue in the thick multiple outer layer of *Poga*; *Combretocarpus* lacks both the multiple inner layer and the hypodermal tissue of the multiple outer layer. Corner (1976, vol. 1: 57) has considered the limitation of a multiple mechanical tissue (probably like that of *Poga*) into one cell-layered as one of specialization trends of seed coat. Following Corner, we may be able to postulate that the successive or simultaneous reduction of the multiple inner layer and the hypodermal tissue of the multiple outer layer had occurred in the seed coat evolution of Anisophylleaceae so that only the epidermis was persistent, as in *Combretocarpus.* Although we did not observe the anatomy of the testa of *Polygonanthus,* it was confirmed that the (outer) integument shows a secondary multiplication, a condition that is clearly different from that in *Combretocarpus.* Therefore it seems very likely that *Polygonanthus* would form a mature seed with as thick a testa as in *Poga.*

TABLE 3. Evolutionary trend of karyological and some embryological characters in Anisophylleaceae.

Characters	Plesiomorphy	Apomorphy
1. Number of integuments	2	1
2. Tapetal nuclei	Not fused	Fused
3. "Outer layer" of the "thick" seed coat (thickness)	Thick	Thin, 1 cell thick
4. Chromosome number	$n = 7$	$n = 8$
5. Pattern of embryo sac formation	*Polygonum* type	*Allium* type
6. "Inner layer" of the mature seed coat	Present	Absent
7. Accumulation of starch grains in developing embryo sac	Absent	Present
8. Vasculature of integuments	Present	Absent

The accumulation of starch grains in the developing embryo sac (*Combretocarpus*) is known to occur in many unrelated families of dicotyledons (see Davis, 1966). Even within a family, however, their occurrence is in general restricted to certain genera. Therefore the occurrence of starch grains seems to have been acquired secondarily by particular groups in many unrelated families, probably because of the necessity of different metabolic activity during megagametogenesis.

Embryos with moderately developed cotyledons are almost universal among dicotyledons and therefore must be primary. On the contrary, because of their restricted occurrence (see Natesh & Ram, 1984), embryos lacking cotyledons seem to be secondary in the evolutionary trend. In this respect, it might be interpreted that an embryo with small cotyledons (*Combretocarpus*) seems less specialized than that which lacks cotyledons, or at the most has rudimentary ones (*Anisophyllea* and *Poga*). Such differences in the degree of size reduction of cotyledons, however, may be a matter of degree, because it seems to be more fundamentally important that Anisophylleaceae share a conspicuous hypocotyl, a truly significant and unusual feature.

It may be difficult to determine whether the chromosome base number of Anisophylleaceae is $n = 7$ or 8. Noticeably $n = 8$ occurs only in *Combretocarpus*, a genus that is furnished with many advanced and fewer primitive character states as discussed above. In contrast, $n = 7$ is shared by *Anisophyllea*, *Poga*, and *Polygonanthus*, all of which—particularly the latter two—retain a combination of primitive character states. Thus it seems likely that $n = 7$ is the base number of the family, and $n = 8$ the derived.

The fusion of tapetal nuclei (*Anisophyllea* and *Combretocarpus*) certainly seems secondary to the condition in which the two nuclei remain distinct (*Poga* and *Polygonanthus*), as discussed earlier. These nuclei also remain distinct in most Myrtales (Tobe & Raven, 1983).

The results of our evaluation of these character states are summarized in Table 3. On this basis, we constructed a cladogram illustrating the evolutionary interrelationships of the genera (Fig. 71). The cladogram indicates that the proto-Anisophylleaceae, a hypothetical ancestor of the family, had nearly all of the embryological features that are presently retained by *Poga* and *Polygonanthus*: a chromosome number of $n = 7$, *Polygonum* type embryo sac (although actually uncertain in *Poga* and *Polygonanthus*), bitegmy, vascularized integument, thick seed coat consisting of a multiple inner layer and a multiple outer layer, no starch grain accumulation during megagametogenesis, and non-fused tapetal nuclei. An ancestral evolutionary line seems to have diverged into two main branches: one leading to *Combretocarpus* and *Anisophyllea*, and the other leading to *Poga* and *Polygonanthus*. In the former branch, the ovule became unitegmic; tapetal nuclei fusion has been generalized, and the thickness of the multiple outer layer was reduced into one cell layer (i.e., the outer epidermis); all three characters are synapomorphies common to *Combretocarpus* and *Anisophyllea*. This branch further diverged into two branchlets: one leading to *Combretocarpus*, and the other leading to *Anisophyllea*. In the branchlet leading to *Combretocarpus*, chromosome base number changed to $n = 8$; the *Allium* type embryo sac and unitegmy were derived; complete reduction of seed coat tissue except for the outer epidermis (i.e., of both a multiple inner layer and the hypodermal tissue of the original thick seed coat) and reduction of integumentary vasculature occurred nearly simultaneously; and accumulation of starch grains during megagametogenesis was generalized. With respect to embryological characteristics, no striking change has occurred in the other branchlet

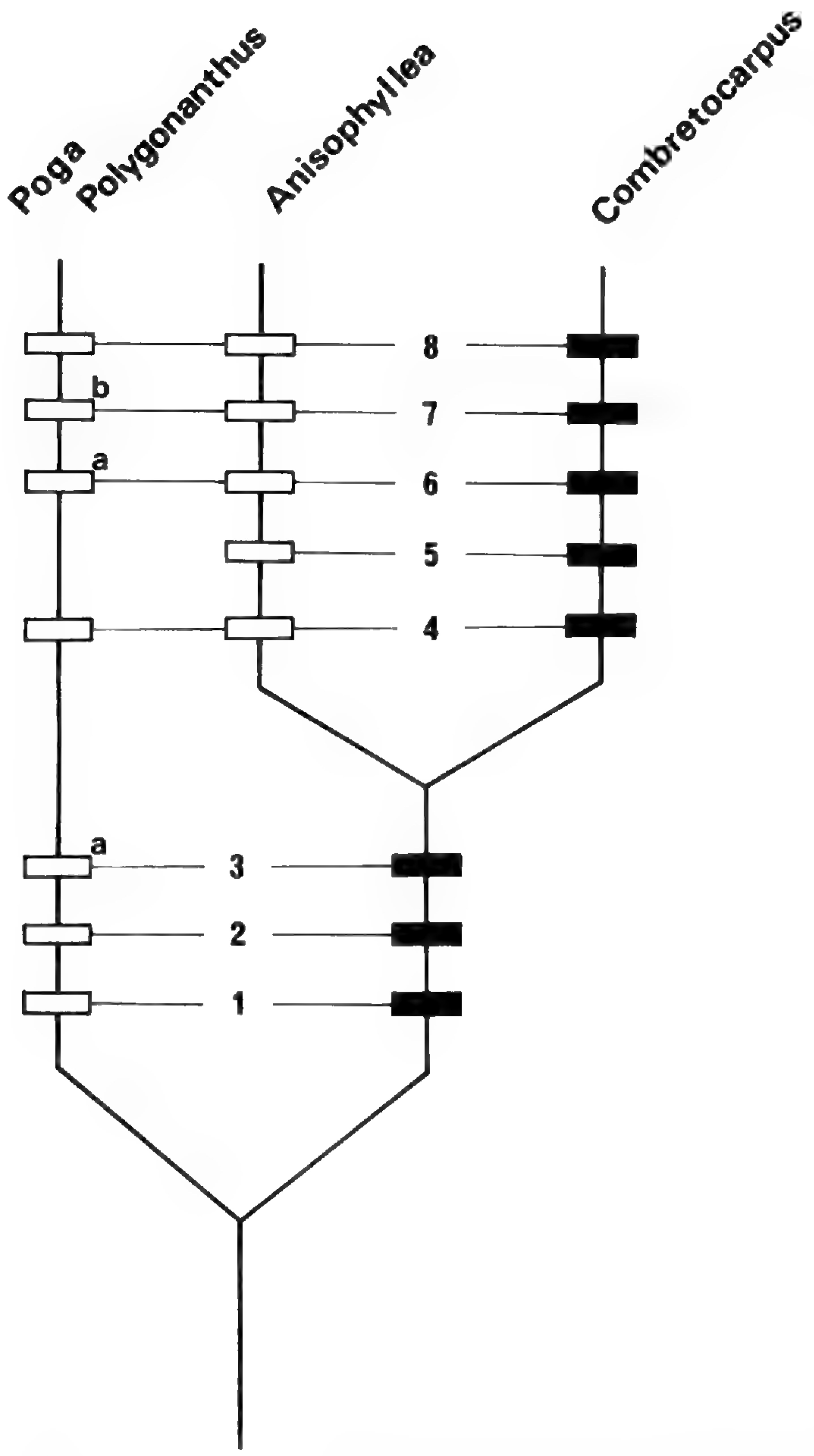


FIGURE 71. A cladogram illustrating postulated evolutionary interrelationships of the genera of Anisophylleaceae. Corresponding characters numbered 1 to 8 and their evolutionary states are shown in Table 3. Shaded rectangles indicate apomorphies. [a]Character state uncertain in *Polygonanthus*; [b]Character state uncertain in *Poga*.

leading to *Anisophyllea*, or in the other main evolutionary line leading to *Poga* and *Polygonanthus*.

Consequently, *Combretocarpus* differs substantially from the three other genera and is apparently the most specialized member of the family. In contrast, most plesiomorphies are referred to *Poga* and *Polygonanthus*, which both retain a combination of primitive embryological character states common to the ancestor of Anisophylleaceae. *Anisophyllea* stands in a more or less intermediate position between *Combretocarpus*, on the one hand, and the group comprising *Poga* and *Polygonanthus*, on the other. Indeed *Anisophyllea* shares most of its archaic features with *Poga* and *Polygonanthus* but shares its apomorphies, including unitegmy and tapetal nuclear fusion, with *Combretocarpus*.

Phylogenetic interpretations of the infrafamilial relationships as discussed above are primarily based on embryological character state evaluation and chromosome number. The cladogram shown in Figure 71 is to be regarded as limited in this respect and provisional. The evolutionary trend in certain characters (such as chromosome number and seed coat structure) might be the opposite of what we have proposed, and certain characters (such as tapetal nuclear condition) might be of much less fundamental significance than others. Earlier studies on Anisophylleaceae never discussed the interrelationships of these genera at much length, however, because the interest earlier was primarily directed toward whether or not *Polygonanthus* was closely related to the other three genera (for instance, Pires & Rodrigues, 1971) or whether or not Anisophylleaceae ("Anisophylleae") should be excluded from Rhizophoraceae (for instance, Van Vliet, 1976). We now regard both of these questions as definitively solved and hope that our phylogenetic diagram will stimulate further research on the family from various other points of view and will thus be improved as a result of these investigations.

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TRAPLINERS IN THE TREES: HUMMINGBIRD POLLINATION OF *ERYTHRINA* SECT. *ERYTHRINA* (LEGUMINOSAE: PAPILIONOIDEAE)[1]

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Abstract

Erythrina sect. *Erythrina* comprises 36 species of hummingbird-pollinated trees and shrubs, distributed principally in Mesoamerica. Avian floral visitors—including nectar thieves as well as pollinators—were observed at 17 populations of 13 species in southern Mexico and Costa Rica. Legitimate pollinators were all "high-reward traplining" hummingbirds with long bills and non-territorial foraging behavior, including in particular two species of *Heliomaster.* Nectar thieves included a variety of short-billed hummingbirds and passerine birds. Measurements of nectar volume, sugar concentration, and flowering behavior indicate that the caloric value of nectar in open flowers produced by one tree per day is insufficient to support a single hummingbird's energetic requirements; therefore, territorial defense by a hummingbird of a single tree is precluded. The traplining hummingbirds appear to be effective agents of pollen flow among conspecific trees in the typically low-density *Erythrina* populations. The pollination system of sect. *Erythrina* is a canopy-level analogue of the high-reward traplining systems involving hermit hummingbirds and understory plants such as *Heliconia* (Musaceae).

Erythrina L. (Leguminosae: Papilionoideae) comprises about 112 species distributed throughout the tropical regions of the world and extending into warm temperate areas in both the northern and southern hemispheres (Krukoff & Barneby, 1974; Neill, in press). Most species are trees or shrubs, but about 10 species occurring in climates with pronounced dry and/or cool seasons are perennial herbs with large, woody rootstocks. *Erythrina* species occur in a very wide variety of habitats, from lowland tropical rain forests to very arid subtropical deserts to highland coniferous forests above 2,500 m in elevation.

Erythrina species have red or orange flowers and copious nectar and are adapted to pollination by nectarivorous birds. Two distinct syndromes of ornithophily are evident. All 42 of the Old World species and 15 of the 70 New World species are pollinated by "perching birds" of several families in the order Passeriformes. Passerine birds cannot hover efficiently or for any length of time, and the inflorescences of passerine-pollinated *Erythrina* are oriented in such a way that the birds can perch while feeding on nectar from the flowers. The corolla standard is usually broad and the flowers are open, with exposed reproductive parts. Pollen is deposited on the feeding bird's breast (Cruden & Toledo, 1977). In contrast, 55 of the New World species of *Erythrina* (nearly half the genus) are pollinated by hummingbirds (Trochilidae), which occur only in the New World. Hummingbirds are the most specialized of nectarivorous birds and are the only ones that hover while feeding. The corolla standard of hummingbird-pollinated *Erythrina* is narrow and conduplicately folded to form a "pseudotube," concealing the wing and keel petals as well as the reproductive parts. The flower resembles the tubular corollas of many gamopetalous hummingbird-pollinated plants, but in *Erythrina* the pseudotube is not sealed on the ventral side where the margins of the corolla standard meet. The inflorescence axis of the humming-

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bird-pollinated species is erect and the flowers are oriented outward, providing no perch for the hovering hummingbirds.

The American hummingbird-pollinated species are included in six different sections of subg. *Erythrina*; these I believe to have been derived from passerine-pollinated groups by convergent evolution in several independent lineages. The largest by far of the hummingbird-pollinated groups is sect. *Erythrina* (36 species) with its center of diversity in northern Central America and southern Mexico (Neill, in press). Most species of sect. *Erythrina* are canopy or subcanopy trees, ranging in height from 5 m in semiarid scrub to 25 m or more in lowland rain forest or cloud forest. A few species inhabit the understory and light gaps of wet forests. Many have restricted ranges and are edaphic specialists; an example is *E. tuxtlana*, which grows only on limestone outcrops in lowland wet forests in southeastern Mexico.

A number of field studies of pollination in *Erythrina* have been conducted in recent years, including observations of passerine-pollinated as well as hummingbird-pollinated species (Toledo, 1974; Toledo & Hernández, 1979; Hernández & Toledo, 1979, 1982; Cruden & Toledo, 1977; Feinsinger et al., 1979; Morton, 1979; Steiner, 1979; Guillarmod et al., 1979). An extensive survey of hummingbird pollination of *Erythrina* tree species, however, was lacking prior to the research reported here.

HUMMINGBIRD FORAGING BEHAVIOR: A REVIEW

Hummingbird species differ in size, bill morphology, and foraging behavior as do the floral morphology and flowering patterns of the plant species they visit (Feinsinger & Colwell, 1978). The two principal behavioral types are territorialists, which feed at large patches of flowers, defending the flowers against usurpers; and trapliners, which do not defend territories but rather visit small, widely spaced clumps of flowers on repeated foraging circuits. The latter may be further subdivided into "low-reward" trapliners, relatively small, short-billed birds, and "high-reward" trapliners, birds with relatively large bodies, high energetic requirements, and long or curved bills. High-reward trapliners are the most "specialized" of hummingbirds in the sense that they have the highest fidelity to particular plant species. These are the only birds capable of pollinating plants with long-tubular flowers, and they provide effective cross-pollination service to plant species with low population densities. The most well-studied of the high-reward trapliners are the hermit hummingbirds (Phaethorninae), which forage principally in lowland and mid-elevation wet forest understories on widely spaced, nectar-rich herbs and shrubs.

Stiles (1978, 1981) noted that very few hummingbird-pollinated plants are canopy trees; in contrast, many ornithophilous plants of the Old World, pollinated by passerine birds, are trees. Stiles reasoned that this difference is related to the social systems of the two bird groups. Passerine nectarivores generally forage in large flocks, whereas hummingbirds are virtually always solitary. A large concentration of flowers on a large tree would be parceled up into feeding territories by hummingbirds, thus drastically reducing cross-pollination. A large flock of passerine birds, in contrast, could quickly exhaust the resources of even a large tree, and the flock would be compelled to move on to the next tree, thus effecting cross-pollination.

Erythrina is an exception to the general paucity of hummingbird-pollinated canopy or subcanopy trees. It should be instructive to determine by observations in the field whether Stiles's prediction holds true for hummingbird-pollinated *Erythrina*. If hummingbirds parcel the crown of a tree into several feeding territories, they may reduce intertree pollen flow; alternatively, hummingbird-pollinated *Erythrina* trees may possess adaptations that reduce territorial behavior and promote intertree movement of the hummingbird pollen vectors.

In the present study of hummingbird pollination in natural populations of trees of sect. *Erythrina*, several questions were addressed: Do the hummingbirds that pollinate *Erythrina* behave as territorialists or as trapliners? How specialized are *Erythrina* pollinators? Another goal was to assess the potential for pollen transfer between different species of *Erythrina*. Experimental hybridization studies (Neill, in press) indicate that species of sect. *Erythrina* are highly interfertile, but unless the hummingbird pollen vectors carry pollen from one species to another, hybridization will not take place under natural conditions. This assessment required information about the flight and foraging patterns of the birds, and whether the *Erythrina* species shared the same pollinators or had different, host-specific pollinators.

MATERIALS AND METHODS

FLORAL BIOLOGY AND BREEDING SYSTEMS

Observations on phenology and other details of *Erythrina* floral biology, as well as experimental studies of genetic self-incompatibility, were made on wild populations in Mesoamerica and on cultivated trees in Hawaii. The experimental methods for the breeding system studies are described by Neill (in press).

OBSERVATIONS OF FLORAL VISITORS

Floral visitors to 17 populations of 13 species of hummingbird-pollinated *Erythrina* trees were observed in Mesoamerica. These included four wet season-flowering species in Costa Rica, July–September 1981, and nine dry season-flowering species in southern Mexico, January–April 1983. All but one of the species is in sect. *Erythrina*; the exception is *E. gibbosa* from Costa Rica, in the monotypic sect. *Gibbosae.* Flowering and pollination patterns in this species are very similar to those in sect. *Erythrina.*

For the 13 species a total of 195 person-hours of observation was conducted. For a population the number of observation hours ranged from 2.5 to 45.5. Most of the observations were made between dawn and 12 P.M., because floral visitor activity is usually greater in the early morning and drops substantially by noon. Some observations were conducted in the late afternoon when avian floral visitors typically become more active after the midday lull.

At the beginning of each observation day I counted the number of open flowers on each tree. For each bird visit to a tree crown, I recorded the time, duration of visit, number of flowers probed, and direction of arrival and departure. I judged qualitatively the frequency of the visitor's contact with the reproductive parts of the flower, as a measure of potential pollination efficacy. Many of the non-pollinating passerine bird visitors actually destroyed or removed a considerable number of flowers daily, reducing the number available to subsequent visitors to the tree. This activity was recorded and entered into the daily flower censuses.

NECTAR PRODUCTION

I sampled daily nectar production in four species in sect. *Erythrina*: *E. globocalyx* and *E. costaricensis* inhabiting wet forests in Costa Rica, and *E. chiapasana* and *E. goldmanii* in dry forests of Chiapas, Mexico. Because the inflorescences in the tree crowns were difficult to reach from the ground, repeated sampling of nectar secretion of individual flowers over the course of a day was not possible; only a day's total production was sampled.

In the late afternoon, flowers due to open the following day were bagged with mosquito netting. These "first-day" flowers were removed at about 4 P.M. the following day, and nectar volume from each flower was measured by repeated probing with a 10- or 25-ml calibrated micropipette.

Nectar production for "second-day" flowers of *E. goldmanii* and *E. chiapasana* was estimated in the following manner: inflorescences were bagged with mosquito netting in the late afternoon as for first-day flowers, and nectar was allowed to accumulate in the isolated flowers for two days. Total nectar accumulation was measured at 4 P.M. on the second day. The mean first-day accumulation of nectar subtracted from the mean 2-day accumulation yields the estimated second-day nectar production. (This method assumes that nectar removal does not influence secretion.) All bagged flowers fell off by the morning of the third day.

Sugar concentration expressed as percent sucrose equivalence (Bolten et al., 1980) was measured for each flower or for the pooled nectar of several flowers using an American Optical model 10431 temperature-compensated hand refractometer. With the figures for nectar volume and sugar content, the mean caloric value of the nectar per flower was calculated for each population sampled.

RESULTS

FLORAL BIOLOGY AND BREEDING SYSTEMS

In most passerine-pollinated species of *Erythrina* the stamens and stigma are well separated at anthesis and the flowers are homogamous, i.e., pollen is released from the anthers and the stigma becomes receptive simultaneously on the first day of flowering. In sect. *Erythrina* and the other hummingbird-pollinated sections of the genus, in contrast, the stamens and stigma are held in close proximity, tightly enclosed in the floral pseudotube, and the flowers are protandrous.

On the first day of anthesis the staminal fila-

TABLE 1. Observations of avian floral visitors to *Erythrina* tree species.

					Nectar Thieves & Robbers	
Species	Locality[1]	Trees[2]	Hours[3]	Pollinators	Hummingbirds	Passerines
1. *E. americana*	Mexico: Oaxaca Coatlán	4	9	*Heliomaster constantii*	—	*Icterus galbula*
2. *E. berteroana* × *E. folkersii*	Mexico: Chiapas Palenque	5	3.5	*Anthracothorax prevostii*	*Anthracothorax prevostii*	*Icterus maculialatus* *Pheucticus ludovicianus*
3. *E. berenices*	Mexico: Veracruz Tequila	2	2	*Eugenes fulgens*	—	—
4. *E. chiapasana*	Mexico: Chiapas El Sumidero	8	15.5	*Heliomaster constantii*	—	*Icterus wagleri*
5. *E. chiapasana*	Mexico: Chiapas Teopisca	6	18	*Eugenes fulgens*	*Hylocharis leucotis*	*Diglossa baritula* *Icterus galbula*
6. *E. cochleata*	Costa Rica: Heredia La Selva	6	20	*Heliomaster longirostris*	*Chalybura urochrysia*	—
7. *E. costaricensis*	Costa Rica: Puntarenas San Vito de Java	1	5	*Heliomaster longirostris*	*Phaeochroa cuvierii*	—
8. *E. gibbosa*	Costa Rica: Alajuela Monteverde	2	11	*Phaethornis guy*	*Lampornis hemileucus*	—
9. *E. globocalyx*	Costa Rica: San Jose Las Nubes	5	8.5	*Eugenes fulgens* *Campylopterus hemileucurus*	—	—
10. *E. goldmanii*	Mexico: Chiapas El Sumidero	12	45.5	*Heliomaster constantii*	—	*Icterus gularis* *I. pectoralis* *I. wagleri*
11. *E. folkersii*	Mexico: Veracruz Los Tuxtlas	2	3.5	*Phaethornis superciliosus* *Campylopterus hemileucurus* *C. curvipennis*	—	—
12. *E. folkersii*	Mexico: Chiapas Palenque	2	4.5	*Phaethornis superciliosus*	*Amazilia tzacatl*	*Icterus galbula* *I. prosthemelas*
13. *E. lanata*	Mexico: Oaxaca Puerto Escondido	2	4.5	*Heliomaster constantii*	—	—
14. *E. lanata*	Mexico: Jalisco Chamela	2	7.0	*Heliomaster constantii*	—	*Cassiculus melanicterus*
15. *E. pudica*	Mexico: Chiapas El Aguacero	8	16.0	*Heliomaster constantii*	—	*Icterus gularis*
16. *E. tuxtlana*	Mexico: Chiapas Malpaso	3	15.0	*Heliomaster constantii* *Anthracothorax prevostii*	*Amazilia cyanocephala* *A. tzacatl*	*Coereba flaveola* *Cyanerpes lucidus* *Icterus graduacauda*

Table 1. Continued.

					Nectar Thieves & Robbers	
Species	Locality[1]	Trees[2]	Hours[3]	Pollinators	Hummingbirds	Passerines
				Eugenes fulgens		*Pheucticus ludovicianus*
17. *E. tuxtlana*	Mexico: Veracruz Uxpanapa	1	5.5	*Campylopterus curvipennis*	*Eupherusa eximia*	—

[1] Complete locality and voucher data for each observation are listed in Appendix.

[2] Number of individual trees observed.

[3] Person/hours of observation.

ments are fully grown and pollen is released from the stamens situated near the apex of the corolla within the pseudotube. At this stage the style is shorter than the stamens and the stigma is not receptive. The style and ovary continue to elongate during the night after the first day of flowering. By the second day, when most of the pollen has been removed by floral visitors, the stigma, now receptive and with a sticky exudate on its surface, is held a few mm beyond the anthers, just inside the mouth of the pseudotube at the apex of the corolla. Each flower, then, is functionally male on the first day and functionally female on the second. Unpollinated flowers usually abort after the second day but sometimes remain for a third or fourth day before aborting; the stigma appears to remain receptive during this time.

The inflorescence of sect. *Erythrina* is a pseudoraceme with fascicles of three flowers each arranged spirally on the erect rachis. Anthesis occurs sequentially from bottom to top of the inflorescence, and usually one or two fascicles of flowers open each day. An individual inflorescence, with 30–50 fascicles, blooms for two or three weeks. An inflorescence in "full bloom" is composed of three to nine functionally female flowers at the bottom (in one to three fascicles), three to six functionally male flowers in the fascicles just above the females, and above them floral buds at progressively younger developmental stages.

Inflorescence development in an individual *Erythrina* tree is staggered, so a tree often blooms for two to three months or more. Blooming among trees in a population is also staggered, so a population is often in bloom for four to five months annually or even longer. Some species remain in bloom for a shorter period, one to two months within a population. Detailed, multi-year phenological data for any particular site, however, is not available.

Most species of sect. *Erythrina* flower during the dry season, from January to May in Mesoamerica, and are leafless when in flower. Leaves flush, in general, after flowering has ceased and while fruits are developing, prior to or just after the onset of the rainy season in May or June. Some species flower during the rainy season, June to October. These species also usually shed all their leaves before flowering and flush a new set of leaves as flowering ceases. This behavior is unusual: few other tree taxa in the Neotropics, especially in very wet forests, shed leaves during the rainier portion of the year and retain them during the drier portion.

The data presently available suggest that all *Erythrina* species are genetically self-compatible (Neill, in press). The fitness of progeny resulting from self-pollination is significantly lower than that of progeny resulting from outcrossing; outcrossing appears to be predominant in the breeding systems of *Erythrina*. Some seed set from geitonogamous pollinations and even from occasional autogamy, which probably occurs in natural populations.

FLORAL VISITORS

The avian visitors to the flowers of most observed *Erythrina* populations included hummingbird and passerine "illegitimate" visitors, which obtained nectar but did not effect pollination, as well as "legitimate" hummingbird pollinators (Table 1). Pollination records for each *Erythrina* species are summarized in Table 2, which encompasses prior reports on hummingbird-pollinated tree species: *Erythrina lanceo-*

TABLE 2. Species of hummingbirds observed as legitimate pollinators on 15 species of *Erythrina*. Abbreviations in parentheses refer to the countries in which species were observed (M = Mexico, C = Costa Rica, and T = Trinidad).

Hummingbirds	*Erythrina* Species														
	E. goldmanii (M)	*E. pudica* (M)	*E. lanata* (M)	*E. lanceolata* (C)	*E. chiapasana* (M)	*E. americana* (M)	*E. cochleata* (C)	*E. costaricensis* (C)	*E. tuxtlana* (M)	*E. pallida* (T)	*E. berteroana* (M, C)	*E. berenices* (M)	*E. globocalyx* (C)	*E. folkersii* (M)	*E. gibbosa* (C)
Heliomaster constantii	+	+	+	+	+	+									
H. longirostris							+	+	+	+	+				
Eugenes fulgens					+	+			+			+	+		
Campylopterus hemileucurus												+	+	+	
C. curvipennis									+					+	
Anthracothorax prevostii									+		+			+	
Phaethornis guy													+		+
Ph. superciliosus														+	
Glaucis hirsuta										+					

lata in Costa Rica (P. Feinsinger, pers. comm.) and *E. pallida* in Trinidad and Tobago (Feinsinger et al., 1979).

For this discussion I have adopted a modified version of Inouye's (1980) terminology for floral larceny: "nectar robbers" make a hole or otherwise damage floral tissue to gain access to the nectar, while "nectar thieves" use the opening used by legitimate pollinators, but a mismatch of the morphologies of flower and animal precludes pollination. The distinction between nectar thieves and robbers is important because robbers may damage the ovary or stylar tissue and often destroy or remove the entire flower, and thus may have a much greater effect in reducing the reproductive potential of the plant than do nectar thieves.

Bill lengths (obtained primarily from Ridgway, 1911) of the hummingbird species observed as pollinators and illegitimate visitors to *Erythrina* trees are compared in Figure 1. Legitimate pollinators all have bills longer than 28 mm, whereas nectar thieves and robbers, with one exception, have bills shorter than 22 mm.

POLLINATORS

Nine species of hummingbird were observed as legitimate pollinators of the 15 species of *Erythrina* trees. All of the hummingbird pollinators may be characterized as long-billed, high-reward trapliners, although some behaved as territorialists or even nectar thieves on certain occasions, as detailed below.

I observed two species of hermit hummingbirds (Phaethorninae) pollinating *Erythrina*: *Phaethornis guy* and *P. superciliosus*. A third hermit species, *Glaucis hirsuta*, was reported as a pollinator of *E. pallida* in Trinidad by Feinsinger et al. (1979). The hermits visited principally the smaller understory species of *Erythrina* but rarely were in the forest canopy. Their foraging behavior at understory *Erythrina* is similar to that documented for understory herbs such as *Heliconia* (Stiles, 1975) or shrubs such as *Aphelandra* (McDade, 1984).

The remaining six *Erythrina* pollinators are non-hermits (Trochilinae); all are long-billed, high-reward trapliners which forage like hermits, but usually in the forest canopy or open areas rather than in the understory. *Heliomaster constantii* is the principal or sole known pollinator of at least six *Erythrina* species in the dry forests on the Pacific slope of Mesoamerica. Its congener *H. longirostris* has been reported from four *Erythrina* species in more humid lowland forests on both the Pacific and Caribbean slopes of Me-

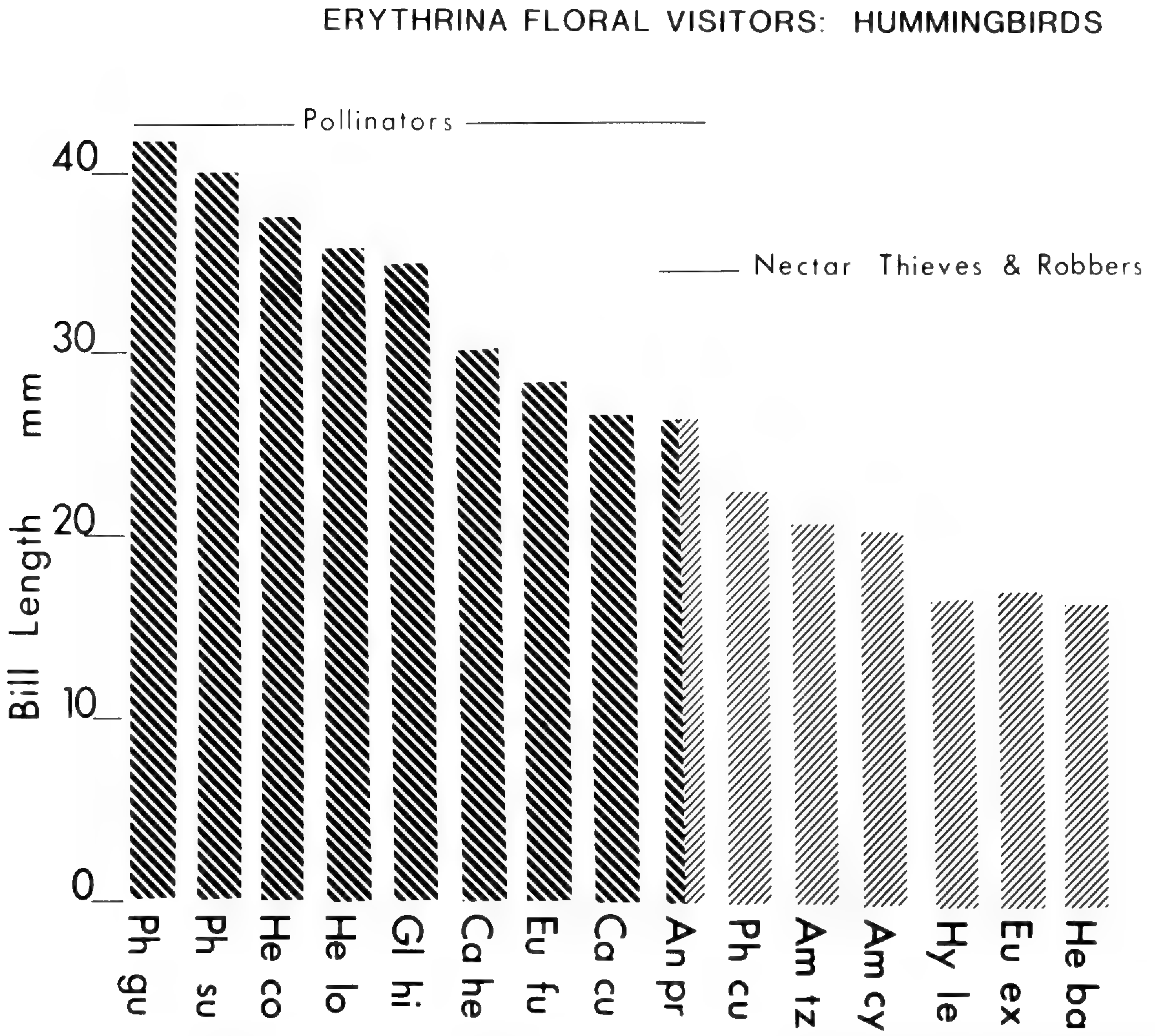
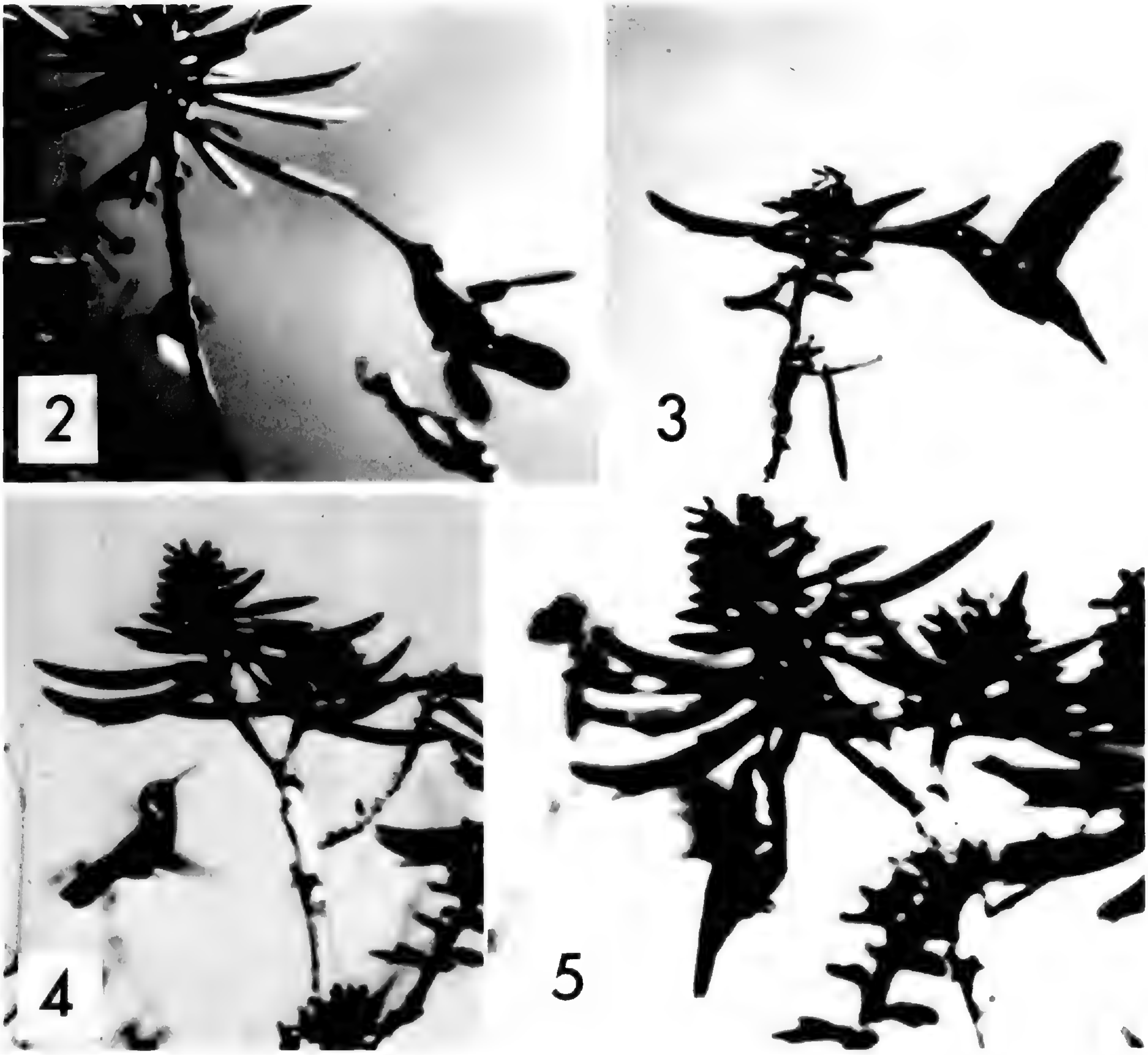


FIGURE 1. Bill lengths of hummingbird visitors to *Erythrina* trees, including pollinators and illegitimate visitors. Ph gu = *Phaethornis guy*; Ph su = *Phaethornis superciliosus*; He co = *Heliomaster constantii*; He lo = *Heliomaster longirostris*; Gl hi = *Glaucis hirsuta*; Ca he = *Campylopterus hemileucurus*; Eu fu = *Eugenes fulgens*; Ca cu = *Campylopterus curvipennis*; An pr = *Anthrocothorax prevostii*; Ph cu = *Phaeochroa cuvierii*; Am tz = *Amazilia tzacatl*; Am cy = *Amazilia cyanocephala*; Hy le = *Hylocharis leucotis*; Eu ex = *Eupherusa eximia*; He ba = *Heliothryx barroti*.

soamerica, and from *E. pallida* in Trinidad (Feinsinger et al., 1979). *Eugenes fulgens* is found mostly in the highlands of Mesoamerica above 1,500 m. It is the principal pollinator of at least four highland species of *Erythrina*, and I also observed it below 1,000 m pollinating *E. tuxtlana* in southern Mexico. *Campylopterus hemileucurus* is a bird of wet forests from near sea level to 1,800 m and has been observed pollinating three *Erythrina* species in such habitats. *Campylopterus curvipennis* was observed as a pollinator of two *Erythrina* species in low- to mid-elevation wet forests of southern Mexico.

Anthracothorax prevostii was the least consistent *Erythrina* pollinator. This bird of low- to mid-elevation humid forests sometimes behaved as a legitimate pollinator and contacted the reproductive parts of *Erythrina* like the other long-billed trapliners. More frequently, however, *Anthracothorax* was a nectar thief, as described below.

The species of hummingbirds that pollinate sect. *Erythrina* all behave in a similar manner when feeding at the flowers. The hummingbird first approaches the inflorescence and hovers to align its bill precisely with the axis of the first flower it is to visit (Fig. 2). It inserts its bill at the apex of the flower; at full penetration the reproductive parts of the flower always contact the bird's throat, upper chest, or the base of the



FIGURES 2–5. Hummingbird pollinators and nectar thieves of *Erythrina* sect. *Erythrina*.—2. Pollinator *Heliomaster constantii* positioning self to feed at flowers of *E. lanata*; dry forest near the Pacific coast, Pochutla, Oaxaca, Mexico. Bill is inserted at apex of corolla.—3. *Eugenes fulgens* pollinating *E. chiapasana*; highland pine-oak forest, Teopisca, Chiapas, Mexico. At full insertion of the bill, pollen is deposited at base of bill or on upper throat.—4–5. *Hylocharis leucotis*, a short-billed nectar thief, approaching and foraging at flowers of *E. chiapasana*; same locality as in Figure 3. The bill is inserted into the mouth of the calyx or the slit of the corolla "pseudotube" to obtain nectar; reproductive parts of the flower are not contacted.

bill (Fig. 3). The bird remains hovering at this position for up to five seconds, then withdraws and moves to another flower in the inflorescence or to another inflorescence.

The pollination records summarized in Table 2 indicate that there is no species-specific, one-to-one relationship of *Erythrina* species and hummingbird species. The ecological and geographic distribution of any single *Erythrina* species does not correspond precisely with that of any pollinator species. Most of the hummingbirds have been observed at several species of *Erythrina* at different localities in the birds' range, and more than one pollinator has been recorded for many of the *Erythrina* species. The bird species are quite similar to one another behaviorally and morphologically, and the tree species are also quite similar to one another in terms of floral morphology, flowering behavior, and nectar rewards (the last is discussed below). *Erythrina* sect. *Erythrina* and related groups are evidently adapted to pollination by the high-reward trapliner guild of hummingbirds as a whole. This, however, is a small subset of all hummingbirds.

In Mesoamerica, there are very few additional hummingbird species with the appropriate morphology and behavior for *Erythrina* tree pollination, other than the nine species listed in Table 2. (*Doryfera ludoviciae* in the highlands of Costa Rica and Panama may be the only high-reward trapliner in the region *not* reported as an *Erythrina* pollinator [P. Feinsinger, pers. comm.].)

On the local community level, often only a single high-reward traplining hummingbird is present so that many populations of *Erythrina* are pollinated by a single bird species. In the lowland dry forests of Pacific Mesoamerica, *Heliomaster constantii* is the only appropriate hummingbird present, so it is undoubtedly the sole pollinator of the *Erythrina* tree species restricted to Pacific dry forests.

The hummingbirds are not strict specialists on *Erythrina*. Well-studied species such as *Eugenes fulgens* have been reported visiting a number of other plant species. The two *Heliomaster* species may be more specialized as *Erythrina* foragers than are the other hummingbird genera. During the course of his extensive community-level studies of hummingbirds, P. Feinsinger (pers. comm.) observed *Heliomaster longirostris* on Trinidad to feed only at *Erythrina pallida* and at the apocynaceous vine *Mandevilla hirsuta*; while at Monteverde, Costa Rica, *Heliomaster constantii* visited exclusively different species of the same two plant genera.

NECTAR THIEVES

The nectar thieves of *Erythrina* sect. *Erythrina* are primarily short-billed, small-bodied, generalist hummingbirds. Observed nectar thieves include several species of *Amazilia, Hylocharis leucotis, Eupherusa eximia,* and *Chalybura urochrysia* (Table 1). The short bills of these birds preclude them from reaching the floral nectar by inserting their bills at the apex of the corolla. Nectar thieves take advantage of the incompletely sealed tube of the *Erythrina* corolla. They approach the flower from below (Fig. 4) and, often with some struggle and manipulation of their bills and bodies, slip their bills into the proximal end of the ventral slit of the pseudotube formed by the corolla standard, or into the mouth of the calyx (Fig. 5). They are thus able to gain access to the nectar within the pseudotube without damaging reproductive tissue. Nectar thief activity is concentrated at the base of the corolla, and thieves were never observed to contact the reproductive parts of the flowers at the apex of the corolla. Unlike the pollinators, thieves frequently grasp the flowers with their feet when feeding and clamber over the inflorescence to reach adjacent flowers. They may damage the surface of the corolla somewhat, but they do not appear to damage the ovary itself. Small nectar thieves may lack the power to pierce the thick *Erythrina* perianth as do the larger-bodied nectar robbers.

Most of the hummingbird nectar thieves are small species with bills under 21 mm long and bodies weighing less than 6 g. An exception is *Anthracothorax prevostii,* whose bill length of 28 mm is within the low end of the range of the legitimate pollinators and whose body size of 10 g is equivalent to that of the pollinators. *A. prevostii* was occasionally seen visiting *Erythrina* flowers in the manner of a true pollinator, but more often it behaved as a nectar thief in a manner similar to the smaller opportunistic birds.

NECTAR ROBBERS: HUMMINGBIRDS

Nectar-robbing hummingbirds have shorter bills than the pollinators but are larger in body size and more powerful than the nectar thieves. The robbers pierce the calyx or base of the corolla with their needle-like bills to gain access to *Erythrina* nectar.

I observed the large (12 g) hummingbird *Phaeochroa cuvierii* repeatedly robbing flowers of a roadside *Erythrina costaricensis* near San Vito de Java in southern Costa Rica. Hovering beneath or beside the inflorescence, the bird placed the tip of its bill against the fleshy calyx and with three or four sharp thrusts punctured through the calyx to plunder the nectar. Usually the robber hovered while piercing the flower, but sometimes it perched on the inflorescence. Flowers strewn on the ground below the tree had up to six puncture holes through the underside of the calyx, indicating that *Phaeochroa* returned to a single flower several times to drain it of nectar. Most pierced flowers were soon aborted, and some had signs of damage to the ovary caused by the robber's bill. On two successive mornings, a *Phaeochroa* repeatedly robbed an *E. costaricensis* tree that was also visited at intervals by a legitimate pollinator, *Heliomaster longirostris.* When on occasion the two birds arrived to feed at the tree simultaneously, a territorial fight ensued.

In the same region of southern Costa Rica where I made the foregoing observations of *E. costaricensis*, Skutch (1971) reported that *Heliomaster longirostris* pollinated the flowers of *Erythrina berteroana* while *Phaeochroa cuvierii* and another short-billed hummer, *Heliothryx barrotii*, robbed them by piercing the calyx. *Erythrina costaricensis* flowers during the Mesoamerican rainy season, August–November, while *E. berteroana* flowers during the dry season, late December to March. The similarity of visitation patterns reported for these two species with different flowering phenologies in the same region (they are not strictly sympatric) suggests that together they support the same pollinators and illegitimate visitors in succession for a considerable portion of the year.

NECTAR ROBBERS: PASSERINE BIRDS AND PARROTS

All of the non-hummingbird visitors to *Erythrina* sect. *Erythrina* are nectar robbers and generally destroy the reproductive potential of the flowers they visit. These robbers include passerine birds in the families Icteridae, Coerebidae, and Fringillidae, and the non-passerine parrot family Psittacidae. Icterids and coerebids are legitimate pollinators of some *Erythrina* species in the Neotropics, but on sect. *Erythrina* they are strictly parasitic.

I observed seven species of orioles (*Icterus* spp.) robbing eight species of *Erythrina* in Mexico and the icterid *Cassiculus melanicterus* robbing one *Erythrina* species. Orioles were the most frequently observed of all robbers and exhibited the most complex behavior to obtain the nectar. Typically, an oriole would pluck a flower with its bill, then hold it against a branch with one foot and jab its bill into the mouth of the calyx to reach the nectar. After plundering the flower, the oriole would drop it and pluck another. The calyx was split open in this process, and the ground beneath a tree preyed upon by orioles would typically be littered with split flowers. This allowed me to count the number of flowers consumed daily by the orioles. Sometimes an oriole would impale a flower on a thorn of an *Erythrina* tree branch to hold it in place while the oriole imbibed the nectar; the impaled flowers were left hanging on the branch.

Oriole species vary in their degree of specialization as nectar feeders (Stiles, 1981). Some evidently obtain a high proportion of their caloric requirements from floral nectar, at least during certain seasons of the year. Orioles are important legitimate pollinators of some *Erythrina* species such as the widespread *E. fusca* (sect. *Duchassaingia*) (Morton, 1979) and the central Mexican endemic *E. oliviae* (sect. *Olivianae*) (Toledo & Hernández, 1979). These passerine-pollinated *Erythrina* species are presumed to represent an ancestral condition with respect to the hummingbird-pollinated groups including sect. *Erythrina*. Orioles and other icterids are known to behave as nectar robbers, in a similar manner to their behavior at *Erythrina*, at other plant species in the Neotropics, including banana (*Musa paradisiaca*), which was introduced from the Old World tropics (Skutch, 1954). In the case of *Erythrina*, the evolutionary relationship of the orioles' nectar-robbing behavior of the hummingbird-pollinated species to their legitimate pollination of the putatively ancestral passerine-pollinated species remains an open question. Did orioles switch to nectar-robbing after having evolved nectar-feeding behavior as legitimate pollinators, or was the order reversed?

Several species of the honeycreeper family (Coerebidae) are nectar robbers of *Erythrina* flowers. I observed the flower-piercer *Diglossa baritula* robbing *E. chiapasana* in the highlands of southern Mexico by holding the corolla with its specialized hooked upper mandible and piercing it with its lower mandible to extract the nectar. Hernández and Toledo (1979) observed similar behavior by the same bird species at *Erythrina leptorhiza*, an herbaceous species of highland central Mexico.

Two coerebid bird species, the shining honeycreeper *Cyanerpes lucidus* and the bananaquit *Coereba flaveola*, were nectar robbers of *Erythrina tuxtlana*. These birds sometimes pierced calyces in the manner of *Diglossa*, and at other times slipped their bills into the calyx mouth without puncturing it, in the manner of the short-billed hummingbird nectar thieves. Like the orioles, these two honeycreepers that behave as robbers of hummingbird-pollinated *Erythrina* species are also important legitimate pollinators of passerine-pollinated *Erythrina* including *E. poeppigiana* in Trinidad (Feinsinger et al., 1979) and *E. megistophylla* in Ecuador (Steiner, 1979).

The migrant rose-breasted grosbeak *Pheucticus ludovicianus* (Fringillidae) nectar-robbed a living fencepost row of hybrid *Erythrina berteroana* × *E. folkersii* and natural populations of *E. folkersii* and *E. tuxtlana*, all on the Atlantic slope of Chiapas, Mexico. Unlike the other pas-

TABLE 3. Daily nectar production in flowers of *Erythrina* sect. *Erythrina.*

Species (Locality)	Nectar Volume $\bar{x}$ µl ± s.d.	$\bar{x}$ Sucrose Equivalence Wt/Vol	$\bar{x}$ Calories per Flower	N
A. First-day flowers				
E. costaricensis (San Vito de Java)	36.4 ± 14.7	29%	43.8	10
E. globocalyx (Las Nubes)	31.4 ± 19.5	22.8%	29.3	10
E. chiapasana (El Sumidero)	29.6 ± 12.0	27.3% ± 3.9%	33.3	12
E. goldmanii (El Sumidero)	31.9 ± 14.6	28.9% ± 2.2%	38.2	10
B. Two-day accumulation of nectar				
E. chiapasana (El Sumidero)	49.8 ± 26.1	27.3	56.0	6
	Estimated caloric production of second-day flower (B-A):		22.7	
E. goldmanii (El Sumidero)	52.3 ± 14.1	31.1	68.1	9
	Estimated caloric production of second-day flower (B-A):		29.9	

serine robbers, grosbeaks actually consumed floral tissue as well as nectar. Usually they plucked the flower and either crushed the calyx with their bills and dropped the flower or consumed the entire flower. At times grosbeaks merely bit off the end of the corolla (and pistil), leaving the flower attached with the calyx and corolla stump. On several occasions I observed the short-billed hummingbird *Amazilia tzacatl* follow a foraging grosbeak and insert its bill into the decapitated *Erythrina* corolla tube to extract the remaining nectar.

On a number of occasions I observed parrots (Psittacidae) consume immature seeds of *Erythrina* trees, but never the flowers. Skutch (1971), however, reported the orange-chinned parakeet *Brotogeris jugularis* to be an important nectar robber of *Erythrina berteroana* in southern Costa Rica. The parakeets plucked the flowers with their bill or feet, bit through the calyx to extract the nectar, and dropped the flowers without consuming floral tissue.

NECTAR PRODUCTION AND CALORIC VALUE

Daily nectar production per flower in the sampled populations of *Erythrina chiapasana, E. costaricensis, E. globocalyx* and *E. goldmanii* is shown in Table 3. Within populations, the variance in nectar production per flower was high (for example, the range in *E. globocalyx* was 10–67 µl). The mean nectar volume for each of the four populations (30–36 µl) was quite similar, however. The sugar concentration of the nectar varied relatively little within or among populations (23%–29%). The calculated mean caloric value of the nectar per flower ranged from 29 to 43 cal among the sampled populations, with an overall mean of 36 cal.

Nectar continued to accumulate on the second day of flowering in the bagged flowers of *E. chiapasana* and *E. goldmanii.* The estimated caloric production of the second-day flowers (overall mean = 27 cal) was somewhat less than in the first-day flowers, but this may have been due to inhibition of production by the accumulation of large nectar volumes in the protected flowers, in the absence of removal by nectarivores.

The results of the nectar sampling from the different species were similar enough to allow a rough estimate of the daily caloric production per flower for hummingbird-pollinated sect. *Erythrina* in general. For purposes of the discussion below, an average caloric production of 35 cal per flower per day is assumed as an approximation. This is somewhat less than the values reported by Stiles (1975) for hermit-pollinated *Heliconia* species (48–141 cal) but is an order of magnitude or greater than the production typical of plants pollinated by short-billed generalist hummingbirds (Feinsinger, 1978).

HUMMINGBIRD ENERGETICS AND NECTAR REWARDS

Macmillen and Carpenter (1977) derived a regression equation for the 24-hour energy costs of nectar-feeding birds, based on empirical data on basal metabolic rates and energetic costs of flight for hummingbirds, Hawaiian honeycreepers, and African sunbirds. Using this equation, the daily energetic cost for a *Heliomaster* weighing 8.0 g is calculated to be 10.9 kcal. This is the equivalent of 311 *Erythrina* flowers at 35 cal/flower. (Hummingbirds do gain some nourishment by consuming arthropods, so the actual daily nectar consumption of an *Erythrina* pollinator may be somewhat less.)

Erythrina species in sect. *Erythrina*—even large canopy trees at the peak of their blooming period—do not generally produce as many as 300 flowers per day. Therefore an individual is probably not "worth" defending as a feeding territory by a hummingbird; several trees must be visited daily to satisfy the bird's energetic requirements.

Intertree movement of the foraging birds, and consequent pollen flow between trees, is evidently promoted by the limited number of flowers produced on an individual tree. In contrast, the extended blooming period of *Erythrina* and the predictability of the nectar resource promotes the high fidelity of visitation exhibited by the traplining pollinators. This syndrome is exemplified by my data on flowering behavior and pollination observations of populations of several different species of *Erythrina*, discussed below.

Erythrina cochleata. *Erythrina cochleata* is a 25-m tall canopy tree at La Selva Biological Station, a tropical wet forest site in Costa Rica. I attempted to locate every reproductively mature individual of this species in an area of about 2 km^2 at La Selva and found a total of 10 trees. This species is confined to the alluvial terraces of the rivers and major streams, so on a large scale the trees were clumped, but no individual was less than 50 m from its nearest conspecific neighbor. *Erythrina cochleata* flowers during the wet season, and the population was in flower continuously at least from May through September 1981.

I observed flower production and floral visitors for six days at four different individual trees. The trees averaged 112.5 (range 84–181) open flowers per day. The pattern of floral visitation each day was very consistent. The only pollinator and regular visitor was *Heliomaster longirostris*. Each morning between 7:00 A.M. and 8:30 A.M. a solitary *Heliomaster* would arrive, visit as few as four to as many as 45 *Erythrina* flowers, and depart. These visits were repeated at sporadic intervals during the morning. (Birds were not tagged, so subsequent visits may have been made by different individual birds.)

On only two occasions was more than one hummingbird seen at a time in an *Erythrina cochleata* crown, and both times the interloper (once another *Heliomaster*, once a nectar-thieving *Chalybura urochrysia*) was chased away by the *Heliomaster*.

Heliomaster longirostris is considered an "uncommon" bird at La Selva (Slud, 1960), yet I saw this species every time I looked for it at flowering *Erythrina* trees. Evidently the small, scattered population of *Erythrina cochleata* supports the nutritional requirements of, and receives consistent pollination service from, a small population of *Heliomaster* for a period of several months each year. What the *Heliomaster* hummingbirds do when the trees cease flowering is unknown. They may migrate to populations of other *Erythrina* species on the Atlantic slope of Costa Rica, such as *E. steyermarkii*, that flower during the dry season, or they may forage at other canopy flowers such as *Mandevilla* spp. vines (besides *Erythrina*, there are no other hummingbird-pollinated canopy-level *trees* in the region).

Erythrina goldmanii. The habitat and population structure of *Erythrina goldmanii* at Cañon del Sumidero National Park in Chiapas, Mexico, where I observed this species, are very different from those of *E. cochleata* at La Selva, but the pollination systems of the two species are quite similar.

Erythrina goldmanii is a dry forest species and is rather scrubby, rarely attaining a height of over 6 m. At El Sumidero, on a slope above the semi-arid basin of the Rio Grijalva, *E. goldmanii* forms dense populations of small trees in disturbed secondary forest. I made observations in a 2 ha plot containing 54 plants. Most trees had only one or two inflorescences in bloom, with less than 10 flowers per tree; the largest tree had 36 flowers. In all there were 475 flowers in the 2 ha plot at peak flowering.

Heliomaster constantii was the only pollinator and the only hummingbird visitor seen at *Erythrina goldmanii* in over 45 hours of observation. At least three *Heliomaster* individuals were regularly in the area, with considerable movement between *Erythrina* plants, and I frequently watched them forage up and down the slope well beyond the boundaries of the plot. Their fidelity to *Erythrina* was very high: only twice did I see a *Heliomaster* visit any other plant, and then only for single floral probes.

Orioles were frequent visitors to *Erythrina goldmanii,* and they destroyed an estimated 21% of the flowers daily in the manner described previously. There may have been competition for nectar resources between the orioles and the *Heliomasters,* but I never observed any aggressive interactions between orioles and hummingbirds.

Species of *Erythrina* sect. *Erythrina* are usually allopatric, being separated by elevation and habitat; but at El Sumidero two species come into contact. *Erythrina goldmanii* inhabits the dry lower slopes at about 800 m, and *E. chiapasana* occurs in the moister forest on top of the plateau at 1,100 m. *Heliomaster constantii* visited *Erythrina chiapasana* just as it did *E. goldmanii* less than a kilometer away downslope. Both *Erythrina* species and spontaneous hybrids were found in the intermediate zone, on the upper slopes of the El Sumidero escarpment (Neill, in press). The birds evidently do not discriminate among *Erythrina* species when the species occur together. *Heliomaster* hummingbirds are certainly the pollen vectors implicated in interspecific gene flow between *Erythrina* species at El Sumidero.

Erythrina tuxtlana. One final observation indicates that traplining hummingbirds will sometimes behave as facultative territorialists if they are given the opportunity. I observed floral visitors to a 20 m tall *Erythrina tuxtlana* in mid-elevation wet forest near Malpaso, Chiapas. The tree had a broad-spreading crown with 1,400 open flowers. According to the estimates of nectar production in other species, this should have been enough to support several hummingbirds. In fact, three hummingbirds of three different species (*Heliomaster longirostris, Eugenes fulgens,* and *Anthracothorax prevostii*) partitioned the crown of the tree into feeding territories and maintained the territories throughout the morning. When not feeding, each bird generally perched within its territory, and many aggressive interactions ensued when one bird crossed into another's territory. This was the only instance of consistent within-tree territoriality I observed in any *Erythrina* population.

Conclusions: Is It Coevolution?

The flowers of *Erythrina* sect. *Erythrina* provide a rich nectar resource that is fed upon by many species of birds besides the legitimate pollinators. The pollinators, however, constitute a small guild of "high-reward traplining" hummingbirds, about eight species in Mesoamerica. These are mostly non-hermits of the subfamily Trochilinae. Predominant among these is the genus *Heliomaster.* The pollinators are highly faithful visitors to *Erythrina,* which provides them with a consistent nectar resource for long periods. The limited caloric value of nectar produced per tree per day usually precludes the maintenance of permanent feeding territories at a single tree by the hummingbird visitors. The consequent nomadic or "traplining" behavior of the hummingbirds and the dispersal patterns of the pollen they transport among the scattered individual *Erythrina* trees may be a critical factor in the mating systems and genetic structure of the low-density *Erythrina* populations.

The pollination system of sect. *Erythrina,* in summary, is a canopy-level analogue of the high-reward traplining pollination systems of *Heliconia* and similar understory plants. In this sense the pollination system of sect. *Erythrina,* together with the other hummingbird-pollinated sections of *Erythrina* trees (sects. *Stenotropis, Pseudo-edules, Gibbosae,* and *Corallodendra*; cf. Neill, in press) may be unique. Hummingbird-pollinated canopy and subcanopy trees are in themselves uncommon (Stiles, 1978), and I know of no other genus of canopy trees besides *Erythrina* that is adapted to pollination by the traplining guild of hummingbirds.

To what extent have species of sect. *Erythrina* and their hummingbird pollinators coevolved? To what extent is this a specialized mutualism? Feinsinger (1983) indicated that a highly specialized, one-to-one relationship between hermit hummingbirds and their food plants is a rare occurrence; although they may specialize on a particular plant species temporarily, most hermit species forage on a number of different plants. Similarly, most hermit-pollinated plants are serviced by several species of hermits, although shorter-billed birds are excluded as pollen vectors. If one's definition of coevolution requires a high degree of one-to-one species specificity in such mutualistic interactions, then hermits and hermit-pollinated plants cannot be considered very "tightly coevolved." Feinsinger (1983) considered that "most hermits, hermit-like hummingbirds and their food plants exemplify diffuse coevolution between two diverse groups of species."

Species of sect. *Erythrina* vary in the degree of specificity of their association with the hummingbird pollinators. *Erythrina* species of the dry forests of the Pacific slope are pollinated exclusively by *Heliomaster constantii,* so the plant's fitness is directly dependent on the behavior and morphology of a single bird species. The opportunity for the plant to evolve adaptations to specific traits of the bird is clear. *Heliomaster constantii,* however, feeds upon and pollinates a number of *Erythrina* species throughout the bird's geographic range, and it also feeds upon and pollinates at least one other plant genus (*Mandevilla*; Feinsinger, pers. comm.). Although there is undoubtedly a temporary sort of exclusivity in the *Erythrina-Heliomaster* association in certain ecological communities at certain seasons of the year, the association cannot really be considered an obligate mutualism.

The plant-pollinator association is less specific for *Erythrina* species of highland and wet-forest communities, where several species of traplining hummingbirds often visit and pollinate an individual tree on a single day. Hummingbirds such as *Eugenes* and *Campylopterus* visit a rather wide variety of plants besides *Erythrina.* Even in these cases, however, such plant-pollinator associations involving high-reward traplining hummingbirds are much more exclusive than those involving short-billed generalist hummingbirds and short-corolla plants.

Among the species of sect. *Erythrina,* there is little differentiation in floral morphology, flowering patterns, or morphology and behavior of the pollinators—the pollination system of all species is quite similar. Rather, species are differentiated by their restriction to distinct climatic and edaphic conditions. This large group of species, as a whole, has evolved a particular set of adaptations to the guild of high-reward traplining hummingbirds.

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Appendix

Locality and Voucher Data for *Erythrina* Populations Used in Observations of Floral Visitors (Numbers correspond to those listed in Table 1)

1. *E. americana* Miller. Mexico: Oaxaca, 5 km E of San Pablo Coatlan. 16°12'N; 96°47'W. Elev. 1,450 m. Disturbed gallery forest with *Taxodium*, and cultivated fields. Tree to 20 m, along intermittent stream. 9–10 Feb. 1983. *Neill 5421, 5424.*

2. *E. berteroana* Urban × *E. folkersii* Krukoff & Moldenke. Mexico: Chiapas, 3 km S of Palenque. Elev. 100 m. 17°28'N; 92°00'W. Fencepost bordering field. Tree to 8 m. 18 March 1983. *Neill 5533.*

3. *E. berenices* Krukoff & Barneby. Mexico: Veracruz, Tequila. 19°45'N; 97°03'W. Elev. 1,650 m. Coffee plantation; Premontane Wet Forest. Tree to 12 m. 26 Jan. 1983. *Neill 5381.*

4. *E. chiapasana* Krukoff. Mexico: Chiapas, El Sumidero National Park, Km 14–16. Elev. 1,100 m. 16°47'N; 93°06'W. Disturbed Premontane Dry Forest, transition to moist mixed *Quercus* forest. Tree 15 m. 2–4, 9, 25 March 1983. *Neill 5455, 5458, 5465.*

5. *E. chiapasana* Krukoff. Mexico: Chiapas, 13 km E of Teopisca. Elev. 2,000 m. 16°30'N; 92°25'W. Pine-oak forest. Tree 7 m. 22–23 March 1983. *Neill 5445.*

6. *E. cochleata* Standley. Costa Rica: Heredia, La Selva Biological Station. Elev. 200 m. 10°24'N; 84°00'W. Tropical Wet Forest. Tree 25 m. 15–18 Aug., 18–21 Sept. 1981. *Neill 5015, 5101.*

7. *E. costaricensis* Micheli. Costa Rica: Puntarenas, San Vito de Java, Las Cruces Botanical Garden. Elev. 1,200 m. 8°45'N; 82°55'W. Premontane Rain Forest, roadside. Tree 6 m. 11–12 Sept. 1981. *Neill 5099.*

8. *E. gibbosa* Cufodontis. Costa Rica: Alajuela, upper Penas Blancas Valley, below Monteverde Reserve. Elev. 1,400 m. 10°20'N; 84°45'W. Premontane Rain Forest; edge of pasture. Tree to 4 m. 4–6 Sept. 1981. *Neill 5057.*

9. *E. globocalyx* Porsch & Cufodontis. Costa Rica: San Jose, Las Nubes. Elev. 1,700 m. 9°53'N; 24°00'W. Fencepost row, border of pasture. Tree to 8 m; sporadic along stream. 14 Aug., 25 Sept. 1981. *Neill 5033, 5142.*

10. *E. goldmanii* Standley. Mexico: Chiapas, El Sumidero National Park, Km 7. Elev. 900 m. 16°47'N; 93°06'W. Tropical Dry Forest; secondary, disturbed scrub. Tree 8 m. 25 Feb.–1 March 1983. *Neill, 5497, 5498.*

11. *E. folkersii* Krukoff & Moldenke. Mexico: Veracruz, Los Tuxtlas Biological Station. Elev. 200 m. 18°31'N; 95°03'W. Tropical Wet Forest. Understory/subcanopy tree to 8 m. 28 Jan. 1983. *A. Gentry* 32490.

12. *E. folkersii* Krukoff & Moldenke. Mexico: Chiapas, Palenque Archaeological Site. 17°29'N; 92°01'W. Tropical Wet Forest; forest edge. Tree 5 m. 19 March 1983. *Neill 5534.*

13. *E. lanata* Rose. Mexico: Oaxaca, 37 km W of Puerto Escondido. Elev. 20 m. 15°90'N; 97°20'W. Tropical Dry Forest, scrub. Tree 6 m. 13 Feb. 1983. *Neill 5430.*

14. *E. lanata* Rose. Mexico: Jalisco, Chamela Biological Station. Elev. 250 m. 19°30'N; 105°03'W. Tree 7 m. 13 Jan. 1983. *Neill 5329.*

15. *E. pudica* Krukoff & Barneby. Mexico: Chiapas, Rio de la Venta, Cascada El Aguacero. Elev. 750 m. 16°46'N; 93°33'W. Tropical Dry Forest, scrub. Tree 6 m. 27, 31 March 1983. *Neill 5512.*

16. *E. tuxtlana* Krukoff & Barneby. Mexico: Chiapas, 25 km N of Ocozocuautla. Elev. 700 m. 16°48'N; 93°25'W. Premontane Wet Forest; karst limestone. Tree to 20 m. 28 March, 9 April 1983. *Neill 5486, 5621.*

17. *E. tuxtlana* Krukoff & Barneby. Mexico: Veracruz, Uxpanapa. Elev. 90 m. 17°11'N; 94°39'W. Tropical Wet Forest; karst limestone. Tree 15 m. 16–17 April 1983. *Neill 5642.*

A COMPARISON OF THE DIVERSITY, DENSITY, AND FORAGING BEHAVIOR OF BEES AND WASPS ON AUSTRALIAN *ACACIA*[1]

Peter Bernhardt[2]

Abstract

Twenty-seven bee taxa and 24 wasp taxa were collected on the open inflorescences and/or extra-floral nectaries of eight *Acacia* species in Victoria, Australia. Despite this superficial similarity in taxonomic diversity, bees outnumbered wasp foragers by 88% of the combined catch of winged Hymenoptera. Representatives from five families of bees were recorded, with the short-tongued Halictidae and Colletidae comprising the largest unit of native Apoidea on the *Acacia* species studied. Pollen foraging female bees of the genera *Lasioglossum* (Halictidae) and *Leioproctus* (Colletidae) comprised 83% of the combined catch of the two short-tongued families. The number of bee taxa collected on the *Acacia* species tended to increase from late winter through late autumn. Polylectic foraging bee taxa expanded from mid spring through late summer when the flowering of nectariferous Myrtaceae peaked. There was no correlation between the density and diversity of bees foraging on *Acacia* species bearing secreting extra-floral nectaries and those species that lacked extra-floral nectar while the inflorescences were blossoming. Representatives of seven families of wasps were collected on the eight *Acacia* species. No wasps, however, were collected on var. *retinodes* of *A. retinodes.* Approximately 66% of the wasps collected belonged to the families Sphecidae and Tiphiidae. Wasps repeatedly foraged on extra-floral nectar before foraging on nectarless inflorescences. The density and taxonomic diversity of wasps remained highest on the *Acacia* species that offered the greatest volume of sucrose-rich, extra-floral nectar (i.e., *A. terminalis*). Bees are probably more important pollinators of *Acacia* in southeastern Australia than are wasps. The direct influence of wasps on polyad dispersal appears to be nominal except in those *Acacia* species bearing functional extra-floral nectaries.

Winged Hymenoptera (bees and wasps) have been observed to forage frequently on inflorescences of Australian *Acacia.* In contrast to the Psyllidae and some Coleoptera, bees and non-parasitic wasps are not destructive to the small flowers that comprise an *Acacia* head or spike (Bernhardt, 1982). Instead evidence suggests that Hymenoptera are often pollinators of some *Acacia* species in southeastern Australia (Bernhardt, 1982; Bernhardt et al., 1984; Knox et al., 1985).

The flowers of all Australian *Acacia* examined thus far are nectarless (Bernhardt, 1982; Bernhardt et al., 1984; Bernhardt & Walker, 1984, 1985; J. Kenrick & G. Beresford, pers. comm.). The pollen grains, which are fused together to form polyads, are the primary edible reward. When the anthers dehisce the eight polyads present in each anther are extruded, or partially extruded, from their respective sacs (Kenrick & Knox, 1979; Knox & Kenrick, 1982). Consequently, bees, wasps, and certain flies easily collect polyads from the synchronously opening florets in an inflorescence.

Female bees are known to collect *Acacia* polyads to feed to their larvae. Foraging bees remove polyads from the anthers via thoracic vibration of whole inflorescences (Buchmann, 1983) or by scraping anthers directly with their forelegs (Vogel, 1978), or both (Bernhardt & Walker, 1984, 1985). *Acacia* species are usually self-incompatible. Seed set tends to occur only when pollinators move between genotypes belonging to the same species (Knox & Kenrick, 1982; Bernhardt et al., 1984; Kenrick et al., 1984b).

Capture records of insects foraging on *Acacia* in southeastern Australia and analyses of their pollen loads suggest that Hymenoptera are often more important as polyad vectors than are either

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beetle or fly taxa. Calliphorid and syrphid flies transport polyads from *Acacia* inflorescence to inflorescence without damage, but they may occur on *Acacia* inflorescences at lower density and diversity than Hymenoptera (Bernhardt et al., 1984; Knox et al., 1985).

Excluding the rare documentation of pollination by birds or marsupials (see review by Turner, 1982; Knox et al., 1985) the flowering behavior, floral presentation, and polyad presentation of most *Acacia* species would be expected to favor a system of generalist entomophily (Bernhardt, 1982; Bernhardt et al., 1984). That is, all insects that forage for polyads have immediate access to the inflorescences of *Acacia* and could effect deposition of polyads on respective stigmas.

Therefore the purpose of this study was to determine which groups within the Hymenoptera were major vectors of *Acacia* polyads with sufficient fidelity to regularly effect seed set. To accomplish this end the density and taxonomic diversity of polyad foragers were compared to their respective activities on *Acacia* inflorescences.

MATERIALS AND METHODS

Acacia species and study sites. Eight *Acacia* were selected to determine interspecific and intraspecific foraging preferences of Hymenoptera. The species of *Acacia* may be found in flower throughout the year (Kenrick et al. 1984a, 1984b; Bernhardt, 1982) with the majority flowering from August through October (Costermans, 1983). Therefore the eight selected species represented the 12-month flowering season of the genus but emphasized the period of intensively overlapping floral phenology from the last month of winter (August) until the second month of spring (October). The periods of fieldwork, study sites, and habitats of each *Acacia* species are listed below. Descriptions of floristic alliances follow Specht and colleagues (1979).

1) *Acacia longifolia* Willd. 31/viii/84–28/ix/84. Langwarren Reserve: Tall shrubland with disrupted epacrid heath (Bernhardt, 1986).
2) *A. mearnsii* De. Wild. 8/xi/84–21/xi/84. Coranderrk Reserve: Moist sclerophyll woodland/shrubland (see Bernhardt & Calder, 1981).
3) *A. mitchelii* Benth. 16/vii/82–21/i/83. Brisbane Ranges National Park: Dry sclerophyll woodland/shrubland (see Bernhardt & Walker, 1984).
4) *A. myrtifolia* Willd. 19/viii/82–7/x/82. Brisbane Ranges National Park: Dry sclerophyll woodland/shrubland (see Bernhardt & Walker, 1984).
5) *A. paradoxa* DC. (syn. *A. armata* R. Br.). 12/ix/84–31/x/84. Brisbane Ranges National Park: Dry sclerophyll woodland/shrubland (see Bernhardt and Walker, 1984).
6) *A. pycnantha* Benth. 11/viii/82–16/ix/82. Brisbane Ranges National Park: Dry sclerophyll woodland/shrubland (see Bernhardt & Walker, 1984).
7) *A. retinodes* var. *retinodes* Schdl. 16/i/82–17/i/82. Grampians National Park: Montane and valley dry sclerophyll forest/shrubland with adjacent epacrid heaths (see Bernhardt & Walker, 1985).
8) *A. retinodes* var. *uncifolia* J. Black. 15/xi/81–5/iii/82. Cape Schanck National Park: Coastal calcareous dune flora consisting of tall shrubland and invasive, naturalized shrubs and herbs (see Bernhardt et al., 1984).
9) *A. terminalis* Macbr. 18/iii/83–28/iv/83. Erica-Moe (south Gippsland) and Boolah Boolah State Forest. Moist sclerophyll woodland/forest with a rain forest element (see Knox et al., 1985).

Analysis of Hymenoptera. The foraging behavior of Hymenoptera was observed and recorded over the respective periods of fieldwork every day or every other day. Insects were collected selectively from 8 A.M. until 2 P.M. as foraging behavior becomes negligible by mid afternoon.

Insects were collected only if they were observed foraging on the open inflorescences of *Acacia* and/or taking nectar from extra-floral nectaries on the leaves or phyllodes of *A. longifolia, A. myrtifolia, A. pycnantha* (Bernhardt & Walker, 1984), and *A. terminalis* (Knox et al., 1985). Foraging is defined here as the active removal of polyads from anthers or the probing of flowers and extra-floral nectaries with mouthparts (Bernhardt et al., 1984). Terminology for bouts of foraging by bee taxa follows Michener (1979).

Insects were killed communally in jars containing fumes of ethyl acetate. To determine the presence of pollen, each insect was observed under a dissecting microscope. To analyze pollen species carried by insects, each insect was placed on a clean glass slide and "bathed" in a couple of drops of 100% ethanol. When ethanol had evaporated, the white residue remaining on the

TABLE 1. Bee taxa collected on the inflorescences of *Acacia*.

Bee Taxon	*Acacia* Species on Which Bee Taxon Was Captured[a]									No. Bees
	LO	ME	MI	MY	PA	PY	RR	RU	TE	
Anthophoridae:										
Exoneura (*Brevineura*) spp.	0	4	0	0	0	0	0	0	0	4
Exoneura (*Exoneura*) spp.	0	18	0	0	0	0	2	0	11	31
										35
Apidae:										
Apis mellifera[b]	A	1	1	5	4	A	A	A	A	
Colletidae:										
Amphylaeus sp.	0	0	0	0	0	0	0	0	1	1
Callomelitta perpicta	0	0	0	0	0	0	0	0	4	4
Callomelitta spp.	0	0	1	2	0	0	1	0	1	5
Euhesma spp.	0	0	0	0	0	3	8	0	0	11
Euryglossa spp.	1	0	0	0	2	0	0	0	0	3
Hylaeus sp.	0	0	0	0	0	0	1	0	0	1
Leioproctus metallescens	0	0	0	0	0	0	0	14	0	14
L. plumosus	0	0	0	0	0	0	0	1	0	1
Leioproctus (*Euryglossidia*) spp.	0	0	0	0	42	0	2	0	0	44
Leioproctus (*Leioproctus*) spp.	3	0	2	12	7	23	19	0	2	79
Trichocolletes sp.	0	0	0	0	1	0	0	0	0	1
										164
Halictidae:										
Homalictus brisbanensis	0	2	0	0	0	0	0	10	0	12
H. demissus	0	0	0	0	0	0	1	0	0	1
H. dixoni	0	0	0	0	0	0	0	0	5	5
H. holochorus	1	0	0	0	0	0	0	0	0	1
H. megastigmus	0	0	2	0	7	0	1	0	0	9
H. oxoniellus	0	0	0	0	0	0	0	4	0	4
H. punctatus	0	0	0	1	0	0	1	0	0	2
Lasioglossum (*Australictus*) spp.	0	12	0	0	0	0	0	0	0	12
La. (*Austrevylaeus*) spp.	0	0	0	0	0	0	0	0	1	1
La. (*Chilalictus*) spp.	0	9	12	5	2	2	6	1	4	41
La. (*Parasphecodes*) spp.	2	1	9	9	22	6	16	71	22	158
Nomia spp.	0	5	5	0	0	0	0	0	0	10
										256
Megachilidae:										
Megachile sp.	0	0	0	0	0	0	0	2	0	2
										2
Grand Total	7	51	31	29	83	34	58	103	51	457

[a] LO = *A. longifolia*; ME = *A. mearnsii*; MI = *A. mitchelii*; MY = *A. myrtifolia*; PA = *A. paradoxa*; PY = *A. pycnantha*; RR = *A. retinodes* var. *retinodes*; RU = *A. ret.* var. *uncifolia*; TE = *A. terminalis*.

[b] A = Abundant (no more than five bees caught but far more than that number were identified on sight on this *Acacia* species).

slide was mounted in one or two drops of Calberla's fluid (Ogden et al., 1974). Identification of pollen was made under light microscopy. However, since insects were killed in the same jar, contamination of pollen species was possible. Therefore an *Acacia* species or species of Epacridaceae was not counted as present on an individual unless 25 polyads could be counted in that single sample. Taxa producing monad pollen were not counted as present in a sample unless 25 individual grains were identified on a single slide (Bernhardt et al., 1984). Insects washed of pollen were air dried, numbered, placed in individual glassine bags, and identified.

TABLE 2. Characteristics of the secretion of extra-floral nectar in four *Acacia* species.[a]

Characteristics of the Nectary or Nectar	LO	MY	PY	TE
Nectary secretes throughout the flowering seasons	+	+	+	+
Nectary secretes ≥1 ml every morning[b]	−	−	−	+
Nectar hexose rich	?	−	+	−
Nectar sucrose rich or sucrose dominant	?	+	−	+

[a] Derived from Bernhardt (1982), Bernhardt and Walker (1985) and Knox et al. (1985).

[b] Observations and collections of nectar made between 7–9 A.M.

LO = *A. longifolia*; MY = *A. myrtifolia*; PY = *A. pycnantha*; TE = *A. terminalis*.

RESULTS

BEES

Bees foraged for polyads on each of the eight *Acacia* species (Table 1). A total of 457 bees were caught on the eight *Acacia* species. The greatest numbers of bees collected belonged to the short-tongued family of Halictidae. Of all five families the Halictidae offered the greatest number of genera collected. *Lasioglossum* (subgenus *Parasphecodes*; Halictidae) species were collected in greater numbers on *Acacia* compared to all other genera and subgenera of native Apoidea.

The naturalized honeybee, *A. mellifera*, was locally abundant on half of the *Acacia* species studied and could be identified effortlessly on sight (Table 1). This bee was the dominant forager on *A. longifolia*.

Five bee families were identified on eight *Acacia* species. However, seven out of the 27 bee taxa represented single captures. The long-tongued families Apidae and Megachilidae were represented by only one taxon each. The third long-tongued family, Anthophoridae, was represented by two subgenera of *Exoneura* (Table 1). All remaining bee taxa belonged to the short-tongued families Halictidae and Colletidae. Eighty-four percent of the Colletidae collected belonged to the genus *Leioproctus* s.l. Eighty-three percent of the Halictidae belonged to the genus *Lasioglossum* s.l. (Table 1). *Lasioglossum* (subgenus *Parasphecodes*) species and *A. mellifera* were the only bee taxa collected on each of the eight *Acacia* species (Table 1). *Leioproctus* (subgenus *Leioproctus*) species were caught on seven out of eight *Acacia* species.

Representatives from the families Anthophoridae, Apidae, Colletidae, and Halictidae were recorded as foraging on the extra-floral nectaries of *A. longifolia, A. myrtifolia, A. pycnantha,* and *A. terminalis* (Tables 1, 2). There was no evidence that *Acacia* inflorescences growing on shoots bearing extra-floral nectar received greater numbers of bees (or more bee taxa) compared to those *Acacia* species lacking extra-floral nectar (Table 1).

There was no obvious correlation between the number of bee taxa collected on an *Acacia* species and the habitat in which the species was studied (Table 3). At the intraspecific level, though, the dry sclerophyll woodlands and heaths of the Grampians National Park offered a wider fauna for *A. retinodes* var. *retinodes* than did the coastal dunes of Cape Schanck (Table 3). The number of bee taxa below the family level collected on four *Acacia* species sympatric through the Brisbane Ranges National Park varied from five to eight. No more than four families of bees were collected on any *Acacia* species (Tables 1, 3).

Variation in the number of bee taxa on an *Acacia* species did correlate positively with the flowering seasons of the plants and increased from mid winter (July) until the end of autumn (May; see Table 4). The number of bee taxa collected from mid winter to early spring (September) on *A. longifolia* and *A. pycnantha* doubled from early autumn (March) to early winter (June) on *A. terminalis* (Table 4). The greatest number of bee taxa was collected on the summer-flowering *A. retinodes* var. *uncifolia* (Table 4).

The majority of bee taxa foraging on the eight *Acacia* species visited a wide range of plants for pollen and/or nectar (Tables 4, 5). Technically these bees must be classified as polylectic foragers (Armstrong, 1979; Michener, 1979). From mid winter until late spring, and then from autumn to early winter, 21–55% of the bees captured on any *Acacia* species carried the polyads of that species mixed with the pollen of one or more sympatric species. Furthermore 63–91% of the bees captured on *Acacia* from late spring to late summer carried the pollen of one or more sympatric plants mixed with *Acacia* polyads (Table 4). Bees collected on *A. pycnantha* showed

TABLE 3. Variation in the number of bee taxa collected at different sites.

Site[a]	*Acacia* Taxon	No. Bee Taxa (No. Families)
Brisbane Ranges	MI	7 (3)
	MY	6 (3)
	PA	8 (3)
	PY	5 (3)
Cape Schanck	RU	8 (4)
Coranderrk Reserve	ME	8 (3)
Erica-Moe; Boolah Boolah	TE	10 (4)
Grampians	RR	12 (4)
Langwarren Reserve	LO	5 (3)

[a] See study sites for description of habitat.

MI = *A. mitchelii*; MY = *A. myrtifolia*; PA = *A. paradoxa*; PY = *A. pycnantha*; RU = *A. ret.* var. *uncifolia*; ME = *A. mearnsii*; TE = *A. terminalis*; RR = *A. retinodes* var. *retinodes*; LO = *A. longifolia*.

the lowest level of polylectic foragers, whereas bees collected on *A. mearnsii* showed the highest (Table 4).

Sixty-three percent of the bees bearing loads of *Acacia* polyads that were mixed with the pollen of other plants carried monads of one or more genera of Myrtaceae (Table 5). Ninety-two percent of the bees carrying mixed pollen loads carried the pollen of plants that bear floral nectaries (Table 5).

WASPS

Wasps were collected on all *Acacia* species excluding *A. retinodes* var. *retinodes*. Only 58 wasps were collected on the *Acacia* species representing seven wasp families (Table 6). Sixty-four percent of the wasps were divided equally between the Sphecidae and Tiphiidae. The greatest numbers belonged to *Cerceris* s.l., but these insects were collected only on *A. paradoxa* and *A. terminalis* (Table 6).

A total of 24 wasp taxa below the family level were collected on *Acacia*. Eleven of these represented single captures. No wasp taxon was recorded on more than two *Acacia* species. *Acacia* species offering extra-floral nectar appeared to attract a minimum of twice as many wasp taxa as those lacking extra-floral nectar (Tables 2, 6). Wasps observed and collected on *A. longifolia*, *A. myrtifolia*, and *A. terminalis* consistently flew to the extra-floral nectary before attempting to forage on the nectarless florets.

TABLE 4. Flowering patterns of *Acacia* species as correlated with the taxonomic diversity and foraging behavior of the bees.

Flowering Period and *Acacia* Species	No. Bee Taxa on *Acacia* sp.	No. Bees Bearing[a] *Acacia* Polyads	Ratio[b]
Mid Winter–Early Spring			
A. longifolia	5	22 (9)	0.40
A. pycnantha	5	41 (9)	0.21
Mid Winter–Mid Spring			
A. myrtifolia	6	29 (16)	0.55
Early Spring–Late Spring			
A. paradoxa	8	96 (50)	0.52
Late Spring			
A. mearnsii	8	59 (45)	0.91
Early Summer–Mid Summer			
A. mitchelii	7	32 (25)	0.78
Early Summer–Late Summer			
A. retinodes var. *retinodes*	12	67 (56)	0.8
A. retinodes var. *uncifolia*	8	121 (77)	0.63
Autumn–Early Winter			
A. terminalis	10	50 (16)	0.32

[a] The first number in the column refers to the total number of bees caught on the particular *Acacia* sp. that carried polyads of *Acacia* on their bodies. The second number, in parentheses, refers to the total number of bees that carried *Acacia* polyads plus the pollen of other genera.

[b] The ratio = number of bees that carried *Acacia* polyads plus pollen of other genera divided by total number of bees that carried *Acacia* polyads.

Acacia terminalis offered more extra-floral nectar per gland on a daily basis than did the three other nectariferous species (Table 2). *Acacia terminalis* received 33–66% more wasp taxa than were captured on the other three nectariferous species.

Wasps foraged selectively on *Acacia* species with functional, extra-floral nectaries. These *Acacia* species flowered during mid winter to mid spring and from autumn to early winter (Tables 4, 6). Consequently the density and diversity of wasps on *Acacia* was heaviest during the coldest seasons.

Seventeen wasp taxa carried the polyads of at least one of the *Acacia* species on which they were caught: *Antamenes* sp., *Anthobosca* sp.,

TABLE 5. Comparative frequencies of pollen from other spermatophyte families as identified on bees carrying *Acacia* polyads.

Spermatophyte Family[a]	No. of Bees Bearing *Acacia* Polyads Mixed with Pollen of Other Families Captured on each *Acacia* spp.									
	LO	ME	MI	MY	PA	PY	RR	RU	TE	Total
Compositae + −	0	4	0	0	3	1	6	26	0	40
Dilleniaceae −	0	0	3	0	4	1	0	0	0	8
Epacridaceae +	0	0	0	1	3	1	0	0	3	8
Leguminoseae (Papilionoidae)+	1	4	0	0	23	0	0	0	0	28
Liliaceae s.l. + −	0	6	0	0	2	0	0	0	0	8
Myrtaceae +	2	47	19	2	26	0	71	43	15	225
Pinaceae −	9	0	0	0	1	1	0	0	0	11
Pittosporaceae +	0	0	0	0	0	0	2	0	0	2
Proteaceae +	0	0	0	4	0	3	0	0	0	7
Rhamnaceae +	0	0	0	12	2	4	0	0	0	18

[a] + = bees bearing pollen of genera with nectariferous flowers; − = bees bearing pollen of genera with nectarless flowers.

LO = *A. longifolia*; ME = *A. mearnsii*; MI = *A. mitchelii*; MY = *A. myrtifolia*; PA = *A. paradoxa*; PY = *A. pycnantha*; RR = *A. retinodes* var. *retinodes*; RU = *A. ret.* var. *uncifolia*; TE = *A. terminalis*.

Cerceris antipodes, Cerceris sp., *Labium* sp., *Lissopimpla excelsa, Lissopimpla* sp., *Lophocheilus anilitatus, Neourys* sp., *Phymatothynnus pygidalis, P.* sp. near *nonilicornis, Podagritus* sp., *Pseudozethus* sp., *Rhagigaster comparatus, Sphex* sp., *Tachynomia moerens,* and the unidentified species of Tiphiidae. Mixed loads of *Acacia* polyads plus the pollen of sympatric plants were confined to those angiosperm families with nectariferous flowers: Compositae, Epacridaceae, Myrtaceae, Rhamnaceae, and Solanaceae.

DISCUSSION

Wasps versus bees as Acacia pollinators. The taxonomic diversity of wasps versus bees on Australian *Acacia* appears almost evenly matched. Wasps, however, comprise only 11% of the total population of foraging Hymenoptera. This supports previous reports that bees forage for *Acacia* polyads in far greater numbers than do wasps (Bernhardt, 1982; Bernhardt et al., 1984; Bernhardt & Walker, 1984, 1985; Knox et al., 1985). Female bees appear to forage primarily for polyads and secondarily for extra-floral nectar (Bernhardt & Walker, 1984; Knox et al., 1985). The results presented in this paper indicate that wasps tend to forage preferentially for extra-floral nectar.

Large quantities of extra-floral nectar fail to assure polyad transport by wasp foragers (Knox et al., 1985). Almost equal numbers of bees and wasps foraged for nectar and polyads on valley populations of *A. terminalis,* but bees consistently carried polyads of *A. terminalis* more often than did wasps (Knox et al., 1985). The low density of wasp populations on flowering *Acacia,* combined with the foraging preferences of these insects, suggests that wasps are of secondary importance to seed set, at best. Under certain circumstances, pollen-eating flies are probably superior polyad vectors compared to wasps (Bernhardt et al., 1984).

This does not mean to suggest that wasps are always nominal pollinators of the Australian flora. Unfortunately few studies have been done to assess the selective pressure of wasp foraging on other angiosperms (Armstrong, 1979). Wasps are important pollinators of nectariferous and nectarless (pseudocopulatory) Orchidaceae in Australia (Beardsell & Bernhardt, 1982). Wasps may also pollinate the nectariferous Epacridaceae (Bernhardt, pers. obs.; Knox et al., 1985). Of course, wasps are important pollinators of *Prosopis* (Simpson et al., 1977), but these mimosoid shrubs bear floral nectaries.

Bee diversity on Acacia species. Although all representatives from all five families of Apoidea found in Australia (Armstrong, 1979) were identified on *Acacia* in this study, some families were more common than others. This is partially explained by biogeography. The Apidae are poorly represented in Australia (Michener, 1979), and the native genus *Trigona* is uncommon south of the Tropic of Capricorn (K. Walker, pers. comm.).

TABLE 6. Wasp taxa collected on the inflorescences of *Acacia* species.

Wasp Taxon	*Acacia* spp. on Which Wasp Was Captured									No. Wasps
	LO	ME	MI	MY	PA	PY	RR	RU	TE	
Braconidae:										
Apanteles sp.	1	0	0	0	0	0	0	0	0	1
										1
Eumenidae:										
Antamenes sp.	0	3	0	0	0	0	0	0	0	3
Pseudozethus sp.	0	0	0	0	0	0	0	0	5	5
Unidentified sp.	0	0	1	0	0	0	0	0	0	1
										9
Ichneumonidae:										
Biconus sp.	0	0	0	1	0	0	0	0	0	1
Labium spp.	1	0	0	0	0	0	0	0	3	4
Lissopimpla excelsa	0	0	0	1	0	0	0	0	0	1
Lissopimpla sp.	0	0	0	0	0	0	0	0	2	2
										8
Pergidae:										
Neourys sp.	0	0	0	0	0	1	0	0	9	1
										1
Pompilidae:										
Chirodamus sp.	0	0	0	0	0	0	0	0	1	1
Pompilius sp.	0	0	0	0	0	0	0	0	1	1
										2
Sphecidae:										
Cerceris antipodes	0	0	0	0	0	0	0	0	7	7
Cerceris spp.	0	0	0	0	1	0	0	0	6	7
Harpactophilus sp.	1	1	0	0	0	0	0	0	0	2
Rhopalum sp.	0	0	0	0	0	0	0	0	1	1
Sphex sp.	0	0	0	1	0	0	0	0	0	1
										18
Tiphiidae:										
Anthobosca sp.	0	0	0	0	0	0	0	3	2	5
Lophocheilus anilitatus	0	0	0	1	0	1	0	0	0	2
Phymatothynnus pygidalis	0	0	0	0	0	1	0	0	9	1
Phymatothynnus sp. nov. n. *nonilicornis*[a]	0	0	0	0	0	3	0	0	0	3
Phymatothynnus sp.	0	0	0	1	0	0	0	0	0	1
Rhagigaster comparatus[a]	0	0	0	0	0	2	0	0	0	2
Tachynomia moerens[a]	0	0	0	0	0	2	0	0	0	2
Unidentified spp.	2	0	0	0	1	0	0	0	0	3
										19
Total No. Wasps/ *Acacia* species	5	4	1	5	2	10	0	3	28	58
Total No. Wasp Taxa/ *Acacia* species	4	2	1	5	2	6	0	1	9	

[a] Refers to wasp taxa caught *en copula*.

LO = *A. longifolia*; ME = *A. mearnsii*; MI = *A. mitchelii*; MY = *A. myrtifolia*; PA = *A. paradoxa*; PY = *A. pycnantha*; RR = *A. retinodes* var. *retinodes*; RU = *A. ret.* var. *uncifolia*; TE = *A. terminalis*.

Trigona may be important in the pollination of paleotropical *Acacia* through northeastern Australia (Bernhardt, 1982; Armstrong, 1979).

Biogeography alone, however, cannot explain the comparative dearth of anthophorid and megachilid bees on *Acacia* species in southeastern Australia. While it is true that neither family approaches the taxonomic diversity of Colletidae in Australia (Michener, 1979), there are far more megachilid and anthophorid taxa in Victoria than were sampled in this study (Michener, 1965). The Anthophoridae and Megachilidae are considered families of long-tongued bees. Although they may be common throughout the habitats described in this paper, evidence suggests that they forage preferentially on flowers offering pollen *and* nectar (Armstrong, 1979). In particular, Megachilidae often are associated with zygomorphic flowers, particularly papilionoid legumes (Michener, 1965; Armstrong, 1979). The only anthophorid bees relatively common on *Acacia* were *Exoneura.* These bees were largely confined to the only two arborescent *Acacia* species studied bearing bipinnately compound leaves: *A. mearnsii* and *A. terminalis.* This is probably coincidental, but it would be worthwhile exploring "presumed" foraging preferences that *Exoneura* may express towards sections of *Acacia* s.l.

Climatic conditions may also influence the diversity of bee taxa on *Acacia* with overlapping distributions. During the spectacular drought of 1982 and 1983 no specimens of *Leioproctus* (subgen. *Euryglossidia*) were collected on *Acacia* in the Brisbane Ranges (Bernhardt & Walker, 1984). The Brisbane Ranges had a cool, wet spring in 1984, and in that year *Leioproctus* (subgen. *Euryglossidia*) far outnumbered previously abundant *Leioproctus* (subgen. *Leioproctus*).

Considering the broad polylecticism of the bee taxa on these eight *Acacia* species, one cannot refer to any bee taxon as an "acacia bee" as some entomologists speak of "clover bees," "orchid bees," and "squash and gourd bees" (Michener, 1974, 1979). The very absence of floral and extra-floral nectar in so many Australian *Acacia* species forces bees to forage on other sources. Oligolecty continues to decline as bees exploit co-blooming sources of nectar and additional pollen in competition with *Acacia.*

Lasioglossum (Halictidae) and *Leioproctus* (Colletidae) remain the predominant polyad foragers of many *Acacia* species (Bernhardt, 1982; Bernhardt et al., 1984; Bernhardt & Walker, 1984, 1985; Knox et al., 1985). *Lasioglossum* species may be more important pollinators than *Leioproctus* species. *Lasioglossum* were caught on all *Acacia* species studied and were collected in greater numbers than were *Leioproctus.*

Parsphecodes and *Chilalictus* were the most commonly collected subgenera on six out of the eight *Acacia* species studied. *Parasphecodes* bees outnumbered *Chilalictus* bees. These allied subgenera may exert preferential foraging patterns when nectarless angiosperms have overlapping flowering periods. From later winter through late spring *Acacia* species and some *Hibbertia* species (Dilleniaceae) have overlapping flowering periods. *Lagioglossum* subgen. *Chilalictus* species forage preferentially on *Hibbertia* (Bernhardt, 1984, 1986), but *Parasphecodes* forage in greater numbers on *Acacia* (Bernhardt & Walker, 1985).

Polylecticisms and the role of polylectic bees in Acacia cross-pollination. The Halictidae and Colletidae are both families of short-tongued bees that forage for nectar on flowers with shallow perianths. They are found most commonly on the flowers of Myrtaceae, the largest and most widely distributed family of nectariferous angiosperms in Australia (Costermans, 1983). Most shrubby Myrtaceae flower through the warm spring–summer months when the greatest number of bees (both short- and long-tongued) are active. Out of the four most important nectariferous families that were patronized most frequently by bees in this study, three have flowers with short-tubular or shallow-bowl perianths (Faegri & van der Pijl, 1979): Myrtaceae, Compositae, and Rhamnaceae. The keeled "flag" flowers of the papilionoid legumes are also visited by short-tongued bees probably because the weight of comparatively large-bodied *Leioproctus* and *Lasioglossum* triggers access to the concealed nectaries.

Bees that pollinate nectarless flowers tend to belong to polylectic genera: *Apis* (Michener, 1974), *Bombus* (Buchmann, 1983), *Centris* (Frankie et al., 1983), *Lasioglossum* (Bernhardt, 1984; Bernhardt & Burns-Balogh, 1986). It is not unusual for an individual bee that belongs to a taxon in which foragers are not fed by siblings to visit one to four nectarless but pollen-rich species and six to eight nectariferous species during flowering seasons (Macior, 1968; Bernhardt & Montalvo, 1979; Bernhardt, 1984; Bernhardt & Burns-Balogh, 1986).

Acacia species in Australia are, in general, mass-flowering plants that are also highly self-incompatible. Seed set will not occur unless bees move spontaneously from one shrub to another. The absence of floral nectar forces polyad foragers to break their bouts on *Acacia* species with trips to nectariferous flowers growing on nonphylogenetically related plants (Bernhardt & Walker, 1984, 1985). When the bees are replete with chemical energy (i.e., nectar) they may return to *Acacia*, but in the mosaic distribution of sclerophyll shrubs it will probably be to a shrub different from the one abandoned for nectar.

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FLOWER LONGEVITY AND PROTANDRY IN TWO SPECIES OF *GENTIANA* (GENTIANACEAE)[1]

C. J. WEBB AND JAN LITTLETON[2]

ABSTRACT

Both *Gentiana saxosa* and *G. serotina* are protandrous. When flowers open, pollen is presented extrorsely around the closed stigma for one to six days. As the stigma opens, the stamens curve toward the corolla lobes. The length of the female phase, and therefore reproductive flower life, is determined by pollination, although in both species the corolla may remain fresh for longer than one month. Fresh female-phase flowers close at night and fail to reopen on the day following pollination. After five days in the female phase, flowers reacted less quickly to pollination and seed production was reduced; flowers pollinated on their tenth day of stigma presentation produced no seed although they appeared fresh. Senescence of unpollinated flowers differed between species: in *G. saxosa* the flowers remained open and gradually deteriorated, but in *G. serotina* the flowers eventually closed before full senescence. Pollination-induced flower senescence has been demonstrated for a number of other angiosperms, and the usual reactions to pollination are corolla abscission, color change, or wilting. In *Gentiana*, the closed corolla enfolds the large superior ovary and may serve to protect it from predators as well as prevent further pollinator visits. Pollination-induced flower senescence probably also minimizes flower maintenance costs by ensuring that the flower functions no longer than necessary. One correlate of this phenomenon in hermaphroditic flowers is protandry, which ensures pollen dispatch before flower closure.

Floral senescence may be either time-dependent (endogenous) or exogenous (usually pollination-induced). However, there have been few detailed investigations of the factors that determine floral senescence, and hence, floral longevity (Primack, 1985). Most such studies have concentrated on corolla color changes or other physiological reactions that follow pollination and signal senescence (e.g., Arditti et al., 1973; Arditti, 1976; Gottsberger, 1971; Gori, 1983; Strauss & Arditti, 1984; Casper & La Pine, 1984; Halevy, 1984), and less attention has been afforded structural changes such as wilting, flower closure, and corolla abscission (Mayak & Halevy, 1980). Most of this research is concerned with the proximate determinants of floral longevity rather than the evolution of particular responses (but see Stead & Moore, 1979; Gori, 1983; Casper & La Pine, 1984; Devlin & Stephenson, 1984). The paucity of research on the evolutionary aspect of flower senescence is somewhat surprising, because pollination-induced senescence in particular may have important consequences for the pollination system and ultimately for the plant's overall reproductive strategy. For instance, in hermaphrodite flowers pollination-induced flower senescence will limit the duration of pollen and stigma presentation and so may influence or be influenced by the extent and nature of dichogamy (Lloyd & Webb, 1986).

New Zealand species of *Gentiana* (in the southern group of Philipson, 1972) are protandrous (Thomson, 1881; Simpson & Webb, 1980; Webb, 1984a). Their large, relatively simple flowers make them particularly suitable subjects for experimental studies of flower function. This paper describes the response of flowers of two species to pollination and reports the results of experiments to determine the functional duration of male and female phases in terms of pollen presentation and seed production.

MATERIALS AND METHODS

The two species of *Gentiana* selected were those that grew best in cultivation. *Gentiana saxosa* Forster f. grows naturally in coastal sites of southern South Island and Stewart Island, New Zealand; plants were collected from Curio Bay, Southland. *Gentiana serotina* Cockayne occurs in grassland in inland central South Island; plants were collected from Lake Lyndon, Canterbury. The plants were grown in clay pots in an insect-proof cage in greenhouses at Lincoln, Canter-

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TABLE 1. Results of controlled pollinations to determine self-compatibility in *Gentiana saxosa* and *G. serotina*.

	Treatment	Number of Flowers	Capsules Produced	% Seeds Produced per Capsule
G. saxosa	Cross-pollinated	10	10	94.2
	Self-pollinated	10	10	94.2
	Unpollinated	10	0	–
G. serotina	Cross-pollinated	5	5	57.9
	Self-pollinated	5	5	67.6
	Unpollinated	5	0	–

bury. Field observations were made at Lake Lyndon.

To test for self-incompatibility and autogamy 10 flowers in *G. saxosa* and five flowers in *G. serotina* were assigned to each of three treatments: self- and cross-pollination by hand, and unpollinated (Table 1). Flowers were tagged individually and observed daily. When capsules matured, they were harvested and good seeds and aborted seeds or undeveloped ovules were counted.

The duration of male and female phases was determined for individual tagged flowers. Pollen and stigma presentation were observed daily until petals withered and turned brown. Of 61 flowers of *G. saxosa* observed daily, five were cross-pollinated on each of the first to tenth days of their female phase, and 11 left unpollinated. Of 34 flowers of *G. serotina,* eight were pollinated on each of the first, fifth, and eighth days of their female phase, five on the tenth day, and five flowers were left unpollinated. For *G. serotina,* three flowers from each of the first, fifth, and eighth day pollinations were collected two days after pollination, the stigma dissected out, fixed, stained with aniline blue, and examined under fluorescent microscopy to determine the extent of pollen germination and pollen tube growth. For the remaining flowers, the responsiveness of each to pollination was quantified as the number of days until (a) the flower closed completely, (b) closed to its greatest extent (for flowers that closed incompletely), or (c) the number of days until the corolla withered and turned brown (for flowers that never closed). When capsules were mature they were harvested and seed production scored.

At Lake Lyndon, 10 fresh, unbagged, female-phase flowers of *G. serotina* were cross-pollinated by hand, and ten were left unpollinated. These flowers were examined the following day.

RESULTS

Flower form, phenology, and pollination. Both *Gentiana saxosa* and *G. serotina* are perennial herbs with a central leafy rosette and stout taproot. The flowers are on annual, leafy, lateral flowering branches that bear from one to eight flowers in *G. serotina* and one to 30 or more in *G. saxosa.* The corolla is deeply 5-lobed, white with translucent stripes on the lobes and upper tube (Fig. 1), and greenish-yellow toward the base of the tube. The five stamens are attached to the corolla tube; the anthers are purple and the pollen is cream to brownish-yellow. Nectar is produced between the bases of the filaments near the base of the tube. The central ovary contains an average of 29 ovules in *G. saxosa* and 47 in *G. serotina* (Webb, 1984a). The flowers lack a well-defined style; the stigma is 2-lobed, distinctly papillate, and dry.

In the field, *G. saxosa* blooms in summer and autumn (January to May), and *G. serotina* from late summer to autumn (February to May). Under greenhouse conditions *G. saxosa* reached peak flowering in December and *G. serotina* in March. The flowers are sweetly scented and visited on fine days by a range of insects. At Lake Lyndon, *G. serotina* was most frequently visited by syrphid flies and solitary bees (*Lasioglossum sordidum*). During anthesis, flowers opened completely only on fine days, and almost completely closed at night. On wet or cold, dull days few new flowers opened, and in those that had opened previously the corolla lobes did not spread completely.

Both *G. saxosa* and *G. serotina* are self-compatible (Table 1); however, flowers that were not pollinated and from which insects had been excluded failed to produce any seed, so biotic pollination is necessary for seed set.

Protandry. The flowers of both species are distinctly protandrous. In neither was there any obvious synchrony of male and female phases among flowers within a plant or even a flowering branch, so that within large plants pollen and

FIGURES 1–8.—1–7. Protandry and reaction to pollination in flowers of *Gentiana serotina* (bars = 0.5 cm).—1. First day open, male phase.—2. Fourth day, stigma opening.—3. Seventh day, stigma open, anthers near corolla.—4. Flower closing, one day after pollination of fresh female-phase flower.—5. Flower closed, two days after pollination of fresh female-phase flower.—6. Flower incompletely closed, five days after pollination on eighth day of female phase.—7. Unpollinated flower, 18 days.—8. Unpollinated flower of *G. saxosa,* 30 days (bar = 0.5 cm).

stigmas were presented simultaneously in different flowers and geitenogamy could occur.

When a flower first opens, the anthers have already dehisced to present pollen extrorsely near the center of the flower and the stigmatic lobes are tightly closed (Fig. 1). Later in the male phase, the corolla lobes open further, the stigma begins to open, and the stamens move outwards toward the corolla (Fig. 2). In *G. saxosa,* the stigma may open and stamens recurve late on the first day of anthesis, or as late as the fifth day. The mean duration of the male phase is 1.41 days (N = 57). In *G. serotina,* the stigma opens and stamens recurve between the third and seventh days (mean =4.73 days, N = 30). In *G. saxosa,* anthers have usually moved halfway toward the corolla when the stigma opens and have reached the corolla lobes in up to three days after that. In *G. serotina,* the anthers reach the petals and usually wither one or two days after the stigma opens (Fig. 3), and in some cases they eventually protrude between the corolla lobes. Although pollen is no longer presented in a central position by the time the stigma opens, there may be some overlap between pollen and stigma presentation within the flower, especially in *G. saxosa,* for which the male phase is shorter. However, under field conditions, little pollen usually remains by the time the stigma opens.

When the stigma opens the two lobes occupy the position in which pollen was presented in the newly opened flower (Figs. 1, 3). The duration of the female phase is dependent on pollination.

Reaction of the flower to pollination. Both species showed similar reactions to pollination. When fresh, first-day, female-phase flowers were pollinated, they partially closed that night and failed to reopen the following day (Fig. 4). Two days following pollination the corolla lobes were imbricate to form a neat, tight structure similar to, but slightly larger than a late bud (Fig. 5). The petals slowly turned brown and withered as the capsule reached maturity after about four weeks.

When the flower was pollinated on the second to fifth days of the female phase, the corolla reacted as quickly and folded as neatly as it did following first-day pollination. After the fifth day, although the flowers and their stigmas still appeared fresh, they reacted more slowly following pollination (Fig. 9), either taking several days to close or closing incompletely (Fig. 6). About one-third of the flowers pollinated after the fifth day of their female phase never closed completely. There was some variation among flowers of the

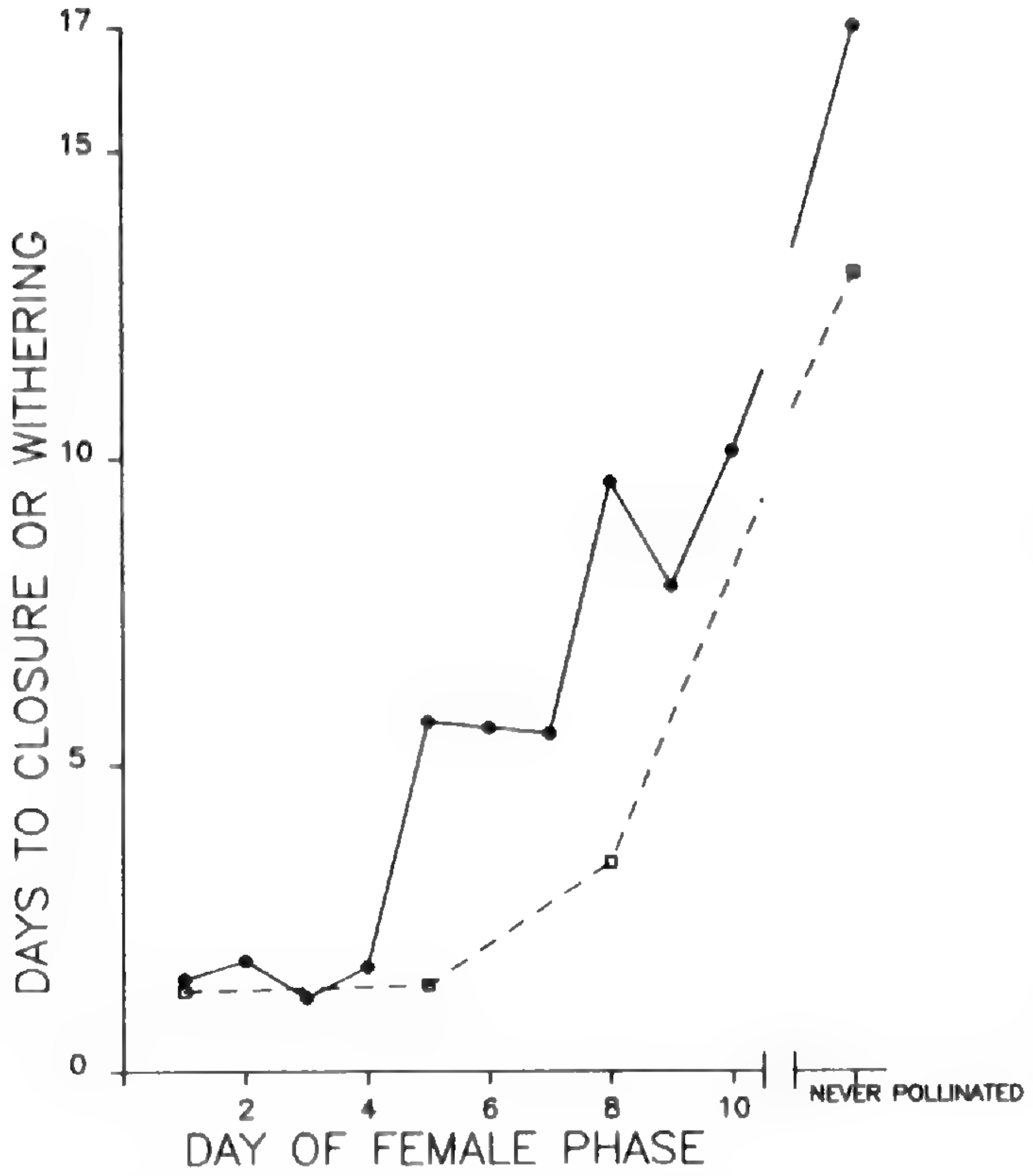

FIGURE 9. Days taken for flowers of *Gentiana saxosa* (solid dots) and *G. serotina* (open squares) to close or wither following pollination on different days of female phase.

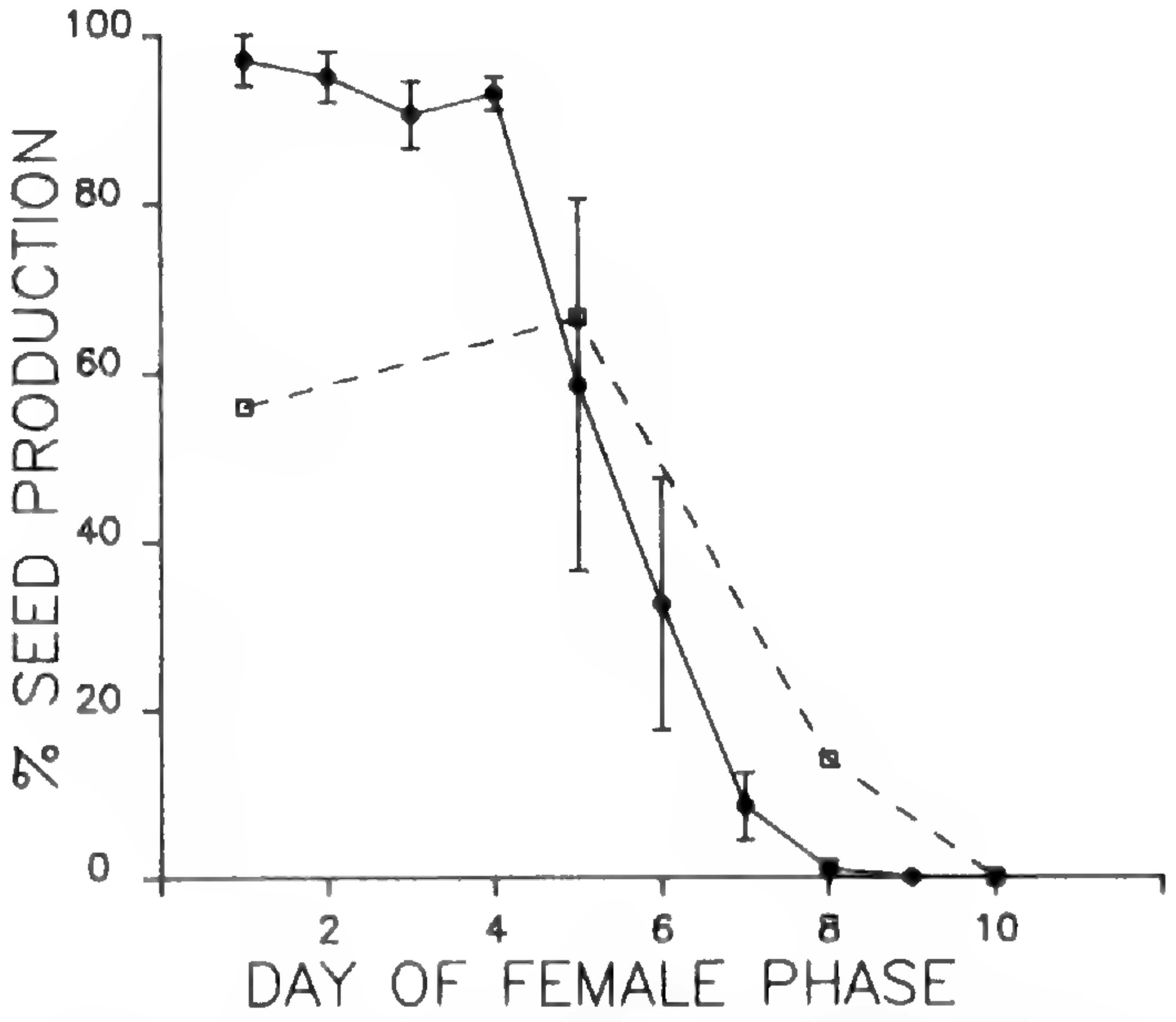

FIGURE 10. Average percentage of ovules producing seed for flowers of *Gentiana saxosa* (solid dots) and *G. serotina* (open squares) following pollination on different days of female phase (mean ± standard error for *G. saxosa*, mean only for *G. serotina*).

same age, but the trend to decreasing reactivity with increasing age was clear in both species (Fig. 9).

In the field, flowers of *G. serotina* reacted similarly to those in the greenhouse. Ten fresh female-phase flowers were all closed on the day following hand pollinations, whereas eight of 10 flowers not pollinated by hand had reopened.

Under fluorescent microscopy, all three stigmas from flowers of *G. serotina* that had been pollinated on the first day of the female phase had numerous germinating pollen grains and many well-formed pollen tubes penetrating the stigma. Of the three stigmas pollinated on their fifth day, two showed good pollen germination and the third had only a few germinating grains. Two of the three stigmas that had not been pollinated until their eighth day had no pollen germinating, and the third had good germination.

The proportion of ovules that developed into good seeds was clearly affected by the age of the stigma when it was pollinated and related well to the responsiveness of flowers to pollination. In both species there was a sharp decrease in seed production for flowers pollinated later than the fourth or fifth days of the female phase (Fig. 10). In *G. saxosa,* flowers pollinated on the first to fourth days of the female phase consistently matured a high proportion of their ovules. Those pollinated on the fifth to seventh days were more variable in seed production, and seed production was related to reactivity of individual flowers. For example, a flower pollinated on the fifth day failed to close and produced no seed, whereas a flower pollinated on the seventh day closed almost completely and had 25% seed production. Few flowers pollinated on the eighth day of the female phase, and none pollinated on the ninth or tenth days produced seed. The pattern of seed production for flowers pollinated at different ages in *G. serotina* was similar (Fig. 10), but the smaller sample size does not allow a detailed analysis.

Thus, although the corolla and stigma may appear fresh for much longer, the functional female phase in both species is only four to eight days. Adding together male and female phases, one gets a reproductively functional flower life of five to 12 days for *G. saxosa,* and six to 14 days for *G. serotina.*

The reaction of flowers that were never pollinated differed between species. In *G. serotina,* the corolla lobes continued to diverge as the flower aged, but eventually began to close (Fig. 7), finally reaching a position similar to that of a late-pollinated flower (Fig. 6) before turning brown after an average of 26 days. However, in *G. saxosa* the corolla lobes reached a strongly recurved position and in all but one of 11 flowers showed no sign of returning to a closed position (Fig. 8) and turned brown after an average of 17 days. In both species some flowers had white, turgid corollas for longer than a month, although the stigmas were dull and blackened by this time and the stamens had altogether withered.

DISCUSSION

Floral longevity of individual flowers may be defined in terms of reproductive function as the period over which a flower is able to receive and/or dispatch pollen. However, outside this period, flowers may perform functions not directly related to their own reproductive success, as in the case of supplemental pollinator attraction provided by late buds and older flowers. Thus, a more practical definition of floral longevity in terms of reproductive success of whole plants may be the period for which a flower is able to attract pollinators. For many plants, particularly tropical species, floral longevity appears to be a predetermined, endogenous characteristic with many such species having 1-day flowers (Dobkin, 1984; Primack, 1985). In some such species, non-induced floral changes, which indicate that the flower is no longer reproductively functional, may occur before full senescence (indicated by abscission or wilting of petals). In others, flowers may be reproductively functional until full senescence (Gori, 1983). The second major pattern is provided by those species in which flower life may be curtailed by pollination (Kerner, 1902; Arditti, 1976; Stead & Moore, 1979; Devlin & Stephenson, 1984). It is important to note that for species in which floral changes are pollination-induced, the potential flower life is still endogenously determined and the pollination-induced changes occur within this outer limit.

Gori (1983) recognized and summarized available data on five basic types of floral change that follow pollination or indicate the end of reproductive function before full senescence: color change, termination of odor and/or nectar production, change in flower orientation, collapse of flower parts, and corolla abscission. To this may be added flower closure as described here for *Gentiana,* and reported by Kerner (1902) for *Mammillaria glochidiata.* In fact, flower closure is likely to be the response in many species in which petals close regularly at night or in dull weather. Although floral changes may prevent or deter pollinator visits, the reproductive, functional end of flower life occurs when no viable pollen is available for dispatch and the stigma ceases to be receptive. In *Gentiana serotina* and *G. saxosa,* the end of reproductive flower life is indicated either by flower closure or the loss of responsiveness of the flower to pollination. Once this occurs, pollen does not germinate on the stigma, and no seeds are produced. The beginning of flower life is marked by the corolla lobes opening to expose the dehisced anthers; all pollen is normally lost before the beginning of the female phase, so pollen availability does not determine the end of flower life, although it may affect flower longevity if the male phase is prolonged by a paucity of pollinator visits as in *Lobelia cardinalis* (Devlin & Stephenson, 1985).

When full senescence of a flower finally occurs, floral changes as listed above may occur. In addition, the whole flower may be aborted, even if pollination has occurred, especially in species that use flower abortion as a means of maternal regulation (Lloyd, 1980; Bawa & Webb, 1984). Within a species, it is possible that the floral changes that occur following pollination may differ from those of flowers that are never pollinated. In both *Gentiana saxosa* and *G. serotina,* fresh female-phase flowers closed in response to pollination; in *G. saxosa,* but not *G. serotina,* the reaction of never-pollinated flowers differed in that flower closure did not occur and petals withered in a recurved position. However, the end of functional pollen and stigma presentation in never-pollinated flowers occurred well before the morphological change of flower closure in *G. serotina* and corolla wilting in *G. saxosa.* The persistence of these flowers well beyond their reproductively functional life may add to the overall floral display of the plant.

Pollination-induced changes in flowers have been interpreted as signals that direct pollinators to unvisited flowers (Allen, 1898; Kerner, 1902; Arditti, 1976; Stead & Moore, 1979; Casper & La Pine, 1984) or help to conceal the developing seeds within pollinated flowers from predators (Allen, 1898), or simply minimize costs of flower maintenance by retaining the perianth no longer than is necessary (Kerner, 1902). Gori (1983) considered three aspects of the first alternative: avoidance of pollinator interference within pollinated flowers, increasing the pollinator's foraging efficiency and so increasing the residence time on the plant, and increasing pollination efficiency by restricting pollinators to receptive (reproductively functional) flowers. In the two species of *Gentiana* studied here, corolla closure clearly signals that the flower is unavailable for visits; in fact it precludes visits, and the corolla also tightly enfolds the developing ovary until it is almost mature, making it less accessible to predators. Field experiments, as described by Gori (1983) for *Lupinus*, would be necessary to determine the precise function of pollination-induced flower closure in *Gentiana*. In many insect-pollinated species, the end of flower life is signalled by corolla abscission and the developing ovary is either inferior or enclosed within infolded bracts or calyx lobes as in *Malvaviscus arboreus* (Webb, 1984b). Corolla closure, rather than abscission, may be necessary to protect the ovary in *Gentiana* because the large superior ovary extends well beyond the small calyx lobes.

In terms of natural selection, flower life for a particular species is likely to be a trade-off between the cost of maintaining the flower in a receptive state and the probability that it has been pollinated. Thus, as originally suggested by Kerner (1902), flower life is likely to be longer for species that normally experience unpredictable weather conditions allowing fewer suitable times for pollinator visits, for species with few, large flowers per plant, and for species that are obligately outcrossing. These suggestions are supported by data on flower life that show that many tropical plants, particularly those flowering in the lowlands during the dry season, have 1-day flowers (Dobkin, 1984; Primack, 1985). Under those conditions pollination is predictable. In contrast, plants of higher altitudes and of temperate areas have long-lived flowers, as might be expected when many days are unsuitable for flower visits. That many large orchid flowers with complex outcrossing mechanisms are long-lived is to be expected because they may have low rates of flower visitation.

There are three strategies that might to some extent ameliorate the difficulty of unpredictable pollination. First, if flower life is pollination-dependent, as in the two species of *Gentiana* described here, then flower maintenance costs are minimized. There is, however, probably a cost in maintaining enzyme systems responsible for pollination-induced floral changes (Gori, 1983). Second, under conditions unfavorable to pollinators, autogamy may occur (Kerner, 1902; Faegri & van der Pijl, 1979); the evolution of autogamy often involves loss of dichogamy or herkogamy, and also a reduction of flower life (Morin, 1983). In some species selfing may be delayed until an opportunity for outcrossing has been provided or may even be a direct response to unfavorable weather conditions. In *Gentiana lineata*, the flowers open fully in warm sunny weather suitable for insect pollination, but on wet or dull days the flowers open only partly so that the anthers dehisce directly onto the stigma (Webb, 1984a); this type of mechanism was termed induced selfing by Schoen and Lloyd (1984). Third, flower life may be much longer during weather unfavorable to pollination, or flowers may open only on suitable days with the floral parts protected during inclement weather (Kerner, 1902).

When floral changes are pollination-induced, flowers are likely to be non-dichogamous or protandrous because flower closure, corolla abscission, and other reactions to pollination, all curtail the time over which pollen can be presented (Lloyd & Webb, 1986). The pollination-induced flower closure described here for *Gentiana* can be effective only if flowers are protandrous; protogyny would preclude pollen presentation, and adichogamy would severely limit the male phase.

Flower life may appear to be the simple result of proximate causes—especially of weather conditions and pollinator availability. However, the average flower life for a population, the particular response of flowers to pollination, and the cues used to determine the time of senescence, must all be the result of natural selection. Yet, the selection of these factors has seldom received the attention of reproductive biologists in spite of the important part they play in determining the success of plants as pollen or seed parents.

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NOTES ON THE BREEDING SYSTEMS OF *SACOILA LANCEOLATA* (AUBLET) GARAY (ORCHIDACEAE)[1]

Paul M. Catling[2]

Abstract

To document breeding systems in the widespread neotropical terrestrial orchid, *Sacoila lanceolata*, pollination and seed development were studied in the field and in cultivated plants. In the southern Florida study area, plants of var. *lanceolata* were not pollinated and hummingbird pollinators were apparently absent. When plants from southern Florida were moved to a situation where hummingbirds were abundant in southern Ontario, hummingbird-pollination was observed on numerous occasions and the incidence of pollination was approximately 90%. Pollination experiments demonstrated a reliance on pollen vectors in plants of var. *lanceolata* from central Guyana, where a variety of hummingbird pollinators are available, but the plants of the same variety from southern Florida were found to be agamospermic. Examination of serial sections of ovaries in successive developmental stages indicated that agamospermy is by adventitious embryony, the embryos (one or more) being formed by proliferation of the inner integument. Adventitious embryony can be detected through association with polyembryonic seed, is characteristic of Florida populations of var. *lanceolata*, and occurs also in portions of the tropical range. Plants of *S. lanceolata* var. *paludicola* from southern Florida were found to self-pollinate. The pollinator-independent breeding systems in southern Florida populations of *S. lanceolata* var. *lanceolata* and var. *paludicola* and the apparent absence of races totally reliant upon pollen vectors are associated with pollinator-paucity.

Sacoila lanceolata (Aublet) Garay var. *lanceolata* is a reddish- to orange-yellow- or occasionally pale greenish-flowered, terrestrial orchid with a broad neotropical distribution extending from northern Florida and northern Mexico to northern Uruguay (Luer, 1972). The smaller-flowered var. *paludicola* Luer is restricted to extreme southern Florida [the Fahkahatchee Strand in Collier Co. (Luer, 1971a), Kendall Hammock in Dade Co. (pers. obs.), and from one location in the Everglades (McCartney, 1985)] and the Caribbean region (based on examination of specimens at AMES, DAO, SEL, and FTG—acronyms from Holmgren et al., 1981). Both var. *lanceolata* and var. *paludicola* have gaping tubular flowers with an adnate spur (Fig. 1). In terms of flower color and morphology and absence of a detectable odor, the flowers of both varieties are representative of the bird pollination syndrome (Pijl & Dodson, 1966).

Casual observations of seed development in a few cultivated plants that were maintained in the absence of any potential pollen vectors suggested that both var. *lanceolata* and var. *paludicola* may have pollinator-independent breeding systems in southern Florida. Since the breeding systems of tropical and subtropical terrestrial orchids are relatively poorly known, a study was undertaken to document the breeding systems of *S. lanceolata*.

Methods

FIELD STUDIES OF POLLINATION IN SOUTHERN FLORIDA

In order to gather information on natural pollination, populations of *S. lanceolata* var. *lanceolata* were observed for an overall total of 20 hours in southern Florida during mid-May 1978 and 1984. The presence of potential pollinators, including hummingbirds and large bees particularly, was noted. Large bees are the regular pollinators of some related species (Pijl & Dodson, 1966; Catling, 1983).

Since pollination of orchid flowers involves removal of the pollinarium from the anther, it is possible to obtain an approximation of the incidence of pollination by recording pollinaria

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[1] Living plants of *Sacoila lanceolata* var. *paludicola* were provided by C. A. Luer, H. Brown, and G. Matous. C. A. Luer and V. R. Brownell assisted with field work. Useful criticisms were provided by S. C. H. Barrett (University of Toronto), C. A. Luer (Missouri Botanical Garden), N. R. Morin (Missouri Botanical Garden), and N. H. Williams (Univ. of Florida). W. Wojtas kindly assisted with the anatomical work.

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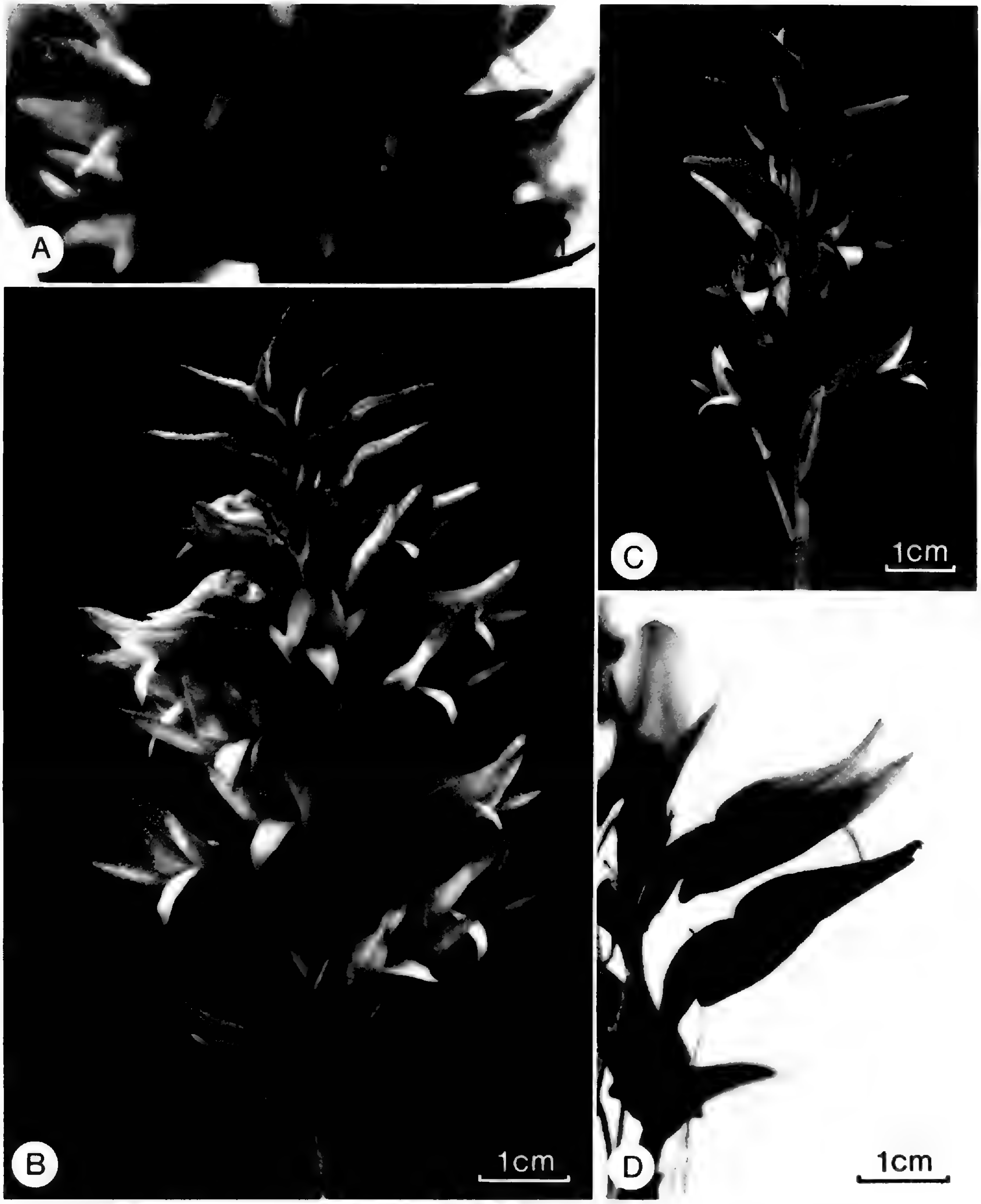

FIGURE 1. A, B, D. *S. lanceolata* var. *lanceolata.*—A. Frontal view of flowers, Immokalee, Collier Co., Florida, 15 May.—B. Flower spike of cultivated plant from central Guyana, South America, 13 January.—D. Side view of flowers, Immokalee, Collier Co., Florida, 15 May.—C. *S. lanceolata* var. *paludicola,* flower spike, cultivated plant from Fahkahatchee Strand, Collier Co., Florida, 15 February.

removal. This is more easily recorded than the presence of pollen tubes in the deteriorating column of faded flowers. It is, however, only an approximation since pollinaria removal is occasionally (although apparently rarely) prevented by malformation or drying out of the viscidium or by the difficulty of attaching to an existing excess load of pollinaria. The incidence of pollination in southern Florida, as determined by the absence of the pollinaria in faded flowers, was determined by examining 500 flowers from a total of 100 inflorescences representing eight locations.

STUDIES OF POLLINATION OF TRANSPLANTS

Plants from the Sarasota and Immokalee areas of southern Florida were observed for approximately 33 hours after transplanting into a rural setting in southeastern Ontario, Canada, in late May 1984. The presence of potential pollinators was again recorded. The approximate incidence of pollination was determined by pollinaria removal (see above) in five groups of five experimental plants each, including a total of 429 flowers.

POLLINATION EXPERIMENTS

Pollination experiments were performed on plants maintained in a glass house in Ottawa in April and May 1984 from which potential pollinators (insects, hummingbirds) were excluded. Voucher specimens are contained in the Agriculture Canada herbarium of the Biosystematics Research Institute in Ottawa, Ontario (DAO). The experiments were performed on three groups of plants: 1) 60 plants of *S. lanceolata* var. *lanceolata,* four from each of 15 localities in southern Florida distributed in a broad band, ca. 30 km wide, from Sarasota south to Immokalee; 2) three plants of *S. lanceolata* var. *lanceolata* from near Mahdia, central Guyana, South America; and 3) six plants of *S. lanceolata* var. *paludicola* including three from the Fahkahatchee Strand, Collier Co. and three from Kendall Hammock, Dade Co., both in southern Florida.

Starting from the base of a spike, each sequence of five flowers was treated in the same way. Following the first day after all flowers in the sequence had fully opened, the first flower was left undisturbed, the pollinarium was removed from the second flower, the third was self-pollinated, the fourth pollinated with pollen from a different flower on the same plant (geitonogamous pollination), and the fifth was pollinated with pollen from a flower on a different plant (cross-pollination). With the exception of the plants from Guyana, cross-pollination was carried out using plants from different localities. Each ovary was appropriately tagged to indicate the treatment of the corresponding flower. The number of expanded ovaries was recorded as well as the percentage of embryo sacs containing embryos. The latter value was estimated by emptying the capsule and determining the presence or absence of embryos in the first 200 embryo sacs observed. This was followed by a scan of a few thousand to make certain that the value obtained was representative. If the value was considered not representative, two more samples of 200 were scored and the average percentage was then recorded.

ANATOMICAL STUDY

Each of the three groups of plants used in the pollination experiments was studied anatomically to determine whether or not pseudogamy (asexual seed development requiring pollination) was operating and to determine the method of agamospermy in plants producing seed without any pollination. Serial sections of ovaries were examined in successive developmental stages. Ovaries fixed and preserved in formalin-acetic acid-alcohol (FAA) were dehydrated, embedded in paraffin, sectioned, mounted, and stained using a safranin-hematoxylin combination (Lillie, 1969; Jensen, 1958). Mature seeds of experimental plants were stained for examination using the differential stain technique described by Owczarzak (1952). The percentage of polyembryonic seed was determined in the same way as the percentage of embryo sacs containing embryos (see above).

STUDY OF DRIED MATERIAL

An attempt was made to determine the distribution of breeding systems through the examination of herbarium material from AMES, MICH, SEL, FTG, and DAO (acronyms from Holmgren et al., 1981). This is made possible, to a degree, by association of various morphological features with a specific breeding system. Plants were considered agamospermic if they possessed any polyembryonic seed. Relatively small flower size was considered potentially indicative of autogamy (see Ornduff, 1969). Lack of expansion of some ovaries in fruiting material was considered suggestive of obligately cross-pollinated races.

RESULTS

FIELD STUDIES OF POLLINATION IN SOUTHERN FLORIDA

In southern Florida, insects (including larger bees) were present but were not observed visiting the flowers of *S. lanceolata* var. *lanceolata.* No

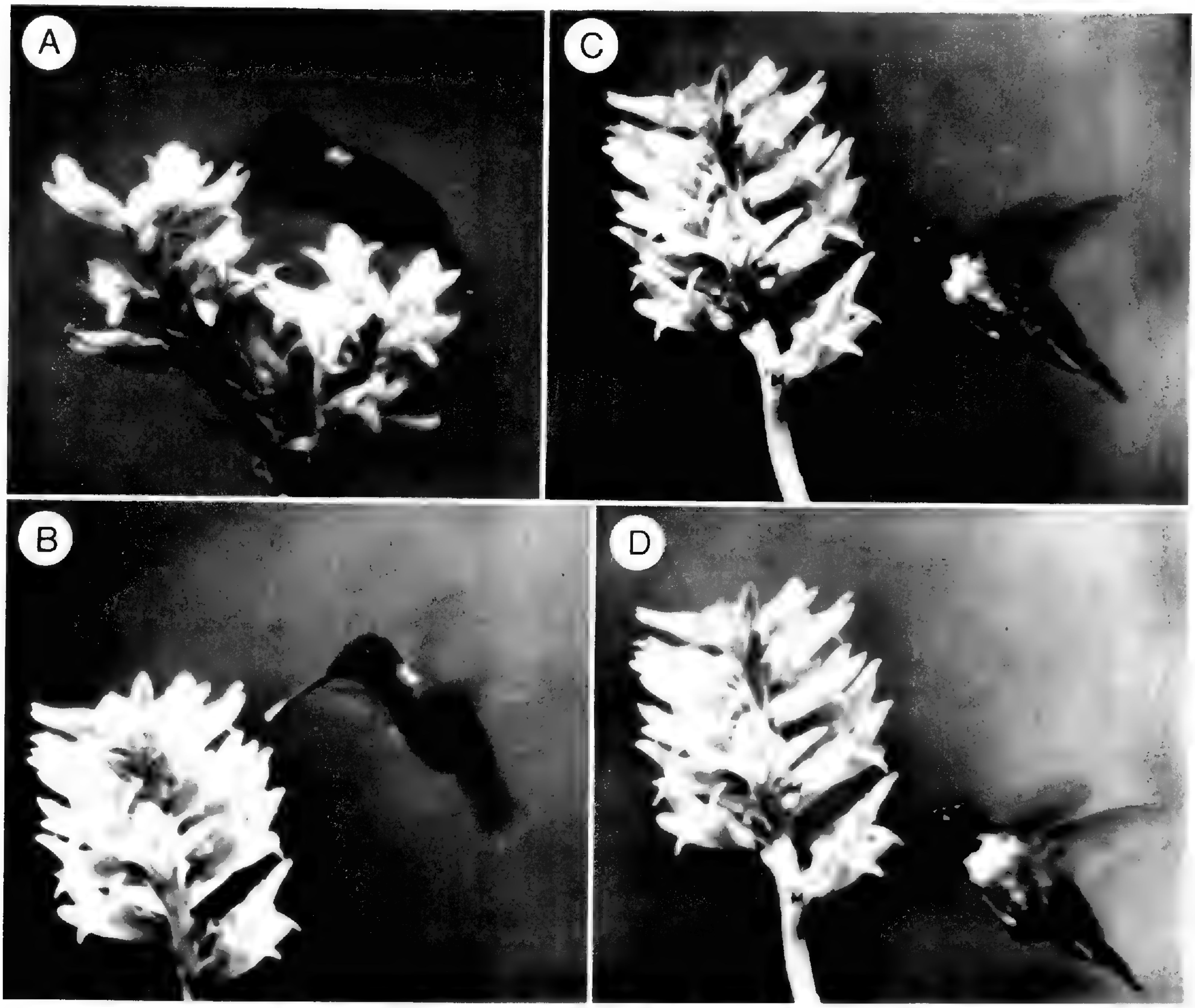

FIGURE 2. Ruby-throated Hummingbird (*Archilochus colubris*) pollinating *Sacoila lanceolata* var. *lanceolata* from Sarasota Co., Florida, 25 May.—A. Female probing flower directly through the floral tube.—B. Female withdrawing with a pale yellowish pollinia attached to the tip of the bill.—C. Male probing a flower from the right side below the lip.—D. Male probing flower directly.

hummingbirds were observed. There was no evidence of pollination, in the form of pollinarium removal, in any of the eight southern Florida locations.

STUDIES OF POLLINATION OF TRANSPLANTS

In southeastern Ontario, large insects including large bees were common, but they totally ignored the flowers. Ruby-throated Hummingbirds (*Archilochus colubris*) were also common. These birds regularly visited the flowers of *S. lanceolata* var. *lanceolata* and acted as effective pollinators. Females were observed visiting inflorescences on 25 separate occasions and males on 46. A visit usually involved probing three to five flowers on an inflorescence and visiting one to three inflorescences in a group of five. Visits were 15 minutes to two hours apart and were most regular in the morning between 9 A.M. and 11:30 A.M. Visits by one or more females (i.e., female visits) involved a direct probing of the flowers (Figs. 2A, 3A), the pollinia becoming attached, by the elongate cushion-type viscidium that sheaths the rostellum (Fig. 3C, D, E, and Greenwood, 1982), to the distal portion of the bill (Figs. 2B, 3B). Male visits involved probing from the side and below the lip approximately 50% of the time (Fig. 2C, D). Probably as a consequence of this "robbing," male visits resulted in pollinia removal only eight of 46 times, as compared with 15 of 25 in the case of female visits. In the 25 experimental plants, which were observed being pollinated by the hummingbirds, the incidence of pollination was 90% (i.e., 386 of 429 flowers).

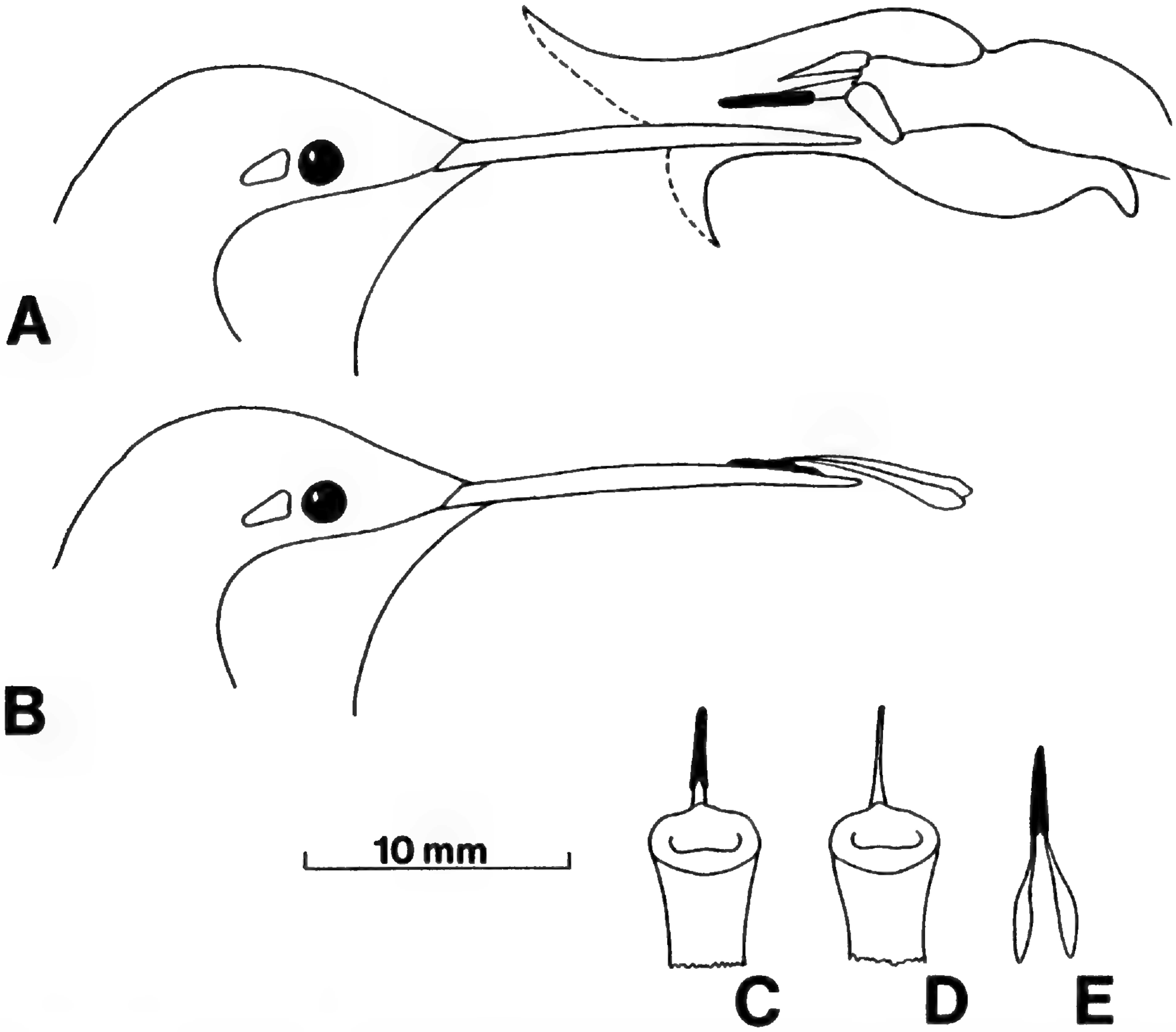

Figure 3. A, B. Diagrams of a Ruby-throated Hummingbird (*Archilochus colubris*) removing pollinia from a flower of *Sacoila lanceolata* var. *lanceolata*.—A. Bird with bill inserted in flower, prior to upward movement that will bring it into contact with the viscidium (darkened).—B. Bird with pollinia attached near tip of bill.—C. Column viewed from below prior to removal of pollinarium, the rostellum inserted into the viscidium.—D. Column viewed from below after removal of pollinarium leaving the long narrow rostellum.—E. Pollinarium viewed from below showing viscidium (darkened) and pollinia. All diagrams based on material from Sarasota Co., Florida.

POLLINATION EXPERIMENTS

Pollination was clearly necessary for seed development in *S. lanceolata* var. *lanceolata* from central Guyana (Table 1). In these pollinator-dependent plants, the flowers last for 10–15 days in the absence of pollination. Pollination at any time is followed by fading in two or three days.

In *S. lanceolata* var. *lanceolata* from southern Florida, seed developed regardless of pollinarium removal (Table 1), and these plants were clearly autonomously agamospermic. The flowers lasted 5–15 days in the absence of pollination, but pollination resulted in fading within two days.

Seed development occurred in undisturbed flowers of *S. lanceolata* var. *paludicola*, but not when the pollinarium was removed from the flower at an early stage (Table 1), indicating autogamy (self-pollination) or pseudogamy (pollination-induced agamospermy) in this variety. Self-pollination occurred after the flowers had been open for one or two days. The flowers are short-lived, lasting for approximately five days. The mechanism of self-pollination is a simple one involving contact between the stigmatic surface and the pollen masses (Figs. 4B, 5). Such contact is not possible in var. *lanceolata* because of the separation resulting from the relative lengths of the pollinia and the basal part of the column (Fig. 4A).

ANATOMICAL STUDY

The Guyana plants of var. *lanceolata* and plants of var. *paludicola* from southern Florida demonstrated a normal sequence of pollination, pol-

TABLE 1. Pollination experiments with *Sacoila lanceolata.*

Treatment	No. of Plants	No. of Ovaries	No./% Ovaries Expanded*	No./% Ovaries with Seed*	% Sacs with Embryos*
S. lanceolata var. *lanceolata*—Guyana					
Undisturbed	3	6	0/0	0/0	0
Pollen removed	3	6	0/0	0/0	0
Self-pollination	3	6	6/100	4/66	50–100
Geitonogamous-pollination	3	6	6/100	4/66	60–100
Cross-pollination	3	6	6/100	4/66	60–100
S. lanceolata var. *lanceolata*—South Florida					
Undisturbed	60	200	200/100	200/100	90–100
Pollen removed	60	180	180/100	180/100	97–100
Self-pollination	60	180	180/100	180/100	96–100
Geitonogamous-pollination	60	180	180/100	180/100	97–100
Cross-pollination	60	180	180/100	180/100	97–100
S. lanceolata var. *paludicola*—South Florida					
Undisturbed	6	25	25/10	25/10	95–100
Pollen removed	6	12	0/0	0/0	0
Self-pollination	6	12	12/100	12/100	95–100
Geitonogamous-pollination	6	12	12/100	12/100	95–100
Cross-pollination	6	12	12/100	12/100	95–100

* As a percentage of the total ovaries tested.

len tube growth, fertilization, and embryo development (see Catling, 1982). In plants of var. *lanceolata* from Florida, the gametophyte degenerated and one or more cells of the inner integument proliferated to become embryos. The proliferation of these cells was indicated by the more deeply staining protoplasts, relatively large nuclei, and well-developed nucleoli (Fig. 6). Proliferation had initiated in the ovaries of flowers open for five days and may have initiated earlier but was not evident in mature ovaries with buds on the point of opening. Using ovaries of increasing age within an inflorescence, it was possible to trace the darkly staining and proliferating micropylar integument to embryos in mature seeds. The seed resulting from adventitious embryony (Fig. 7C) differs from that resulting from fertilization (Fig. 7A, B) in having a proportion of the seeds polyembryonic (range 28–95%, mean 71.3%, standard deviation 17, based on 15 flowers representing 15 different southern Florida populations).

Five capsules from flowers cross-pollinated on the first day of opening and five capsules from flowers from which the pollinarium was removed demonstrated similar levels of polyembryony (range 56–94%, mean 73.5%, standard deviation 17.9; range 30–84%, mean 57.2%, standard deviation 23.5, respectively).

STUDY OF DRIED MATERIAL

Many more collections and some supporting fieldwork would be necessary to allow a reliable assessment of the distribution of different breeding systems throughout the range of *S. lanceolata.* However, an appraisal of the extent to which the breeding systems of the southern Florida populations are unique was possible with the material examined.

Agamospermy, as evidenced by polyembryonic seed, was found in all fruiting plants from Florida and in some plants from Guatemala, Belize (British Honduras), and Bolivia. In some cases this was associated with non-opening (i.e., cleistapogamous, see Sheviak, 1982) flowers (for example, district of Peten, Guatemala, 12 June 1933, *C. L. Lundell 3896,* MICH). The occurrence of agamospermy within the main tropical range is not clearly associated with relatively high altitude, a situation that involves some of the same effects as high latitude, and the sample is not large enough or sufficiently well documented to reliably reflect a trend.

Relatively small flowers (lateral sepals 14–17 mm long), suggestive of self-pollination, were characteristic of plants from a number of Caribbean islands (for example, Bahamas, St. Vincent, based on specimens at AMES and FTG). Limited

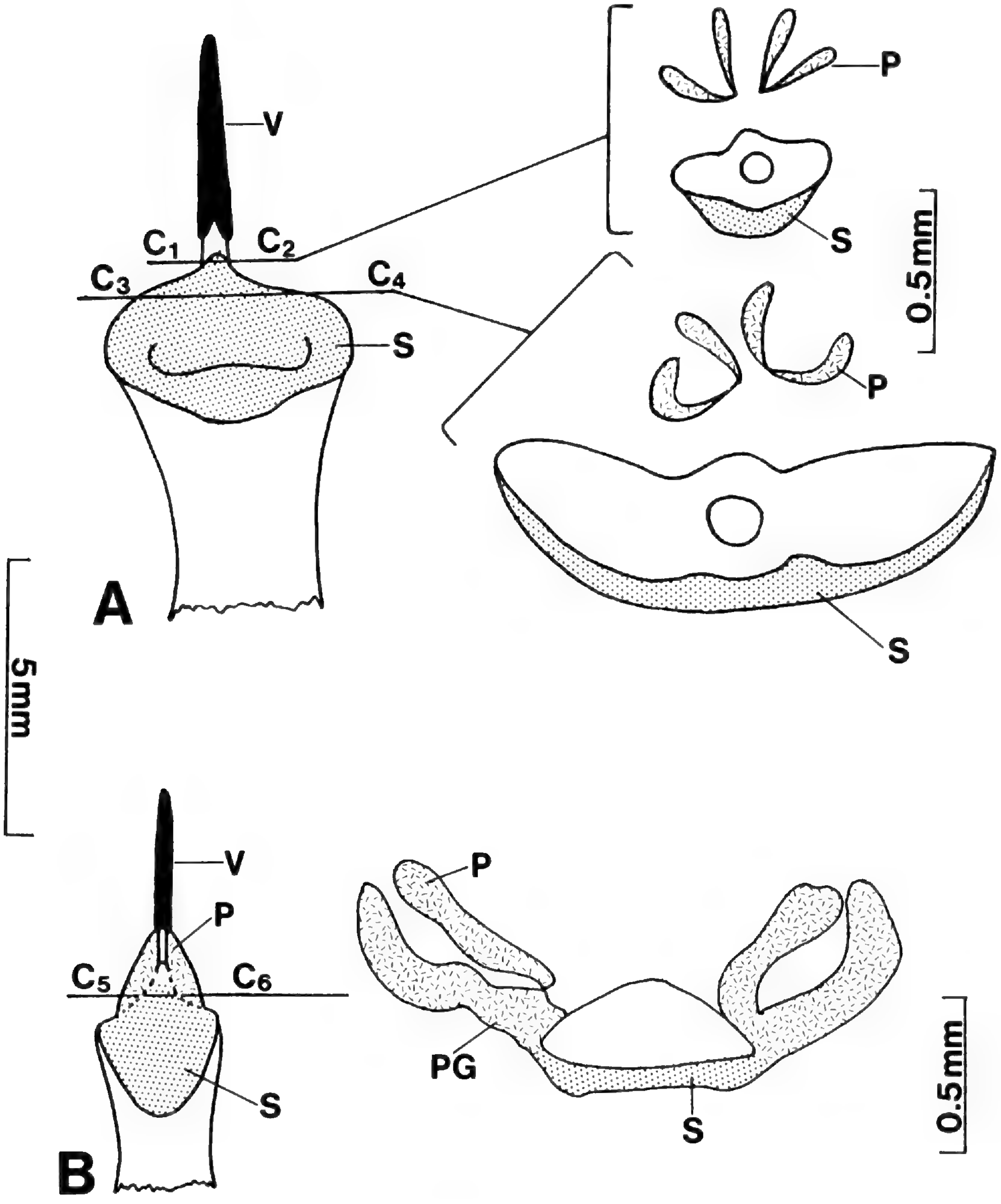

FIGURE 4. A. Column of *Sacoila lanceolata* var. *lanceolata* viewed from below (left) and diagrams of cross-sections (right) based on material from Sarasota Co., Florida.—B. Column of *Sacoila lanceolata* var. *paludicola* viewed from below and diagram of cross-section (right) of flowers originating from Collier Co., Florida. C_1–C_6, cross-sections illustrated on the right-hand side of the figure: P, pollinarium; PG, pollen germinating; S, stigmatic surface; V, viscidium.

fruit set, suggestive of obligate cross-pollination, was restricted to Costa Rica and northern South America.

DISCUSSION

Agamospermy is uncommon in the orchid family, having been previously reported only in *Zeuxine, Nigritella,* and *Spiranthes* (Maheshwari, 1952; Catling, 1982), *Prasophyllum* (Bates, 1984a), *Microtus* (Bates, 1984b), *Paracaleana* (Jones, 1977), *Dactylorhiza* (Dressler, 1981), *Zygopetalum* (Dressler, 1981), and *Pterygodium* (Schelpe, 1970). Autogamy is much more prevalent than agamospermy in vascular plants generally and in the orchid family, where it has been reported in over 60 genera (Catling, unpubl. data).

In *S. lanceolata* var. *lanceolata,* it is not known whether agamospermy is facultative. Although there is no evidence of seed resulting from cross-fertilization in terms of a lower incidence of poly-

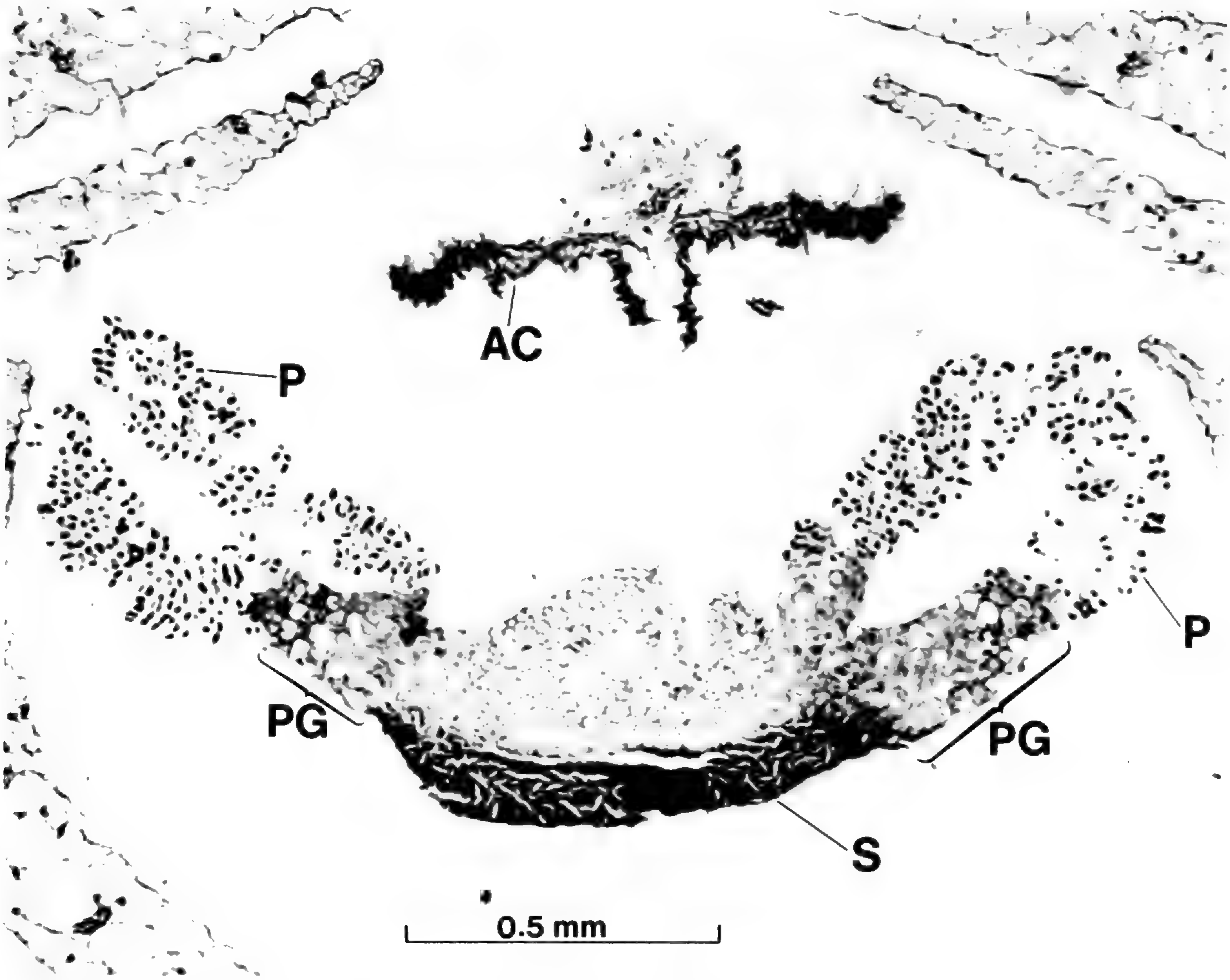

FIGURE 5. Cross-section of column of *S. lanceolata* var. *paludicola,* from Collier Co., Florida. This section represents the position C_5–C_6 in Figure 4B. AC, anther cap; P, pollinarium; PG, pollen germinating; S, stigmatic surface.

embryony, this may have been the result of cross-pollinations using genetically identical individuals with some degree of self-incompatibility. Although the crossings involved plants from different localities in southern Florida, it is conceivable that the different populations had the same agamospermic origin and are genetically identical.

Pollination by hummingbirds in *S. lanceolata* is to be expected on the basis of various floral features such as the tubular, horizontally oriented, reddish flowers without internal marking and lacking odor (Austin, 1975; Pijl & Dodson, 1966), but no previous observations of hummingbird pollination have been reported. The only feature of characteristically bird-pollinated orchid flowers that is lacking is a dark pollinarium (Dressler, 1971), that of *S. lanceolata* being pale yellow. Although the observation of hummingbird-pollination reported here involved transplanted and cultivated plants, there seems to be no reason to doubt that these observations are indicative of the pollination mechanism in various other situations where one or more species of hummingbirds are available.

The suggestion of a lack of natural pollinators in southern Florida pineland is of interest insofar as it may provide an explanation for the pollinator-independent breeding systems. Although self-pollination and agamospermy are associated with pollinator-paucity and colonization of new territory (for example, Allard, 1965; Jain, 1976; Lloyd, 1978) the actual absence of pollinators has not often been well established (for example, Kevan, 1972); nor has "newness" been quantified.

In the southern Florida pinelands in May, *Erythrina herbacea* and *Ipomea microdactyla* are among the few characteristic hummingbird blossoms available, and these species were not observed near colonies of var. *lanceolata.* Only one species of hummingbird (*A. colubris*) is present,

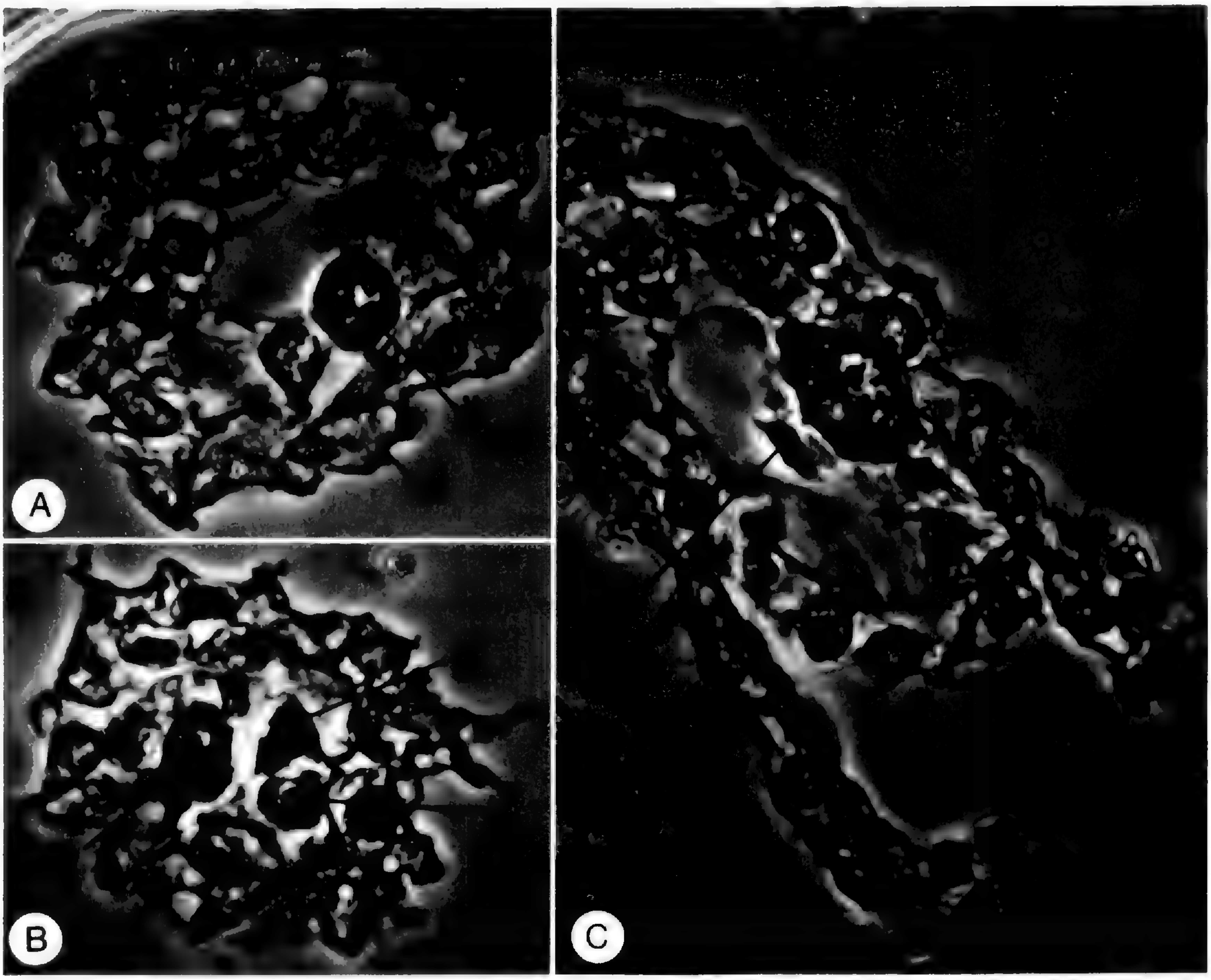

FIGURE 6. A, B. Cross-sections of ovules of *S. lanceolata* var. *lanceolata* from Sarasota Co., Florida.—C. Longitudinal section. g = degenerate gametophyte, ii = proliferating inner integument, oi = outer integument. Material from Sarasota Co., Florida.

and by April and May it has already migrated through the area (Austin, 1975). Breeding of *A. colubris* south of Lake Okeechobee may be very localized (Sprunt, 1954), and there is very little evidence of breeding in southern Florida (Robertson, 1974). Thus there is relatively little to attract hummingbirds to the vicinity of many *S. lanceolata* colonies in southern Florida during the May blooming period, and there is only one potential hummingbird pollinator, which is apparently not abundant. The var. *paludicola* also exists in the absence of a diverse hummingbird-pollinated flora in southern Florida, although a few bromeliads exhibiting the syndrome do flower simultaneously in the hammocks. The situation over much of the range of var. *lanceolata* is quite different since many different hummingbird species are available and there is a diversity and continuity of hummingbird-pollinated blossoms on a year-round basis (Grant & Grant, 1968).

Populations of five other tropical orchids (*Epidendrum rigidum, E. nocturnum, Encyclia cochleata* var. *triandra, E. boothiana* var. *erythronoides* and *Bletia purpurea*) in many parts of southern Florida possess a column structure that promotes self-pollination. This is in contrast to parts of (or all of) the warmer continental neotropics where these same species have a column structure adapted to cross-pollination, or where this latter column structure is at least predominant (Luer, 1971b, 1972; Pijl & Dodson, 1966; pers. obs.). Pollinators are not clearly lacking in the case of these species. It is possible that continual near extinctions due to frost (Singleton, 1936; Stowers & Le Vasseur, 1983), hurricanes (Craighead & Gilbert, 1962; Alexander, 1967) and sea-level fluctuations (Fairbridge, 1974;

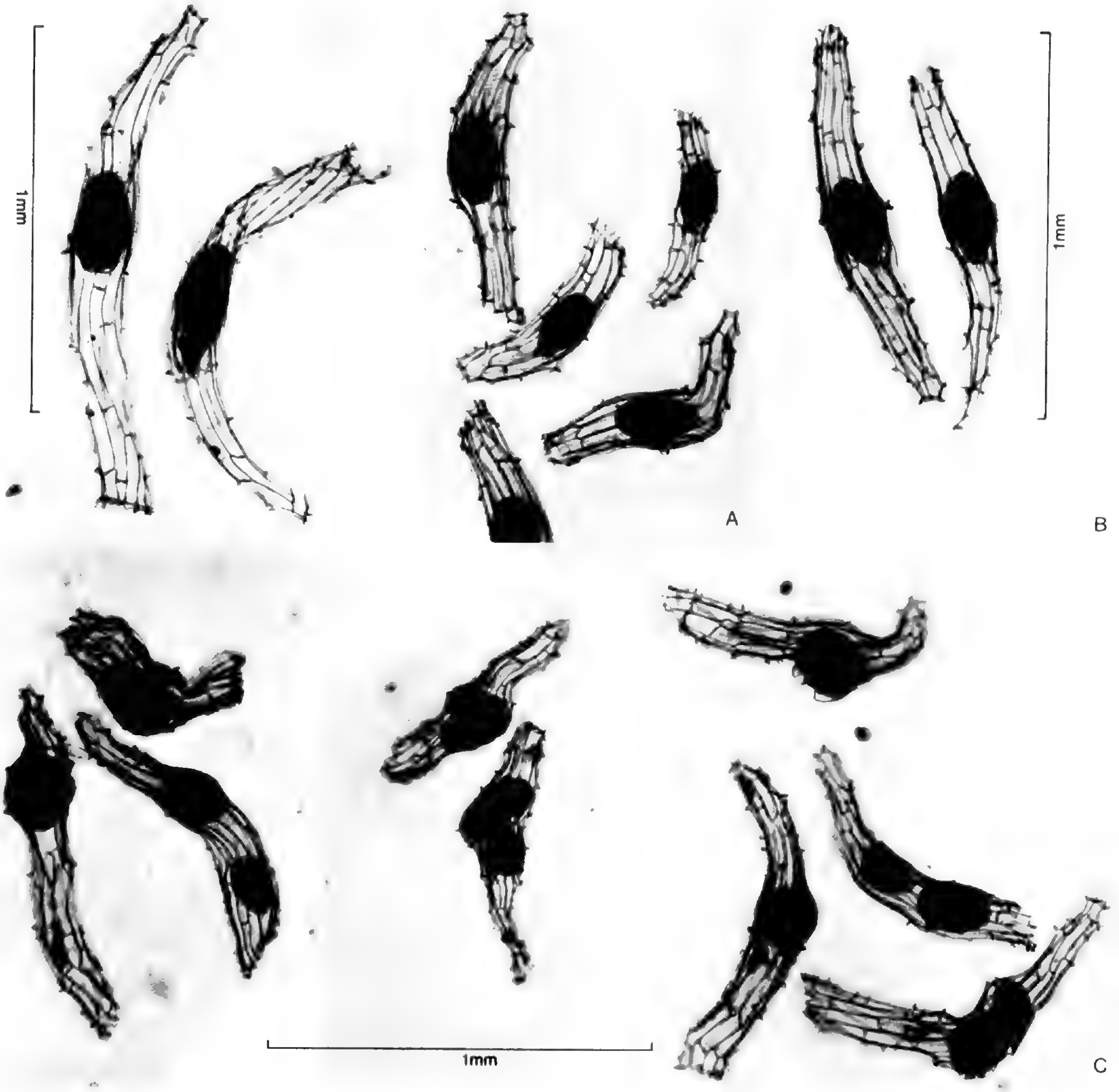

FIGURE 7. A, B. Seed of *Sacoila lanceolata* var. *paludicola*.—A. Collier Co., Florida.—B. Dade Co., Florida.—C. Seed of *S. lanceolata* var. *lanceolata* from Sarasota Co., Florida.

Long, 1974) resulted in a strong selection for colonizing ability, regardless of pollinator-availability. With their terrestrial habit and drier elevated habitats, it seems unlikely that the two varieties of *S. lanceolata* would be as strongly influenced by these factors. Consequently pollinator-paucity is considered to provide an adequate explanation for their pollinator-independent breeding systems in southern Florida.

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FLOWER AND FRUIT BIOLOGY IN SOUTHERN SPANISH MEDITERRANEAN SHRUBLANDS[1]

Javier Herrera[2]

Abstract

Flower and fruit biology was studied in a coastal, southern Spanish scrub community composed of 30 plant taxa. Data on breeding systems; rewards offered to vectors; flower, fruit, and seed sizes; and fruiting intensities are reported. Most taxa in the community have insect-pollinated, hermaphroditic flowers that are largely unspecialized in morphology. Dioecious species are relatively well represented (27% of the total), as are vertebrate-dispersed species (43%). Bagging experiments demonstrated that pollinators were required for maximum fruit production, but the existence of incompatibility systems was not tested. When the relationship between fruiting intensity and the ability to perform vegetative regeneration was investigated, it was found that sprouting taxa had, on average, lower fruit production than those that were unable to sprout. Low fruit production is discussed in relation to reproductive allocation trade-offs.

Mediterranean-type vegetation has been the subject of research for investigators who wish to emphasize convergence phenomena in geographically distant areas with similar environmental factors (Specht, 1969; Mooney & Dunn, 1970; Cody & Mooney, 1978). Also, a great emphasis has been put upon plant development and the adaptive features of plants in this highly seasonal climate (Mooney & Parsons, 1973; Mooney et al., 1974; Kummerov, 1983). Comparatively little is known, however, about other characteristics in the biology of mediterranean species, such as their reproductive biology. The paucity of information is particularly noticeable with respect to plants living in the Mediterranean region itself (but see C. M. Herrera, 1981, 1984; Jordano, 1982, 1984, for plant-frugivorous bird relationships, and J. Herrera, 1985, for nectar secretion patterns in scrub). Some information is available for mediterranean areas in America, Australia, and South Africa (for example, Moldenke, 1975; Specht et al., 1981; Kruger, 1981). But in spite of this, our present knowledge of the reproductive biology of mediterranean shrublands is low compared to our knowledge of tropical (for example, Frankie et al., 1974, 1983; Heithaus, 1974; Bawa, 1979; Bawa & Opler, 1975; Opler et al., 1980) and temperate plant communities (for example, Mosquin, 1971; Kevan, 1972; Pojar, 1974; Reader, 1977; Primack, 1983).

This paper presents part of a study designed to investigate the reproductive biology of a southern Spanish sclerophyllous scrub community. Flower and fruit features in a number of taxa are used to elucidate reproductive patterns. The relationship between sprouting behavior (the production of new stems from established rhizomes, lignotubers, or burls; James, 1984) and pollination–reproduction variables is also investigated. Pollination relationships at the community level will be dealt with elsewhere (J. Herrera, in prep.).

Study Area and Methods

This study was conducted in the Doñana Biological Reserve (Doñana National Park, Spain). The reserve is located on the Atlantic coast of southwestern Spain, in an area with a mediterranean-type climate where the vegetation is composed mainly of mediterranean sclerophyllous shrublands with some planted pine woods. Annual precipitation averages 537 mm. Mean annual temperature is 16°C, January being the coolest month (9.8°C) and July the hottest (24.6°C). Temperatures rarely descend below zero, and summer drought covers five months on average (May through September). The soil is sandy, and maximum elevation above sea level is 30 m.

Basically the vegetation encompasses two types of scrub formations, distributed according to topographic and edaphic factors. Where the level of the underground water table is relatively near

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soil surface, the scrub becomes dominated by hygrophytic species (heath). Otherwise, a highly xerophytic scrub vegetation is found (see Allier et al., 1974; Rivas-Martínez et al., 1980). The most representative species, both in hygrophytic and xerophytic scrub, were selected for study giving a total of 30 taxa. From December 1982 through March 1984 the study plot was visited weekly, and data on flowering phenology, pollination relationships, and flower–fruit biology of the species were gathered. Here I report only on aspects of flower and fruit biology.

Individual plants or branches were marked before flowering, and their area estimated from maximum and minimum diameters. Flowers were counted every week during the time of study, and the maximum numbers registered for the plants of a species were averaged to give an estimate of flower production per unit area.

Fresh samples of flowers and fruits of all taxa were taken to determine the most outstanding external features, such as dimensions, color, and sex. Ten to 20 flowers of each species were measured (length, maximum and minimum diameters), and 20 to 500 complete flowers without their pedicels were air dried and weighed. The maximum dimension of a flower was found to be directly correlated with its dry weight (r_s = 0.806, N = 30, $P < 0.001$). Therefore dry weight has been used subsequently as an estimate of flower size, since it is less dependent on the architecture of the corolla than on the maximum dimension. Pollination modes of taxa were determined from external features and visitor censuses (J. Herrera, in prep.). Flower forms were referred to those of Faegri and van der Pijl (1979).

Pollen production and the number of ovules in the ovary of each flower were determined for 10 to 15 flowers per plant species. Ovules were counted under a dissecting microscope. Pollen production was assessed in the same flowers by macerating one or two anthers in a known volume of detergent-safranine solution and counting the number of grains in 10 replicates of 5 μl. Pollen-ovule ratios of hermaphroditic species were then compared with those given by Cruden (1977).

To investigate nectar secretion, flowers were observed in the field and in the laboratory under a dissecting microscope. In doubtful cases, the arrival of insect visitors to flowers was precluded by bagging branches with white nylon mesh; flowers were examined after 24 hours and, when possible, the accumulated nectar was quantified. The volume per flower was measured by the length of the column, in mm, inside 5 μl micropipettes. Concentration, on a weight : weight basis, was measured in two ATAGO refractometers (models N1 and N2) compensated to ambient temperature. The milligrams of nectar sugar plus diluted solids (Inouye et al., 1980) were computed by the product of volume × concentration (Bolten et al., 1979).

Percent fruit production in open pollinated flowers of the species was estimated from flower and ripe fruit counts on marked branches. In the same individual plants that were used to estimate percent fruiting, some branches were also bagged with white nylon mesh (or with glassine paper bags in anemophilous taxa) to determine fruiting intensities when pollinators were excluded. Bagging experiments were not carried out with dioecious taxa. Samples of fruit were collected and oven dried to a constant weight, and the number of seeds, along with the weights of the whole fruit, all seeds, and that of an individual seed were averaged and recorded. Notes on fruit and flower predation were also taken and, when possible, the agents responsible were identified.

The ability to perform vegetative regeneration after complete destruction of aboveground biomass (sprouting) was assessed for every species. Data on sprouting of these species were derived from careful observations carried out in the study area on plants damaged by fire, herbivores, or human disturbance during the years 1982 through 1985.

RESULTS

FLOWER BIOLOGY

The names of the species studied, together with their most distinctive floral features, are summarized in Table 1. Our set of mediterranean plants consists of 30 taxa in 17 families and 25 genera. Most families contribute one or two species, with only Cistaceae, Leguminosae, Labiatae, and Ericaceae being relatively well represented (5, 4, 3, and 3 species, respectively).

Pollination by insect vectors is dominant in the community, where entomophilous species account for more than 80% of the total (Table 1). Only five species rely on wind for pollen dispersal. Hermaphroditism is the most common breeding system with 21 taxa (70%), although dioecious species are relatively well represented (27%). *Thymus tomentosus* is the only species with a different sexual condition (gynodioecy).

TABLE 1. Floral attributes of 30 scrub species. (BS, breeding system; PM, pollination mode; FF, flower form; DW, dry weight of individual flowers, in mg; P, mean number of pollen grains per flower, in thousands; P:O, pollen-ovule ratio.) Flower number indicates the mean number in individual plants at peak bloom per m^2, followed by the standard error; number of plants is indicated in parentheses. When there are differences among sexes in dioecious taxa, the value corresponding to female flowers is given first.

Species	BS[1]	PM[2]	FF[3]	Color[4]	Reward[5]	DW	P	P:O	Flower Number		Predation
Armeria velutina Welw. ex Boiss. & Reuter	H	E	d	p	N	2.0	1	979	2,553 ± 621	(10)	–
Asparagus aphyllus L.	D	E	d	g	N	0.8–1.5	37	—	599 ± 237	(10)	+
Calluna vulgaris (L.) Hull	H	E	b	p	N	2.3	24	1,047	16,495 ± 4,847	(12)	–
Chamaerops humilis L.	D	A	a	y	—	8.3–4.1	214	—	366 ± 118	(10)	–
Cistus libanotis L.	H	E	d	w	P	24.5	55	2,482	177 ± 27	(10)	–
Cistus salvifolius L.	H	E	d	w	P	65.5	106	1,908	68 ± 12	(10)	–
Corema album (L.) D. Don	D	A	a	brown	—	0.5–0.1	229	—	—		–
Cytisus grandiflorus D.C.	H	E	f	y	P	22.4	69	6,179	244 ± 53	(10)	–
Daphne gnidium L.	H	E	t	cream	N	2.8	9	9,040	854 ± 301	(10)	+
Erica ciliaris L.	H	E	b	p	N	4.6	35	129	52 ± 23	(7)	+
Erica scoparia L.	H	A	b	g	—	0.8	92	2,008	56,902 ± 13,699	(5)	+
Halimium commutatum Pau	H	E	d	y	P	11.6	13	2,024	256 ± 41	(10)	–
Halimium halimifolium L. (Willk.)	H	E	d	y	P	26.8	55	1,179	89 ± 21	(9)	–
Helianthemum croceum (Desf.) Pers.	H	E	d	y	P	15.4	53	3,039	498 ± 114	(10)	–
Helichrysum picardii Boiss. & Reuter	H	E	d	y	P	0.1	2	2,075	26,561 ± 8,488	(10)	–
Lavandula stoechas L.	H	E	t	purple	N	1.5	4	1,030	4,683 ± 669	(10)	–
Lonicera periclymenum L.	H	E	t	cream	N	19.1	10	850	48 ± 3	(4)	–
Myrtus communis L.	H	E	brush	w	P	16.8	599	12,323	266 ± 72	(4)	–
Osyris alba L.	D	E	d	g	N	2.6–1.8	5	—	3,497 ± 754	(8)	–
Osyris quadripartita Salzm. ex Decne	D	E	d	g	N	1.8–0.8	3	—	7,281 ± 1,897	(10)	–
Phillyrea angustifolia L.	H	A	d	w	—	1.6	72	71,932	11,727 ± 2,861	(7)	–
Pistacia lentiscus L.	D	A	a	p-y	—	0.4–2.1	35	—	—		–
Rhamnus lycioides L.	D	E	d	g	N	0.6	15	—	—		–
Rosmarinus officinalis L.	H	E	t	w	N	2.7	5	1,346	2,226 ± 403	(14)	–
Rubus ulmifolius Schott.	H	E	d	p	N	53.7	54	11,022	13 ± 2	(10)	–
Smilax aspera L.	D	E	d	w	?-P	1.8–1.4	13	—	527 ± 616	(11)	–
Stauracanthus genistoides (Brot.) Samp.	H	E	f	y	P	5.1	20	3,579	970 ± 245	(10)	–
Thymus tomentosus Willd.	G	E	t	w	N	0.6–0.7	5	1,148	2,859 ± 531	(8)	–
Ulex minor Roth.	H	E	f	y	P	3.0	13	1,824	687 ± 170	(14)	–
Ulex parviflorus Pourret	H	E	f	y	P	8.0	19	2,943	111 ± 44	(8)	–

[1] H, hermaphrodite; D, dioecious; G, gynodioecious.

[2] E, entomophilous; A, anemophilous.

[3] d, disc; b, bell; a, apetalous; f, flag-blossom; t, tube.

[4] p, pink; g, green; y, yellow; w, white.

[5] N, nectar; P, pollen

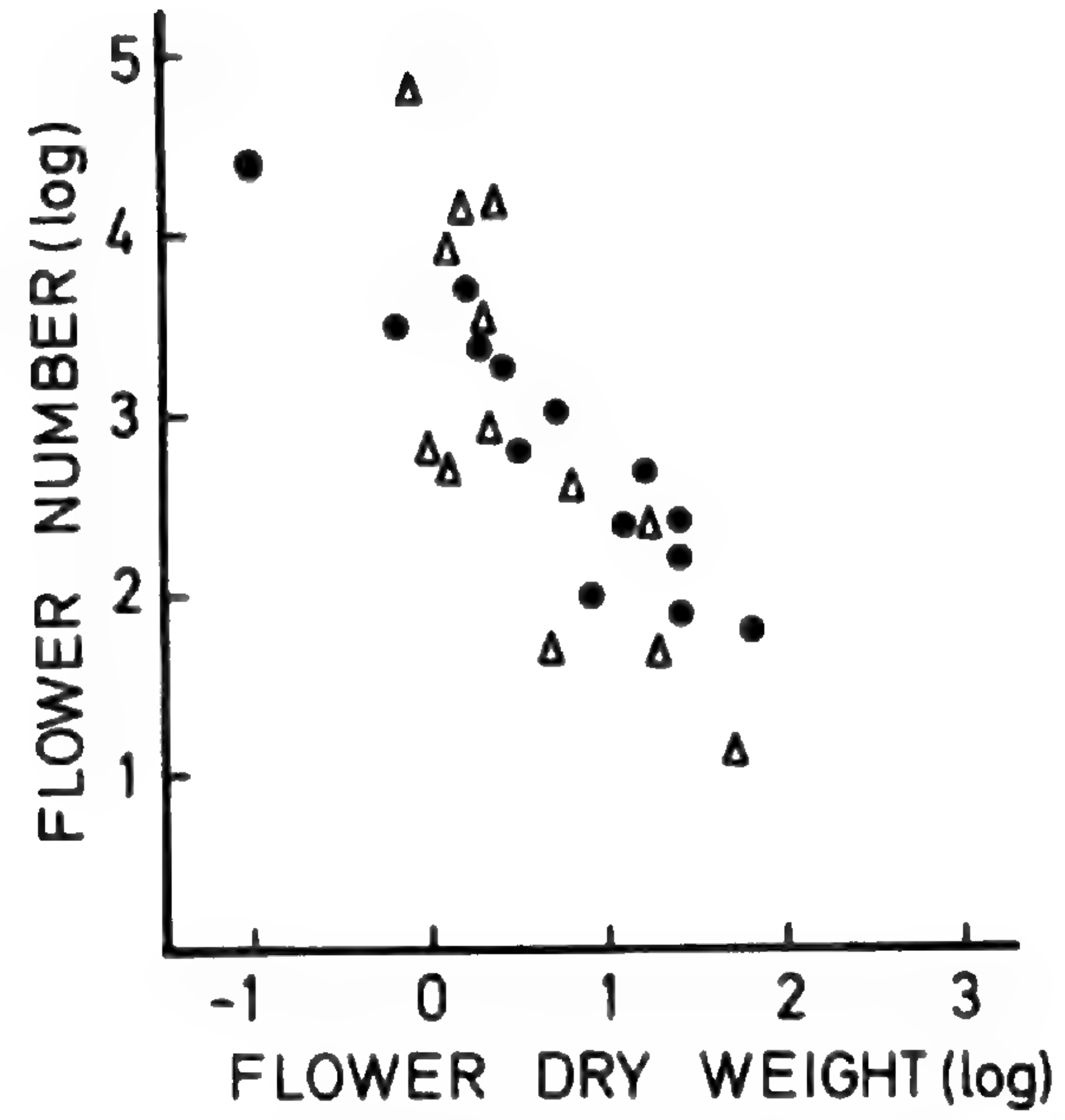

FIGURE 1. Relationship between the weight of an individual flower and the mean number of flowers per square meter in peak blooming plants. Triangles = sprouting taxa; circles = nonsprouting taxa.

Flower sizes (as dry weight of the complete flower) in the sample range between 2.2 mg for the female flowers of *Pistacia lentiscus* and 65.5 mg for *Cistus salvifolius*. More than 50% of the taxa have flowers of 5 mg or less in dry weight. Floral dry weight is not independent of the breeding system in this set of species. If taxa are segregated in two categories, less or more than 5 mg (a value that is near the median in the frequency distribution), dioecious taxa predominate in the lower class (8 out of 9), whereas hermaphroditic taxa are evenly distributed among the two classes (10 and 11, respectively). The differences are statistically significant ($G = 5.04$, df $= 1$, $P < 0.025$).

The predominant flower morphology is of the dishbowl type (Faegri & van der Pijl, 1979), which is present in the Cistaceae and also in all the entomophilous dioecious taxa. Species in the Labiatae have short, tubular corollas; while the legumes present typical flag blossoms. The only long-tubed flowers are those of *Lonicera periclymenum*. Generally speaking, flowers are small and/or have corollas that impose little or no restriction on floral visitors (except for *L. periclymenum* and the legumes). All species in the Leguminosae and three in the Cistaceae have yellow flowers, which is the most common color (nine of total); whereas six species have white corollas. Many of these yellow- or white-flowered taxa offer pollen as the main reward to pollinators (Table 1). There are five species with pink flowers, which provide predominantly nectar as the reward.

Among entomophilous taxa, pollen and nectar are offered by approximately the same number of species (12 and 13, respectively). However, since wind-pollinated taxa are also occasionally used as a pollen source by insects (pers. obs.), this food material is more readily available in our community than is nectar, at least in terms of plant taxa. Furthermore, we have succeeded in quantifying the secretion in only six out of 13 species in which nectar is the main reward. These species were *Daphne gnidium* (0.17 mg sugar/flower per 24 hr.), *Erica ciliaris* (0.08 mg), *Lavandula stoechas* (0.15 mg), *Lonicera periclymenum* (2.00 mg), *Rosmarinus officinalis* (0.20 mg), and *Rubus ulmifolius* (1.20 mg). In the remaining seven species the yield of nectar sugar per flower per 24 hr. was too scarce to be quantified with our method (presumably less than 0.08 mg). Maximum concentration values ranged between 9.5% (*Erica ciliaris*) and 60% (*Rubus ulmifolius*); volumes per flower on a daily basis ranged between 0.9 μl (*Lavandula stoechas, Daphne gnidium*) and 10 μl (*Lonicera periclymenum*).

Pollen yield of the individual flowers is given in Table 1. The lowest is that of *Armeria velutina* (10^3 grains) and the highest that of *Myrtus communis* (599×10^3), which has insect-pollinated, nectarless flowers of the brush type common in the Myrtaceae. Since pollen production is not independent of flower size, a more correct estimate of staminate effort on a per flower basis would be the number of pollen grains produced per milligram of flower dry weight (Relative Staminate Effort, RSE). Defined in this way, RSE is minimum for entomophilous taxa such as *Armeria velutina* (500) and *Lonicera periclymenum* (524). The former has dimorphic pollen grains and stigmas, and the latter has the most specialized (long-tubed, highly nectariferous) flowers in the sample. Maximum values of RSE are found in anemophilous species such as *Corema album* (2.3×10^6) and *Erica scoparia* (120×10^3). Mean RSE is significantly higher for anemophilous taxa than for entomophilous ones ($U = 121$, N = 5, 25, $P < 0.001$).

Values of pollen-ovule ratios for hermaphroditic species are given in Table 1. In most taxa this ratio is greater than 2,000 and thus referable to the allogamous class of Cruden (1977). Only three species have pollen-ovule ratios lower than 1,000. Mean number of flowers for plants in peak bloom are also shown in Table 1. A highly significant relationship exists between flower num-

TABLE 2. Fruit and seed characteristics for 29 scrub species. Numbers in parentheses are sample sizes.

Species	Type[1]	Mean Number of Seeds	Mean Dry Weight (mg)			Predation
			Whole Fruit	All Seeds	Individual Seed	
Armeria velutina	D	1	3 (50)	1	1 (50)	+
Asparagus aphyllus	F	1.2	46 (100)	23	19 (122)	+
Calluna vulgaris	D	3.6	2 (100)	0.2	0.1 (325)	−
Chamaerops humilis	F	1	1,364 (18)	781	781 (18)	+
Cistus libanotis	D	22.3	59 (20)	23	1 (445)	+
Cistus salvifolius	D	51	137 (12)	53	1 (612)	+
Corema album	F	3	57 (30)	35	12 (90)	−
Cytisus grandiflorus	D	6.9	214 (20)	39	6 (137)	−
Daphne gnidium	F	1	18 (75)	8	8 (75)	−
Erica ciliaris	D	17.9	5 (80)	0.2	0.01 (1,150)	+
Erica scoparia	D	6.5	1 (60)	0.1	0.02 (1,000)	+
Halimium commutatum	D	2.6	33 (20)	14	6 (52)	+
Halimium halimifolium	D	25.7	59 (20)	15	0.6 (514)	−
Helianthemum croceum	D	10.3	34 (15)	15	1 (155)	+
Helichrysum picardii	D	1	0.6 (750)	0.6	0.6 (750)	−
Lavandula stoechas	D	2.3	4 (50)	1	0.6 (114)	+
Lonicera periclymenum	F	2.3	52 (30)	15	7 (30)	−
Myrtus communis	F	5.7	108 (75)	56	10 (430)	−
Osyris alba	F	1	157 (30)	90	90 (30)	+
Osyris quadripartita	F	1	131 (75)	73	73 (75)	+
Phillyrea angustifolia	F	1	35 (100)	12	12 (100)	−
Pistacia lentiscus	F	1	22 (80)	13	13 (80)	−
Rhamnus lycioides	F	1.6	63 (30)	26	16 (30)	−
Rosmarinus officinalis	D	2.9	4 (20)	2	0.6 (59)	+
Rubus ulmifolius	F	40.4	213 (30)	87	2 (30)	−
Smilax aspera	F	1.4	78 (100)	51	36 (140)	−
Stauracanthus genistoides	D	2.5	59 (15)	13	5 (38)	+
Ulex minor	D	2.1	22 (20)	7	3 (35)	+
Ulex parviflorus	D	2	47 (10)	12	6 (20)	+

[1] D, dry fruits; F, fleshy, vertebrate-ingested fruits.

ber and flower size (dry weight); this relationship can be easily appreciated in Figure 1 ($r = -0.826$, $N = 27$, $P < 0.001$).

Damage of flowers by insect predators, mostly noctuid larvae, coleopteran larvae, and other unidentified insects, was observed in only four species (Table 1).

FRUIT BIOLOGY

Table 2 summarizes various characteristics of the fruits in our set of mediterranean plant species. Fruit production in *Thymus tomentosus* was so sparse that we were unable to gather a reasonable sample of fruits and seeds; this species has therefore been excluded from the analyses. According to the way in which their seeds are dispersed our taxa are easily divided in two groups: those whose seeds are dispersed by vertebrates (13 taxa) and those whose seeds are dispersed by the wind or in a largely passive way (16 taxa). The former have fleshy fruits, while the latter have dry fruits (mostly capsules, legumes, or achenes). Seed collecting by ants has been observed in a few taxa, but data are not conclusive enough to recognize a third (ant-dispersed) class. Most vertebrate-dispersed plant species in the sample have ornithochorous diaspores (C. M. Herrera, 1984a).

Mean number of seeds per fruit ranges between 1 and 51, and the fruit size (fruit dry weight) between 0.6 mg (*Helichrysum picardii*) and 1,364 mg (*Chamaerops humilis*). The lightest seeds are those of *Erica ciliaris* (2×10^{-2} mg) and the heaviest those of *Chamaerops humilis* (781 mg). Predation of fruits, mainly by Curculionidae, larvae of Tortricidae, Noctuidae, and parasitic hymenopterans, is far more common than flower predation (55% and 13% of species, respectively). Damage by predators was observed more frequently on dry than on fleshy fruits ($G = 4.02$, $df = 1$, $P < 0.05$).

TABLE 3. Results of independence tests performed between the type of fruit (dry or fleshy) and other variables of flowers and fruits. Class intervals considered were weight of fruit, less than 20 mg, 20–40 mg, 40–60 mg, or more than 60 mg; weight of the individual seed, less than 10 mg, or more than 10 mg; number of seeds per fruit, less than 2, 2–4, or more than 4.

Independence of Fruit Type	G	df	P
Sexuality (hermaphroditism, dioecy)	11.72	1	<0.001
Weight of fruit	8.04	3	<0.05
Weight of individual seed	23.32	1	<0.001
Seeds per fruit	13.85	2	<0.001

G, value of the statistic in the G test of independence; df, degrees of freedom.

Results of tests for the independence of fruit type and a few variables of flowers and fruits are given in Table 3. There is a significant tendency for species with hermaphroditic flowers to produce dry fruits, and for species with unisexual flowers to produce fleshy fruits. The independence hypothesis of fruit type and breeding system (Bawa, 1980) is thus rejected (Table 3). The only gynodioecious taxon in the sample has been included (conservatively) in the dioecious class for this analysis. The independence hypothesis for the type of fruit and the variables weight of fruit, weight of an individual seed, and seeds per fruit are all rejected. In fact, fleshy fruits tend to be, on average, heavier than dry ones ($U = 185.5$, N = 16, 13, $P < 0.05$) and to have fewer and heavier seeds ($U = 203$, N = 16, 13, $P < 0.001$). Note that we are reporting *dry weights,* so that differences are not due to the high water content of fleshy, vertebrate-ingested fruits.

Fruiting intensities for 28 of the studied species can be seen in Table 4. Data are not available for two dioecious species, *Corema album* and *Rhamnus lycioides.* Fruit production after exclusion of pollinators is also reported for hermaphroditic taxa. Percent of fruit production in open pollinated flowers ranged between 2% for *Thymus tomentosus* and *Daphne gnidium,* and 92% for *Halimium commutatum.* Bagging of flowers in most cases had a clear effect of decreasing fruit production—to levels as low as 0–1% in 15 species. There was just one taxon that was unaffected by exclusion of pollinators (*Daphne gnidium,* 2% fruit production under both treatments). Some fruit was produced (10–31%) in bagged flowers of a few taxa (*Calluna vulgaris, Erica scoparia, Myrtus communis,* and *Rosmarinus officinalis*), but even in such cases pollinating vectors were needed for fruiting to arrive at its maximum.

REPRODUCTIVE TRADE-OFFS

Figure 2 shows the relationship between percent fruiting and the quotient of the fruit dry weight to the flower dry weight (fruit : flower size ratio hereafter), which indicates about how high the increase in size is from the first reproductive unit to the second. This variable will be employed below to investigate some patterns of reproductive allocation in our set of species. A highly significant negative relationship exists between percent fruit production and fruit : flower size ratio ($r = -0.6780$, N = 26, $P < 0.001$, log transformed data). Thus species in which there is a great increase in dry weight during the transition from flower to fruit are those with the lowest percent fruiting, whereas species in which this process involves little gain in weight have relatively greater fruiting success.

Species known to perform vegetative regeneration (sprouting) are distinguished from nonsprouting ones in Table 4, and their respective distribution in the relationship defined by percent fruit production and fruit : flower size ratio is shown in Figure 2. Sprouting taxa tend to have low values of fruiting and high values of fruit : flower size ratio. Mean percent fruit production is not, however, significantly different for sprouting and nonsprouting taxa ($U = 109$, N = 14, 12, $P > 0.2$); differences in mean dry weight increase from flower to fruit are weakly significant ($U = 117.5$, $P > 0.05$). Species in the Ericaceae lower the coherence of the sprouting group, since they are well-known sprouters but have relatively low fruit : flower size ratios. If the Ericaceae are removed, the sprouting group is entirely composed of taxa with few-seeded, vertebrate-ingested fruits; with the exclusion of ericaceous taxa, the nonsprouting group overlaps entirely with the dry fruit group, and the sprouting group does likewise with the fleshy fruit group. Differences in mean percent fruit production and fruit : flower size ratio are now significant ($U = 101.5$, $P < 0.05$; $U = 116.5$, $P < 0.002$, N = 12, 11, respectively).

Figure 1 shows an inverse relationship between the number of flowers at peak blooming and flower dry weight. Both sprouting and nonsprouting species are evenly distributed along this continuum, so that mean number of flowers at

TABLE 4. Fruit production in open pollinated and bagged flowers of the studied species. Numbers in parentheses indicate the number of flowers, and N the number of plants. The sample of the only gynodioecious species (*Thymus tomentosus*) includes three hermaphrodites and four female plants. Species known to be capable of sprouting are marked with an asterisk.

	Fruit Production (%)		
Species	Open Pollinated	Bagged	N
Armeria velutina	59 (478)	3 (476)	5
*Asparagus aphyllus**	24 (804)	—	6
*Calluna vulgaris**	88 (100)	24 (50)	5
*Chamaerops humilis**	4 (4,560)	—	7
Cistus libanotis	55 (5,822)	0.2 (538)	4
Cistus salvifolius	50 (3,014)	0 (92)	10
Cytisus grandiflorus	12 (150)	0 (134)	4
*Daphne gnidium**	2 (23,749)	2 (2,660)	10
*Erica ciliaris**	45 (147)	1 (105)	10
*Erica scoparia**	89 (85)	31 (65)	5
Halimium commutatum	92 (100)	0 (100)	5
Halimium halimifolium	41 (70)	1 (1,259)	5
Helianthemum croceum	—	0 (171)	3
Helichrysum picardii	68 (1,308)	1 (1,443)	5
Lavandula stoechas	69 (200)	0.4 (1,040)	10
*Lonicera periclymenum**	8 (1,537)	4 (211)	4
*Myrtus communis**	68 (857)	23 (78)	4
*Osyris alba**	7 (1,385)	—	8
*Osyris quadripartita**	5 (2,400)	—	5
*Phillyrea angustifolia**	14 (1,229)	0 (735)	5
*Pistacia lentiscus**	16 (1,368)	—	5
Rosmarinus officinalis	31 (256)	10 (797)	5
*Rubus ulmifolius**	78 (931)	0 (158)	10
*Smilax aspera**	9 (4,053)	—	5
Stauracanthus genistoides	40 (115)	0.2 (651)	4
Thymus tomentosus	2 (210)	0 (210)	7
Ulex minor	16 (238)	0 (221)	10
Ulex parviflorus	5 (310)	0 (471)	5

peak blooming is not significantly different between them ($U = 101$, $P > 0.1$); neither is mean flower dry weight significantly different ($U = 113.5$, $P > 0.1$, $N = 14, 13$). Both sprouting and nonsprouting taxa may be many- and small- or few- and big-flowered.

DISCUSSION

The 30 mediterranean plant species studied represent a relatively small sample of the regional flora (more than 2,000 taxa for southern Spain, of which nearly 300 are woody). Furthermore, shrublands have many different and diverse species compositions in southern Spain, depending on elevation, rainfall, edaphic factors, etc., so that the results reported here should be extended only with caution to other scrub communities in the region. Nevertheless many of the studied taxa are widespread, and the community they form is undoubtedly a clear example of coastal scrub on sandy soils, which is characteristic of other areas in southern Spain.

In the studied community a sizeable heterogeneity in reproductive traits was likely to occur, since 30 plant species were distributed among 17 families. However, certain groups (virtually Cistaceae, Leguminosae, Ericaceae, and Labiatae) contributed with more taxa to the sample than did others. Hence a phylogenetic component in the reproductive patterns recognized should not be ruled out, in addition to an ecological component and to the fact that the plants form a steady, long-lasting community achieving reproduction year after year. Several aspects in the reproductive patterns are not restricted to our particular community. The relative dominance of taxa in which nectar yield is low or even zero,

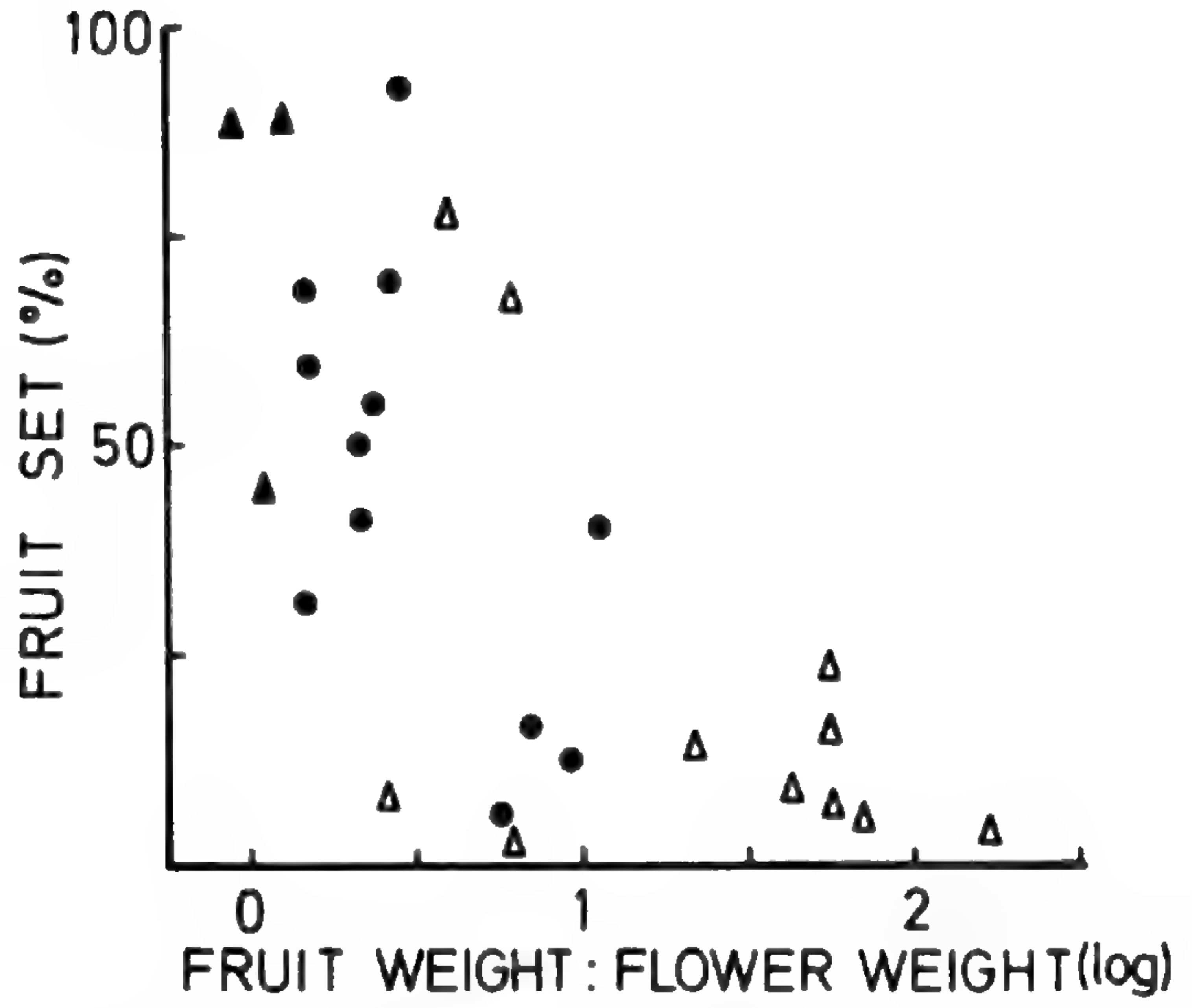

FIGURE 2. Relationship between fruit : flower dry weight ratio and percent fruiting for 26 scrub taxa. Triangles = sprouting species; circles = nonsprouting species; black triangles = species in the family Ericaceae.

for example, is general in the region (J. Herrera, 1985). The consequences of this factor upon the pollination relationships will be dealt with elsewhere (J. Herrera, in prep.). Dispersal by inanimate or vertebrate agents creates a dichotomy that is also found in other mediterranean-type communities (Bullock, 1978, chaparral; C. M. Herrera, 1984b; Jordano, 1984, southern Spain). As has been reported in other woody communities (Reader, 1977; Ruiz-Zapata & Arroyo, 1978; Bawa, 1979; Bawa & Beach, 1983) pollinators are needed for maximum fruit production. Further investigations will determine the extent to which incompatibility systems occur in shrublands of southern Spain.

Sprouting is also a common regenerative strategy of woody plants in many and diverse ecosystems (James, 1984). It is particularly important in regions of a mediterranean-type climate that experience summer droughts and frequent fires. This aspect has received much attention in the Californian chaparral (Wells, 1969; Keeley, 1977), where two general reproductive strategies (in fact, extremes of a continuum) have been recognized: the "seeder" strategy consists of obligate seed reproduction and incapacity to form new stem sprouts after destruction of aerial parts; the "sprouters" can produce stem or root sprouts that enable repeated shoot production despite frequent damage (Malanson & Westman, 1985; see James, 1984, for an extensive review). It appears that both strategies also are found among sclerophyllous species of the Mediterranean Basin. In our community most plants fall clearly into one category or the other, although species in the Ericaceae could be easily included in both: they produce plenty of seeds and are also able to sprout, which was reported some time ago for *Calluna vulgaris* (Kayll & Gimingham, 1965).

It has been hypothesized that pollination-reproduction variables may be associated with each of the sprouting or nonsprouting strategies. In seeders, for example, the pollination system must be efficient enough to assure the release of numerous seeds (which could open a way to self-compatibility), produce numerous flowers highly attractive to pollinators, and offer a greater reward per flower than sprouters (Carpenter & Recher, 1979). In contrast, sprouting taxa are proposed to have a high rate of outcrossing, although often with a low production of flowers, which would be relatively low rewarding (Fulton & Carpenter, 1979; Carpenter & Recher, 1979). These hypotheses are supported in part by our data.

A high rate of outcrossing has to be expected in the sprouting group of species, since many dioecious taxa are included in that group. There are no evident signs, however, of a high incidence of self-pollination in the nonsprouting group. In contrast, mean percent fruit production was significantly higher for nonsprouters than for sprouting species, which confirms the hypothesis outlined above. Low pollination efficiency due to unisexuality can be reasonably proposed to explain low fruit production in the sprouting group, but we wish to put forward a complementary view. Percent of fruit production was found to be inversely related to fruit : flower size ratio (i.e., the increase in mass needed to produce a fruit from a flower). Such a relationship suggests the existence of a trade-off between the energy that a plant allocates to an individual fruit or seed and the number it can successfully form. Low fruit production in vertebrate-dispersed, big-seeded species may reflect low pollination success and/or the impossibility of developing every fruit with pollinated ovules, due to the relatively high costs involved in the ripening process. It has been demonstrated, for example, that some species experience low fruit production despite good levels of pollination, which is apparently due to intrinsic regulatory mechanisms (Lloyd, 1980; Wyatt, 1981; Casper & Wiens, 1981; Casper, 1983; Bookman, 1983; Bawa & Webb, 1984; see Stephenson, 1981, for a review). Flower size and number showed a negative relationship too, but the predicted tendency for sprouting taxa to appear at one end of this continuum has not been detected by us.

Wells (1969) pointed out that the capacity to sprout vegetatively from underground parts is probably an ancestral trait. James (1984), however, suggested that sprouting cannot always be seen as an ancestral trait in woody dicotyledons. In the present study the capacity to sprout is associated with other traits, such as the production of fleshy, vertebrate-ingested fruits, heavy seeds, and low fruit production, along with a relatively high incidence of dioecy (species in the genera *Asparagus, Chamaerops, Lonicera, Osyris, Pistacia, Rhamnus* and *Smilax,* for example). This group of taxa has subtropical affinities: sclerophyllous species in these genera existed well before the Pleistocene and the evolution of true mediterranean climatic conditions (Raven, 1973; Axelrod, 1975; Pons, 1981). In contrast, species in the genera *Armeria, Cistus, Cytisus, Halimium, Lavandula, Rosmarinus,* or *Thymus* are nonsprouters; and the high number of taxa endemic to the Mediterranean Basin makes clear that species in these genera originated much more recently (Quezel, 1978, 1981; Pons, 1981). The capacity to sprout is thus lacking in the typically mediterranean taxa but is present in the more ancient, pre-mediterranean ones. This supports the view of Wells (1969) that sprouting is an ancestral trait, and it may indicate that only those "tertiary flora" subtropical sclerophyllous taxa with a capacity to sprout were able to survive the shift to seasonal dryness associated with the mediterranean climate.

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REPRODUCTIVE SYSTEMS AND CHROMOSOME RACES OF *OXALIS PES-CAPRAE* L. AND THEIR BEARING ON THE GENESIS OF A NOXIOUS WEED[1]

Robert Ornduff[2]

Abstract

In its native South Africa, *Oxalis pes-caprae* is represented by diploid and tetraploid races; the short-styled, sterile pentaploid race reported as a noxious weed elsewhere is apparently uncommon there. South African plants have trimorphic flowers, but the three morphs usually are not present in equal proportions in natural populations. The diploid and tetraploid races of the species have a well-developed incompatibility system associated with their floral trimorphism. Outside South Africa, the species is represented not only be a fairly sterile short-styled pentaploid, but sexual tetraploids are known as well. Although the latter may have resulted from independent introductions, low levels of sexuality in the pentaploids also could account for the origin of tetraploidy in situ as a consequence of the union of diploid gametes, and may account for the occasional spontaneous appearance of mid-styled plants in populations of the short-styled pentaploid. Pentaploidy likely resulted from the union of an unreduced gamete of a tetraploid with a haploid gamete of a diploid and presumably developed in South Africa. Since weediness is characteristic of many populations of the native diploids and tetraploids in South Africa, pentaploidy per se cannot be implicated in the origin of weediness, nor is there evidence of any aggressive superiority of the short-styled morph in the sexual races in South Africa. Why the pentaploid is such a successful weed outside South Africa, but apparently less successful as a weed than the diploids and tetraploids within South Africa, is unknown.

Oxalis pes-caprae L. is a troublesome and widespread agricultural and garden weed, particularly in areas of the world with a mediterranean climate such as central Chile, the Mediterranean basin, parts of Australia, and California (Salter, 1944; Young, 1958; Munz, 1959; Michael, 1964). The species is native to southern Africa, where it is variable (Salter, 1944), and where it is distributed from Namibia (South West Africa) southward to the Cape region and around the Indian Ocean coast at least as far north as the Knysna area, sometimes ranging well inland. There it occurs as a "well-behaved" native of relatively undisturbed sites as well as a weed, and it is particularly common in vineyards and along roadsides. In southern Africa, the species is tristylous (Fig. 1), but throughout most of its exotic range it is represented by a short-styled form, which is pentaploid ($2n = 35$), and which reproduces asexually via bulbils. In parts of its exotic range, tetraploid and presumably sexual populations also occur, though less commonly than the sterile pentaploid.

In view of the importance of this species as a weed, certain features of the reproductive biology and chromosome cytology of plants originating in South Africa were studied in the hopes of elucidating the events that led to the origin of the aggressive weedy races from the native races.

Materials and Methods

Bulbs collected from natural populations of *Oxalis pes-caprae* in the Cape Province region in South Africa in 1970 and 1971 were later grown at Berkeley for chromosome studies. One collection was provided by Sherwin Carlquist. Chromosome numbers were determined by examining microsporogenesis in flower buds of these cultivated plants preserved in 3 : 1 ethanol : acetic acid and stained in acetocarmine. Bulbs collected by Peter Goldblatt from two localities in 1984 provided plants used in an artificial crossing program to determine the presence and nature of an incompatibility system in this tristylous species. These localities are an abandoned farm near Noordhoek, Cape Peninsula, and a vineyard at Rustenberg, near Stellenbosch, Cape Province. The two localities are ca. 50 km from each other. Crosses were made in the spring of 1985 and 1986 by transferring pollen from

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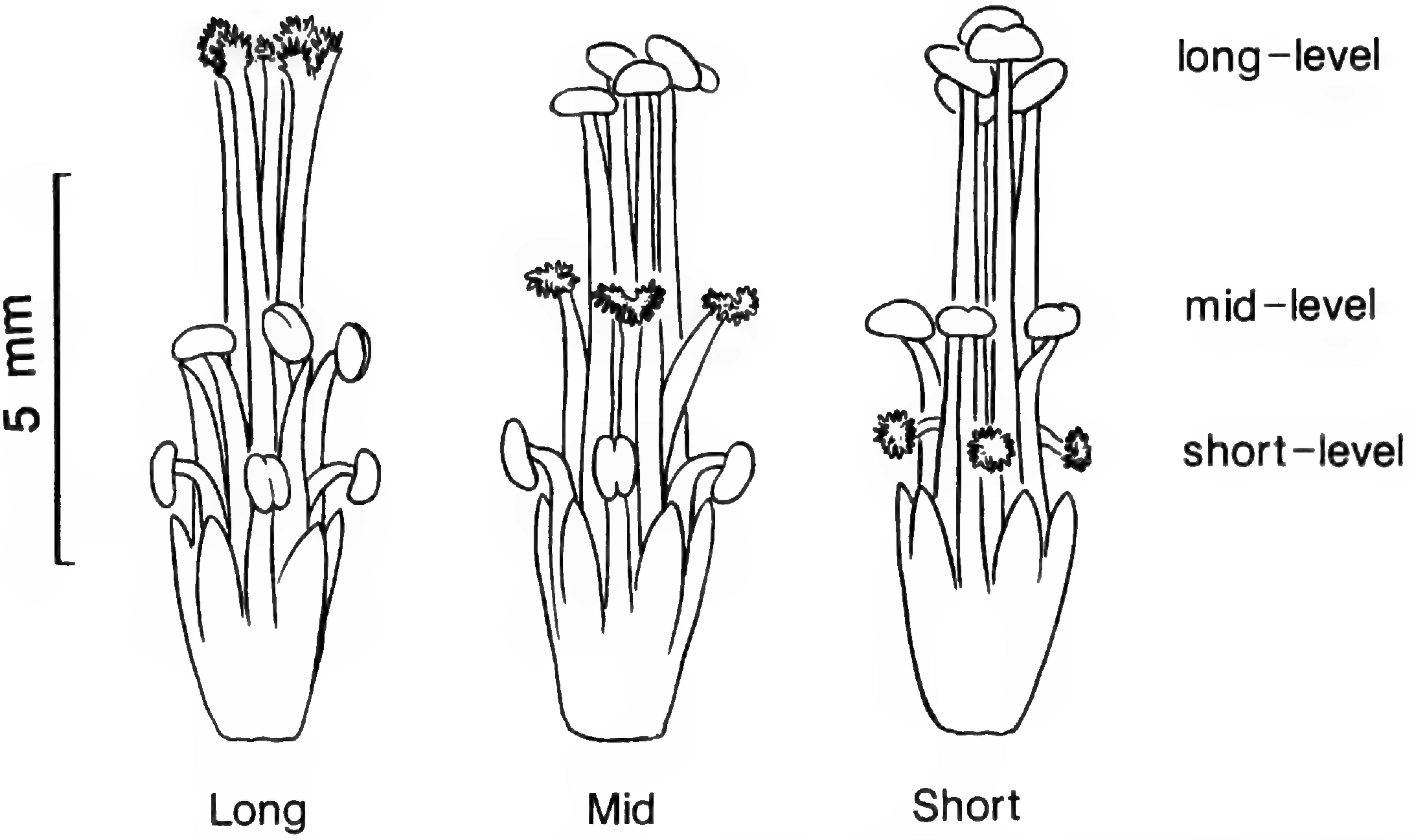

FIGURE 1. Illustrations of gynoecia and androecia of the three floral forms of *Oxalis pes-caprae*. The designation of each floral form is given below each illustration. The stigma and anther level designations used in the text are given to the right of the figure.

dehisced anthers to stigmas under insect-free conditions. Seed set was determined by collecting nearly mature capsules and counting the seeds released by them in seed packets. Pollen size for the three morphs was determined by mounting fresh grains in aniline blue-lactophenol and measuring them with an ocular micrometer; pollen stainability was determined by counting the number of stained grains in a sample of 100 mounted in this medium.

RESULTS

Chromosome numbers. Seven of the nine native populations examined were tetraploid ($n = 14$); two were diploid ($n = 7$; Table 1). Previously published reports, summarized in Table 2, indicate only tetraploidy and pentaploidy for the species.

Weediness. The two diploid populations and four of the tetraploid populations were growing under disturbed conditions such as roadsides, vineyards, or grainfields and were considered weedy; the others occurred in undisturbed conditions and were considered non-weedy (field data are lacking for one tetraploid population; Table 1).

Morph ratios. Morph ratios have been reported earlier (Ornduff, 1974). In two populations, morph ratios of Longs : Mids : Shorts were 1 : 1 : 1, both populations were considered, with some doubt, to be non-weedy. In four populations, morph ratios deviated from equality. In one of these, Longs were deficient; in another, Mids; in third, Shorts; and in the fourth, Longs and Mids were greatly outnumbered by Shorts. Three of these four populations were characterized as weedy (two for which chromosome counts are available were tetraploid).

Pollen size and stainability. Pollen size of diploids and tetraploids is trimorphic (Table 1). Pollen from the long-level anthers is largest, that from mid-level anthers is smaller, and that from short-level anthers is smallest. Pollen from anthers at equivalent levels in different morphs was generally of the same size within a population, but there were interpopulation differences in pollen size from equivalent anther sets. There was no correlation between differences in pollen size and in chromosome number of the diploids and tetraploids. Pollen from presumed pentaploids collected in California was extremely variable in size, even from an individual anther. Pollen stainability of diploids and tetraploids was variable, but was mostly over 60%. One Short tetraploid (*7038*, Table 1) had pollen with 12% and 25% stainability from its two sets of anthers. One

TABLE 1. Chromosome numbers, pollen size (μm), and pollen stainability in *Oxalis pes-caprae.*

Collection (author's or collector's field number)	Chromosome Number	Floral Morph	Origin of Pollen (size; standard deviation; stainability in percent) Long-level Anthers	Mid-level Anthers	Short-level Anthers
Cape Province, South Africa:					
7035: Worcester, riverbank, non-weedy	$n = 14$	Long		41.7; 1.83 (—)	35.8; 2.03 (—)
		Mid	45.7; 2.65 (—)		33.0; 2.05 (—)
7038: Klapmuts, roadside, weedy	$n = 14$	Short	54.1; 3.94 (12%)	41.2; 3.10 (25%)	
7041: Stellenbosch, vineyard, weedy	—	Short	49.5; 3.20 (66%)	41.8; 1.83 (69%)	
7096: Mamre Road Station, roadside, weedy	$n = 7$	Mid	46.4; 1.95 (99%)		33.7; 1.91 (98%)
7248: Gouda/Hermon, roadside, weedy	$n = 7$	Mid	42.7; 3.94 (—)		31.1; 2.20 (—)
7292: Hopefield/Malmesbury, field, non-weedy	—	Long		41.8; 1.83 (89%)	42.7; 4.84 (88%)
		Mid	50.1; 2.38 (86%)		38.9; 1.83 (78%)
		Short	50.4; 4.15 (93%)	41.5; 2.93 (98%)	
7301: Hopefield/Langebaan, field, non-weedy	$n = 14$	Long		39.0; 1.83 (78%)	30.3; 3.92 (79%)
		Mid	46.2; 1.68 (83%)		31.2; 1.54 (81%)
		Short	48.3; 5.73 (81%)	34.4; 2.03 (77%)	
8053: Calvinia, grain field, weedy	$n = 14$	Long		42.6; 2.42 (65%)	36.2; 2.52 (60%)
		Mid	52.2; 2.67 (64%)		35.0; 1.81 (40%)
		Short	47.2; 2.75 (74%)	38.0; 2.55 (73%)	
8055: Clanwilliam, veld, non-weedy	—	Long		38.2; 2.49 (75%)	32.6; 2.07 (68%)
		Mid	45.1; 2.89 (94%)		32.6; 2.30 (86%)
		Short	48.3; 2.87 (88%)	38.8; 2.83 (82%)	
Goldblatt *s.n.*: Rustenberg, near Stellenbosch, abandoned farmland	$n = 14$	Long		—; — (90%)	—; — (84%)
		Mid	—; — (66%)		—; — (62%)
		Short	—; — (70%)	—; — (81%)	
Goldblatt *s.n.*: Noordhoek, Cape Peninsula	$n = 14$	Long		—; — (93%)	—; — (88%)
		Mid	—; — (81%)		—; — (79%)
		Short	—; — (88%)	—; — (78%)	
Carlquist *s.n.*: Southwestern Cape Province	$n = 14$	Long		40.2; 2.46 (80%)	32.0; 1.93 (46%)
		Mid	50.8; 4.84 (92%)		34.5; 2.01 (96%)
		Short	49.7; 4.37 (67%)	41.8; 3.71 (63%)	
California, U.S.A.:					
Ornduff *s.n.*: Univ. California campus, Berkeley	—	Short	—; — (62%)	—; — (87%)	
	—	Short	—; — (58%)	—; — (51%)	
R. Dulberger *s.n.*: as above	—	Mid	—; — (49%)		—; — (58%)
R. Dulberger *s.n.*: College Ave., Berkeley	—	Mid	—; — (32%)		—; — (29%)

set of anthers of a few other collections (e.g., *8053* Mid, Carlquist *s.n.* Long) had pollen with low stainability. The two collections used in the crossing program had pollen stainabilities exceeding 62%. Presumed Short pentaploids collected in California had pollen stainabilities ranging from 29% to 87%. However, these pollen grains were variable in size, and the total number per anther was reduced compared with pollen production of diploids and tetraploids as estimated from the density of the pollen grains on the prepared slides.

TABLE 2. Published chromosome counts of *Oxalis pes-caprae*.

Chromosome Number	Locality of Population Examined	Reference
$2n = 28$	Cape Town, South Africa	Marks, 1956
	India (garden plants)	Mathew, 1958
	Madeira	Borgen, 1974
	South Australia	Oram in Symon, 1961
	Western Australia	Michael, 1964
$2n = 34$	India (Punjab)	Bir and Sidhu, 1978, 1979, 1980 Sidhu, 1979
$2n =$ ca. 35	Italy	Vignoli, 1935, 1937
$2n = 35$	Unknown	Yamashita, 1935
	South Australia	Oram in Symon, 1961
	Western Australia	Franklin in Michael, 1964
	Cape Town, South Africa	Franklin in Michael, 1964

Compatibility relationships. Table 3 presents summarized results for various crosses using parent plants from Rustenberg and Noordhoek. Legitimate pollinations are those between anthers and stigmas at equivalent levels; all other pollinations are termed illegitimate (Darwin, 1877). Only 4% of the illegitimately pollinated flowers produced capsules compared with 87% of the legitimately pollinated flowers. The average number of seeds per pollination obtained from legitimate crosses was 15.9; from illegitimate ones it was 0.2. Self-pollinations produced 0–0.2 seeds per pollination. Intermorph, illegitimate pollinations produced 0–0.5 seeds per pollination. Intermorph, legitimate pollinations produced 13.0–20.9 seeds per pollination. The two populations used in the crossing program produced similar results for all classes of crosses. Seed production of Shorts following legitimate pollinations was slightly greater than that of the other two morphs. Both populations are tetraploid (Table 1).

DISCUSSION

In its native range in South Africa, *Oxalis pes-caprae* is represented by indigenous weedy and non-weedy races with a conventional tristylous floral morphology, including pollen-size trimorphism, and a fully developed trimorphic incompatibility system. Individuals are strongly self-incompatible and illegitimate cross-pollinations produce little or no seed. Legitimate pollinations produce considerable quantities of seed. The pentaploid form has been reported from that country as well (Michael, 1964), but it is unclear how common this race is there.

In South Africa, tetraploids are apparently more common than diploids, but weedy populations of both are known. Unequal morph ratios may be more common in weedy South African races than in non-weedy ones and are likely a consequence of vegetative propagation that is enhanced by physical disturbances of the habitat during agricultural or road-building activities. Morph ratios were found in which Longs, Mids, and Shorts, respectively, were deficient in numbers. Each unequal morph ratio differed from the others, with no morph(s) predominating overall. Thus there is no basis from observation of native races that accounts for the fact that the aggressive morph outside South Africa is short-styled.

Over most of its exotic range of distribution, *Oxalis pes-caprae* appears to be represented by a fairly sterile, pentaploid short-styled morph. As early as 1887, Hildebrand noted the prevalence of this short-styled form and its lack of seed set. Henslow (1891, 1910) also noted these features and described in some detail the means of vegetative reproduction later amplified by Galil (1968). Where introduced, the species is distributed by human agents and, in places, by other animals such as the mole-rat (Galil, 1967) or by birds (Young, 1958).

Despite the high level of pollen sterility of the short-styled pentaploid, it apparently reproduces occasionally by seed. This may result from self- or geitonogamous pollinations in populations where Shorts alone are represented. Illegitimate pollinations of sexual Shorts carried out in the present study produced small amounts of seed, which offers support for this suggestion. Vignoli (1937), in an embryological study of the species, noted rare sexual reproduction in the pentaploid but concluded also that apogamy may rarely occur in this race. Another line of evidence for

TABLE 3. Results of legitimate and illegitimate pollinations in two populations of *Oxalis pes-caprae*. The first figures summarize results for the Rustenberg population; the second figures summarize results for the Noordhoek population.

Style Length (♀ parent) × Anther Level/Style Length (♂ parent)[1]	Number of Flowers Pollinated	Number of Flowers Producing Capsules	Number of Seeds Obtained	Average Number of Seeds/ Pollination
Self-pollinations (all illegitimate):				
L × m/L selfed	18; 55	0; 6	0; 34	0; 0.6
L × s/L selfed	20; 12	0; 0	0; 0	0; 0
M × l/M selfed	38; 33	0; 1	0; 5	0; 0.2
M × s/M selfed	23; 35	0; 0	0; 0	0; 0
S × l/S selfed	18; 20	1; 0	1; 0	0.1; 0
S × m/S selfed	15; 12	0; 0	0; 0	0; 0
Intermorph, illegitimate pollinations:				
L × s/M	26; 20	0; 0	0; 0	0; 0
L × m/S	23; 13	1; 2	10; 7	0.4; 0.5
M × s/L	25; 29	0; 2	0; 8	0; 0.3
M × l/S	15; 26	0; 1	0; 1	0; 0
S × l/M	15; 21	0; 3	0; 9	0; 0.4
S × m/L	25; 30	1; 4	17; 6	0.7; 0.2
Intermorph, legitimate pollinations:				
L × l/M	18; 48	12; 41	279; 738	15.5; 15.4
L × l/S	27; 34	23; 30	430; 583	15.9; 17.2
M × m/L	33; 37	29; 38	413; 533	12.5; 14.4
M × m/S	54; 42	46; 34	797; 546	14.8; 13.0
S × s/L	13; 22	11; 20	222; 460	17.1; 20.9
S × s/M	11; 29	11; 25	255; 588	23.2; 20.1
Summary of all legitimate, illegitimate pollinations:				
Legitimate	156; 212	132; 188	2,396; 3,448	15.4; 16.3
Illegitimate	261; 306	3; 19	28; 70	0.1; 0.2

[1] Notation is as follows: "L × m/L selfed" means a long-styled flower (L) was self-pollinated with its own pollen from the mid-level (m) set of anthers. "L × s/M" means a long-styled flower was pollinated with pollen from the short-level stamens of a mid-styled flower. Figure 1 illustrates the three flower types.

occasional sexual reproduction of this form comes from the spontaneous appearance of Mids in otherwise short-styled populations as noted in southern Italy by Vignoli (1935) and in central California by Dulberger (pers. comm.). It also has been suggested that in Western Australia, where the pentaploid sometimes exists in mixed populations with tetraploids, hybridization between the two may occur (Michael, 1964). The variability of the species there would suggest frequent sexual reproduction (Peirce, 1973). Tetraploid populations with all three style lengths are known in South Australia (Symon, 1961) and Western Australia (Michael, 1964) and these presumably reproduce sexually as well as asexually. Tetraploids also have been reported from India and Madeira (Mathew, 1958; Borgen, 1974), but it is unknown whether these are composed of more than one morph.

Although the occurrence of tetraploids and pentaploids in Australia as a consequence of independent introductions is documented (Michael, 1964), it is possible to explain the origin of tetraploids within pentaploid populations by another mechanism. The pentaploids produce some viable pollen (Table 1; Vignoli, 1937; Bir & Sidhu, 1980; Michael, 1964). The illustrations and discussion of microsporogenesis in pentaploids by Vignoli (1935, 1937) indicate that pollen grains with $n = 14$ can be produced by such plants. If megasporogenesis also results in eggs with $n = 14$, fertilization of these eggs by diploid sperm would result in a tetraploid zygote.

The place and mode of origin of the weedy pentaploid race are uncertain. Lower (1963) suggested that it may have originated outside South Africa. A 5*x* chromosome count reported by Michael (1964) indicates that this race is present in South Africa, but it is apparently not common (although this remains to be documented). The origin of the weedy pentaploid race can only tentatively be reconstructed, but I believe that it likely occurred in South Africa. The simplest explanation for the origin of pentaploidy is that it resulted from the union of an unreduced gamete of a tetraploid plant with a haploid gamete from a diploid plant. Since diploids are unknown outside South Africa, this event must be assumed to have occurred in South Africa. Although diploids and tetraploids are not known to be sympatric in South Africa, they have been collected very near each other, so sympatry may occur. Weediness clearly preceded the occurrence of pentaploidy since sexual diploids and tetraploids are frequently aggressively weedy: they commonly occur in cultivated fields and along roadsides. Pentaploidy itself has not conferred weediness on the species. Likewise, prodigious means of vegetative reproduction occur in diploids and tetraploids with a fully developed sexual apparatus, so that the almost exclusively vegetative propagation characteristic of the pentaploid is a condition that likewise preceded the origin of pentaploidy.

Present evidence, although scanty, suggests that the largely sterile pentaploid race is less successful as a weed in South Africa than are the sexual diploids and tetraploids. Outside South Africa, however, the pentaploid seems to prevail, possibly as a consequence of its greater competitive success over sexual races under exotic conditions (as, for example, seems to be the case in Australia) or as a consequence of a series of coincidences of introduction that led to this race being more abundant than its apparent diploid and tetraploid precursors. There is a possibility that there are competitive differences among the chromosomal races of *Oxalis pes-caprae,* or among its morphs (as suggested by Peirce, 1973). The reduced pollen stainability of some field collections suggests the possibility that, in these, the sexual apparatus may be impaired and that asexual mechanisms are more important in their reproductive mode. Both suggestions merit study. Nevertheless, the sequence of events leading to the origin of pentaploidy and the routes of human-aided migration and introduction of this species to other continents will probably never be fully reconstructed.

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FLORA OF THE VENEZUELAN GUAYANA—II

JULIAN A. STEYERMARK[1]

ABSTRACT

A total of 18 species, four subspecies, and one variety are newly described from the Venezuelan Guayana, nearly one-half of them originating from Cerro Marahuaca of Territorio Federal Amazonas, while the others are from Cerro de la Neblina, Guaiquinima, Huachamacari, Auyan-tepui, Ptari-tepui, and Sipapo. The following new taxa are included: *Brocchinia oliva-estevae* (Bromeliaceae); *Peperomia gentryi, P. marahuacensis,* and *Piper gentryi* (Piperaceae); *Euphronia acuminatissima* (Vochysiaceae); *Ilex liesneri* (Aquifoliaceae); *Sauvagesia marahuacensis, S. guianensis* subsp. *sipapoensis* and subsp. *guaiquinimensis* (Ochnaceae); *Bonnetia bolivarensis, B. guaiquinimae, B. ptariensis,* and *B. tristyla* subsp. *nervosa* (Theaceae); *Lissocarpa stenocarpa* (Lissocarpaceae); *Chomelia stergiosii, Coccocypselum croatii, Pagameopsis maguirei* subsp. *neblinensis* var. *pirapucuensis* and subsp. *pusillus, Psychotria guanchezii* and *P. ronaldii, Schradera marahuacensis,* and *Sipanea setacea* (Rubiaceae); and *Gongylolepis terramarae* (Compositae). A reevaluation of *Euphronia* gives evidence for the maintenance of three species, instead of one as previously treated by Lleras, and provides a key to the known species. A study of the variation in *Sauvagesia guianensis* (Ochnaceae) reveals the occurrence of five morphologically closely related but geographically separated subspecies isolated on different sandstone table mountains. A key to the subspecies and the newly described *Sauvagesia marahuacensis* is provided, as well as a key to the newly described species of *Bonnetia.*

BROMELIACEAE

Brocchinia oliva-estevae Steyerm. & Lyman B. Smith, sp. nov. TYPE: VENEZUELA. Bolívar: summit of Auyan-tepui, extreme north end above Angel Falls, Dec. 1984, *Francisco Oliva Esteva s.n.* (holotype, VEN). Figure 1.

Planta parva caulescens florifera 3.7 dm alta, caule erecto folioso 13 cm alto; foliorum laminis majoribus ligulato-lanceolatis acutis mucronatis 10 cm longis, 1.7–1.8 cm latis, inferioribus ovatis acuminatis 1.5–2.8 cm longis, 1–1.4 cm latis, ca. 10-nervatis, nervis paullo obscuris; scapo folioso, scapi bracteis lanceolato-ligulatuis 6–8 cm longis, 1.4–1.7 cm latis; inflorescentia erecta laxe bipinnatim paniculata 2.1 dm longa tenui, rhachidi sparsim brunneo-furfuracea obtecta, axibus lateralibus gracillimis racemosis brevibus 3.5–6 cm longis, quoque axe 15–17-flora; bracteis primariis ad 3 cm longis, 0.8 cm latis; bracteis florigeris lanceolatis acutis vel acuminatis 3–3.5 mm longis, 0.7 mm latis; floribus adscendentibus brevipedicellatis, pedicellis 1–2 mm longis minute furfuraceis; petalis albidis lanceolatis subacutis vel obtuse acutis haud unguiculatis 3 mm longis, 1 mm latis; antheris suborbiculari-oblongis 0.5 mm longis; ovario inferiore subclavato-cylindrico 3 mm longo; ovulis extremitatibus appendicibus caudatis.

Caulescent, small, herbaceous plant, flowering 3.7 dm tall; stem erect, 13 cm tall. Leaves ascending, pale dull green both sides with about 10 parallel, slightly darker longitudinal lines becoming bronzy where entering sheath, submembranous, flexible, concave above, convex below, not contracted at base, the larger ones ligulate-lanceolate, acute, mucronate, 10 cm long, 1.7–1.8 cm wide, lower leaves ovate, acuminate, 1.5–2.8 cm long, 1–1.4 cm wide, the upper ones longer than the internodes, minutely pale lepidote. Scape foliose, scape bracts lanceolate-ligulate, 6–8 cm long, 1.4–1.7 cm wide. Inflorescence erect, laxly bipinnately paniculate, 2.1 dm long; rachis slender, covered with a scattered brown furfuraceous indument, with 5 short, racemose, lateral axes 3.5–6 cm long, each axis 15–17-flowered, the uppermost part of the inflorescence elongated to 10 cm; primary bracts subtending the lower three axes ascending, lanceolate, acute, 3 cm long, 0.8 cm wide, entire; floral bracts lanceolate, acute to acuminate, 3–3.5 mm long, 0.7 mm wide at the base. Flowers shortly pedicellate, pedicels 1–2 mm long, minutely furfuraceous. Sepals pale green, lanceolate, acute, 3–4.5 mm long, 1 mm wide, dorsally sparsely furfuraceous in lower half. Petals white, lanceolate, subacute or obtusely acute, not unguiculate, 3 mm long, 1 mm wide. Anthers suborbicular-oblong, 0.5 mm long, basally bilobed; filaments white, 1.2 mm long. Ovary inferior, pale green, subclavate-cylindric, 3 mm long, 1 mm wide at summit, 0.7 mm wide at base, pale brown furfuraceous; ovules caudate-appendaged at both ends.

This species of *Brocchinia* is characterized by its bipinnate inflorescence with lepidote, simple,

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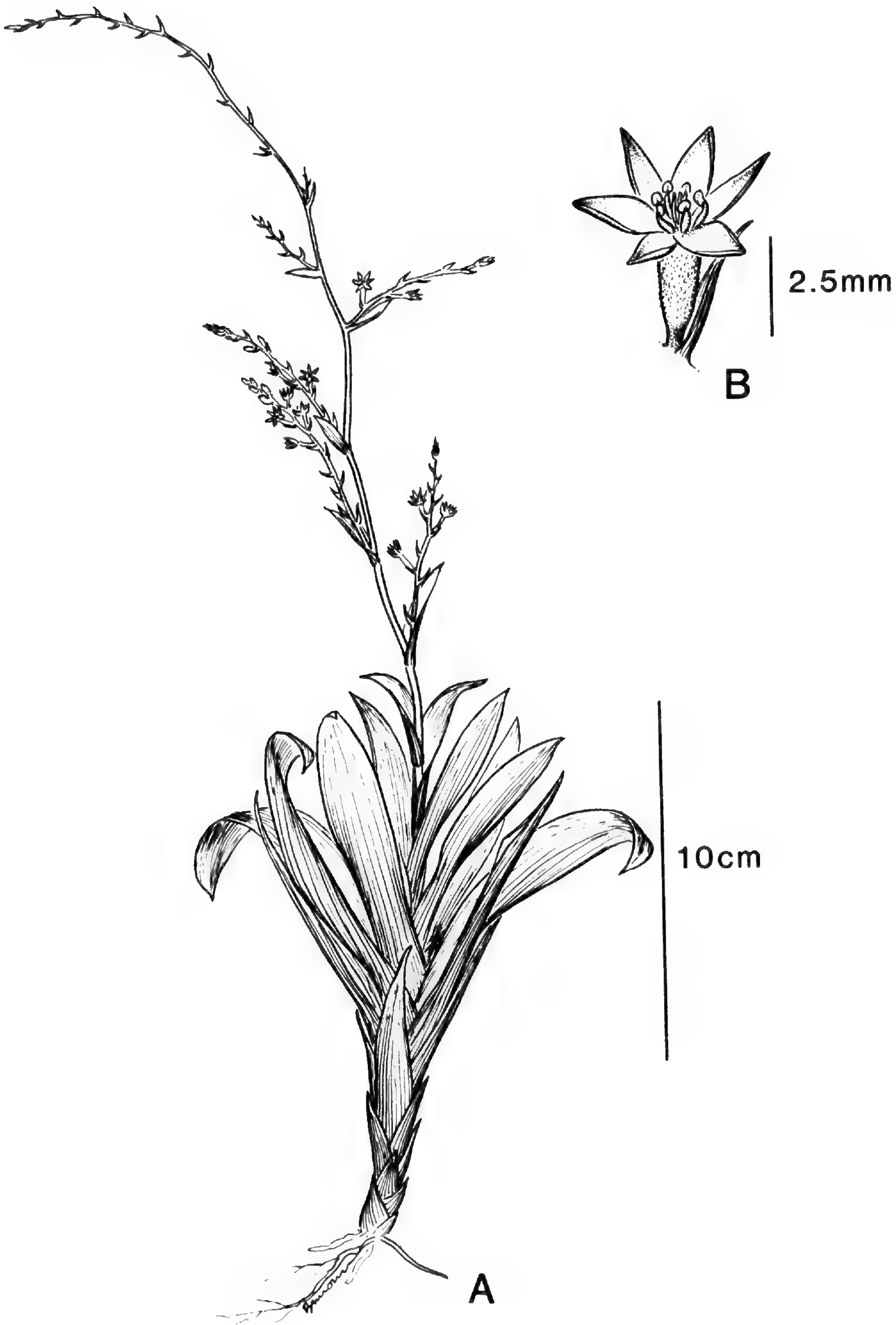

FIGURE 1. *Brocchinia oliva-estevae.*—A. Habit.—B. Flower with bract.

racemose axes, primary bracts extending from ¼ to ½ the length of the rachis, shortly pedicellate flowers, non-unguiculate petals, and narrow submembranous, slightly nerved, short leaves only 10 cm long by 1.8 cm wide, which are not contracted toward the base. It is most closely related to *B. cowanii* L. B. Smith of Cerro Moriche, Terr. Fed. Amazonas, Venezuela, in having a bipinnate inflorescence with non-unguiculate petals, but differs from that taxon in the scape bracts shorter than the internodes and in the shorter sepals and petals.

It is a pleasure to name this interesting species for Mr. Francisco Oliva Esteva, Venezuelan landscape architect, an avid student of Bromeliaceae, and author of several books on ornamental plants of Venezuela.

PIPERACEAE

Peperomia marahuacensis Steyerm., sp. nov. TYPE: VENEZUELA. Territorio Federal Amazonas: Depto. Atabapo, Cerro Marahuaca, summit, in a zanjón, "Sima" south and southeast of Summit Camp, 3°37′N, 65°23′W, 2,520–2,620 m, 26–27 Feb. 1985, *Julian A. Steyermark & Bruce Holst 130742-A* (holotype, MO; isotype, VEN). Figure 2C.

Herba effusa; caulibus elongatis 8 dm longis, 2.5–3 mm latis praeter apices dense pubescentes ramorum juvenalium sparsim puberulis; foliis alternis orbiculari- vel triangulari-ovatis apice acuminatis basi truncatis vel late rotundatis, majoribus 3–4.5 cm longis, 2.5–4 cm latis, palmatim 5-nervis, nervis tribus conspicuis nervis duobus lateralibus inconspicuis, supra nervis principalibus pilosulis, demum glabris, subtus nervis sparsim pilosulis pilis patentibus 0.2–0.5 mm longis ceterum glabris vel glabratis, marginibus parte suprema ¼–⅕ ciliolatis ceterum glabris; petiolis 5–20 mm longis, laminis 2–3-plo brevioribus pilosis.

Sprawling herbaceous plant with stems elongated to 8 dm, 2–3 mm diam., sparsely puberulous except at the densely pubescent younger tips. Leaves alternate, orbicular- to triangular-ovate, acuminate at apex, truncate or broadly rounded at base, larger blades 3–4.5 cm long, 2.5–4 cm wide, palmately 5-nerved with 3 of them conspicuous and 2 lateral nerves faint, glabrous on the upper surface except pilosulous along the main nerves, lower surface glabrous or glabrate, but the nerves sparsely pilosulous with spreading hairs 0.2–0.5 mm long; leaf margins ciliolate in the uppermost ¼–⅕, elsewhere glabrous; petioles 5–20 mm long, ⅓–½ length of leaf blade, pilose.

From the related *P. foveolata* Steyerm. of Cerro de la Neblina, the new taxon differs in the palmately five-nerved leaves, which are pubescent along the nerves of the upper and lower surfaces, and in the shorter, pubescent petioles, which are proportionately shorter in relation to the length of the leaf blade. Compared with *P. peltoidea* Kunth, it differs in the non-peltate, non-sulcate leaves with pilosulous nerves on the upper surface, but mainly glabrous below on the leaf surface itself, with leaf margins ciliolate only in the uppermost ¼–⅕, and in the petioles shorter than the leaf blades.

Peperomia gentryi Steyerm., sp. nov. TYPE: VENEZUELA. Territorio Federal Amazonas: Cerro de la Neblina, Camp V, valley north base of Pico Cardona, 0°49′N, 66°0′W, 1,250 m, 21–24 Mar. 1984, *Ronald Liesner & Brian Stannard 16901* (holotype, MO; isotype, VEN).

Herba repens; foliis alternis late ovatis vel subrhombico-ovatis apice acutis vel subacutis basi truncatis vel late obtusis 4.5–9 cm longis, 3–5.5 cm latis a 5–11 mm infimis 5–7-plinerviis praeter margines superiores ciliatos glabris; spicis geminis 2–3.5 cm longis; drupis ellipsoideo-ovoideis rostratis.

Repent herb with elongated glabrous stems 2 mm diam.; internodes 4–9 cm long. Leaves alternate, broadly ovate to subrhombic-ovate, acute to subacute at apex, truncate to broadly obtuse at base, 5–7-plinerved, the innermost lateral nerves forking off the midrib within the lowermost 5–11 mm, 4.5–9 × 3–5.5 cm, moderately pilose-ciliate on the upper margins; petiole 3.5–7 cm long. Inflorescence with paired spikes; primary peduncle 2.8–5 cm long, minutely puberulent; secondary peduncle subtending the spike 1.5–2 cm long, sparsely puberulent basally or glabrous; spikes 2–3.5 cm long, 1.5–2 mm diam. Fruit basally attached, ellipsoid-ovoid, rostrate, the body 0.5 × 0.3 mm, the beak 0.2–0.3 mm long; stigma anterior near base of beak.

Paratype. Same locality as type, 12 Apr. 1984, *Gentry & Stein 46542* (MO, VEN). Figure 2A, B.

This species is related to both *P. distachya* and *P. schwackei*. From *P. distachya* (L.) A. Dietr. this species differs in the 5–7-plinerved broadly ovate to subrhombic-ovate leaves, which are acute to subacute instead of acuminate at the apex and truncate to broadly obtuse at the base.

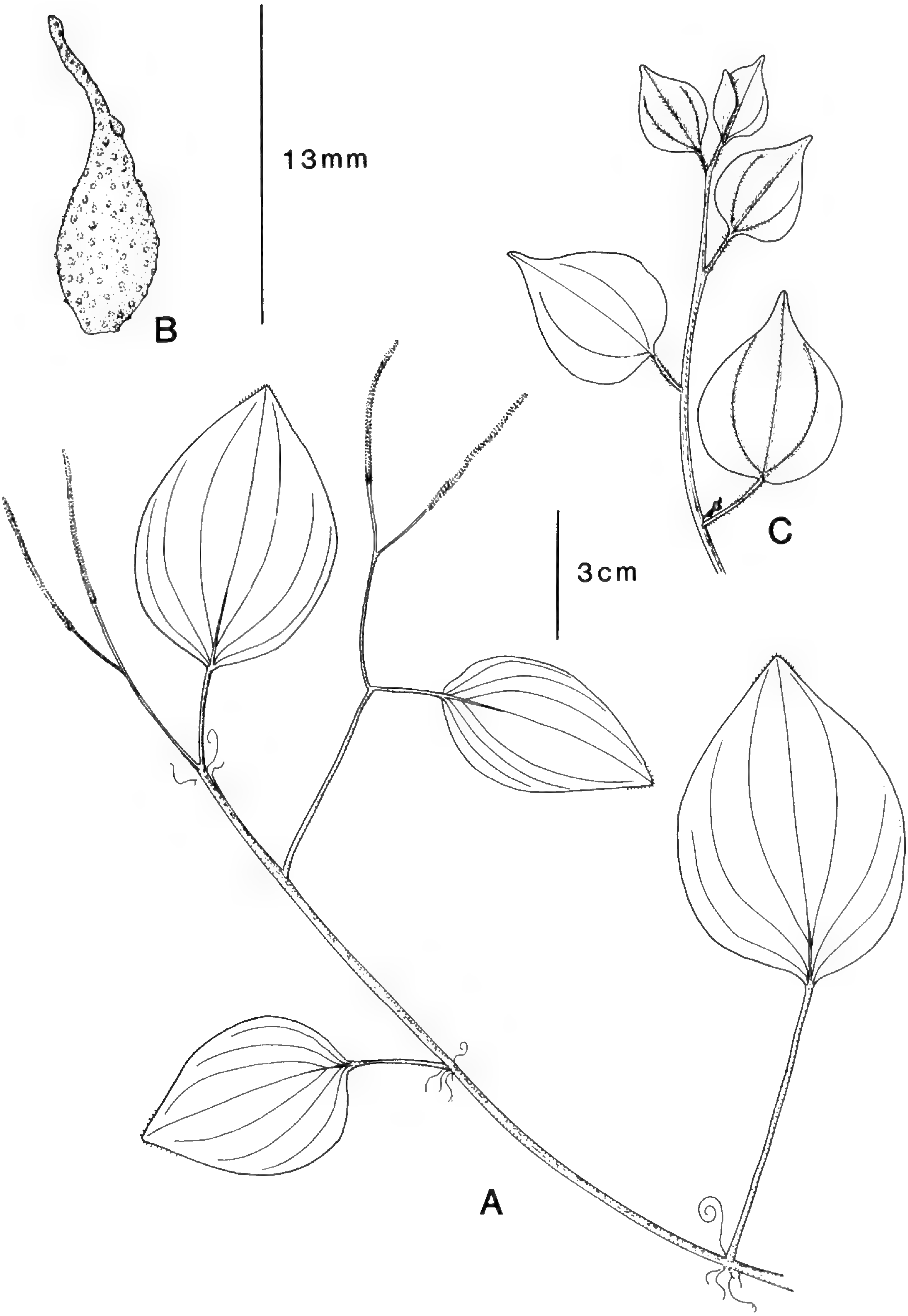

Figure 2. *Peperomia*. A, B. *P. gentryi*.—A. Habit.—B. Beaked fruit.—C. *P. marahuacensis*.—Habit.

From *P. schwackei* C. DC. of southern Brazil, it differs in the 5–7-plinerved, acute to subacute leaves and longer secondary peduncle, which supports the spike.

Piper gentryi Steyerm., sp. nov. TYPE: VENEZUELA. Territorio Federal Amazonas: Cerro Neblina, trail due south from Base Camp, stunted swampy forest, alt. 140 m, 23 Apr. 1984, *Alwyn Gentry & Bruce Stein 46887* (holotype, MO).

Frutex 1.5-metralis, internodiis 2–3.5 mm diam. glabris; foliis grosse rugosis lanceolato-ellipticis vel oblongo-ellipticis apice acutis vel acuminatis basi subaequilateraliter acutis vel subacutis 17–22 cm longis, 5.5–7.5 cm latis supra glabris subtus ad nervos hirsutulis ceterum glabris, nervis lateralibus utroque latere 11–15 totis pinnatim venosis; petiolis 5–12 mm longis breviter hirsutulis; spicis 2 cm longis, 6–7 mm latis; pedunculis 3 mm longis glabris; bracteis floriferis fimbriatis.

Shrub 1.5 m tall, internodes 2–3.5 mm diam., glabrous. Leaves lance-elliptic or oblong-elliptic, acute to acuminate at apex, subequally acute or subacute at base, 17–22 cm long, 5.5–7.5 cm wide, broadest at the middle, pinnately nerved throughout to apex, glabrous above, punctate, glabrous below on leaf surface but hirsutulous with short, spreading hairs on the midrib and lateral nerves, grossly rugose both sides, venation sulcate above, elevated below, the areoles formed by the tertiary veins averaging 5–7 mm diam.; lateral nerves 11–15 each side, spreading at an angle of 15–20°, sulcate above, subelevated below, anastomosing at 5–10 mm from the margin; petioles 5–12 mm long, shortly hirsutulous, vaginate to the base of the blade. Spikes erect-ascending, 2 cm long, 6–7 mm wide; peduncle 3 mm long, 1 mm wide, glabrous, erect. Floral bracts triangular at the summit, 1.5 mm across the summit, ciliate on margins. Fruit round from above, depressed at summit, 2 mm diam., glabrous.

This species is related to *P. holtii* Trel. & Yuncker, from which it differs in the glabrous stems and peduncles, more numerous lateral nerves, and floral bracts conspicuously fimbriate.

VOCHYSIACEAE

A REEVALUATION OF THE GENUS *EUPHRONIA* (VOCHYSIACEAE)

In his publication on a revision and taxonomic position of the genus *Euphronia*, Lleras (1976) showed that the generic name *Lightia* must be replaced by the earlier *Euphronia*. Furthermore, he transferred the genus from the Trigoniaceae, where it had been placed previously, to the Vochysiaceae, the family he considered as showing the closest affinity.

Although two species had previously been recognized under *Lightia* in Warming's treatment of the genus (1875), Lleras considered these taxa as constituting one variable taxon, which he designated *E. hirtelloides* Martius ex Martius & Zucc. His decision in considering this a polymorphic species was based on what he judged as extreme variability in leaf morphology and lack of geographical or other "consistency."

While preparing a taxonomic treatment for the flora of the Venezuelan Guayana, I have concluded that three distinct taxa are involved worthy of specific recognition. Consistent differences have been found in characters such as type of inflorescence, length of pedicels, apex of calyx lobes, and quality of pubescence present on the exterior of the calyx lobes and pedicels. Moreover, the three taxa demonstrate distinct geographical areas to which they are limited.

KEY TO THE SPECIES OF *EUPHRONIA*

1a. Calyx lobes caudate-acuminate, the exterior portion covered by a dense, uniform, appressed, lanuginose tomentum; inflorescence subfasciculate; flowers 1–6, crowded near the upper portion of the rachis; pedicels 7–8 mm long, nearly equaling the calyx, covered with an appressed lanuginose tomentum .... *E. acuminatissima*

1b. Calyx lobes acute, subobtuse, or subrotundate at apex, the exterior portion with loose, ascending to spreading hairs throughout or at least on midrib; flowers 3–23, racemose, the pedicels arising along an elongated rachis; pedicels 1.5–5 mm long, shorter than the calyx, with loosely ascending to spreading pubescence 2

   2a. Floriferous portion of rachis usually conspicuously elongated beyond the leafy branch, mainly (7–)15–23-flowered, 4–10 cm long; leaf blades 4.5–7.5 cm long, mainly lance- to oblong-elliptic, generally acute to subacute at apex, 2–2.5 times longer than broad; calyx lobes (dried state) more or less uniformly gray-green; exterior of calyx lobes with loose sericeous or ascending hairs along midportion, elsewhere with shortly appressed tomentum .... *E. hirtelloides*

   2b. Floriferous portion of rachis only shortly elongated, mainly 3–8-flowered, 1–4 cm long; leaf blades (0.6–)1.5–3(–4.8) cm long, mainly ovate to ovate-elliptic, gen-

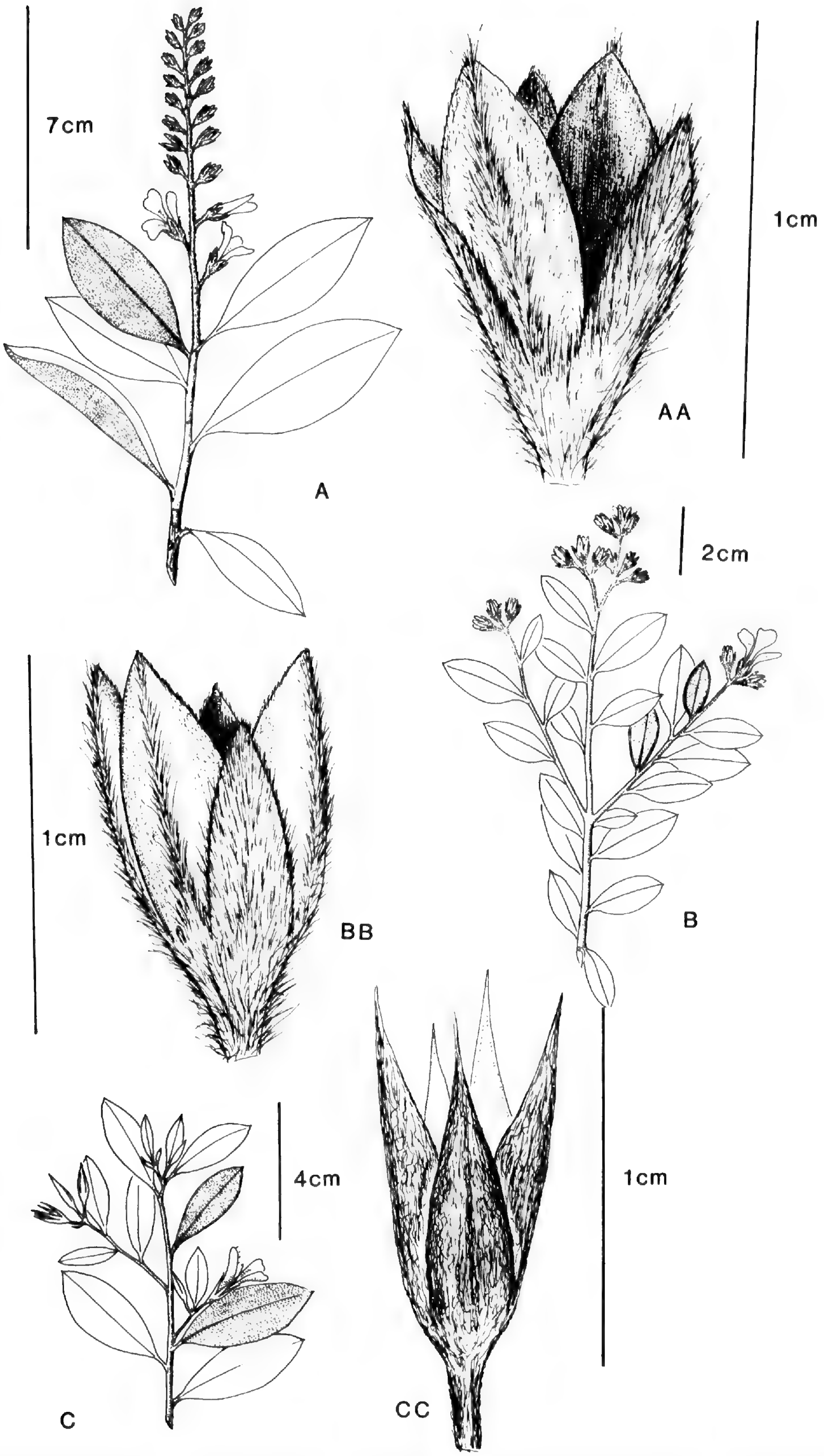

FIGURE 3. *Euphronia.*—A. *E. hirtelloides.*—A. Habit of flowering branch.—AA. Calyx.—B. *E. guianensis.*—B. Habit of flowering branch.—BB. Calyx.—C. *E. acuminatissima.*—C. Habit of flowering branch.—CC. Calyx.

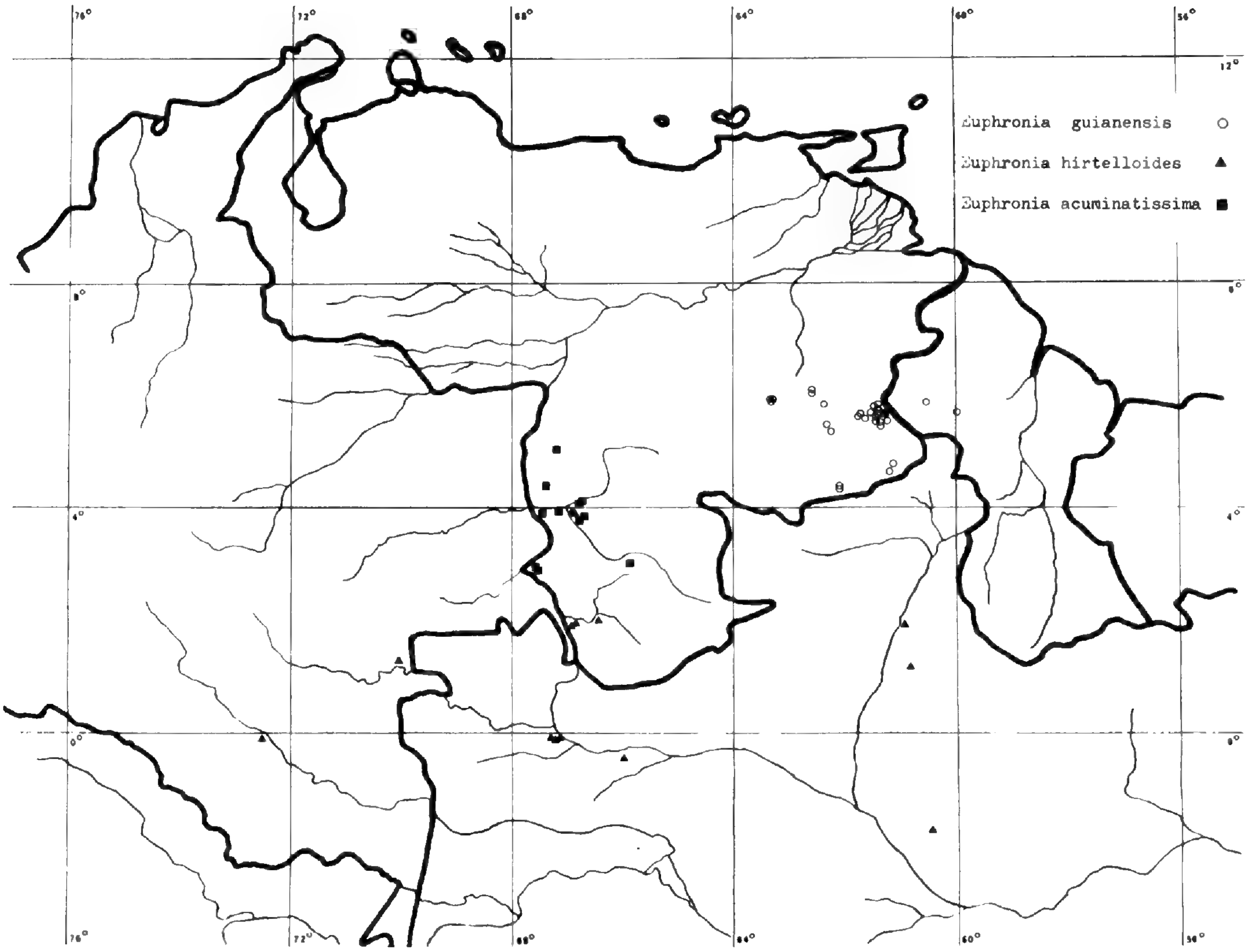

FIGURE 4. Map showing distribution of *Euphronia*.

erally rounded to obtuse at apex, 1.75–2 times longer than broad; inner calyx lobes (dried state) with conspicuous broad white borders; exterior of calyx lobes with dense, loosely ascending to spreading hairs over the entire surface ..... *E. guianensis*

Euphronia acuminatissima Steyerm., sp. nov. TYPE: VENEZUELA. Territorio Federal Amazonas: Río Orinoco, Sabana Cumare on right bank of Caño Cumare, Río Atabapo, 20 km above San Fernando de Atabapo, 125–150 m, 5 Aug. 1959, *John J. Wurdack & L. S. Adderley 43762* (holotype, MO; isotype, NY). Figures 3C, CC, 4.

Frutex vel arbuscula 0.2–5-metralis; foliis oblongo-ellipticis vel lanceolato-ellipticis apice rotundatis vel obtusis abrupte cuspidatis basi acutis vel subacutis 2–4.5 cm longis, 1–2 cm latis; inflorescentia subfasciculata plerumque (2–)3–6-flora pedunculata, pedunculo 7–8 mm longo; pedicellis 7–8 mm longis, indumento lanuginoso pilis adpressis munitis; calycis lobis anguste lanceolatis apice caudato-acuminatis 7–9 mm longis, indumento lanuginoso pilis adpressis munitis.

Subshrub to small tree 0.2–5 m tall; stems gray-white lanuginose, becoming glabrescent or glabrous on older or lower portions. Leaves coriaceous, dark green above, white below, oblong-elliptic to lance-elliptic, rounded to obtuse at the abruptly cuspidate apex, acute to subacute at base, 2–4.5 cm long, 1–2 cm wide, 2.6–3 times longer than broad, gray-floccose above on young leaves, becoming glabrous on older leaves, white-pannose below; petioles 2–6 mm long, gray-white lanulose. Inflorescence terminal or axillary, subfasciculate, sessile or shortly pedunculate, (2–)3–6-flowered, the flowers crowded at or near the summit of the abbreviated rachis; peduncle 0.5–1 cm long, together with the rachis gray-white lanuginose. Bracts subtending pedicels subulate, caudate-acuminate, 3.5–4 mm long, 0.4–1 mm wide, lanuginose, more persistent than in other species. Pedicels 7–8 mm long, nearly equaling the calyx, densely gray-white lanuginose with appressed, more or less uniform indument. Calyx 10–12 mm long, densely gray-white lanuginose without, the hairs closely appressed; tube campanulate-turbinate, 2.5–4 mm long, 3–5 mm wide at summit; lobes narrowly lanceolate, tapering to a long caudate acuminate apex, 7–9 mm long, 1.5–2.5 mm wide, gray-white lanuginose without, minutely sericeous within. Petals lavender or lilac, spatulate, rounded at apex, unguiculate, (15–)18–23 mm long, (4–)6–9 mm wide near summit, 1.5 mm wide at or below middle, loosely pilose within along middle, glabrous elsewhere, sericeous without, bearing shorter hairs in upper portion, glabrous elsewhere. Anthers oblong, rounded, above bilobed basally, 2.5 mm long; filaments 9–11 mm long, the sterile one retrorsely pilose, the others glabrous. Style 10 mm long, antrorsely pilosulous. Fruit cylindric, 13–14 mm long, gray-white lanuginose.

Distribution. Mainly on white sand savannas of the Territorio Federal Amazonas, Venezuela, at altitudes of 100–150 meters.

Paratypes. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Río Guainía, Sabana El Venado, left bank of Caño Pimichín, 2 km above Pimichín, 120–140 m, 10 Oct. 1957, *Maguire, Wurdack & Keith 41813* (MO, NY); same locality, *Maguire & Wurdack 35638* (NY); base of Cerro Yapacana, 125–130 m, *Maguire, Cowan & Wurdack 30479-A, 30509* (NY); Bajo Río Ventuari, alrededores de Canaripó, a unos 20 km al E de la confluencia con el Río Orinoco, 4°03'N, 66°49'W, 98 m, *Huber 1070, 1877* (NY, VEN); Río Ventuari, frente al caserío de Canaripó, 4°09'N, 66°50'W, 100 m, *Huber 2441* (NY, VEN); Río Orinoco, poco más río abajo de Santa Barbara, 4°02'N, 67°15'W, 100 m, *Huber 2471* (NY, VEN); E del Caño Perro de Agua, a unos 30 km al SE de la confluencia Orinoco-Ventuari, 3°47'N, 67°00'W, 100 m, *Huber & Tillett 2824* (NY, VEN); 10 km al S del Río Autana, 15 km al SW del Cerro Autana, 4°44'N, 67°33'W, 100 m, *Huber 4063* (NY, VEN); Caño San Miguel between Limoncito and Caño Ikebeme (about 70 km from river mouth), 100–140 m, *Wurdack & Adderley 43249* (NY); middle Caño Yagua, NE and E base of Cerro Cucurito, 3°36'N, 66°34'W, *Huber & Tillett 2925* (VEN); 20 km NW of Yavita, headwaters of Caño Pimichín, 3°1'N, 67°33'W, 120 m, *Huber & Medina 5947* (VEN); 4 km west of Serranía del Cuao, 4°59'N, 67°32'W, *Huber & Tillett 5293* (VEN); Río Sipapo, 4–6 km downstream from mouth of Río Guayapo, 4°32'N, 67°36'W, 90–100 m, *Guanchez 2571* (MO, TFAV); 15–20 km S of Tama-Tama, 90 m, *Guanchez 2021* (MO, TFAV). BOLIVAR: Uarupata, *Maguire 33282* (NY).

This species differs markedly from both *E. hirtelloides* and *E. guianensis* in the longer, caudate-acuminate calyx lobes and fewer-flowered, subfasciculate inflorescence with longer pedicels. The pubescence, moreover, is quite different from either of the other species, with both pedicels and the exterior of the calyx lobes covered by a short, appressed, finely lanuginose indument, the other two taxa having a pubescence of longer, loose, spreading to ascending hairs on the pedicels and on a part or whole of the outer surface of the calyx lobes.

Euphronia guianensis (R. H. Schomb.) H. Hallier, Meded. Herb. Leid. 35: 13. 1918, in obs.: *Lightia guianensis. Lightia guianensis* Schomb. in Linnaea 20: 757. 1847; Warm. in Martius's Flora Brasiliensis 13(2): 122. 1875. Figures 3B, BB, 4.

Shrub or tree (0.2–)2–10 meters tall, branches gray-lanuginose, becoming glabrous below or in age. Leaves coriaceous, gray to silvery white below, shortly petiolate to subsessile, mainly ovate to subovate, generally rounded or obtuse at a minutely mucronate apex, less frequently subacute, chiefly rounded to obtuse at base, (0.6–)1.5–3(–4.8) cm long, (0.5–)1–2(–2.5) cm wide (rarely sterile shoots of juvenile branches elliptic-oblong, 7 × 3–3.5 cm), revolute, densely white tomentose below with elevated tomentose midrib, young leaves gray-white floccose above, older ones mainly glabrous above with narrowly sulcate midrib, sometimes white-tomentose along upper midrib; petioles 1–4 mm long, densely gray tomentose. Inflorescence terminal or axillary, mainly simple and short racemose or occasionally the axis with a branch at base, 2–6 cm long including the peduncle, the flowering portion 1–4 cm long, 1–2 cm wide, 3–8-flowered; peduncle 0.6–2.5(–4) cm long, together with the rachis densely tomentose. Bracts subulate, 4–5 mm long, tomentose, caducous. Pedicels 1–5 mm long, shorter than the calyx, densely tomentose with subspreading to loosely ascending hairs. Calyx 6–9 cm long, tube shallowly campanulate, 1.5–3 mm long, 3–4 mm wide at summit, densely gray tomentose with short spreading-ascending hairs; calyx lobes slightly unequal, broadly lanceolate to oblong-lanceolate, acute, the outer lobes dull gray nearly throughout with narrow paler margins, the inner lobes with conspicuous broad white margins and a narrow gray-green median zone, the longer inner lobes 6.5–7 mm long, 3 mm wide, the shorter outer lobes 4.5–5.5 mm long, 2.5–3 mm wide. Petals bluish, purplish, or rose (varying according to different collectors), spatulate, rounded at apex, unguiculate, 10–15 mm long, 4–7 mm wide, shortly and inconspicuously appressed-pubescent without to glabrescent, conspicuously long pilose within except near apex. Anthers narrowly oblong, 2–2.5 mm long; filaments 10–11 mm long, the sterile one retrorsely pilose, the others glabrous. Style 8–10 mm long, antrorsely pilose. Fruit oblong-cylindric, 9–20 mm long, gray short-tomentose.

Common name. "Curataquilla"; "sacaraiyek" (arekuna dialect).

Distribution. Rocky savannas and open sandstone exposures of the eastern portion of Bolívar in the Venezuelan Guayana from the region of the Gran Sabana at Cerro Roraima westward to the summit of Cerro Guaiquinima, and in the adjacent Pakaraima Mountains of Guyana, at altitudes of 300–1,200 m, ascending to 1,600 m on the slopes of Ptari-tepui. [*Cardona 2726* from the summit of Auyan-tepui at an altitude of 2,500 meters was cited as *Euphronia hirtelloides* by Lleras (1976). It is actually *Myrtus alternifolia* Gleason, as cited in Flora of Auyantepui (Steyermark, 1967).]

Specimens examined. GUYANA. Mt. Ayanganna, Pakaraima Mountains, between Chinowieng and Chi-Chi Landing, 1,000 m, *Maguire, Bagshaw & C. K. Maguire 40647* (NY); Kamarang Station, Pakaraima Mountains, 500 m, *Maguire & Fanshawe 32614* (NY).

VENEZUELA. BOLIVAR: Gran Sabana, El Dorado-Sta. Elena road, 2.5 km before turnoff at San Rafael, 1,030 m, *Luteyn, Lebrón-Luteyn & Steyermark 6294* (MO, NY); km 146 along El Dorado-Sta. Elena road, 1,280 m, *Luteyn, Lebrón-Luteyn & Steyermark 6291* (MO, NY); between Santa Teresita de Kavanayen and base of Ptari-tepui, 1,220 m, *Steyermark 60307* (F, NY); between Ptari-tepui and Sororopán-tepui, 1,615 m, *Steyermark 60274* (F, MO); Cerro Manacauaray, headwaters of Río Caroní, basin of Río Yuruguaní, 1,130 m, *Cardona 3024* (NY); Río Ambetere, Alto Caroní, 420 m, *Cardona 2583* (NY); slopes of Auyan-tepui, 1,100 m, *Cardona 2609* (NY); alrededores de Sta. Elena de Uairén, *Lasser 1273* (NY, VEN); Gran Sabana, 27 km N of Kama-Merú, carretera El Dorado-Sta. Elena road, 5°30′N, 61°20′W, 1,300 m, *Holst, Steyermark & Manara 2222* (MO); 5 km east of Kavanayen, 1,200 m, *Maguire 33717* (NY); Uarupata, *Maguire 33283* (NY); Kamarang head, Gran Sabana, 800–950 m, *Maguire 33293* (NY); región de los rios Icabaru, Hacha y cordillera sin nombre, 450–850 m, *Bernardi 2626, 2679* (NY); cumbre del Cerro Guaiquinima, 5°44′4″N, 63°41′8″W, 730–900 m, *Steyermark, Berry & Dunsterville 117285* (NY, VEN); same locality, *Steyermark, G. C. K. & E. Dunsterville 113455, 113119-A* (NY, VEN); km 150, valley of Río Uarama, NE of Luepa, 1,220 m, *Steyermark & Nilsson 581* (NY, VEN); km 175 south of El Dorado, 1,200 m, *Steyermark 111296* (NY, VEN); Urimán, 300 m, *Steyermark 75330* (F, MO, NY); Río Caroní below Urimán, 393 m, *Steyermark & Wurdack 3* (F, MO, NY); región of Canaima, 6°15′N, 62°47′W, 200–500 m, *Agostini 258* (NY, VEN); Hacha Falls, Canaima, *Prance 16550* (NY, US); between Luepa and Kavanayén, 1,317–1,375 m, *Badillo & Holmquist 6255* (MY); km 135–137 south of El Dorado, *Badillo & Holmquist 6196* (MY); 148 km south of El Dorado, 1,350–1,400 m, *Steyermark & Dunsterville 104162* (MY, VEN); Cerro Akurimá, Sta. Elena, *Tamayo 2699* (US); between Parupa and Kavanayén, *Ramírez 792* (VEN); 7.5 km NE of Santa Elena, 4°40′N, 61°4′W, 880 m, *Steyermark & Liesner 127592* (MO, VEN).

This species is characteristic of the eastern portion of the Venezuelan Guayana in the state of Bolívar, where it is a common shrub on rocky open sandstone outcrops and savannas.

Warming (1875) gave only a brief description of *Lightia guianensis*, mentioning a few salient characters such as "*foliis minoribus, ovatis v. obovatis, basi rotundato-cuneatis; racemis brevivissimis 4-6-floris*" in differentiating this species from *Lightia licanioides* (= *Euphronia hirtelloides*). However, his reference to "staminibus glabris" has been found to be incorrect. Careful examination of specimens from eastern Venezuela shows the filaments of the fifth sterile stamen to be retrorsely pilose and the four fertile stamens as glabrous, characteristic of the genus.

Although united by Lleras with *E. hirtelloides* (loc. cit.), *E. guianensis* is amply distinct not only in its shorter, fewer-flowered racemes and smaller, differently shaped leaves, as mentioned by Warming, but also in the hairs of the outer part of the calyx lobes and pedicels uniformly loosely ascending to spreading. Moreover, dried specimens manifest broad white marginal zones on the inner calyx lobes with only a relatively narrower gray-green central midrib. This latter character is in contrast to the more uniformly gray-green calyx lobes of *E. hirtelloides* with only the central median portion with a loose, dense, ascending sericeous pubescence.

The specimens of *Prance 16550* and *Agostini 258* from the Canaima region need some comment. The material of Prance is sterile with the leaves larger than usual, and that of Agostini has inflorescences (up to 7 cm long) and peduncles (3.5–4 cm long) longer than usual, thus attaining dimensions similar to those of *E. hirtelloides*. However, the short flowering portion (2–3 cm) is like that of *E. guianensis*.

Euphronia hirtelloides Martius, Nov. Gen. et Sp. 1: 121, *t. 73*. 1825. *Lightia licanioides* Spruce ex Warm. in Martius's Flora Brasiliensis 13(2): 121. 1875. *Euphronia licanioides* (Spruce ex Warm.) H. Hallier, l.c. in obs.: *Lightia licanioides*. Figures 3A, AA, 4.

Shrub or tree mainly 2–10 m tall, branches gray lanuginose, becoming glabrous below. Leaves coriaceous, gray-green above, white below, shortly petiolate, lance- to oblong-elliptic or ovate, shortly acute at apex, acute to obtuse at base, 4.5–7.5 cm long, 1.5–4 cm wide, densely and closely white tomentose below with elongated midrib, glabrous above or sometimes white-tomentose in the sulcate groove; petioles 5–7 mm long. Inflorescence terminal or axillary, simply racemose, or with 1 or 2 lateral axes branching from the base, 5–11.5 cm long including the peduncle, flowering portion 4–10 cm long, 2–2.5 cm wide, (7–)15–23-flowered; peduncle 1–4 cm long, together with the rachis gray-lanulose. Bracts lanceolate, acute, 3.5–4 mm long, 0.8–1 mm wide, sericeous without, caducous. Pedicels 1.5–5 mm long, mainly shorter than the calyx, with dense, loosely ascending to spreading hairs. Calyx 6–9 mm long, tube shallowly campanulate, 2 mm long, 2–4 mm wide at summit, gray-tomentellose, lobes unequal, inner ones oblanceolate-obovate, shortly acute, broader than the outer and broadened above the middle, outer ones broadly lanceolate, more narrowed above the middle, (2.5–)5–8 mm long, 2–3 mm broad, sericeous both sides, more abundantly long-sericeous with longer, looser hairs on outer midrib, rather uniformly gray-sericeous elsewhere, externally with shorter appressed hairs. Petals rose, purplish, or lavender, the limb spotted with violet (fide Clark and Maquirino), spatulate, rounded at base, unguiculate, short-sericeous or sometimes glabrescent, long pilose within at base and median portion, glabrous elsewhere at apex. Anthers 1.8–2.5 mm long; filaments 10–11 mm long, the sterile one retrorsely pilose, the others glabrous. Style 11–12 mm long, antrorsely pilose. Fruit cylindric, 15–23 mm long, 5–6 mm wide, subobtusely trigonous, gray lanate.

Distribution. Amazonian Brazil in Estado Amazonas and Territorio do Roraima, Amazonian Colombia in Vaupés and Caquetá, and Territorio Federal Amazonas of southern Venezuela, at altitudes of 100–150 meters.

Specimens examined. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: ad flumina Casiquiari, Vasiva et Pacimoni, 25–26 Feb. 1854, *Spruce 3413-x* (type of *Lightia licanioides*; isotype, NY; photo of type, F, MO); San Carlos de Rio Negro, 1°56'N, 67°03'W, 119 m, *Clark & Maquirino 7338, 7363* (NY); NW base of Cerro Yapacana, 150 m, *Maguire & Wurdack 34525* (MO, NY), *34546* (NY); Savanna No. 3, Cerro Yapacana, *Maguire, Cowan & Wurdack 30594* (NY).

COLOMBIA. AMAZONAS: Río Caquetá, Araracuara savannas, *Maguire, C. K. Maguire & Fernandez 44153* (MO, NY); Vaupés: lower Río Paraná-pichuna, at Mitú, *Zarucchi 1986* (GH).

BRAZIL. AMAZONAS: Rio Curicuriary, affluent Rio Negro, *Ducke 337* (GH, MO, NY, US); same locality, *Ducke 159-A, 23869* (NY, US); Manaus-Caracarai Road (BR-174), km 115, campina adjacent to Igarapé Lajes, *Zarucchi, Almeida & Coêlho 2544* (NY); Rio Negro, Preto, *Fróes 22753* (MO, NY, US); Rio Uneiuxi, 100–200 km above mouth, basin of Rio Negro, *Prance et al. 15502* (NY, US); Rio Negro, *Nascimento 608* (NY). Territorio Federal Roraima: Rio Branco, São José de Anauá, *Silva 4514* (NY); estrado Manaus-Caracarai, km 350, north of Rio Brancinho, *Steward et al. 86* (MO, NY, US); Caracarahy, Rio Branco, *Ducke 1407* (GH, NY, US); Rio Negro, Rio Tea 40 km above mouth, village Bacuri, *Kubitzki et al. 79-240* (US).

In his description of *Lightia licanioides* (=*Euphronia hirtelloides*), Warming (1875) incorrectly described all five filaments of the stamens as retrorsely pilose, and plate 22 (1875) depicts three of the stamens with retrorse pubescence. However, dissection of specimens pertaining to this taxon reveals the retrorse pilosity present only on the fifth sterile filament, while the other four fertile ones are glabrous. As indicated in the present key to the species and in comments under *E. guianensis*, *E. hirtelloides* is distinct in having a more elongated, many-flowered inflorescence; larger, more acutely tipped leaves; and the pubescence of pedicel and outer surface of calyx lobes of a different type. It should be noted here that the calyx of *Euphronia* is gamophyllous [Lleras (1976) describes the calyx as consisting of five sepals], consisting of a calyx tube and five lobes, as originally defined by Martius and Zuccarini (1826), Robert Schomburgk (1847, as *Lightia*), and Warming (1875, as *Lightia*).

AQUIFOLIACEAE

Ilex liesneri Steyerm., sp. nov. TYPE: VENEZUELA. Territorio Federal Amazonas: Depto. Atabapo, Cerro Marahuaca, 1–2 km N of "Sima" Camp, 3°43'N, 65°31'W, 1,100 m, 8–9 Mar. 1985, *Ronald Liesner 18469* (holotype, MO; isotype, VEN).

Frutex 1–2 m altus glaber; foliis anguste elliptico-lanceolatis ad apicem obtuse attenuateque angustatis ad basin acutate attenuateque angustatis 4.5–9 cm longis, 0.5–1.5 cm latis subtus sparsim punctulatis, ad margines crenato-serrulatis, utroque latere 5–13-crenulato; inflorescentiis axillaribus et lateralibus solitariis trichotome cymosis pedunculatis, cymis plerumque 7-floris; pedunculis 0.8–1.5 cm longis gracilibus; inflorescentiae pedicellis filiformibus sub anthesi 4–5 mm longis sub fructu 4–8 mm longis; floribus 4-meris; floribus ♂: calycis lobis suborbicularibus rotundatis 1.8 mm longis, 1.5 mm latis; floribus ♀: calycis lobis 0.5

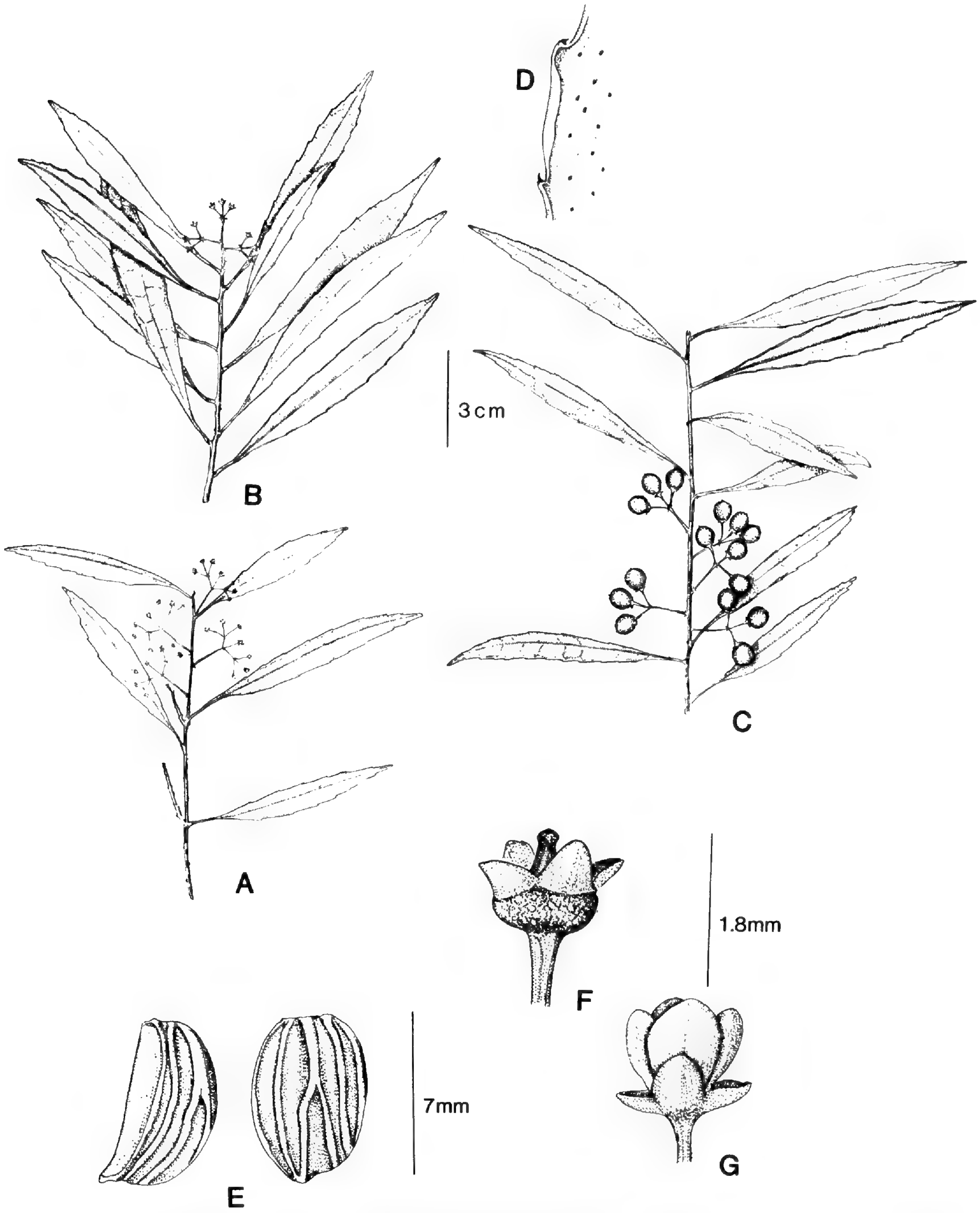

FIGURE 5. *Ilex liesneri.*—A. Habit of flowering branch showing axillary inflorescences.—B. Habit of flowering branch showing terminal inflorescence.—C. Habit of fruiting branch.—D. Detail of portion of lower leaf surface showing punctation, revolute margin, and crenulations.—E. Pyrenes, lateral view, left; dorsal view, right.—F. Pistillate flower.—G. Staminate flower.

mm longis, 1.2 mm latis; petalis suborbicularibus rotundatis 1.5 mm longis, 2 mm latis; fructu subgloboso vel ovoideo-subgloboso 7 mm longo, 7 mm lato; pyrenis 4–5 trigonis 5 mm longis, 3.5–5 mm latis, dorso 3–5-costatis.

Shrub 1–2 m tall with slender branches. Leaves narrowly elliptic-lanceolate, narrowed above to a long obtuse apex, narrowed below to a long acute base, 4.5–9 cm long, 0.5–1.5 cm wide, sparsely punctate below, midrib narrow, sulcate above, slightly elevated below, lower surface enervate, upper surface 7–8-nerved on each side of midrib, subhorizontally spreading, anastomosing 1–2 mm from margin, remotely crenulate-serrulate with 5–13 depressed crenulations on each margin. Petioles 5–15 mm long. Inflorescence axillary and lateral, solitary, trichotomously cymose, pedunculate; cymes simple or compound, few-flowered (usually 7) when simple with one flower on the central axis and three each on the two lateral axes, when compound each of the axes 2–3-flowered, the axes divaricately spreading, 1–3 mm long; pedicels 4–8 mm long. Bracts subtending pedicels spreading, 0.1 mm long. Peduncle slender, 0.8–1.5 mm long. Flowers 4-merous. Staminate flowers: calyx lobes suborbicular, rounded, 1.8 mm long, 1.5 mm wide; anthers suborbicular, 0.8 × 0.8 mm; filaments 0.8 mm long; pistil rudiment ovoid, 1 mm long. Pistillate flowers: calyx lobes 0.5 mm long, 1.2 mm wide; petals suborbicular, rounded, 1.5 mm long, 2 mm wide; ovary ovoid or subglobose, 1–1.5 mm long, constricted slightly at summit into a short style 0.2–0.3 mm long; stigma prominent, ovoid-capitate. Fruit subglobose or ovoid-subglobose, 7 × 7 mm; pyrenes 4–5, trigonous, 5 mm long, 3.5–5 mm wide, dorsally 3–5-costate.

Paratypes. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Depto. Atabapo, Cerro Marahuaca, Río Yameduaka arriba, 3°38′N, 65°28′W, 1,225 m, *Liesner 17604* (MO, VEN); "Sima" Camp, southcentral portion along eastern branch of Cerro Negro, Cerro Marahuaca, 3°43′N, 65°31′W, 1,140 m, *Steyermark & Holst 130575, 130422, 130424* (MO, VEN). Figure 5.

This species is distinguished by the narrowly lance-elliptic, crenulate, punctate leaves, which are long attenuate at each end, the 3–5-dorsally ribbed pyrenes, the slender, solitary peduncles from both axillary and lateral buds, and the filiform pedicels on trichotomous cymose inflorescences.

OCHNACEAE

Tyleria apiculata Sastre (Fig. 6A–G)

This species was recently described by Sastre (Phytologia 59: 313–314. 1986) with only a brief description based upon a single specimen, which I collected. A later expedition in 1985 to Cerro Marahuaca by Bruce Holst, Ronald Liesner, and me resulted in the collection of more ample material. In view of these additional collections, the following more detailed description can be furnished.

Shrub or small tree 2–3 m tall. Leaves erect, crowded, those on sterile branches clustered at the apex, scattered below the inflorescence on fertile branches, subobtuse at apex, sometimes with a minute mucro 2 mm long, the apically clustered leaves on sterile branches 7–8 cm long, 5–10 mm wide, those on fertile branches often shorter and 6–13 mm wide, gradually narrowed to the sessile base, glabrous on both surfaces, margins finely serrulate-ciliate with closely ascending purplish hairs 0.5–0.7 mm long, lateral nerves finely parallel from base to apex, strongly ascending to apex. Stipules ovate-triangular or lanceolate, obtuse to acute, 4–10 mm long, 2 mm wide, finely parallel-veined. Inflorescence paniculate, terminal, many-flowered, 12–14 cm long, 5–7.5 cm wide in the basal half, 3.5–4 cm wide in upper half; flowers pedicellate, pedicels filiform, 10–13 mm long, articulate 1–2 mm above base, dilated below apex, spreading in fruit. Sepals membranous, ovate or elliptic-ovate, obtuse, 8 mm wide, 5 mm long. Petals pink, obovate, rounded at apex, narrowed to the base, 15 mm long, 11 mm wide. Anthers linear-oblong, 4 mm long, acutely apiculate, subsessile; filaments 0.3 mm long. Staminodes spatulate, rounded at apex, 7 mm long, 2.5 mm wide above, adnate 1 mm above the base with dimorphic lateral appendages, the longer appendage deeply cut into an elongated subulate, simple, distal segment 5.5–6 mm long attached to a ligulate multifimbriate portion, and an inner proximal shorter appendage 5 mm long with lateral fimbrillate segments. Pistil 9 mm long; style subulate, 5 mm long; ovary narrowly conic, 4 mm long, 1 mm wide. Capsule oblong-conic, 10–11 mm long.

Specimens examined. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Depto. Atabapo, Cerro Marahuaca, below Salto Los Monos on tributary of headwaters of Río Iguapo, 3°35′N, 65°23′W, 1,500–1,600 m, 11 Mar. 1985, *Liesner 18511* (MO, VEN); Río Yameduaka arriba, 3°38′N, 65°28′W, 1,225 m, 17–18 Feb. 1985, *Liesner 17624* (MO, VEN); "Sima Camp," southcentral portion of forested slopes along eastern branch of Caño Negro, 3°43′N, 65°31′W, 21–22, 24 Feb. 1985, *Steyermark & Holst 130565* (MO, VEN); below Salto Los Monos on tributary of headwaters of Río Iguapo, 3°35′N, 65°23′W, 1,500 m, 13–14 Oct. 1983, *Steyermark 129649* (P, holotype; MO, VEN, isotypes).

Sastre notes that the species is well marked by its

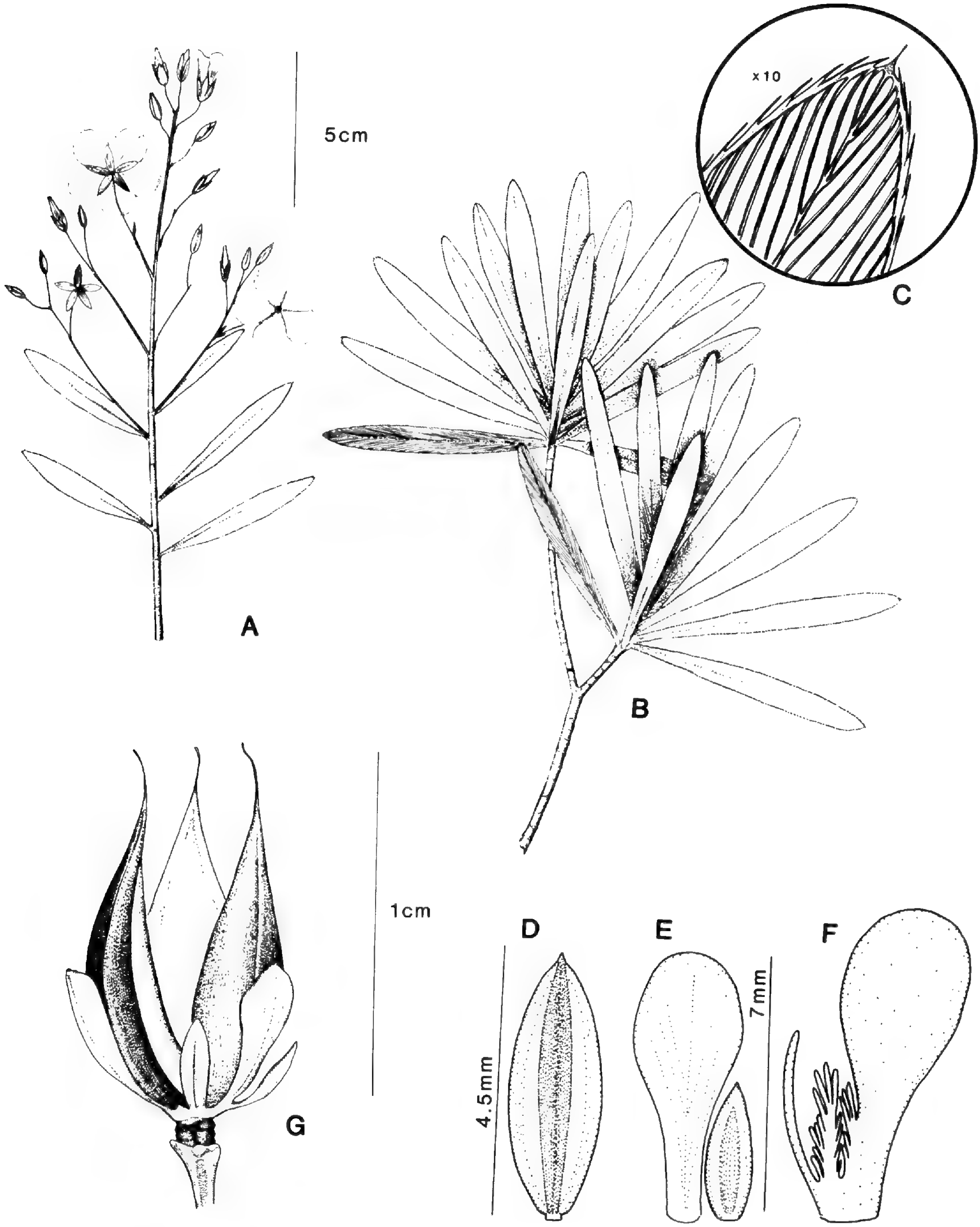

FIGURE 6. *Tyleria apiculata.*—A. Habit of flowering branch.—B. Sterile leafy branch showing terminal clusters of leaves.—C. Detail of leaf apex, lower surface.—D. Anther.—E. Anther and staminode, ventral view.—F. Staminode, dorsal view.—G. Capsule.

apiculate anthers and contrasts it with *T. spectabilis* Mag. & Wurd. and *T. floribunda* Gl. because of its shorter leaves. It also resembles *T. linearis* Gl. of adjacent Cerro Duida in leaf shape but differs from that species in the elongate pedicels in terminal panicles, broader and longer leaves with a subobtuse apex, shorter petals, and larger fimbriate lateral appendages of the staminodes.

Sauvagesia marahuacensis Steyerm., sp. nov. TYPE: VENEZUELA. Territorio Federal Amazonas: Depto. Atabapo, Cerro Marahuaca, Río Yameduaka arriba, 3°38'N, 65°28'W, 1,225 m, *Ronald Liesner 17677-A* (holotype, MO; isotype, VEN). Figure 7.

Suffrutex 0.5-metralis, caulibus virgatis; foliis subsessilibus anguste linearibus vel subulatis apice cuspidatis basi inconspicue angustatis 10–13 mm longis, 0.8–1 mm latis, 10–15-plo longioribus quam latioribus, marginibus revolutis minute glanduloso-serratis 10–11 glandulis adpressis 1 mm longis praeditis, pagina supra depressionibus numerosis praedita, subtus nervis elevatis striatis; floribus ad apices ramulorum axillaribus numerosis pedicellatis, pedicellis 3–3.5 mm longis; sepalis lanceolatis acutis 5–5.5 mm longis, 1.7 mm latis; petalis albidis obovatis apice rotundatis basi subcuneiformibus 7–7.5 mm longis, supra medium 4–5 mm latis; staminibus 5 coronae squamulis alternis; corona 1-seriata basi cum filamentis in columnam brevem 0.3–0.4 mm latam coalita, squamulis quinque 1.2–1.5 mm longis, laminis subulato-spathulatis apice rotundatis 0.7–0.9 mm longis in stipitem 0.5 mm longum, 0.2 mm latum attenuatis; antheris linearibus 2.1–2.7 mm longis, 0.2–0.25 mm latis.

Virgate subshrub 0.5 m tall. Stems dichotomously branched or 3–6-verticillate, densely foliose toward the apex, leafless for most of the length below, 2–3 mm diam. Stipules densely crowded, overlapping, rufous-brown, lanceolate, 2.5–3 mm long, 1 mm wide, dorsally carinate, conspicuously pectinate from base to apex with 15–18 subulate appendages on each side, each one tipped by a filiform, white cilium 1 mm long, lower appendages often deciduous. Leaves subsessile, coriaceous, narrowly linear or narrowly subulate, 10–13 mm long, 0.8–1 mm wide, 10–15 times longer than broad, cuspidate at apex, inconspicuously narrowed at base, margins revolute, minutely glandular serrulate, each margin with 10–11 minute, appressed-ascending teeth 0.1 mm long, upper surface marked with small transverse depressions. Flowers numerous near the apex, conspicuously pedicellate; pedicels 3–3.5 mm long. Sepals lanceolate, acute, 5–5.5 mm long, 1.7 mm wide. Petals white, obovate, rounded above, narrowed to a subcuneiform base, 7–7.5 mm long, 4–5 mm wide. Stamens 5; anthers linear, 2.1–2.7 mm long, 0.2–0.25 mm wide; filaments 0.6 mm long. Staminodes 5, subulate-spatulate, rounded at apex, 1.2–1.5 mm long, narrowed basally, the claw 0.5–0.7 mm long, 0.2 mm wide, the laminar portion 0.7–0.9 mm long, the summit of the laminar portion attaining one-third to one-quarter length of anther. Ovary ovoid, 1 mm long; style subulate, 2.9–3 mm long.

This species differs from *S. guianensis* (Eichl.) Sastre and varieties in the narrower linear-subulate leaves 10–15 times longer than broad with depressed areas on the upper surface and in the long-pedicellate, more numerous flowers conspicuous at the ends of the leafy stems as contrasted with the solitary, sessile or barely pedicellate flowers largely hidden amongst the leaves of *S. guianensis*.

SAUVAGESIA GUIANENSIS AND VARIATIONS

A study of *Sauvagesia guianensis* (Eichl.) Sastre (1970) reveals much variation not only in details of leaf morphology but in those of staminodial form as well. This taxon (sensu lato) is distributed in the region of the Guayana Shield, with its greatest concentration in the Venezuelan Guayana, but with outliers in adjacent Guyana and Colombia (Sastre, 1970).

It was originally described by Eichler as *Leitgebia guianensis* (op. cit.), based upon a collection by Richard Schomburgk from the savannas of Guyana. Gleason (1931) referred collections of Tate from the summit of Cerro Duida to this taxon. In 1946 Lasser described a Steyermark collection, also from the summit of Duida, as *Leitgebia gleasoniana*. At this time Lasser (1946) associated a Phelps collection from Cerro Paraque (Sipapo) as conspecific with the Steyermark type.

Sastre (1970) eventually transferred *Leitgebia guianensis* to *Sauvagesia* and referred later collections originating from various parts of the Venezuelan Guayana as one taxon. The variability of this taxon becomes obvious upon more detailed study. It is noted that specimens originating from the Gran Sabana of eastern Venezuela and adjacent Guyana near the type locality have leaves relatively fewer times longer than broad, relatively shorter and with shorter-pointed apices than those from the summits of various table mountains westward in Venezuela. Moreover, the staminodes of specimens from the eastern sector of the range have shorter laminar portions. Additionally, a surprising degree of variation is shown between plants collected from various sandstone table mountains. For example, plants from the summit of Cerro Guaiquinima in Bolívar have leaves with only 2–4 glands on each margin that appear in the upper three-fourths only; whereas specimens from other parts of the range manifest 6–14 glands on each margin, which are distributed from one-fourth to

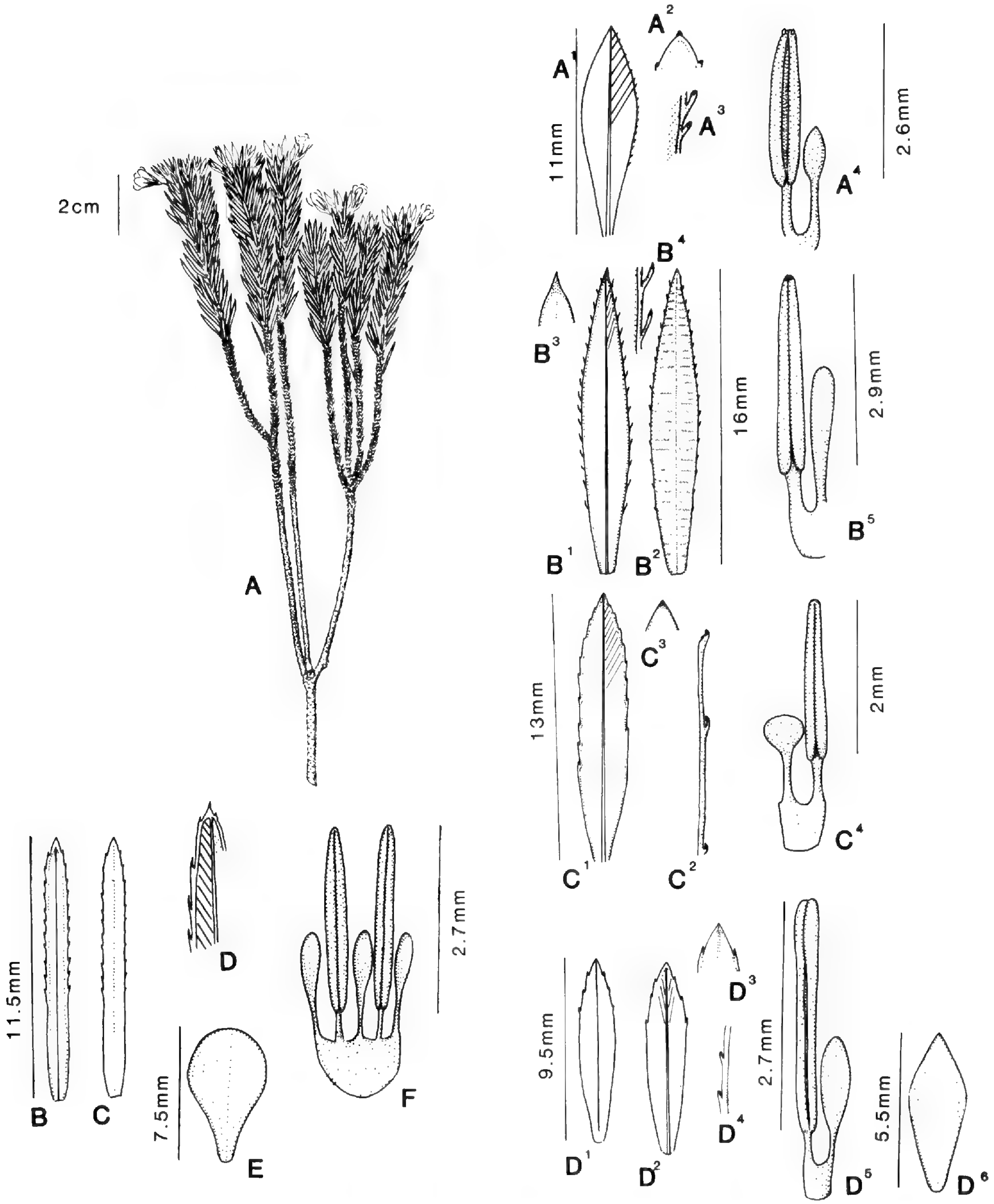

FIGURE 7. A–F. *Sauvagesia marahuacensis.*—A. Habit.—B. Leaf, lower side.—C. Leaf, upper side.—D. Detail of upper apical portion of lower side of leaf.—E. Petal.—F. Portion of stamens and staminodes attached to membrane.—A^1–A^4. *Sauvagesia guianensis* subsp. *guianensis*:—A^1. Leaf, lower side.—A^2. Apical portion of leaf.—A^3. Marginal leaf glands.—A^4. Portion of androecium showing anther and staminode.—B^1–B^5. *S. guianensis* subsp. *gleasoniana*:—B^1. Leaf, lower side.—B^2. Leaf, upper side.—B^3. Apical portion of leaf.—B^4. Marginal leaf glands.—B^5. Portion of androecium showing anther and staminode.—C^1–C^4. *S. guianensis* subsp. *sipapoensis*:—C^1. Leaf, lower side.—C^2. Marginal leaf glands.—C^3. Apical portion of leaf.—C^4. Portion of androecium showing anther and staminode.—D^1–D^6. *S. guianensis* subsp. *guaiquinimensis*:—D^1. Leaf, upper side.—D^2. Leaf, lower side.—D^3. Apical portion of leaf.—D^4. Marginal leaf glands.—D^5. Portion of androecium showing anther and staminode.—D^6. Petal.

halfway up the leaf margin to the apex. Furthermore, petals of the Cerro Guaiquinima plants have acute to subacute apices, whereas those on specimens elsewhere are rounded. Moreover, in contrast to the usually encountered elongated, linear-ligulate, narrowly spatulate, or narrowly elliptic laminar portion of the staminode, plants from the summit of Cerro Sipapo (Paraque) have developed a suborbicular type about as broad as long.

Results obtained from a study of the available material in NY and VEN herbaria indicate that *Sauvagesia guianensis* has undergone differentiation in various portions of its geographical range resulting in populations showing a divergence in various characters. This geographical isolation on several of the sandstone table mountains is recognized in the present study as correlated with taxonomic characters sufficiently distinct as to be considered of subspecific significance.

The following key encompasses the principal differences by which these variations may be recognized within *S. guianensis* as well as distinguishing them from the related *S. marahuacensis.*

KEY TO *SAUVAGESIA GUIANENSIS* AND SUBSPECIES, AND RELATED *SAUVAGESIA MARAHUACENSIS*

1a. Flowers on pedicels 3–3.5 mm long, numerous and conspicuous near apices of the leafy stems; leaves linear-subulate, 0.8–1 mm wide, 10–15 times longer than broad; upper leaf surface with transversely depressed areas ..... *S. marahuacensis*
1b. Flowers subsessile or on pedicels to 2 mm long pedicellate, few and mainly concealed amidst the leaves; leaves linear-oblanceolate, 1–3 mm wide, 3–10 times longer than broad; upper leaf surface without transversely depressed areas 2
  2a. Staminodes 3–3.5 mm long, 1–1.5 mm wide; Colombia ..... 1e. *S. guianensis* subsp. *araracuarensis*
  2b. Staminodes 1–1.9 mm long, 0.2–0.5 mm wide; Venezuela and Guyana 3
    3a. Foliar glands 2–4 on each margin, the lowest starting at ¼ the distance below the apex; petals subacute to acute at apex ..... 1d. *S. guianensis* subsp. *guaiquinimensis*
    3b. Foliar glands 6–14 on each margin, the lowest starting from ½–¾ the distance below the apex; petals rounded at apex 4
      4a. Laminar portion of staminode suborbicular, about as broad as long, 0.5 × 0.4–0.5 mm; upper surface of leaf blade with a conspicuous puncticulate appearance ..... 1c. *S. guianensis* subsp. *sipapoensis*
      4b. Laminar portion of staminode elongated, longer than broad, linear-ligulate, elliptic-spatulate, or narrowly spatulate, 0.8–1.9 × 0.2–0.3 mm; upper surface of leaf blade lacking a puncticulate appearance 5
        5a. Foliar glands 6–11 on each margin; leaves oblanceolate or narrowly oblanceolate, 8–11 mm long, 1.5–3 mm wide, 3–4 times longer than broad; leaf apex shortly acute to bluntly pointed; laminar portion of staminode 0.8–0.9 mm long ..... 1a. *S. guianensis* subsp. *guianensis*
        5b. Foliar glands 11–14 on each margin; leaves linear or linear-lanceolate, 10–18(–22) mm long, 1–2 mm wide, 7–10 times longer than broad; leaf apex prolonged, acuminate; laminar portion of staminode 1.2–1.9 mm long ..... 1b. *S. guianensis* subsp. *gleasoniana*

1a. **Sauvagesia guianensis** (Eichl.) Sastre subsp. **guianensis**. *Sauvagesia guianensis* (Eichl.) Sastre, Caldasia 10: 570. 1970. *Leitgebia guianensis* Eichl. in Martius's Flora Brasiliensis 13(1): 413. pl. 83, fig. 2. 1871. TYPE: Guyana. *Rich. Schomburgk 1553.* Figure 7A^{1}–A^{4}.

Leaves oblanceolate, acute to bluntly pointed at apex, 6–11 mm long, 1.5–3 mm wide, 3.5–4 times longer than broad, foliar glands (6–)7–11 along each margin, appressed to ascending outwardly, short; upper surface with fine transverse lines. Flowers solitary, few, hidden and inconspicuous among the leaves, subsessile to 2 mm long pedicellate. Petals obovate, rounded at apex, 6.8–7.5 mm long, 5 mm wide. Anthers 2.5–3 mm long. Staminode lamina narrowly to broadly elliptic-spatulate, rounded to subacute, 0.8–0.9 mm long, 0.3 mm wide, the narrower lower portion about equaling the lamina in length.

Distribution. Guyana and adjacent southeastern Venezuela, Bolívar.

Additional specimens examined. VENEZUELA. BOLÍVAR: km 177, S of El Dorado, just N of Río Sacaicá, 1,200 m, *Steyermark 111302* (MO, VEN); 52 km N of Kama-merú, carretera El Dorado-Sta. Elena, 5°40′N, 61°25′W, 1,300 m, *Holst, Steyermark & Manara 2201* (MO, VEN).

1b. **Sauvagesia guianensis** subsp. **gleasoniana** (Lasser) Steyerm., comb. nov. *Leitgebia gleasoniana* Lasser, Bol. Acad. Ci. Venez. 9: 246. 1946. TYPE: VENEZUELA. Territorio Federal Amazonas: Cerro Duida, summit, Savanna Hills, Aug. 1944, *Steyermark 58248* (holotype, VEN; isotype, F). Figure 7B¹–B⁵.

Leaves linear or linear-lanceolate, aristate long-pointed at apex, 10–18(–22) mm long, 1–2 mm wide, 7–10 times longer than wide; foliar glands 11–14 each margin, ascending outwardly from margin, elongated, 0.3–0.5 mm long; upper surface usually marked with fine transverse striations. Flowers solitary, few, hidden and inconspicuous among the leaves, subsessile to 1–2 mm pedicellate. Petals obovate, rounded at apex, 8 mm long, 4.5 mm wide. Anthers 2.3–2.9 mm long. Staminode 1.2–1.9 mm long, the laminar portion linear-ligulate or narrowly spatulate, obtuse or rounded, 0.3–1.2 mm long, 0.2 mm wide, much longer than wide, the lower stipitate portion 0.5–1.3 mm long.

Distribution. Summits of Cerro Duida and Huachamacari, Territorio Federal Amazonas, Venezuela.

Additional specimens examined. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Cerro Duida, 3°40'N, 65°45'W, 1,500 m, *Steyermark, Brewer-Carias & Liesner 124569* (MO, VEN); plateau of Huachamacari, 3°50'N, 65°43'W, 1,720 m, 1 Mar. 1985, *Liesner 18057* (MO, VEN); Savanna Hills, Cerro Duida, *Steyermark 58248* (F, VEN).

1c. **Sauvagesia guianensis** subsp. **sipapoensis** Steyerm., subsp. nov. TYPE: VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Serrania Sipapo, cumbre, sección septentrional, 5°N, 67°30'W, 1,500 m, *Steyermark, Brewer-Carias & Liesner 124530* (holotype, MO; isotype, VEN). Figure 7C¹–C⁴.

A subsp. *guianense* squamulorum laminis suborbicularibus apice late rotundatis 0.5 mm longis, 0.4–0.5 mm latis, foliis supra conspicue cellulosis recedit.

Leaves linear-lanceolate, ending in a long cuspidate apex, 10–13 mm long, 2–2.5 mm wide, 5–6 times longer than broad; foliar glands short, 7–10 each margin, incurved-appressed, the lowest ones beginning ⅔ the distance below the apex; upper surface with a conspicuous cellular appearance. Flowers solitary, few, subsessile, inconspicuous among the leaves. Petals obovate, rounded at apex, 5.5 mm long, 4 mm wide. Anthers 2–2.5 mm long. Staminode with the laminar portion suborbicular, broadly rounded, 0.3–0.5 mm long, 0.4–0.5 mm wide, stipitate lower portion 0.7–0.8 mm long.

Distribution. Summit of Cerro Sipapo, Territorio Federal Amazonas, Venezuela.

1d. **Sauvagesia guianensis** subsp. **guaiquinimensis** Steyerm., subsp. nov. TYPE: VENEZUELA. Territorio Federal Amazonas: Cerro Guaiquinima, cumbre, sector occidental, cerca del borde cubierto con bosque bordeando una sabana, 5°45'N, 63°43'W, 1,540 m, 27 May 1978, *Steyermark, Berry, G. C. K. & E. Dunsterville 117498* (holotype, MO; isotype, VEN).

A subsp. *guianense* atque ceteris petalis apice acutis vel subacutis, foliorum glandulis marginalibus utroque latere 2–4 secus longitudinem superiorem ¾ insertis recedit.

Leaves linear-oblanceolate, acute at apex, 6–9.5 mm long, 1.5–2 mm wide, 4–6 times longer than wide; foliar glands 2–4 each margin, inserted along the upper ¾ of the margin, appressed, short; upper surface with few or no transverse lines but with a cellular appearance. Flowers solitary, few, hidden and inconspicuous among the leaves, subsessile. Petals obovate, acute at apex, 5.5 mm long, 2 mm wide above middle. Anthers 2.7 mm long. Staminode 1.6 mm long, the laminar portion ligulate-oblong or ligulate-obovate, rounded or subobtuse at apex, 1.1 mm long, 0.3–0.4 mm wide, narrowed to a stipitate portion 0.5 mm long.

Distribution. Known only from the summit of Cerro Guaiquinima, Bolívar, Venezuela.

Paratypes. VENEZUELA. Cerro Guaiquinima, cumbre, sector suroeste, 5°38'N, 63°45'W, 1,650 m, *Steyermark, Berry, G. C. K. & E. Dunsterville 117434* (MO, VEN); Cerro Guaiquinima, cumbre, sector suroeste-central, 5°45'N, 63°35'W, 950 m, *Steyermark, Berry, G. C. K. & E. Dunsterville 117474* (MO, VEN). Figure 7D¹–D⁶.

1e. **Sauvagesia guianensis** subsp. **araracuarensis** (Sastre) Steyerm., stat. nov. *Sauvagesia guianensis* var. *araracuarensis* Sastre, Bull. Mus. Nat. Hist. Paris 35: 37. 1978. TYPE: COLOMBIA. Com. Amazonas: Río Caqueta, Araracuara, camino a La Sabana, segunda sabana de Tibeyes, 500–600 m, 5 Jan. 1977, *Sastre & Reichel 5139* (holotype, P; isotypes, COL, G).

Staminodes larger than in the other subspecies, 3–3.5 mm long, 1–1.5 mm wide.

Distribution. Known only from savannas over sandstone soils at the type locality.

THEACEAE (BONNETIACEAE)

Since the publication of "Flora of the Venezuelan Guayana—I" (Steyermark, 1984), the following additional new taxa are described in *Bonnetia.*

Bonnetia bolivarensis Steyerm., sp. nov. TYPE: VENEZUELA. Bolívar: Ptari-tepui, cumbre, 5°47′N, 61°47′W, 2,400 m, 19 Nov. 1984, *Otto Huber 9818* (holotype, VEN; isotype, MO).

Frutex 1-metralis; foliis dense rosulatis subsessilibus oblongo-lanceolatis apice obtuse acutis basi obtusis (2–) 2.5–5 × 0.8–1.7 cm; sepalis 11–12.5 × 4–5 mm; petalis 21–22 × 14–16 mm; stylis tribus 3–3.5 mm longis fere usque ad basem divisis.

Leaves crowded at summit of branches, oblong-lanceolate, subsessile, narrowed to an obtusely acute apex, obtuse at base, (2–)2.5–5 × 0.8–1.7 cm, faintly impressed-nerved on both sides or the lateral nerves not evident, midrib slightly elevated below. Flowers solitary, sessile or subsessile; bracts immediately subtending flower oblong-lanceolate, acute to obtuse, 11–12 × 4.5 mm, dorsally carinate, setulose marginally with dark setae 1 mm long; sepals lance-oblong, subacute, 11–12.5 × 4–5 mm, obtusely dorsally keeled basally and apically; petals white, subcuneately obovate, subtruncate apically with unequally rounded sides, narrowed to the base, 21–22 mm long, 14–16 mm wide at summit, 4 mm wide at base. Stamens numerous, multiseriate; filaments 5 mm or less long; anthers 0.5–0.8 × 0.6 mm; pistil 9 mm long; styles 3, 3–3.5 mm long, divided about ⅔ way down.

The larger flowers and larger, subacute leaves differentiate this taxon from *B. chimantensis* Steyerm., *B. tepuiensis* Kobuski & Steyerm., and *B. toronoensis* Steyerm. In its deeply 3-parted style it differs from *B. tepuiensis.*

Bonnetia guaiquinimae Steyerm., sp. nov. TYPE: VENEZUELA. Bolívar: Cerro Guaiquinima, cumbre, sector SE, 5°40′N, 63°26′W, 1,250 m, 26 May 1978, *Julian A. Steyermark, Paul Berry & G. C. K. & E. Dunsterville 117421* (holotype, VEN; isotype, MO).

Frutex 1.5-metralis; foliis subpetiolatis oblongo-lanceolatis vel oblanceolatis apice acutis basi subobtusis vel obtusis 5–6.6 × 1.3–1.6 cm subtus enervatis integerrimis; sepalis minute mucronatis 10–12 × 6–8 mm; petalis 20 × 15–20 mm; filamentis 3.5–7 mm longis; stylo subulato apice leviter 3-lobato.

Leaves coriaceous, entire, oblong-lanceolate to oblanceolate, acute at apex, gradually narrowed to a subacute or subobtuse base, 5–6.5 × 1.3–1.6 cm, enervate below, the midrib subimpressed below, lateral nerves elevated above; petiole 1–2 mm long. Sepals coriaceous, suborbicular-obovate, rounded at a shortly cuspidate apex, 10–12 mm long, 6–8 mm wide above the middle, 3–4 mm wide at base; petals white, obovate, narrowed to a subunguiculate base, 20 mm long, 15–20 mm wide at the summit, 2–3 mm wide at base; filaments distinct, 3.5–7 mm long. Anthers 1.5–1.8 × 0.7 mm; pistil 9 mm long; style merely 3-lobed at apex.

This taxon is characterized by the shallowly 3-lobed style, entire, oblong-lanceolate, acute leaves, which are enervate beneath. It may be distinguished from *B. chimantensis* Steyerm. by the larger petals, shallowly 3-lobed style and larger leaves enervate below. From *B. toronoensis* Steyerm. it differs in the larger sepals and petals and larger, entire leaves enervate below, while from *B. tepuiensis* and subsp. *minor* Steyerm. it is separated by the larger, minutely mucronate sepals, longer filaments, and entire leaves.

Bonnetia ptariensis Steyerm., sp. nov. TYPE: VENEZUELA. Bolívar: Ptari-tepui, cumbre, 5°45′N, 61°45′W, 2,360–2,420 m, 23 Feb. 1978, *Steyermark, Carreño, McDiarmid & Brewer-Carias 115645* (holotype, VEN; isotype, MO).

Frutex 2.5 m; foliis sessilibus lanceolatis apice acutis majoribus 3.5–4.5 × 1–1.5 cm minute obscureque serrulatis; floribus solitariis breviter pedunculatis, pedunculis teretibus vel subteretibus 4–6 mm longis; sepalis lanceolatis vel suboblanceolatis acutis 12–13 × 3–5 mm; petalis luteis obovatis apice rotundatis 16–18 × 12 mm; antheris 0.8 × 0.7 mm; stylis tribus 6 mm longis fere usque ad basem divisis.

Leaves coriaceous, lanceolate, acute at apex, slightly narrowed to the base, the larger ones 3.5–4.5 × 1–1.5 cm, obsoletely pinnately nerved, midrib slightly elevated below, microscopically and obscurely serrulate. Flowers solitary, short-pedunculate; peduncle terete or subterete, 4–6 mm long; bracts immediately subtending flower narrowly oblanceolate, acute, 11–12 × 3–4 mm;

sepals subcoriaceous, lanceolate or suboblanceolate, acute, 12–13 × 3–5 mm, 10-striate, minutely ciliolate, obtusely carinate; petals yellow, obovate, rounded above, 16–18 mm long (pre-anthesis), 12 mm wide near apex, 2 mm wide at base. Filaments 1.5–3.5 mm long (pre-anthesis); anthers 0.8 × 0.7 mm; pistil 10 mm long; 3 styles 6 mm long, free nearly to the base.

From the yellow-flowered *B. wurdackii* Maguire, this species differs in the larger, lanceolate, and acute leaves, longer sepals, larger petals (even in bud), longer filaments, and longer style branches. The leaves, furthermore, do not manifest the pale punctate stomata that are clearly shown in *B. wurdackii.* From *B. tristyla* Gleason it is easily distinguished by the short pedicels, smaller floral parts and smaller leaves; while from *B. huberiana* Steyerm. it is well separated by the larger, lanceolate leaves, shorter pedicels, and larger floral parts.

Bonnetia tristyla Gleason subsp. **nervosa** Steyerm., subsp. nov. TYPE: VENEZUELA. Territorio Federal Amazonas: Cerro Yapacana, below summit, 3°45′N, 66°45′W, 825 m, 5 May 1970, *Julian A. Steyermark & George Bunting 103153* (holotype, VEN).

Frutex vel arbor 1.5–4-metralis; foliis supra costa media necnon nervis lateralibus nonnullis conspicue manifesteque elevatis, nervis lateralibus supra inaequaliter prominentibus; petalis 25–38 × 15–22 mm.

Leaves suboblong, oblong-oblanceolate, or oblong-obovate, obtuse to rounded at apex, narrowed to a subobtuse or subacute base, 4–8 × 1.5–3.5 cm, midrib of upper surface and 6–8 pairs of lateral nerves conspicuous and elevated, other intermediate pairs of lateral nerves less conspicuous and lightly impressed, nerves on lower surface subequal and lightly impressed. Petiole absent or 1–2 mm long. Peduncle 3–4.3 (–6.5) cm long. Sepals 12–20 mm long, the outer 12–15 mm long, the inner 15–20 mm long. Petals 25–38 × 15–22 mm.

Paratypes. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Cerro Yapacana, summit, 1,000–1,200 m, 5 May 1970, *Steyermark & Bunting 103103* (VEN); Cerro Yapacana, 2 Jan. 1951, *Maguire, Cowan & Wurdack 30632* (NY, VEN); Cerro Yapacana, 1,200 m, *Maguire, Cowan & Wurdack 30665* (NY, VEN); Cerro Vinilla, 30 km al SSW de Ocamo, 2°31′N, 65°23′W, 440–600 m, 1–2 Mar. 1984, *Steyermark, Berry & Delascio 130405* (MO, VEN); Cerro de la Neblina, Caño Grande SSW of Cumbre Camp, 1,050–1,100 m, 25 Dec. 1957, *Maguire, Wurdack & C. K. Maguire 42498* (NY, VEN); Cerro de la Neblina, summit, Cañon Grande slopes E of Cumbre Camp, 1,200–1,300 m, *Maguire, Wurdack & C. K. Maguire 42235, 42179* (NY, VEN); Cerro Avispa, Río Siapa, summit, 1°30′N, 65°51′W, 1,510 m, *G. C. K. & E. Dunsterville s.n.* (VEN); same locality and data, *Cardona 3098* (VEN); Serranía de Vinilla, 20 km SW of Ocamo, 2°20′N, 65°22′W, 760 m, *Huber 6168* (VEN); E side of Río Siapa, 1°36′N, 65°41′W, 600 m, *Huber 6006* (VEN).

This taxon differs from typical *B. tristyla* Gleason in having smaller petals, upper surface of the leaf blade with the midrib prominently elevated, and unequally prominent pairs of lateral nerves, with 6–8 of the pairs prominently elevated alternating with finer, lightly impressed intermediate ones. In *B. tristyla* subsp. *tristyla* the large petals 35–42 × 27–30 mm contrast with the smaller ones of subsp. *nervosa.* Moreover, in subsp. *tristyla* the upper midrib is shallowly depressed, not elevated, and all the lateral nerves of the upper surface of the leaf are equally inconspicuous and lightly impressed. The leaf blades in typical *B. tristyla* tend to be larger (5–) 8–15 × 2.5–5.0 cm as contrasted with 4–8 × 1.5–3.5 cm in subsp. *nervosa.* The base of the leaf blade in *B. tristyla* subsp. *tristyla* is cuneately narrowed, whereas that of subsp. *nervosa* is usually slightly obtusely curved or rounded above the junction with the petiole.

The geographical ranges of the two subspecies are distinct. Typical *B. tristyla,* described originally from Cerro Duida, occupies the northeastern sector of the range, from Cerro Duida and Marahuaca east to the Meseta de Jaua and Sarisariñama in Bolívar. *Bonnetia tristyla* subsp. *nervosa,* in contrast, is found in the more western sector, ranging from Cerro Yapacana south to Cerro Vinilla, Avispa, Aracamuni, and Neblina.

The only other species of *Bonnetia* having large yellow petals, *B. steyermarkii* Kobuski, is easily distinguished from *B. tristyla* by the larger acute sepals subtended by 4–6 large sepaloid bracts and the broader, acutely angled ancipital peduncle.

The following key incorporates the newly described taxa of *Bonnetia* with those previously described by the author in 1984.

KEY TO THE SPECIES AND SUBSPECIES OF *BONNETIA*

1a. Style undivided.
  2a. Lateral nerves of upper leaf surface elevated, impressed on lower surface; leaf blades mainly 2–4 × 1.5–2.5 cm .... *B. tepuiensis* subsp. *tepuiensis*

- 2b. Lateral nerves of upper leaf surface faintly impressed, mostly not evident on lower surface; leaf blades 1–2 × 0.8–1.4 cm .... *B. tepuiensis* subsp. *minor*

1b. Style divided into 3 branches nearly or all the way to the base, or shallowly 3-lobed at the apex.
- 3a. Style shallowly 3-lobed .... *B. guaiquinimae*
- 3b. Style divided into 3 branches, parted halfway or more to the base.
  - 4a. Petals white or pink.
    - 5a. Petals 21–22 mm long; sepals subacute, 11–12.5 mm long; leaves obtusely acute at apex, the larger 4–5 × 1.2–1.7 cm .... *B. bolivarensis*
    - 5b. Petals 9–12 mm long; sepals obtuse or rounded at apex, 8–9 mm long; leaves acute to subacute, 1.2–3.1 × 0.5–1.3 cm.
      - 6a. Leaves in a terminal rosette; upper leaf surface enervate or nerves faint; petals 4–6 mm broad .... *B. chimantensis*
      - 6b. Leaves imbricately extending on the branch below its tip; upper leaf surface impressed-nerved; petals 9–10 mm broad .... *B. toronoensis*
  - 4b. Petals yellow.
    - 7a. Peduncle elongate, 3–9 cm long, often surpassing the leaves, ebracteate.
      - 8a. Petals 3.5–4.2 × 2.7–3 cm; lateral nerves of upper leaf surface equally impressed but not elevated; upper midrib shallowly depressed .... *B. tristyla* subsp. *tristyla*
      - 8b. Petals smaller, 2.5–3.8 × 1.5–2.2 cm; lateral nerves of upper leaf surface unequally impressed, 6–8 pairs prominently elevated; upper midrib elevated .... *B. tristyla* subsp. *nervosa*
    - 7b. Peduncle lacking or at most 1.6 cm long, usually hidden among the leaves or much shorter.
      - 9a. Leaves linear-oblanceolate, 2.5–7 mm wide; petals 8 mm long; peduncle 8–16 mm long .... *B. huberiana*
      - 9b. Leaves broadly lanceolate, obovate, or oblong-oblanceolate, 8–15 mm wide (leaves on vegetative shoots sometimes wider); peduncles 3–6 mm long.
        - 10a. Leaves broadly oblong-lanceolate, acute, only slightly narrowed at the base, nearly the same width for most of length, 3.5–4.5 × 1–1.5 cm; leaves finely impressed-nerved beneath, not pale punctate beneath, stomata not manifest; sepals 12–13 mm long .... *B. ptariensis*
        - 10b. Leaves oblanceolate or obovate, obtuse, rounded, or subacute at apex, conspicuously narrowed to the base, broadest above the middle, 1–3.5 × 0.4–1(–1.5) cm; leaves mainly enervate beneath, pale punctate beneath, the stomata manifest; sepals 9–10 mm long .... *B. wurdackii*

LISSOCARPACEAE

Lissocarpa stenocarpa Steyerm., sp. nov. TYPE: VENEZUELA. Territorio Federal Amazonas: Depto. Atabapo, Cerro Marahuaca, riverine forest upstream from "Sima" Camp, along branch of Caño Negro, southcentral portion, 3°43′N, 65°31′W, 28 Feb.–1 Mar. 1985, 1,140 m, *Steyermark & Holst 130880* (holotype, MO; isotype, VEN).

Arbor 10-metralis glabra; foliis subcoriaceis oblongo-ellipticis vel elliptico-ovatis apice obtuse acuminatis basi obtusis vel subacutis 7.5–13 cm longis, (2–) 3–5.5 cm latis, nervis lateralibus numerosis tenuibus, venulis tertiariis laxe tenuiterque reticulatis; petiolis 5–13 mm longis; floribus solitariis bibracteatis supra axillaribus vel axillaribus pedicellatis, pedicellis 3–3.5 mm longis; bracteis ovatis apice rotundatis 2.5 mm longis, 2–2.2 mm latis; corollis cylindricis (alabastro maturo) 8.8 mm longis, basi 1.5 mm latis, medio 2.5 mm latis, lobis 4 ligulato-oblongis rotundatis 4 × 2 mm, coronae segmentis lanceolatis acutis 1.5–2 mm longis; calyce hypanthioque 6 mm longo, calyce 5 mm longo, 1.5–2 mm lato, lobis 4 suborbicularibus rotundatis 2 mm longis, 2 mm latis, minute glandulari-ciliolatis; fructu anguste elliptico-oblongo in prominentiam obtuse triangularem abrupte angustato basi rotundato 3–3.3 cm longo, 1.2–1.7 cm lato, 2.2–2.5 plo longiore quam latiore.

Tree 10 m tall, glabrous throughout. Leaves subcoriaceous, dark green above, paler below, oblong-elliptic to elliptic-ovate, obtusely acuminate at apex with acumen 0.8–1.2 cm long, obtuse to subacute at base, 7.5–13 cm long, (2–) 3–5.5 cm wide, glabrous both sides; midrib elevated above, impressed or less elevated below; lateral nerves numerous, faint, about equally prominulous on both sides as the loosely tertiary reticulate venation; petiole 5–13 mm long. Flowers solitary, superaxillary or axillary on new or old branches, pedicellate, bibracteate at base; pedicels 3–3.5 mm long; bracts ovate, rounded at apex, 2.5 mm long, 2–2.2 mm wide. Corolla green, tubular, 8.8 mm long in mature bud, 2.5 wide at the middle, 1.5 mm wide at base, the constricted basal part 2 mm long; 4 corolla lobes ligulate-oblong, rounded, 4 mm long, 2 mm wide; 8 coronal divisions lanceolate, acute, 1.5–2 mm long. Calyx and hypanthium 6 mm long; calyx

5 mm long, 1.5–2 mm wide, the cylindric tube 4 mm long, 1.5 mm wide; 4 lobes suborbicular, rounded at apex, 2 mm long, 2 mm wide, minutely glandular-ciliolate on margins. Style 1.5 mm long, upwardly thickened to a subtruncate-capitate stigma. Fruit yellow-green, narrowly elliptic-oblong, abruptly narrowed to a bluntly triangular protuberance at apex, rounded at base, 3–3.3 cm long, 1.2–1.7 cm wide, the subtending bracts more or less persistent.

This species differs from *L. benthamii* in the differently shaped fruit which is 2.2–2.5 times longer than broad and narrowly elliptic-oblong, and in the solitary flower instead of the few- to several-flowered, subracemose inflorescence. Additionally, its occurrence in the montane forest on the slopes of Marahuaca at an elevation of 1,140 m is in contrast to the lower altitudes where *L. benthamii* has been collected.

The differences suggested by Gleason (1926) to differentiate *L. guianensis* Gl. from *L. benthamii* cannot be maintained with respect to the more prominent upper midrib and conspicuously reticulate veinlets on both surfaces, supposedly characteristic of *L. guianensis.* Examination of material collected by Liesner from San Carlos de Río Negro, Venezuela, type locality for *L. benthamii,* indicates variation in these characters, some specimens showing prominently raised upper midribs but with only obscure tertiary venation on the lower foliar surface (*Liesner 8692*; *Liesner & Clark 9083*), while others (*Ducke 1117*) have more prominently reticulate veinlets on the lower surface. Similarly, specimens determined by White as *L. guianensis* (*Maguire 34618, 34907*) show only obscure venation on the lower surface.

The leaves of the Marahuaca specimens are prominently reticulate-veined on both surfaces with the upper midrib manifestly elevated. The leaves are relatively small in size as compared with either *L. guianensis* or *L. benthamii.*

Although *L. benthamii* and *L. guianensis* cannot be well separated on vegetative characters, the larger flowers of *L. guianensis* may be the best difference in distinguishing the two taxa. Pending further collections of flowering material, the two taxa may at present be considered as separate species.

RUBIACEAE

Chomelia stergiosii Steyerm., sp. nov. TYPE: VENEZUELA. Bolívar: Anacoco, Río Cuyuní, entre puesto de la Guardia Nacional Acarabisí and Anacoco, 2 Aug. 1981, *Basil Stergios & Gerardo Aymard 2804* (holotype, VEN; isotype, PORT).

Arbor 8-metralis, ramulis glabris; foliis elliptico-ovatis vel lanceolato-ellipticis apice obtuse acutis basi acutis vel subobtusis supra glabris subtus praeter axillas nervorum barbellatas glabris 4.5–7 cm longis, 2–4 cm latis; inflorescentia ebracteata longipedunculata, pedunculo 2.5 cm longo glabro; floribus sessilibus; calycis lobis foliaceis inaequalibus, duobus majoribus patulis vel reflexis oblongo-spathulatis apice rotundatis 3–5 mm longis (1–)1.7–1.8 mm latis, intus dimidio inferiore sparsim pilosulis; hypanthio extus sparsim pilosulo; corolla hypocrateriformi, tubo 20 mm longo, 0.7–1 mm lato ubique glabro, lobis lineari-ligulatis 4 mm longis, 1.2–1.5 mm latis.

Tree 8 m tall, branches slender, glabrous, spines axillary, 18–19 mm long. Leaves membranous, elliptic-ovate to lance-elliptic, obtusely acute at apex, acute to subobtuse at base, glabrous above, glabrous below except barbellate in the leaf axils and sometimes sparsely pilosulous along some of the lateral nerves, 4.5–7 cm long, 2–4 cm wide, with minute dark dots moderately scattered beneath; lateral nerves 4–5 each side, slender, slightly sulcate above, faintly impressed below, ascending, faintly anastomosing near margin; petiole 4–5 mm long, ciliate on upper margins, elsewhere glabrous, canaliculate above. Stipules triangular-ovate, acute, appressed-pubescent without, ciliolate at apex, 2–3 mm long. Inflorescence terminal, long-pedunculate, congested-cymose with 3–6 flowers, ebracteate; peduncle 2.5 cm long, filiform, glabrous; flowers sessile, the central one solitary and sessile, the others on short lateral axes 0.5 mm long. Calyx lobes 4, unequal, the two larger ones oblong-spatulate, rounded at apex, narrowed in the basal third, 3–5 mm long, (1–)1.7–1.8 mm wide in upper part, 1 mm wide in lower third, spreading to reflexed, sparsely minutely pilosulous within in lower half, glabrous without, two smaller lobes ligulate, obtuse, 2 mm long, 0.8 mm wide, spreading to reflexed; hypanthium clavate-turbinate, 2 mm long, 1 mm wide above middle, sparsely pilosulous with loosely spreading hairs. Corolla salverform, tube 20 mm long, 1 mm wide just below summit, 0.7 mm wide at base, glabrous within and without, lobes linear-ligulate, rounded at apex, 4 mm long, 1.2–1.5 mm wide, glabrous within, strigillose without mainly above middle. Anthers slightly exserted, linear, 2 mm long, 2 mm wide, glabrous. Style 13.5 mm long, glabrous.

This species is sympatric with *C. delascoi* Steyerm. but is distinguished from that taxon in the much longer corolla, foliaceous, manifestly unequal, and spreading calyx lobes, which are sparsely pilosulous on the interior surface of the larger pair, and larger leaves. It differs from *C. polyantha* Blake in the glabrous exterior of the corolla tube, the longer corollas, and the longer, spreading calyx lobes.

I take pleasure in naming this species for Dr. Basil Stergios, director of the herbarium of PORT, who has activated a well-organized collecting program in Venezuela and, together with his colleagues, has established an important herbarium in the Venezuelan Llanos of Edo. Portuguesa.

Coccocypselum croatii Steyerm., sp. nov. TYPE: VENEZUELA. Bolívar: vicinity of Icabarú, 4°19'N, 61°44'W, 600 m, 25 Jul. 1982, *Thomas B. Croat 54112* (holotype, MO).

Herba radicans, caulibus repentibus 2 mm diam. glabris; stipulis praeter vaginae marginem ciliatam glabris, subulatis elongatis 8–10 mm longis glabris; foliis petiolatis, petiolis 3–4 mm longis, marginibus superioribus setoso-ciliatis ceterum glabris; laminis obtusis vel rotundatis 4–4.5 cm longis, 1.5–3 cm latis supra costam mediam pilis setosis munitis atque marginibus dense adpresso-setoso-ciliatis, ciliis 0.5–0.7 mm longis ceterum glabris, nervis lateralibus utroque latere 7–9 arcuato-adscendentibus subtus elevatis; inflorescentiis longipedunculatis 5–7-floris, pedunculo 2.5–3 cm longo glabro; floribus subsessilibus; hypanthio glabro, post anthesim 1–1.5 mm longo; calycis lobis lineari-lanceolatis acutis 2.5–3 mm longis, 0.7–0.9 mm latis omnino glabris; bacca (immatura) coerulea 4 mm longa, 7 mm lata glabra.

Creeping herbaceous plant with rooting glabrous stems 2 mm diam.; stipular sheath glabrous except densely ciliate on the summit, prolonged into a glabrous, elongated, subulate appendage 8–10 mm long. Leaves petiolate; petioles 3–4 mm long, upper margins setose-ciliate, otherwise glabrous; leaf blades ovate, shortly acute at apex, obtuse or rounded at base, 4–4.5 cm long, 1.5–3 cm wide, upper midrib setose-ciliate, margins densely appressed setose-ciliate, the incurved hairs 0.5–0.7 mm long, elsewhere glabrous; lateral nerves 7–9 each side, arcuate-ascending, elevated below. Inflorescence long pedunculate, 5–7-flowered; peduncle 2.5–3 cm. Flowers subsessile; hypanthium and calyx glabrous; hypanthium in post-anthesis 1–1.5 mm long; calyx lobes linear-lanceolate, acute, 2.5–3 mm long, 0.7–0.9 mm wide, glabrous throughout. Fruit blue, 4 mm long, 7 mm wide, glabrous.

This species is related to *C. condalia* R. & P. of Peru, from which it differs in the larger ovate leaves, shorter petioles, more elongate setose cilia on the leaf margins, and more numerous, arcuately curved lateral nerves.

Pagameopsis Steyerm.

Recent collections of *Pagameopsis* have necessitated a reevaluation of the specific and subspecific elements within the genus.

Pagameopsis maguirei Steyerm. subsp. **pusillus** Steyerm., subsp. nov. TYPE: VENEZUELA. Territorio Federal Amazonas: Depto. Río Negro, Cerro de la Neblina, Camp III, NW Plateau, 13.5 km ENE of Base Camp, 0°54'N, 66°4'W, 1,750–1,850 m, 16–18 Feb. 1984, *Ronald Liesner 16013* (holotype, MO; isotype, VEN). Figure 8.

Suffrutex 0.1–0.2-metralis; foliis ad apices ramorum congestis rosulatis anguste lanceolato-ellipticis vel lanceolatis apice obtusis vel subobtusis subsessilibus 1–2.5 cm longis, 4–7 mm latis, supra dense adpresso-hirsutulis subtus marginibus dense hirsutulis, nervis lateralibus non manifestis; petiolis 2–3 mm longis dense hirsutulis; stipularum vaginis crebris dense hirsuto-strigosis 1.5–2 mm longis apice dense hispidis, pilis erectis 1.5–2.5 mm longis munitis; inflorescentiis subhemisphericis 7–30 mm longis, 20–30 mm latis pedunculatis; pedunculo erecto 2.5–4.5 cm longo 1–1.5 mm crasso, dense hirsutulo; floribus glomeratis ad apices 4–5 ramorum brevium inflorescentiae, quoque glomerulo 3–4-floribus; corollis 4–5-meris 4 mm longis, tubo lobisque extus praeter basin glabram dense strigosis, lobis 4–5 ligulato-lanceolatis subobtusis 2 mm longis intus dense lanulosis; calycis lobis 4–5 lineari-lanceolatis acutis extus dense strigoso-hirsutis intus glabris in sinubus una glandula nigra munitis.

Dwarf ligneous plant 0.1–0.2 m tall. Leaves densely crowded in an apical rosette, narrowly lance-elliptic or lanceolate, narrowed to an obtuse or subobtuse apex, narrowed to a subsessile base, 1–2.5 cm long, 4–7 mm wide, densely appressed-hirsutulous above, densely hirsutulous below and on margins; midrib elevated below, not evident above; lateral nerves not manifest; petiole 2–3 mm long, scarcely distinguishable from the leaf base. Stipular sheaths closely crowded, 1.5–2 mm long, densely hirsute-strigose, the summit densely loosely hispid with prominent hairs 1.5–2.5 mm long. Inflorescence subcapitate-subcorymbose, many-flowered, 7–30 mm long, 20–30 mm wide, pedunculate, bearing 4–5 short axes, the lowest axes 8–15 mm long,

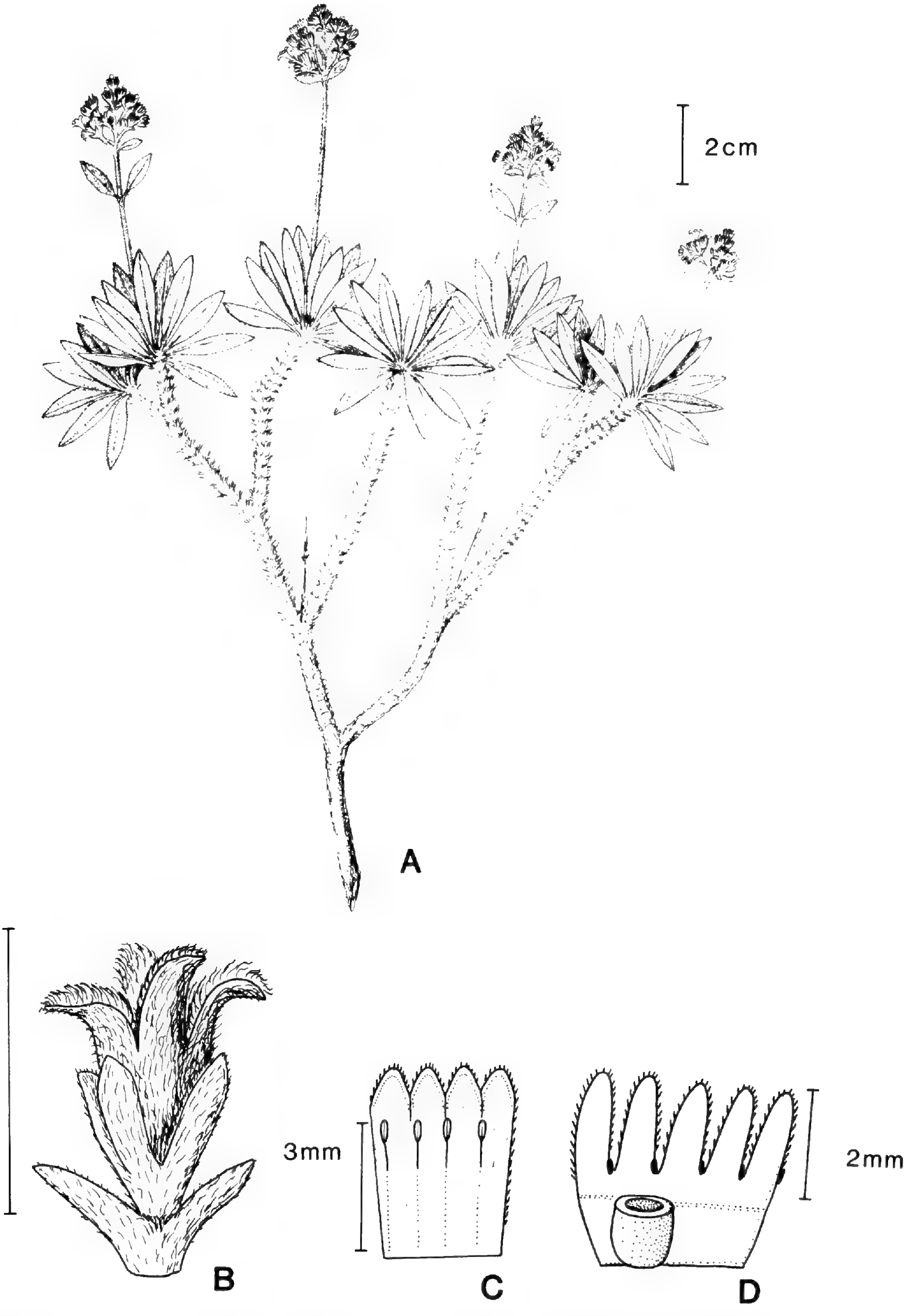

FIGURE 8. *Pagameopsis maguirei* subsp. *pusillus.*—A. Habit.—B. Flower, with subtending bracts.—C. Corolla, interior view.—D. Calyx and hypanthium, with pistil detached from calyx, interior view.

densely hirsute; rachis with 1–3 pairs of horizontally spreading bracts 3 mm long, 1 mm wide, hirsutulous without, glabrous, the inflorescence bibracteate at base with the bracts foliose, linear to oblong-lanceolate, subobtuse, 8–15 mm long, 2–3 mm wide, densely pubescent above, sparsely or moderately so below. Peduncle 2.5–4.5 cm long, 1–1.5 mm thick. Flowers in dense nearly sessile glomerules of 3–4 at the ends of short axes; 2 bracts subtending the base of the calyx navicular, oblong-lanceolate, 1.5–1.8 mm long, 0.8–1 mm wide, glabrous and glandular within. Calyx lobes slightly unequal, 4–5, linear-lanceolate, acute, 1.5–2 mm long, 0.5–0.6 mm wide, densely strigose-hirsute without and on margins, glabrous within with 1 gland between the sinuses of the lobes. Corolla 4 mm long, densely strigose without except where glabrous at base; tube 2 mm long; lobes 4–5, ligulate-lanceolate, subobtuse at apex, 2 mm long, densely lanulose within.

This taxon differs from the other known taxa of *Pagameopsis* in the very small, narrow, densely hirsute leaves and dwarf habit. It is closely related to *P. maguirei* Steyerm. subsp. *neblinensis* in having apical leaf clusters, but differs in the smaller inflorescences with 3–5 axes, and in the dense pubescence.

A glabrous variation of subsp. *pusillus* has been found on nearby Cerro Avispa of Venezuela.

Pagameopsis maguirei subsp. **pusillus** var. **glabrus** Steyerm., var. nov. A subsp. *pusillus* var. *pusillus* foliis glabris recedit. TYPE: VENEZUELA. Territorio Federal Amazonas: summit of Cerro Avispa, Río Siapa, 1°30′N, 65°51′W, 1,510 m, 5 Dec. 1972, *Cardona 3096* (holotype, NY; isotype, VEN).

Another variation of *Pagameopsis maguirei* from adjacent northern Brazil is here described.

Pagameopsis maguirei subsp. **neblinensis** Steyerm. var. **pirapucuensis** Steyerm., var. nov. TYPE: BRAZIL. Serra Pirapucú, 1,300 m, 26 Jan. 1966, *Nilo T. Silva & Umbelino Brazao 60880* (holotype, NY).

Frutex; foliis caulinis dispersis haud omnino apicalibus, longitudinem caulis 2.5–4 cm occupantibus, oblanceolatis apice subacutis 8–8.5 cm longis, 1.3–1.5 cm latis supra adpresso-pubescentibus vel saltem parte inferiore costae mediae pilosis, subtus costa media abundanter substrigosis vel pilosis ceterum sparse puberulis; petiolis utrinque abundanter strigosis vel substrigosis; stipularum vaginis elongatis 7–10 mm longis, 4–8 mm latis, moderatim vel dense strigosis, apice dense hirsutis.

Shrub; leaves arranged along the uppermost length of the stem, not wholly apical, oblanceolate, subacute at apex, 8–8.5 cm long, 1.3–1.5 cm wide, appressed-pubescent above or at least pilose on the lower part of the midrib, abundantly substrigose or pilose below, otherwise sparsely puberulous; petioles abundantly strigose or substrigose throughout. Stipular sheaths elongated, 7–10 mm long, 4–8 mm wide, moderately to densely strigose, the summit densely hirsute.

This taxon differs from the other varieties of subsp. *neblinensis* in the more densely strigose stipular sheaths, which are more densely hirsute at the summit. From var. *neblinensis* it differs in having the leaves dispersed along the stem length for 4 cm, and in the pilose petioles and lower surface. From subsp. *neblinensis* var. *angustifolius* it differs in the leaves pubescent below and above at least along the midrib or surface. From subsp. *maguirei* var. *maguirei* it may be differentiated by the pubescent upper midrib and lower leaf surface.

In order to accommodate the above newly described taxa, the following revised key to *Pagameopsis* is offered.

KEY TO THE SPECIES, SUBSPECIES, AND VARIETIES OF *PAGAMEOPSIS*

1a. Cauline leaves spaced along the upper part of stem for 2.5–11 cm; stipular sheath elongated, usually longer than broad or as long as broad, 3–15 mm long 2

2a. Cilia of leaf margins very conspicuous and dense, the hairs extending divaricately or subascending, 0.5–1 mm long; inflorescence with usually 3–5 densely flowered glomerules on 1–2 pairs of lateral axes, the whole inflorescence 1.5–4 cm long, 2–4 cm wide; leaves mainly 1⅔–3⅙ times longer than broad .... *P. garryoides*

2b. Cilia of leaf margins inconspicuous, appressed or subappressed to ascending, less than 0.5 mm long; inflorescence branched into numerous small glomerules borne on 7 or more branched axes, the whole inflorescence 5–11 cm long, 3–6 cm wide; leaves mainly (2⅞–)3–6 times longer than broad 3

3a. Lower leaf surface glabrous or mainly so, sometimes pubescent; upper leaf surface glabrous 4

4a. Petiolar base short-strigose throughout; calyx lobes densely hirtellous with spreading hairs; corolla lobes ca. 2 mm long, 1–1.25 mm wide .... *P. maguirei* subsp. *maguirei* var. *maguirei*

4b. Petiolar base glabrous above, glabrous to sparsely pubescent below; interior of calyx lobes with short strigose pubescence, the exterior with ascending hirtellous pubescence; corolla lobes 2.2–3 mm long, 0.7–1 mm wide .... *P. maguirei* subsp. *neblinensis* var. *angustifolius*

3b. Lower leaf surface pubescent; upper leaf surface pubescent or glabrescent, the midrib pubescent .... *P. maguirei* subsp. *neblinensis* var. *pirapucuensis*

1b. Leaves apically congested, occupying the uppermost 0.5–1.5 cm length of stem; stipular sheath contracted, broader than long or as broad as long, 1–6 mm long 5

5a. Leaves 2–10 cm long, 0.7–1.8 cm wide; bracts subtending base of inflorescence 15–55 mm long, 4–17 mm wide; inflorescence branching into numerous small glomerules borne in 7 or more branched axes, the whole inflorescence 5–11 cm long, 3–6 cm wide; shrub 0.3–2 m tall .... *P. maguirei* subsp. *neblinensis* var. *neblinensis*

5b. Leaves 1–2.5(–3) cm long, 0.4–0.7 cm wide; bracts subtending base of inflorescence 8–15 mm long, 2–3(–5) mm wide; inflorescence with only 3–5 densely clustered glomerules borne on 1–2 pairs of lateral axes, the whole inflorescence 0.7–3 cm long, 2–3 cm wide; depressed ligneous plant 0.1–0.2 m tall 6

6a. Upper and lower leaf surfaces densely hirsute .... *P. maguirei* subsp. *pusillus* var. *pusillus*

6b. Upper and lower leaf surfaces glabrous .... *P. maguirei* subsp. *pusillus* var. *glabrus*

Psychotria guanchezii Steyerm., sp. nov. TYPE: VENEZUELA. Territorio Federal Amazonas: Río Sipapo junto a la comunidad indígena de la etnia Piaroa, 15 Nov. 1984, *Francisco Guanchez 3644* (holotype, VEN; isotype, TFAV). Figure 9.

Suffrutex 1.5-metralis, ramis glabris; stipulae vagina 2–2.5 mm longa, 1.8–2 mm lata glabra in duobus dentibus subulatis utroque latere 3 mm longis minute ciliolatis desinenti; petiolis 3–9 mm longis glabris; foliorum laminis anguste lanceolatis apice acutis basi acutis utrinque glabris 4–9.5 cm longis, 0.8–2 cm latis, costa media subtus elevata supra impressa, nervis lateralibus 16–20 utroque latere divaricate patentibus; inflorescentia terminali pedunculata, pedunculo gracili erecto 4–4.3 cm longo, 1 mm lato minute sparsimque puberulenti; inflorescentia parva umbellata cymosa 1.2–1.8 cm longa, 1.3–1.8 cm lata, axibus principalibus quattuor, lateralibus tribus patentibus 5–6-floris, 4–6 mm longis, 0.5–1 mm latis, uno axe centrali erecto 7–8-flora, omnibus moderatim vel abundanter puberulentibus; bracteis duobus sub inflorescentia patentibus subulatis 2.5–2.7 mm longis minute moderatimque puberulentibus; bracteis sub fasciculis florium ligulatis vel lanceolatis 2.5–3 mm longis utrinque minute denseque puberulentibus; calyce hypanthioque 1.5–2 mm longo; calycis lobis deltoideis obtusis 0.3 mm longis, 0.8 mm latis; corolla subinfundibuliformi 5–6 mm longa extus praeter basim glabram ipsa dense puberulenti pilis patentibus 0.1–0.2 mm longis munita intus dimidia parte superiore puberula ceterum glabra.

Slender subshrub 1.5 meters tall, branches glabrous. Stipular sheath 2–2.5 mm long, 1.8–2 mm wide, glabrous, terminating on each side in 2 subulate minutely ciliolate teeth 3 mm long. Leaf blades narrowly lanceolate, acute at apex and base, glabrous both sides, 4–9.5 cm long, 0.8–2 cm wide, midrib elevated below, impressed above; lateral nerves 16–20 each side, divaricately spreading at an angle of 5–10°, faintly anastomosing at 1–2 mm from margin; petiole 3–9 mm long, glabrous. Inflorescence small, cymosely umbellate, terminal, 1.2–1.8 cm long, 1.3–1.8 cm wide, on erect, slender peduncle 4–4.3 cm long, 1 mm wide, minutely and sparsely puberulent; axes of inflorescence 4, three lateral ones spreading, 4–6 mm long, 0.5–1 mm wide, one central axis erect and longer, 7–8 mm long, 1 mm wide, all moderately to abundantly puberulent with spreading unequal puberulence, the longest hairs 0.1 mm long; 3 lateral axes 5–6-flowered, 4th axis 7–8-flowered. Bracts subtending base of inflorescence divaricately spreading, subulate, 2.5–2.7 mm long, 0.3 mm wide, minutely and moderately puberulent; bracts subtending flower clusters ligulate to lanceolate, acute to obtuse, 2.5–3 mm long, 0.7 mm wide, minutely densely puberulent on both sides. Calyx and hypanthium 1.5–2 mm long; hypanthium shallowly campanulate, 1 × 1 mm; calyx 1 mm long, 1.2 mm wide, shallowly lobed; lobes deltoid, obtuse, 0.3 mm long, 0.8 mm wide. Corolla infundibuliform, 5–6 mm long; tube 2.2–3.5 mm long, 0.8 mm wide at base, 1.3 mm wide at orifice, densely puberulent, except at very base, with short spreading hairs 0.1–0.2 mm long, pubescent in upper half within from staminal insertion to orifice, elsewhere within glabrous; lobes 4, lanceolate, subacute, 1.7–2.5 mm long, 1.3 mm wide, densely puberulous without. Anthers linear, 1.1–1.2 mm long, included in uppermost part of corolla tube; filaments 0.8 mm long, inserted halfway up corolla tube. Style 4.2 mm long, papillate; stigmas rhomboid, dilated, exserted, 0.8 mm long.

This species is related to *P. capitata* R. & P. but is reduced in the size of all parts. Moreover, the densely puberulous calyx and minute, puberulous corollas, small inflorescence with slender peduncle, and narrow leaves are noteworthy distinguishing characters of the taxon. From *P. piresii* Steyerm. of Amapá, Brazil, it is differen-

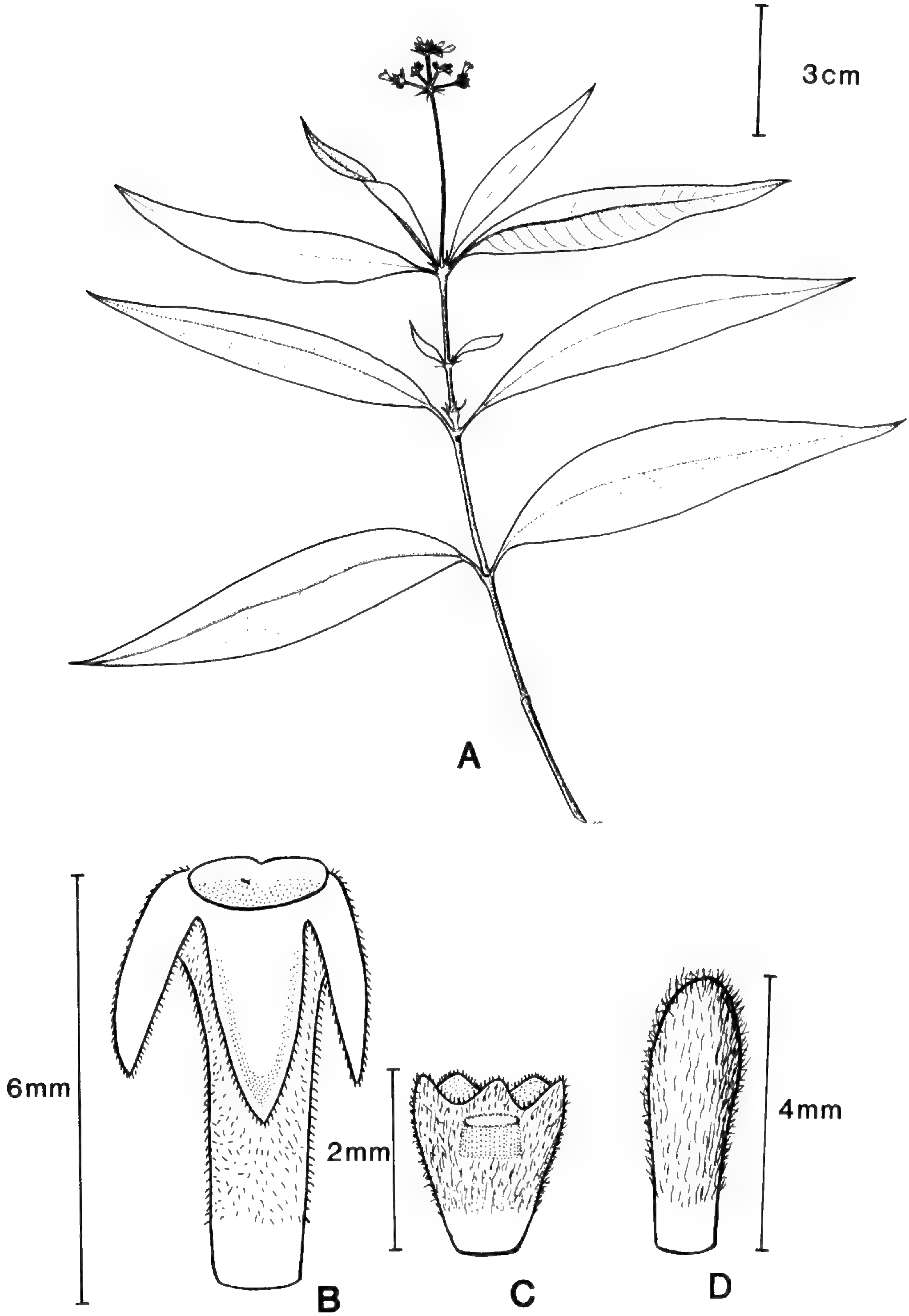

Figure 9. *Psychotria guanchezii.*—A. Habit.—B. Corolla.—C. Calyx and hypanthium, with position of disk indicated.—D. Corolla, pre-anthesis.

tiated by the smaller, 5-merous corollas, shorter stipular teeth, and smaller inflorescence with fewer axes.

Psychotria ronaldii Steyerm., sp. nov. TYPE: VENEZUELA. Territorio Federal Amazonas: Depto. Atabapo, Cerro Huachamacari, forested slope, 3°39′N, 65°42′W, 600–750 m, 4 Mar. 1985, *Ronald Liesner 18214* (holotype, MO; isotype, VEN). Figure 10.

Frutex 2-metralis, caulibus glabris; stipularum vaginis apice late subrotundatis vel interdum paullo subacutis 2.5 mm altis interiusque pubescentibus; foliis late elliptico-obovatis apice caudato-acuminatis acumine 2 cm longo, ad basim acute angustatis decurrentibusque 22–30 cm longis, 8–10.5 cm latis utrinque glabris, nervis lateralibus utroque 14–17 late patentibus; petiolis 1–1.5 cm longis glabris; inflorescentia terminali paniculata parva subhemisphaerica paullo latiore quam longiore 2 cm longa, 2.5–3 cm lata, axibus lateralibus 4–6 patentibus, axium cicatricibus basi fimbriato-pubescentibus; pedunculo erecto 1.8–2.5 cm longo, 1–1.5 mm crasso glabro; floribus sessilibus, bracteis ut videtur nullis; hypanthio calyceque 2.1 mm longo glabro, calyce breviter 5-lobato, dentibus late deltoideis vel fere truncatis; corolla subinfundibuliformi 4.5 mm longa extus glabra, intus infra insertionem filamentorum pilosulo ceterum glabro, lobis 5.

Shrub 2 m tall; stems glabrous. Stipular sheaths broadly semicircular, rounded or slightly acute at apex, buff-pubescent within and on the apical margins, 2.5 mm high, 5 mm wide. Leaves broadly elliptic-obovate, caudate-acuminate at apex with acumen 2 cm long, acutely narrowed to a decurrent base, 22–30 cm long, 8–10.5 cm wide, glabrous both sides; lateral nerves 14–17 each side, widely spreading at an angle of 15°–20°, elevated below, tertiary venation beneath finely grossly reticulate. Petioles 1–1.5 cm long, glabrous. Inflorescence terminal, paniculate, subhemispheric, slightly broader than long, 2 cm long, 2.5–3 cm wide at base; lateral axes divaricately spreading, the lower ones 7–8 mm long, the upper 2–4 mm long; base of axes with fimbriate-pubescent scars; axes terminating in 7–10-flowered clusters. Peduncle erect, 1.8–2.5 cm long, 1–1.5 mm thick, glabrous. Flowers in groups of 7–10. Calyx and hypanthium 2.1 mm long, glabrous; hypanthium 1 mm long, 1 mm wide; calyx 1 mm long, 1.2 mm wide, the border shallowly toothed; calyx teeth broadly deltoid to nearly truncate. Corolla cream-colored, subinfundibuliform, 4.5 mm long, 2 mm wide above, 1 mm wide at base, glabrous without, glabrous within except for a pilosulous zone at the antheriferous level; lobes 5, oblong-lanceolate, subacute, 1.5 mm long, 1 mm wide.

The immediate relationship of this taxon with other species of the genus is not apparent. The species is characterized by the small corollas, glabrous leaves, inflorescence, and stems, and fimbrillate pubescence of the scars on the inflorescence axes.

The species is named for Ronald Liesner, who made important collections on Cerros Huachamacari and Marahuaca during the expedition in 1985 sponsored by the Terramar Foundation.

Remijia marahuacensis Steyerm., sp. nov. TYPE: VENEZUELA. Territorio Federal Amazonas: Depto. Atabapo, Cerro Marahuaca, "Sima" Camp, southcentral portion of forested slopes along eastern branch of Caño Negro, 3°43′N, 65°31′W, 1,140 m, 21–22, 24 Feb. 1985, *Julian A. Steyermark & Bruce Holst 130440* (holotype, MO; isotype, VEN). Figure 11.

Frutex 2 m altus, ramis dense adpresso-hirsutulis; foliis anguste lanceolatis vel lineari-lanceolatis apice longiacuminatis basi acutis vel subacutis 11–18 cm longis, 2.5–5 cm latis, adultis supra glabris subtus costa media nervis lateralibusque adpresso-pubescentibus axillibus barbellatis ceterum glabris, nervis lateralibus utroque latere 9–11; petiolis 0.5–1.5 cm longis adpresso-pubescentibus; inflorescentia axillari sub anthesi capitata 2 cm longa, 1.5 cm lata bracteis foliosis oblongo-ovatis obtusis vel subobtusis 1.7–2 cm longis, 0.8–1.1 cm latis extus adpresso-pubescentibus subtenta; infructescencia breviter racemosa 2–4 cm longa, 3 cm lata elongata; rhachidi dense hirsutula; pedunculo 6–15 cm longo, 2 mm lato, dense adpresso-hirsutulo; floribus heterostylis sub anthesi brevipedicellatis, pedicellis 1.5 mm longis dense hirsutulis, sub fructu 5–7 mm longis; calyce hypanthioque 4–5 mm longo, hypanthio 3–4 mm longo; calyce apice fere truncato extus sericeo-strigoso, intus glabro-eglanduloso; corolla 15–21 mm longa, tubo 10–15 mm longo, 2.5 mm lato, extus dense lanuginoso pilis erectis subadpressis munito, lobis 5 lanceolatis subobtusis 5–6 mm longis extus dense lanuginosis; capsulis maturis cylindricis 1.5–2.3 cm longis, 5–6 mm latis, adpresso-pubescentibus deorsum dehiscentibus, valvis apice solutis; seminibus alatis ligulato-oblongis extremitatibus rotundatis 5 mm longis, corpusculo ovali 1.7–2 mm longo, 1.5 mm lato, alis late oblongis rotundatis 1.5–2.5 mm longis, 1.5 mm latis.

Shrub 2 m tall, young stems densely appressed-hirsutulous. Stipules ligulate-lanceolate, subacute, 1.5–3 cm long, 4–7 mm wide, appressed pubescent without, midrib densely pubescent. Leaf blades subcoriaceous, dark green above, pale green below, linear-lanceolate to narrowly lanceolate, long acuminate at apex, acute to sub-

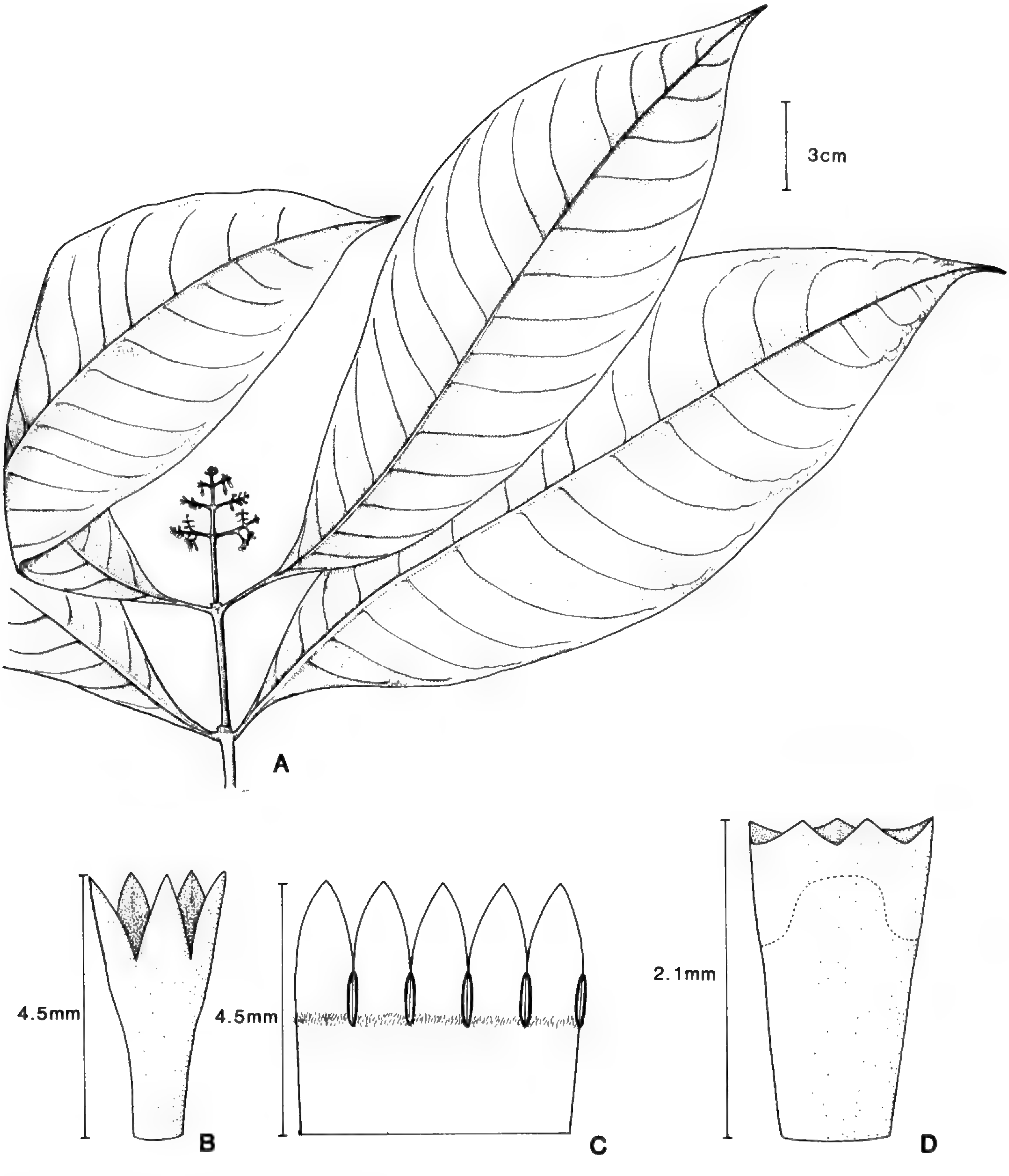

FIGURE 10. *Psychotria ronaldii.*—A. Habit.—B. Corolla.—C. Corolla, interior view.—D. Calyx and hypanthium, with position of disk indicated.

acute at base, 11–18 cm long, 2.5–5 cm wide, glabrous above on mature leaves, lower surface appressed-pubescent on midrib and lateral nerves, barbellate in axils of nerves beneath, lower surface otherwise mainly glabrous; lateral nerves 9–11 each side, sulcate above, elevated below, ascending at an angle of 45–50°, curving into the margin, tertiary venation finely reticulate below. Inflorescence axillary, capitate in anthesis, 2 cm long, 1.5 cm wide, 6–10-flowered, subtended by 2 foliose, oblong-ovate, obtuse or subobtuse bracts 1.7–2 cm long, 0.8–1.1 cm wide, appressed-pubescent without. Infructescence racemose, 2–4 cm long, 3 cm wide, rachis densely hirsutulous, up to 1.5–2 cm long in fruit. Peduncle 6–15 cm long, 2 mm thick, densely appressed-hirsutulous. Flowers heterostylous, short-pedicellate, in anthesis pedicels 1.5 mm long, in

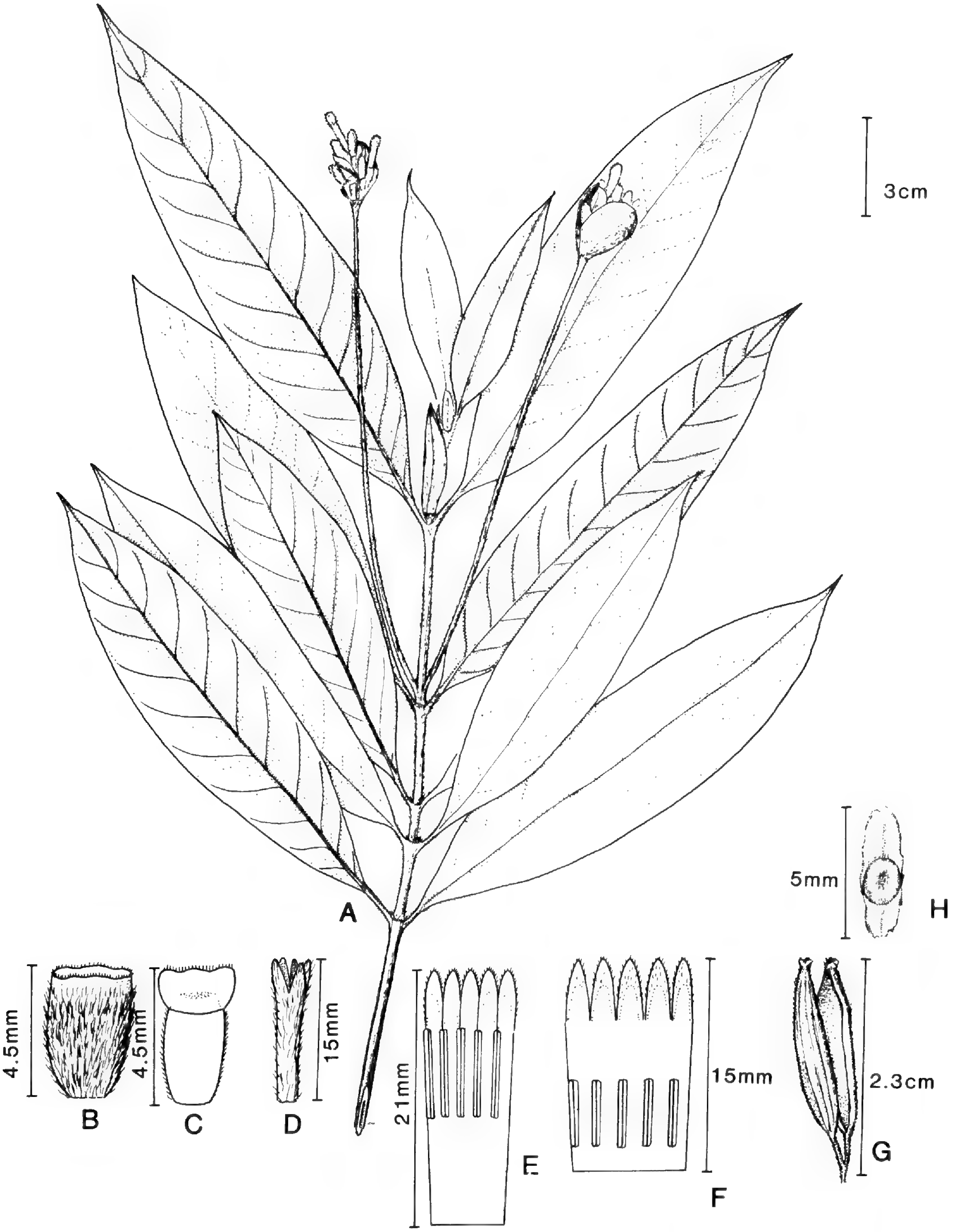

FIGURE 11. *Remijia marahuacensis.*—A. Habit.—B. Calyx and hypanthium, external view.—C. Calyx and hypanthium with disk, internal view.—D. Corolla.—E. Short-styled corolla.—F. Long-styled corolla.—G. Fruiting capsule after dehiscence.—H. Seed.

fruit 5–7 mm long, densely hirsutulous. Calyx and hypanthium short-cylindric, 2.5 mm wide, densely lanuginose without with cream-colored, erect-ascending hairs; calyx 1–1.3 mm long, 2.5 mm wide, truncate or shallowly cupulate, strigose-sericeous without, ciliate on margins, glabrous and eglandular within. Corolla pink, subhypocrateriform, densely buff lanuginose without, 15–21 mm long, tube 10–15 mm long, 2.5 mm wide, glabrous within; lobes 5, lanceolate, subobtuse, 5–6 mm long, 1.2–2 mm wide. Anthers linear, 5.3 mm long, in short-styled flowers inserted in the upper half of the corolla tube, in long-styled flowers inserted 2–3 mm above base of corolla tube. Style 5.5–9 mm long. Mature capsules cylindric, 1.5–2.3 cm long, 5–6 mm wide, appressed pubescent. Seeds ligulate-oblong, winged, 5 mm long, the body pale brown, oval, 1.7–2 mm long, 1.5 mm wide, wings broadly oblong, rounded, 1.5–2.5 mm long, 1.5 mm wide.

Distribution. Forested slopes of Cerro Marahuaca, Territorio Federal Amazonas, Venezuela, at an altitude of 1,140–1,220 meters.

Paratype. Cerro Marahuaca, Upper Río Yameduaka, 3°38′N, 65°28′W, 1,225 m, 22 Feb. 1985, *Liesner 17818* (MO, VEN).

This species is related to *R. maguirei* of Cerro de la Neblina, from which it differs in the smaller seeds, much shorter corolla, eglandular interior of calyx tube, glabrous petioles, lower leaf surface, and densely pubescent branches.

Of the 20 species of *Remijia* presently known from the Guayana, six are endemic to different sandstone table mountains (*R. pilosinervia* from Chimantá, *R. maguirei* from Neblina, *R. argentea* from Yapacana and Moriche, *R. steyermarkii* from Duida, and *R. roraimae* from Roraima and Chimantá). *Remijia densiflora* is widespread on several table mountains and surrounding areas of Bolívar and Territorio Federal Amazonas. *Remijia marahuacensis* becomes the seventh species to add to the list of endemic taxa of this genus.

Schradera marahuacensis Steyerm., sp. nov. TYPE: VENEZUELA. Territorio Federal Amazonas: Depto. Atabapo, Cerro Marahuaca, "Sima" Camp, southcentral portion of forested slopes along eastern branch of Caño Negro, 3°43′N, 65°31′W, 1,140 m, 25 Feb. 1985, *Julian A. Steyermark & Bruce Holst 130721* (holotype, MO; isotype, VEN).

Suffrutex epiphyticus glabrus, stipulis non visis; foliis petiolatis 5–16 mm longis; laminis coriaceis oblongo-ellipticis apice obtusis vel subobtusis basi acutis 9.5–13 cm longis, 2.5–5.5 cm latis, costa media subtus elevata supra paullo anguste sulcata, nervis lateralibus utroque latere 11–12 adscendentibus subtus subprominulis supra obsoletis; capitulis hemisphaericis 10–20-floris 2.5–3 cm diam., 1.5–2 cm altis; pedunculo solitario terminali 3.5–5.5 cm longo, 2–2.5 mm lato infra apicem paullo dilatato; involucro 7–8 mm alto lobato, lobis suborbicularibus 8 mm longis, 10 mm latis; calyce hypanthioque 10 mm longis, 4–5 mm latis; calyce cylindrico-campanulato breviter lateque deltoideo-dentato vel subtruncato; corolla cylindrica 12 mm longa extus glabra intus pilosula, lobis 5 lanceolatis subacutis 5 mm longis, 1.8–2 mm latis; staminibus prope basin tubi corollae insertis.

Woody glabrous epiphyte. Leaf blades coriaceous, oblong-elliptic, obtuse to subobtuse at apex, acute at base, 9.5–13 cm long, 2.5–5.5 cm wide; midrib elevated below, slightly narrowly sulcate above, lateral nerves ascending, 11–12 each side, faint or at most slightly prominulous below, obsolete above. Petioles 5–16 mm long. Inflorescence hemispheric, 10–20-flowered, 2.5–3 cm diam., 1.5–2 cm high. Peduncle solitary, terminal, 3.5–5.5 cm long, 2–2.5 mm wide, slightly dilated below summit. Involucre 7–8 mm high, lobed, lobes suborbicular, 8 mm long, 10 mm wide. Calyx and hypanthium 10 mm long, 4–5 mm wide, calyx cylindric-campanulate, shortly and broadly deltoid-toothed or subtruncate. Corolla fleshy, cylindric, 12 mm long; tube 6 mm long, pilosulous internally; lobes 5, lanceolate, subacute, 5 mm long, 1.8–2 mm wide. Stamens 5, inserted near base of corolla tube; anthers linear, 3.5 mm long, 0.7 mm wide. Pistil 6.5 mm long; stigmas 2, linear.

Distribution. Known only from forested slopes of Cerro Marahuaca, 1,140–1,225 m, Territorio Federal Amazonas, Venezuela.

Paratype. VENEZUELA. TERRITORIO FEDERAL AMAZONAS. Cerro Marahuaca, upper Río Yameduaka, 3°38′N, 65°28′W, 1,225 m, 22 Feb. 1985, *Liesner 17818* (MO, VEN).

Sipanea setacea Steyerm., sp. nov. TYPE: VENEZUELA. Bolívar: Dtto. Piar, Cerro El Venado, 20 km E of Canaima, 6°17′N, 62°41′W, 1,300 m, 31 Aug. 1983, *Otto Huber, G. T. Prance & C. Alarcon 8246* (holotype, NY).

Herba repens, caulibus tenuibus dense pilosulis pilis patentibus 0.2 mm longis praeditis; stipulae appendice setiformi 2–3 mm longa; foliorum laminis ovatis vel elliptico-ovatis apice acutis basi obtusis vel subacutis 1.2–2 × 0.9–1.2 cm utrinque dense subadpresso-pilosis, petiolis 3.5–4.5 mm longis; inflorescentia pedunculata triflora, pedunculo terminali 1–1.7 cm longo dense pilosulo pilis patentibus praedito; floribus subsessilibus, pedicellis ad 0.5 mm longis; corolla purpurea 7.5 mm longa, tubo 4 mm longo, lobis 3.5 mm longis extus pilosulis.

Herbaceous plant; stems creeping, slender, 0.5 mm diam., densely pilosulous with spreading or loosely ascending hairs 0.2 mm long; internodes 1–1.8 cm long. Stipules setaceous, 2–3 mm long, 0.1 mm wide, densely pilosulous. Petioles 3.5–4.5 mm long, 0.5–0.7 mm wide, densely pilosulous with spreading hairs. Leaf blades ovate to elliptic-ovate, acute at apex, obtuse to subacute at base, 1.2–2 cm long, 0.9–1.2 cm wide, densely subappressed-pilose both sides with hairs 0.2–0.5 mm long. Inflorescence terminal, pedunculate, 3-flowered, the peduncle slender, 1–1.7 cm long, densely pilosulous with spreading hairs. Flowers subsessile; pedicels to 0.5 mm long. Bracts subtending inflorescence 2, subulate, acuminate, 2.2 cm long, 0.1 cm wide, glabrous within, setose-ciliate with hairs 0.3–0.5 mm long. Calyx lobes subulate or subsetaceous, 2.2–2.5 mm long, 0.3–0.4 mm wide, densely pilosulous with hairs 0.4 mm long; hypanthium pyriform, densely villosulous with spreading white, non-tuberculate hairs 0.4–0.5 mm long. Corolla "purple" (fide Huber et al.), subsalverform, 7.5 mm long, the tube 4 mm long, shortly pilosulous with hairs within near the base of the stamens; lobes narrowly oblong, obtuse, 3.5 mm long, 1.2 mm wide, moderately pilose without. Anthers linear-oblong, 1.3 mm long, 0.3 mm wide. One setiform squamella 0.15–0.2 mm long situated in each sinus of the calyx lobes.

In its setaceous stipules and pubescent exterior of the corolla lobes, this species differs from other members of sect. *Virecta* subsect. *Cryptotricha*, but resembles them in habit, slender stems, and small leaves. From *S. ovalifolia* Bremek. var. *ovalifolia* and var. *villosissima* Steyerm. it differs in the shorter peduncle and petioles, longer corolla and corolla lobes, 3-flowered inflorescence on a shorter peduncle, shorter, non-tuberculate hairs of the hypanthium, narrower leaves, and purple instead of white corollas. From *S. micrantha* Sandw. it may be distinguished by the spreading pubescence of stems and peduncles, broader ovate leaves with pubescent upper surface, loosely pubescent calyx lobes, and 3-flowered inflorescence. From *S. gleasonii* Steyerm. it is differentiated by the subsessile flowers, shorter petiole, calyx lobes, hypanthium, and corolla tube, smaller leaf blades, shorter foliar pubescence, and non-tuberculate hairs of the hypanthium. Finally, from *S. cowanii* Steyerm. it differs in the densely spreading hairs of the hypanthium, the shorter corolla and calyx lobes, and the 3-flowered inflorescence.

COMPOSITAE

Gongylolepis terramarae Steyerm., sp. nov. TYPE: VENEZUELA. Territorio Federal Amazonas: Depto. Atabapo, Cerro Marahuaca, forested steep sandstone SE-facing slopes and bluffs, above branch of Caño Negro, southcentral portion of meseta, downstream from "Sima" Camp, 3°43′N, 65°31′W, 1,220–1,350 m, 23–24 Feb. 1985, *Julian A. Steyermark & Bruce Holst 130629* (holotype, MO; isotype, VEN).

Arbor 3–4-metralis, caulibus vegetativis ad apices lanulosis, internodiis infra petiolos atque ad nodos minus lanulosis, caulibus floriferis vetustioribusque sparsim pilosulis vel glabris; foliis lanceolato-ellipticis vel oblanceolatis apice obtusis basi angustatis ad petiolum longe decurrentibus 9–24 cm longis, 3–6 cm latis, supra costa media laxe pilosa vel glabrescenti, subtus costa media adpresso-pilosa pilis elongatis munita ceterum utrinque sparsim adpresso-pilosis vel glabris, venulis tertiariis subtus vix manifestis supra magis prominulis; pedunculis corymbosis 1.5–3 cm longis bracteatis breviter pubescentibus; capitulis aliquot campanulatis maturis 3–3.5 cm longis, 2–2.5 cm latis 21-floris; involucro 3 cm longo 5–6-seriato, phyllariis glabris apicibus marginibusque scariosis; pedunculi bracteis ovatis apice acutis 2.5–4 mm longis dorsaliter puberulis vel glabrescentibus; corollis bilabiatis, tubo 11 mm longo, 3 mm lato, lobo exteriore ligulato 14 mm longo, 3.5 mm lato, lobo interiore 2-fisso, segmentis linearibus; achaeniis anguste linearibus nigris 9.5 mm longis, 1.4 mm latis costatis.

Tree 3–4 m tall; tips of vegetative stems lanulose, the internodes below the petioles and at the junction of the petioles sparsely lanulose, the flowering and older stems sparsely pilosulous to glabrous. Leaves coriaceous, dark green above, pale green below, lance-elliptic to oblanceolate, obtuse at apex, narrowed to an acute long-decurrent base, 9–24 cm long, 3–6 cm wide, midrib above loosely pilose to glabrescent, below usually appressed pilose with elongate hairs, elsewhere sparsely pilosulous to glabrous on both surfaces; lateral nerves at an angle of 35–45°, faint on both sides for ⅔–¾ distance to the margin, becoming obsolescent; tertiary venation beneath scarcely or faint only, above slightly or more evidently reticulate. Petiole on flowering shoots not developed, up to 10 cm long on vegetative shoots, sparsely puberulous to lanulose at the base. Inflorescence corymbosely branched, the peduncles 1.5–3 cm long, bracteate, shortly pubescent. Heads several, campanulate, mature ones 3–3.5 cm long, 2–2.5 cm wide, 21-flowered, on bracteolate pubescent pedicels 1.5–4 cm long; bracteoles ovate-lanceolate, acute, 3–3.5 mm long, dorsally pubescent. Involucre green, 3 cm long, 5–6-seriate, outermost bracts ovate, 4–5 mm long, 2.5–3 mm wide, middle ones ligulate-oblong, rounded at apex, 12–13 mm long, 5–6 mm wide, innermost linear-ligulate, rounded at apex, 23–30 mm long, 4 mm wide. Bracts of peduncle ovate, subacute at apex, 2.5–4 mm long, dorsally more or less appressed-puberulous to glabrescent. Corollas white, tube 11 mm long, 3 mm wide, glabrous, external lobe ligulate, 14 mm long, 3.5 mm wide, minutely 3-lobed at apex, lobes rounded; inner lobe 12–13 mm long, 2-parted with linear subacute segments 1 mm wide. Anther 11–12 mm long. Pappus buff, 15–17 mm long, setae numerously barbellate. Achene black, narrowly linear, 9.5 mm long, 1.4 mm wide, costate.

Paratype. VENEZUELA. Cerro Marahuaca, slope between Upper Río Yameduaka and base of cliff, 3°38′N, 65°28′W, 1,225–1,400 m, *Liesner 17751* (MO, VEN).

This species resembles *G. huachamacari* Maguire & Wurd. of Cerro Huachamacari, from which it differs chiefly in the smaller flowers, greatly reduced peduncular bracts, and larger leaves with pubescent midribs. From *G. pedunculata* Mag. & Wurd. of cerros Parú and Huachamacari it differs in the smaller, less numerously flowered heads, corymbose inflorescence, more reduced size of the peduncular bracts, pubescent midrib, and narrower involucral bracts; while from *G. yapacana* Maguire & Wurd. of Cerro Yapacana, it differs especially in the absence of large areolate, strongly reticulate venation, and shorter peduncles.

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A NEW SPECIES OF *JATROPHA* (EUPHORBIACEAE) FROM NICARAGUA[1]

GRADY L. WEBSTER[2]

ABSTRACT

A new species, *Jatropha stevensii*, is described from collections in Dept. Boaco in Nicaragua. It may be assigned to subg. *Curcas* and appears related to *Jatropha fremontioides*, a species from southern Mexico. *Jatropha stevensii* represents yet another extension of the Mexican xerophytic element into Central America, and the second record for *Jatropha* subg. *Curcas*.

When *Jatropha costaricensis* Webster & Poveda was described from Guanacaste, Costa Rica, some years ago (Webster & Poveda, 1978), it was predicted that other xeric relict taxa might be discovered elsewhere in Central America. Recent botanical exploration in Nicaragua has disclosed not only a number of new populations of *Jatropha podagrica* Hook. in rocky areas in Dept. Esteli, but also on basaltic ridges in Dept. Boaco a species that appears to be undescribed. Unlike *J. podagrica,* which belongs to subg. *Jatropha* (Dehgan & Webster, 1979), the plant from Boaco clearly is referable to subg. *Curcas.*

Jatropha stevensii Webster, sp. nov. TYPE: Nicaragua, Dept. Boaco, 1.6 km SW of Santa Cruz, low ridge of basaltic lava, 140–160 m, 12°24'N, 85°50'W, 7 June 1984, *W. D. Stevens 22902* (MO, holotype; DAV, isotype; additional isotypes to be distributed). It should be noted that the type collection includes both glabrous and pubescent specimens and was apparently gathered from several individuals.

Ab *J. olivacea* differt dichasio *menor,* minore stipulis obsoletis, foliis integris marginibus non glanduligeris; ab *J. alamanii* foliis elobatis, sepalis minoribus, petalis tantum ⅓ longitudinis coalitis; ab *J. fremontioide* foliis acuminatis, dichasio non capituliforme.

Deciduous shrub to 3 m high; twigs terete, greyish- or reddish-brown, glabrous or hispidulous, exuding cloudy latex when cut. Leaves alternate or clustered on spur shoots; stipules obsolete; petioles slender, 5–25 mm long; blades thinly chartaceous, ovate contracted to an acuminate tip, cordate at base, loosely tomentose to glabrous beneath, 2–4 cm long, 1–3 cm broad, palmately 5-veined at base, brochidodromous, beneath midrib and secondaries raised, veinlets prominent; margins entire, eglandular. Monoecious; dichasia terminal, often paired, with peduncle 1–2.5 cm long, branches hispidulous; bracts oblong-lanceolate to oblanceolate, glabrous or tomentulose, lower ones 4–5 mm long and 1.2–1.3 mm broad; pistillate flowers 0–2 per dichasium, at lower nodes; staminate flowers 10–15, at upper dichotomies. Staminate flower: pedicel 0.5–0.8 mm long, articulated at base; sepals 5, lanceolate, obtuse or subacute, entire, glabrous or hirsutulous, 2.5–4.8 mm long, 1.2–2 mm broad; petals 5, pale green, oblong, glabrous abaxially, copiously hirsutulous adaxially in lower half, 5.5–6 mm long, coherent into a tube in lower ⅓, midrib with several sharply ascending laterals that dichotomize distally; disk glands 5, cubical, glabrous, 0.5–0.6 mm high; stamens 10, biverticellate, monadelphous below into a slender column 3–4 mm high, outer stamens on filaments ca. 1 mm long. Pistillate flower: pedicel glabrous or tomentulose, becoming 3–11 mm long in fruit; sepals 5, elliptic or lanceolate, obtuse or subacute, becoming in fruit 5.5–6.5 mm long, 2.5–3.8 mm broad; petals 5, ovate at base tapering to oblong obtuse tips, pale green, ca. 5.8–6 mm long, 4–4.2 mm broad, hirsutulous adaxially, coherent in lower ⅓; disk dissected into 5 lobes; ovary smooth, glabrous, sharply carinate, 3-locular; styles ca. 3 mm long, connate in lower ⅓, erect, scarcely bifid; stigmas dilated, elliptic, 0.7 mm long, 0.3 mm broad. Capsule smooth, 3-lobed, prominently 3-carinate on back of cocci, 1.5–1.6 mm in diameter; seeds ellipsoidal, ca. 9 mm long, smooth; caruncle brownish, deeply flabellately lobed, 2.5 mm long, 4 mm broad.

Additional collections examined. NICARAGUA. BOACO: 1 km E of Santa Cruz, 200 m, *Moreno 22467B*

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[1] I wish to thank Ms. Lynn Gillespie for the photograph of the type collection.

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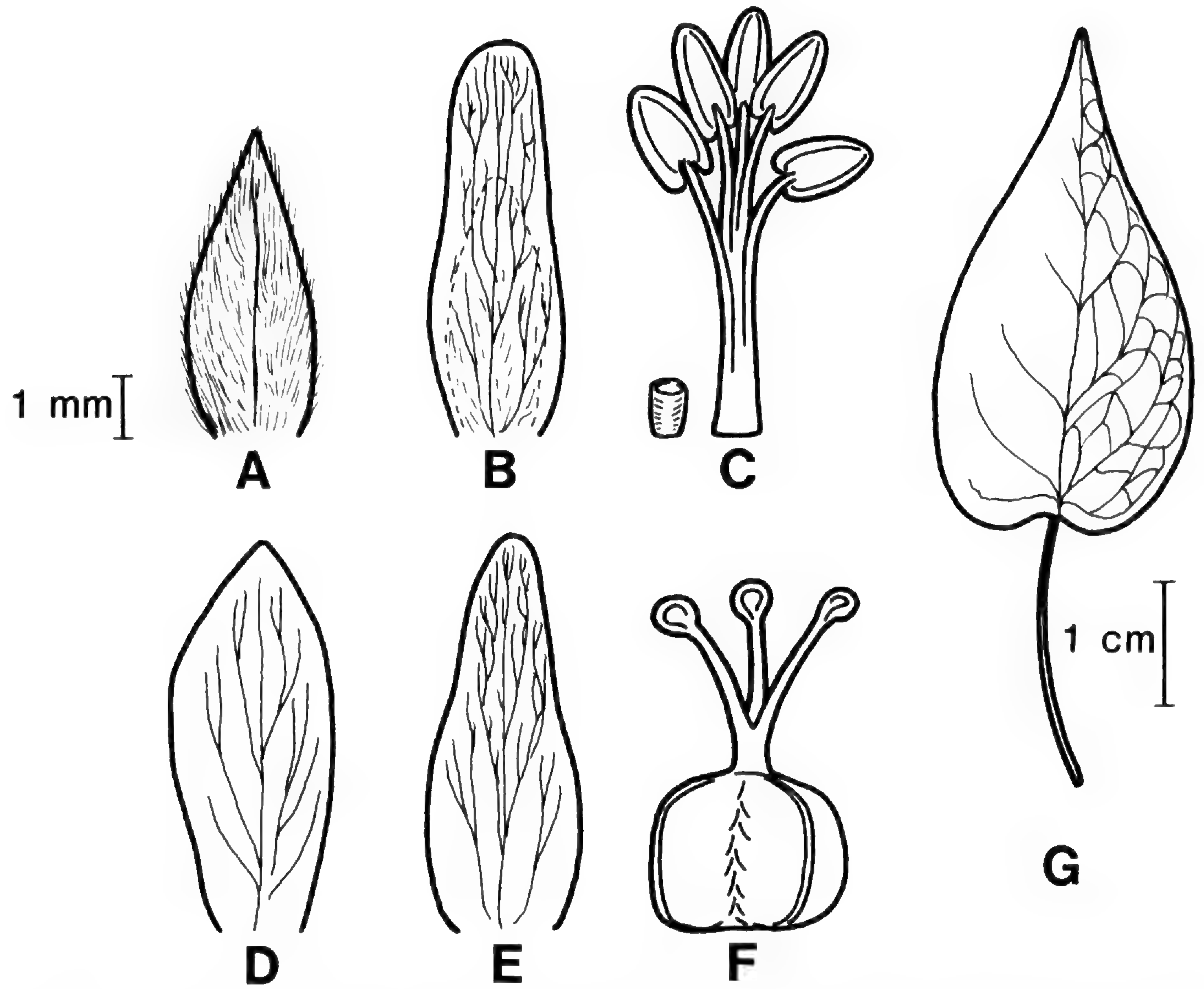

FIGURE 1. Flowers and leaf of *Jatropha stevensii* (*Stevens 22902*).—A–C. Staminate flower.—A. Sepal.—B. Petal.—C. Androecium and disk-segment.—D–F. Pistillate flower.—D. Sepal.—E. Petal.—F. Gynoecium.—G. Leaf.

(MO). Matagalpa: San Juanillo, 8 km SE of Ciudad Darío, 500 m, *Grijalva 2599* (DAV, MO).

Jatropha stevensii, named in honor of Warren Douglas Stevens, the leading student and collector of the Nicaraguan flora, belongs to subg. *Curcas* (Adans.) Griseb. by virtue of its flowers with entire imbricate sepals, coherent petals, and androecium of 10 monadelphous stamens (Dehgan & Webster, 1979). Within subg. *Curcas,* it is referable to sect. *Platyphyllae* Dehgan & Webster because of its 3-locular carinate fruits and biseriate anthers. However, it is divergent from most species of sect. *Platyphyllae* in having elongated seeds with a prominent caruncle. As noted by McVaugh (1945), *J. fremontioides* Standl. from Oaxaca differs from other species of subg. *Curcas* in its prominently carunculate seeds. Furthermore, Dehgan (1980) has indicated that *J. fremontioides* is distinguished by anisocytic stomata, a feature unique in the genus.

The prominently carunculate seeds, monoecious flower production, and small entire cordate leaves link *J. stevensii* with *J. fremontioides* and indicate that the latter is the closest relative of the new species. The two species form a subgroup of sect. *Platyphyllae* differing from more typical species such as *J. platyphylla, J. alamanii,* and *J. ciliata,* which have larger more-or-less lobed leaves, flowers produced dioeciously, and seeds with small caruncles. Nevertheless, the staminate and pistillate flowers of such species as *J. ciliata* are quite similar overall to those of *J. stevensii* and *J. fremontioides,* and the preponderance of evidence does not seem to compel any modifications in the circumscription of sect. *Platyphyllae* at this time.

The discovery of *J. stevensii* in Nicaragua brings to three the number of endemic Central American species of *Jatropha*: *J. podagrica* Hook. (eastern Guatemala to Nicaragua), *J. stevensii*

FIGURE 2. Photograph of type collection of *Jatropha stevensii* (*Stevens 22902*); left-hand glabrous branch with capsule and staminate flowers; right-hand pubescent branch with pistillate flowers.

(Nicaragua), and *J. costaricensis* Webster & Poveda (Guanacaste, Costa Rica). These species belong to two different subgenera and sections, *J. podagrica* in subg. *Jatropha* sect. *Peltatae* and *J. stevensii* and *J. costaricensis* in subg. *Curcas* sect. *Platyphyllae*. However, as noted by Webster and Poveda (1978), *J. costaricensis* is most closely related to *J. alamanii* Muell. Arg. of southern Mexico (Oaxaca) and therefore not to *J. stevensii*.

The Central American species of *Jatropha* appear to represent a depauperate extension of the large assemblage of endemic species in southern Mexico, as remarked by Webster and Poveda (1978). It is interesting that the floristic break for *Jatropha* comes not at the Isthmus of Tehuantepec but in Guatemala; however, there is clearly a decline in diversity east of the Isthmus.

In contrast to studies such as that of Savage (1982) on vertebrate distributions in Mesoamerica, there is clearly no ancient Central American center for xeric Euphorbiaceae such as *Cnidoscolus, Jatropha,* and *Manihot.* Instead, in Mesoamerican *Jatropha* there has been an invasion of one species of subg. *Jatropha* from the south (*J. podagrica*) and two species of subg. *Curcas* from the north (*J. costaricensis* and *J. stevensii*). Gentry (1982) considers that xeric Mesoamerican taxa are ultimately of southern origin. However, for *Jatropha* subg. *Curcas* and other distinctive Mexican xerophyte taxa such as the Fouquieriaceae, this migration from the south must have been so ancient that these taxa may be regarded as autochthonous to Mexico in terms of their evolutionary diversification. In contrast, the invasion of plants ancestral to *J. podagrica* must be more recent, and indeed perhaps subsequent to the closing of the Panamanian gap.

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REUNION OF *PHAEOSPHAERION* AND *COMMELINOPSIS* WITH *COMMELINA* (COMMELINACEAE)

ROBERT B. FADEN[1] AND D. R. HUNT[2]

ABSTRACT

The genera *Phaeosphaerion* and *Commelinopsis* are reunited with *Commelina* because they were separated solely by their indehiscent, conspicuous fruits. Showy fruits similar to those of *Phaeosphaerion* and *Commelinopsis* but dehiscent are reported in undescribed species of *Commelina* from Ecuador and Madagascar. The new combinations *Commelina rufipes* var. *glabrata* and *Commelina mathewsii* are made.

The handful of neotropical species referred to *Phaeosphaerion* Hassk. and *Commelinopsis* Pichon differ from the cosmopolitan genus *Commelina* L. in having indehiscent, conspicuous fruits—fleshy and blue to black in *Phaeosphaerion*; crustaceous and white (with the seeds adhering to the septa) in *Commelinopsis*. Although other characters may yet be found to separate these segregates from *Commelina*, the present, admittedly incomplete evidence suggests otherwise. To date the fruit characters are all that can be used to justify having three genera rather than one.

We formerly have recognized *Phaeosphaerion* and *Commelinopsis* as distinct from *Commelina* (e.g., Hunt, 1981, 1983). New evidence has convinced us, however, that these genera should no longer be maintained. First, the principal species of *Phaeosphaerion* and *Commelinopsis* are so strikingly similar to species of *Commelina* that identifying non-fruiting specimens is sometimes extraordinarily difficult. Indeed, the resemblance of *Phaeosphaerion leiocarpum* (Benth.) Hassk. ex C. B. Clarke to *Commelina texcocana* Matuda (?= *C. pallida* Willd.) is so close, at least in herbarium specimens, that one is tempted to wonder whether the genetic basis of the fruit difference could be a relatively simple one. Similarly, *Commelinopsis glabrata* D. R. Hunt (= *C. persicariifolium* sensu Pichon, non *Commelina persicariifolia* Delile) bears a very strong resemblance to *Commelina obliqua* Vahl (synonym *C. robusta* Kunth), although the two can usually be separated by flower color and leaf pubescence—flowers white and adaxial leaf surface smooth in *Commelinopsis glabrata*; flowers blue and adaxial leaf surface scabrous in *Commelina obliqua*—when fruits are lacking.

The second line of evidence is the recent discovery of two undescribed species of *Commelina* that bridge the narrow gap in fruit morphology between that genus on the one hand and *Phaeosphaerion* and *Commelinopsis* on the other. The first of these species is known from three collections from the vicinity of Guayaquil, Ecuador [*Gilmartin 762* (US); *Asplund 16628* (S); *Asplund 16645* (S)]. The fruits of this species, which resembles *Phaeosphaerion leiocarpum* in habit, are reddish or dark blue and exserted from the spathes at maturity. Unlike the fruits of *Phaeosphaerion*, however, those of the Ecuadorian species are dehiscent when fully mature.

The fruits of the second *Commelina* species, represented by *Bosser 17832* (P) from Madagascar, are also exserted from the spathes at maturity; but they more closely resemble the fruits of *Commelinopsis* than those of *Phaeosphaerion*, being crustaceous and whitish. Unlike *Commelinopsis* fruits, those of *Bosser 17832* seem to be dehiscent when mature.

The conspicuous fruits of *Phaeosphaerion* and *Commelinopsis* and the two undescribed *Commelina* species have undoubtedly evolved for bird dispersal. *Phaeosphaerion* and *Commelinopsis* have closer affinities with distantly related species of *Commelina* than with each other. They clearly represent separate and parallel evolutionary derivatives from *Commelina*. The Ecuadorian *Commelina* is apparently related to *Phaeosphaerion leiocarpum*, but technically it belongs to *Commelina* because of its dehiscent fruit. The Madagascan *Commelina* is unrelated to any of the other conspicuous-fruited species, all of which are neotropical. It represents yet another evolutionary lineage.

The already weak boundaries between *Com-*

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melina and *Phaeosphaerion* and *Commelinopsis,* respectively, are further eroded by these new *Commelina* species. It is evident that *Commelina* has produced species with berry-like fruits in several evolutionary lines. Either each of these lines must be recognized as a distinct genus or all of them must be retained within *Commelina.*

In the course of our discussions on the treatment of the Commelinaceae for the *Flora Mesoamericana,* we have concluded that *Phaeosphaerion* and *Commelinopsis* can no longer be upheld. No new combination in *Commelina* is needed for *Phaeosphaerion leiocarpum* or *Commelinopsis rufipes* because their basionyms are *Commelina leiocarpa* Benth. and *Commelina rufipes* Seubert, respectively. *Commelinopsis glabrata* appears to be conspecific with *Commelina rufipes* and will be treated in the *Flora* as a variety:

Commelina rufipes Seubert var. **glabrata** (D. R. Hunt) Faden & D. R. Hunt, comb. et stat. nov. Basionym: *Commelinopsis glabrata* D. R. Hunt in Kew Bull. 36: 199. 1981.

Phaeosphaerion pseudomonosperma (Kuntze) Steyerm. (basionym: *Athyrocarpus pseudomonosperma* Kuntze) is a synonym of *Commelina rufipes* var. *glabrata.*

The status of the other specific and varietal names in *Phaeosphaerion* and *Commelinopsis* needs to be considered. *Phaeosphaerion efoveolatum* C. B. Clarke from Venezuela is so similar to *Commelina leiocarpa* that it is probably conspecific. We are uncertain about the importance and consistency of the seed character used by Clarke (1881) to separate these taxa, so we decline to transfer *P. efoveolatum* to *Commelina* at this time.

Commelina scabrata Seubert is the basionym for *Phaeosphaerion persicariifolium* var. *scabrata* (Seubert) C. B. Clarke. Seubert's species, however, is a synonym of *Commelina obliqua* Vahl, thus it is not a synonym of any taxon of *Phaeosphaerion* or *Commelinopsis.*

We are less certain about *Phaeosphaerion mathewsii* C. B. Clarke from Peru, which is known definitely only from the type (*Mathews 148*—K). (The original spelling of the specific name, with two 't's is clearly a typographical error.) Although it would appear to belong to *Commelina rufipes,* it does not exactly match collections of either variety. It is perhaps closer to some specimens of *C. obliqua,* especially *Davidse & González 19296* (US) from Venezuela, but it does not match them perfectly either. The type of *P. mathewsii* lacks fruits, and therefore its inclusion in *Phaeosphaerion* by Clarke (1881) is questionable. Because we cannot place this specimen in any named species of *Commelina* with certainty, we are maintaining its status as a species and are transferring it to the genus:

Commelina mathewsii (C. B. Clarke) Faden & D. R. Hunt, comb. nov. Basionym: *Phaeosphaerion mathewsii* C. B. Clarke in DC., Monogr. Phan. 3: 138. 1881.

A comment may be made here about the generic name *Athyrocarpus,* which has sometimes been used interchangeably with *Phaeosphaerion. Athyrocarpus* was first mentioned by Schlechtendal (1855) as a possible genus, but it was not validly published until Hasskarl (1866) included it in his key to the genera of Commelinaceae. Hasskarl also described *Phaeosphaerion* in the same paper, so the priority between the two names must be determined by the earliest publication in which they are combined. Clarke (1881) appears to be the first worker to combine them, placing *Athyrocarpus* in synonymy under *Phaeosphaerion.*

Finally, it should be noted that under Art. 10 of ICBN (Sydney edition, 1983), the type of *Commelinopsis* is the same as that of *Commelina persicariifolia* Delile, which is probably referable to *C. virginica* L. or *C. paludosa* Blume (Hunt, 1981). To retain Pichon's generic concept, it would be necessary to conserve *Commelinopsis* under Art. 10.3 with a specimen that Pichon had examined, or else to choose a new name for the genus.

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CHROMOSOME NUMBERS OF MADAGASCAR PLANTS[1]

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ABSTRACT

Chromosome numbers are reported for 19 species in eight families of flowering plants of Madagascar. Included are first reports for 14 species. First counts for the genera *Kaliphora* ($n = 16$) and *Haronga* ($n = 10$) also are presented. A new low number ($n = 7$) is reported for the genus *Vernonia*, and the possible allopolyploid origin of New World taxa of the genus based on $x = 17$ is discussed.

Although the flora of Madagascar contains many interesting and poorly known genera and families, chromosome counts are available for relatively few species. The present paper inaugurates what is intended to be a sustained effort to record the chromosome numbers of Madagascar plants so they will be available to assist in interpretation of phytogeographic and evolutionary relationships.

MATERIALS AND METHODS

With two exceptions, chromosome numbers reported here were determined from microsporocytes undergoing meiotic divisions. The two counts in the genus *Aloe* were made from microcytes undergoing the first mitotic division of microgametogenesis. All floral bud materials used for chromosomal determinations were preserved in a modified Carnoy's fixative (6 chloroform : 3 absolute ethanol : 1 glacial acetic acid). These were stored in the fixative under refrigeration until they were transported to the University of Hawaii where acetocarmine slide preparations were made according to a modification of Beeks' method (Beeks, 1955). Observations were made with a Zeiss Photoscope III equipped with phase contrast optics. Voucher specimens of all cytological determinations have been deposited in the Herbarium of the Service de Botanique, Université de Madagascar, Tananarive (TAN).

RESULTS

The results are listed in Table 1.

DISCUSSION

Clusiaceae. The count of $n = 10$ for *Haronga madagascariensis* (Table 1) is the first count for this monotypic genus of tropical Africa and Madagascar. The same chromosome number characterizes the related genera *Hypericum* and *Vismia* (Moore, 1973, 1977; Goldblatt, 1983).

Ericaceae. First reports here of $n = 12$ for *Vaccinium emirnense* and *V. secundiflorum* agree with many other reports for the genus (Fedorov, 1974; Moore, 1973; Goldblatt, 1981, 1983).

Crassulaceae. The report of $n = 18$ given here for *Kalanchoë beharensis* (Table 1) agrees with two previous counts for this species (Baldwin, 1938; Friedmann, 1971).

Thymelaeaceae. The report here for the Madagascar endemic, *Gnidia bakeri*, agrees with an earlier report of $n = 9$ for *Gnidia carinata* Thunb. (Venkateswarlu, 1946). This number is also characteristic of at least five other genera of the family (Moore, 1977; Goldblatt, 1981, 1983).

Cornaceae. The chromosome number of *Kaliphora madagascariensis*, an endemic monotypic genus, is here determined to be $n = 16$. *Aucuba* appears to be the only other genus in the family known to possess this number (Fedorov, 1974; Moore, 1973; Goldblatt, 1983).

Compositae. The Madagascar endemic, *Anisopappus anemonifolius*, is here reported to have $n = 7$. The only other report for the genus appears to be $2n = 28$ for *A. africanus* (Hook. f.) Oliv. & Hiern (Auquier & Renard, 1975). Apparently on the basis of this latter count, Merxmüller et al. (1977) proposed the base number of $x = 7$ for the genus. Our determination for *A. anemonifolius* supports their proposal. The first report here for the endemic *Conyza garnieri* is the same as that found in many other species of this genus previously investigated (Fedorov, 1974; Moore, 1973, 1977; Goldblatt, 1981, 1983). A first report of $n = 5$ for the Madagascar endemic, *Emilia citrina* (Table 1) is a number that (along with $n =$

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TABLE 1. Chromosome numbers of Madagascar plants.

Taxon	*n*	Collection Data
Clusiaceae		
Haronga madagascariensis Choisy	10	142–84[1] Ambohitantely
Ericaceae		
Vaccinium emirnense Hook.	12	145–84 Ambohitantely
Vaccinium secundiflorum Hook.	12	148–84 Ambohitantely
Crassulaceae		
Kalanchoë beharensis Drake	18	Cultivated, Université de Madagascar
Thymelaeaceae		
Gnidia bakeri Gilg	9	152–84 Ambohitantely
Cornaceae		
Kaliphora madagascariensis Hook.	16	120–84 Ambohitantely
Compositae		
Anisopappus anemonifolius (DC.) G. Taylor	7	Ankatso
Conyza garnieri Klatt	9	Tsimbazaza
Helichrysum sp.	7	139–84 Ambohitantely
Emilia adscendens DC.	15	Ankatso
Emilia citrina DC.	5	Ankatso
Mikania scandens Willd.	19	143–84 Ambohitantely
Vernonia appendiculata Less.	7	Tananarive
Vernonia diversifolia Bojer	9	101–84 Ambohitantely
Vernonia garnieriana Klatt	30	114–84 Ambohitantely
Vernonia pectoralis Baker	10	Ankatso
Aloeaceae		
Aloe deltoideodonta Baker	7	Station Manambaro[2]
Aloe divaricata Berger	7	Fort Dauphin[2]
Orchidaceae		
Calanthe silvatica Lindley	20	133–84 Ambohitantely

[1] All collection numbers are those of the senior author.

[2] Collected by Lydia Rason.

10) is well established in the genus (Fedorov, 1974; Moore, 1973, 1974, 1977; Goldblatt, 1981, 1983). However, the number $n = 15$ reported here for *E. adscendens* is apparently otherwise known only in *E. sonchifolia* (L.) DC. (Torres & Liogier, 1970). The report here for *Mikania scandens* is in agreement with earlier reports for the species (Fedorov, 1974; Moore, 1973; Goldblatt, 1981). The counts here of $n = 9$ for *Vernonia diversifolia* and $n = 10$ for *V. pectoralis* appear to represent first reports for these endemic species. These numbers agree with previous reports and are found to be frequent in Old World taxa of the genus (Jones, 1979). *Vernonia garnieriana*, another endemic reported for the first time, has $n = 30$ (Table 1). This number appears to have been reported previously for only two species of *Vernonia*, i.e., *V. glabra* (Steetz) Vatke (Jones, 1979) and *V. travancorica* Hook. f. (Narayana, 1979). That these are hexaploids based on $x = 10$ is suggested by the report of both $n = 10$ and $n = 30$ in *V. glabra* by Jones (1979). The first report here of $n = 7$ for the endemic *Vernonia appendiculata* represents a number that is otherwise unknown in the genus. Moreover, this number represents the lowest haploid number known in *Vernonia* and allows speculation of a new, low base number of $x = 7$ for the genus. Jones (1979) has suggested that New World taxa based on $x = 17$ may have originated through aneuploidy from tetraploids based on $x = 9$. However, the discovery of $x = 7$ in *Vernonia appendiculata* offers an alternative explanation. New World taxa based on $x = 17$ could have arisen by way of allopolyploidy involving taxa with $x = 7$ and $x = 10$. In this connection, it may be mentioned that Humbert (1960) divided the 96 species listed for Madagascar into six groups,

according to apparent affinities. The group that includes *V. appendiculata* contains 38 other endemic species. It would be tempting to speculate that at least some of those also exhibit $x = 7$. As Jones (1979) pointed out, much cytological work remains to be done in the Vernonieae.

Aloeaceae. The endemic species *Aloe deltoideodonta* and *A. divaricata* are reported here to have $n = 7$, a number that agrees with previous reports for these and many other species of the genus (Amano et al., 1972).

Orchidaceae. The first report here of $n = 20$ for *Calanthe silvatica* agrees with previous reports for the genus (Fedorov, 1974; Moore, 1973, 1974, 1977; Goldblatt, 1981, 1983).

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CYTOTAXONOMIC STUDIES IN THE GENUS *URGINEA* STEIN IN WEST AFRICA. II. KARYOTYPE EVOLUTION IN *URGINEA ALTISSIMA* (L.) BAKER[1]

S. O. OYEWOLE[2]

ABSTRACT

Mitotic and meiotic studies were carried out on *Urginea altissima* with $2n = 22$. At pachynema-diakinesis pollen mother cells had 9 (1.61%), 10 (93.9%), or 11 (5.0%) chromosome bodies. Pollen viability was 93.56%. Statistical analysis showed a strong correlation between the proportion of PMCs with (a) 9 bodies and those with anaphase bridges; (b) 10 bodies and those with normal anaphase movements, and pollen viability; and (c) 11 bodies and those with excluded chromosomes. The eleventh homologue was associated with the second largest homologue in the PMCs with 10 bodies. This association is specific and ensures the successful transmission of the eleventh homologue to the spores. Failure of these two homologues to associate always results in the breakdown of normal meiotic behavior. In mitosis, the eleventh pair behaved normally. Hence the correct diploid number is 20 + 2 homologous fragments.

Urginea Stein is a genus of bulbous geophytes in the Liliaceae. It is represented by the basic chromosome numbers of 5 and 7 (Darlington & Wylie, 1955; Jones & Smith, 1967). The known tropical African members have a somatic complement of 14 (a species endemic to Madagascar), 20 or 20 + 0–6 B chromosomes (Jones & Smith, 1967), or 22 (Oyewole, 1975b). The two West African species with a somatic chromosome number of 22, viz., *U. altissima* (L.) Baker sensu stricto and *U. gigantea* (Jacq.), represent a departure from the established basic chromosome numbers. They therefore offer a novel opportunity for investigating and understanding the evolution of genetic systems in the genus, possibly opening up avenues for understanding the mode of speciation in a family known to contain groups of morphologically similar and closely related taxa. Hence the behavior of the chromosomes of *U. altissima* sensu stricto has been investigated in this work.

MATERIALS AND METHODS

Sample collections from natural populations of *U. altissima* sensu stricto were cultivated in experimental gardens at Ibadan and later at Ilorin. These were investigated cytologically, using root tip squashes for mitosis and flower bud (anther) squashes for meiosis, both pretreated for one hour in sat. aq. solution of p-dichlorobenzene. Twenty-five plant stands from various population locations in western Nigeria were investigated. Conventional methods (Darlington & La Cour, 1942; Marenah & Holden, 1967) of squash preparation were employed. Two percent acetic orcein was used. Viability of pollen from undehisced anthers extracted from open flowers was estimated by observing the ability of grains to stain in 1% acetocarmine within two to three minutes.

RESULTS

All 22 chromosomes of the somatic complement behave normally at mitosis (Fig. 1). None shows differential staining except at the centromeric points. They all move normally at anaphase; the number and form, from one cell generation to another (and indeed in different tissues), remain consistent (Oyewole, 1975b).

The pairing behavior at meiosis, as well as pollen viability estimates (Table 1), shows that the taxon has a stable chromosomal system, with a high average pollen viability of 93.56%. However, meiotic formations of 9, 10 or 11 chro-

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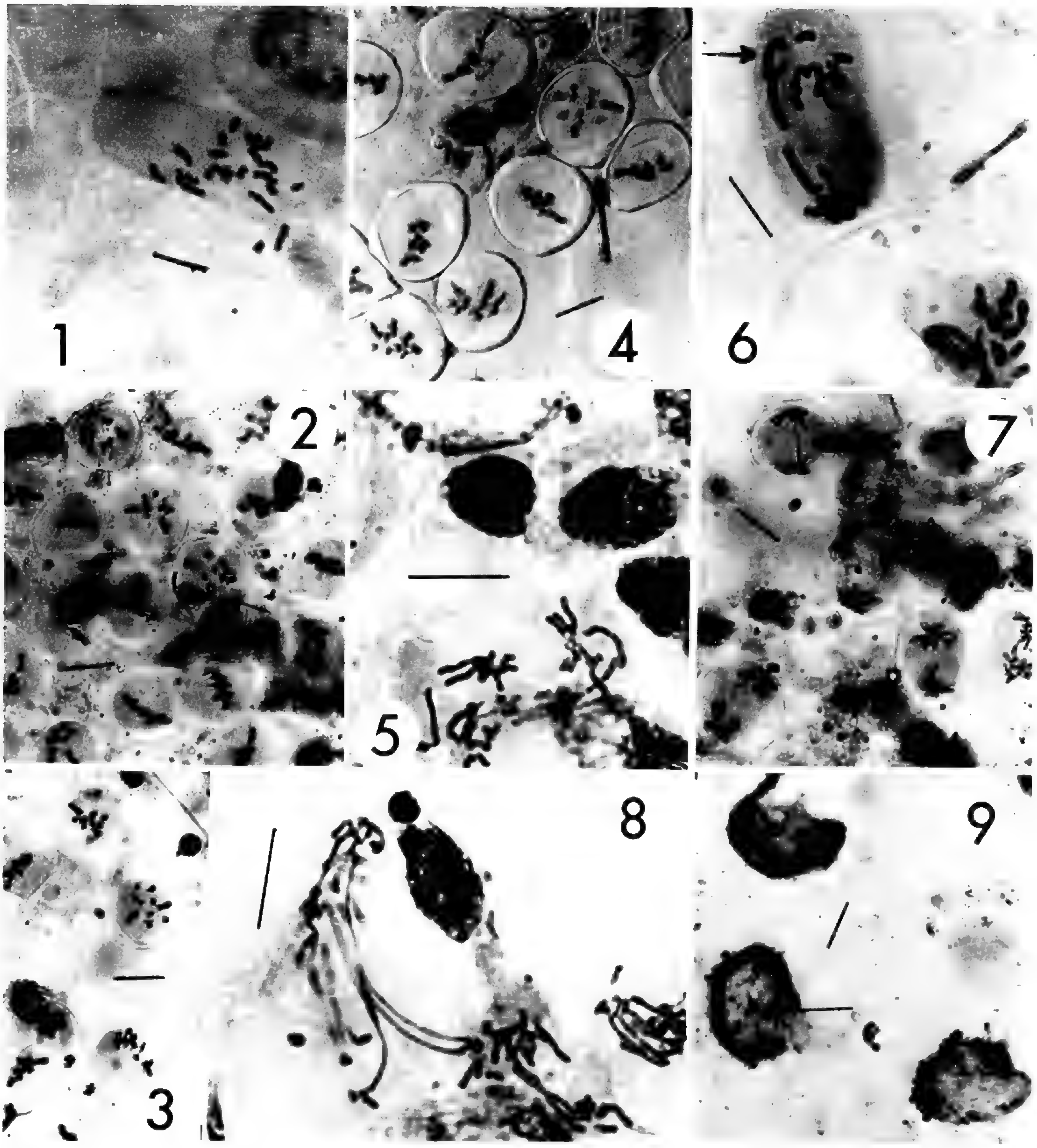

FIGURES 1–9.—1. Somatic complement of 22 chromosomes.—2. PMCs at Metaphase I–Anaphase I, one of which has nine chromosome bodies. The hexavalent is arrowed.—3. PMCs at Metaphase I showing 10 bodies.—4. PMCs at Metaphase I. Arrow indicates the PMC showing 11 bivalents.—5. A PMC with Anaphase I bridge persisting into MII.—6. A PMC at Anaphase I with normal movement. There are 10 chromosomes per group. Second large chromosome, arrowed in one group, shows a conspicuous second arm (cf. Fig. 1).—7. PMC (arrowed) at AI with a chromosome bridge (dicentric).—8. Persistent AI and AII bridges.—9. Telophase I PMCs. One has excluded chromosomes (arrowed).—Each bar (——) represents 10 μm.

mosome bodies per pollen mother cell (PMC) during the first prophase to metaphase were observed (Figs. 2–4). The nine bodies consist of one hexavalent and eight bivalents; the 10 bodies consist of nine bivalents and one quadrivalent; the 11 bodies are all bivalents. These formations occur at frequencies of 1.61%, 93.39%, and 5.0%, respectively. Figures 5–7 demonstrate first anaphases: anaphase bridges (Fig. 5), normal movement (Fig. 6), and lagging and an excluded pair of chromosomes (Fig. 7). These occur at frequencies of 1.23%, 93.51%, and 5.44% respec-

TABLE 1. Meiotic behavior of *U. altissima* Baker sensu stricto.

	Total PMCs				Examined at							Pollen Viability		
	Diplonema–MI				AI–TI				AII–TII					
	Chromosome Bodies Formed			Total PMCs	Normal Anaphase Movement	Anaphase Bridge Formation	Telophase with Excluded Chromosomes	Total PMCs	Normal Anaphase Movement	Anaphase Bridge & Excluded Chromosomes	Total PMCs	Normal Pollen	Aborted Pollen	Total Pollen Examined
	9	10	11											
Number	10	579	31	620	533	7	31	570	309	21	330	4,678	322	5,000
%	1.61	93.39	5.0	100	93.51	1.23	5.44	100	93.64	6.36	100	93.56	6.44	100

PMCs = pollen mother cells; MI = metaphase I; AI = Anaphase I; TI = Telophase I; AII = Anaphase II; TII = Telophase II.

TABLE 2. Results of χ^2 to test the null hypothesis that:

(1) % pollen mother cells (PMCs) showing 10 chromosome bodies, normal anaphase movements, and normal pollen are equal (ratio 1 : 1 : 1 : 1);

(2) % PMCs with 9 chromosome bodies and % PMCs with Anaphase I bridge formation are equal (ratio 1 : 1);

(3) % PMCs with 11 chromosome bodies and % PMCs with Telophase I excluded chromosomes are equal (ratio 1 : 1); and

(4) Total % PMCs with 9 and 11 chromosome bodies, % PMCs with AI bridge formation and TI excluded chromosomes, % PMCs with AII bridge formation and TII excluded chromosomes, and % aborted pollen grains are equal.

	χ^2 Value	Probability Value
(1)	0.000605	$P > 99\%$
(2)	0.0508	$90\% > P > 80\%$
(3)	0.01854	$90\% > P > 80\%$
(4)	0.0096	$98\% > P > 95\%$

Level of significance is set at 0.05. The null hypothesis is proved in each case.

tively. Figures 8 and 9 show Anaphase II (AII) diagonal bridge and Telophase II (TII) excluded chromosomes, which also occur at a total frequency of 6.36% while normal AII movement occurs at a frequency of 93.64%. Statistical analyses of these data (Table 2) show that pollen viability percentage and the frequencies of AI and AII normal movements and the formation of 10 chromosome bodies per PMC during the first prophase to metaphase (93.56%, 93.64%, 93.51%, and 93.39%, respectively) are not significantly different; that the frequency of formation of nine bodies per PMC is not significantly different from the frequency of occurrence of laggards and excluded chromosomes at TI; and that the total frequencies of formation of nine and 11 bodies, AI bridge formation and TI chromosome exclusion, AII diagonal bridge formation and TII chromosome exclusion, and percentage pollen abortion are all not significantly different.

In the formation of nine bodies, the hexavalent is an association involving three small pairs including the eleventh homologue, whereas the quadrivalent in the formation of 10 bodies is an association of the eleventh homologue with the second largest pair (cf. chromosome bodies in Figs. 2–4). When this association occurs, the first and second large pairs become about equal in length at MI (see Fig. 4; see also mitotic chromosome lengths of the two large and eleventh homologues, Oyewole, 1975b). This means that when the eleventh homologue forms a bivalent of its own (in 11 separate bivalents), or associates with any homologues other than the second largest, meiotic behavior becomes erratic and meiotic products are inviable.

DISCUSSION

Some representatives of *Urginea* in other areas have been shown to have B chromosomes (De Wet, 1957; Jones & Smith, 1967), but accessory chromosomes have not been reported in any of the west tropical African materials. Where they have been reported, these accessory chromosomes are known to be different from the autosomal members of their complement. They are heterochromatic, their numbers vary within populations, their transmission at mitosis is not regular, and at meiosis there has not been any mechanism of transmission comparable to that shown in *U. altissima,* where association of the extra pair with a specific pair of autosomes is the mechanism for successful transmission of the extra chromosomes into the spores and thereby into the next generation of the plant. Hence the extra pair of chromosomes in *U. altissima* cannot be seen as essentially inert as in the cases of the B chromosomes reported in other species.

The formation of a hexavalent involving the extra pair and two other pairs may indicate some genetic affinities between the three pairs involved (Battaglia, 1964), or show the probable origin of the extra pair (Wedberg et al., 1968). However, the formation of an association between the extra pair and a specific pair, viz., the second large pair, with a much higher frequency than in the hexavalent formation, and leading to successful meiotic behavior, may identify the true origin of the extra pair. This extra pair cannot be regarded as accessory because it is indistinguishable from the other pairs in mitotic behavior and structure (cf. chromosomes in *Clarkia unguiculata,* and *C. williamsonii* in Mooring, 1960, and Wedberg et al., 1968, respectively). The extra pair behaves normally at mitosis as in the large B chromosomes of *Brachychome lineariloba* (Carter & Smith-White, 1972), but its successful transmission from one generation of the plant to another depends upon a meiotic mechanism of its association with a specific pair of autosomes in the complement. Hence, it differs from the B chromosomes of *B. lineariloba.*

The origin of the extra pair is undoubtedly betrayed in its association with the second large pair—only such association leads to viable spore formation. The mode of origin of the extra pair is probably by fragmentation at a heterochromatic region along the second (short) arm of the parent (second large) autosomal pair. This is why the point of breakage on the otherwise acentric fragment is able to exercise secondarily a spindle-fiber organizing function at mitosis for effective polar movement—and, hence, normal autosomal behavior—but which is incidentally too weak to effectively organize the movement of the fragments at meiosis whenever they form a bivalent of their own. They then remain excluded on the equatorial plane after polar movement of the other chromosomes.

Again, in the formation of 11 normal bivalents, incomplete pairing or total asynapsis in the extra pair, which would lead to early repulsion of its members prior to anaphase movement, was not observed at all. That is, the extra pair shows synapsis (and probably chiasma formation). This means that (1) the extra pair contains essential homologous genic matter to ensure effective pairing, (2) the extra pair came from homologous segments of a homologous pair of parent chromosomes, and (3) the extra pair carries genic matter essential to the survival and success of the plant. This is why its transmission is effected by a genetic mechanism. The failure of this mechanism ultimately leads to the formation of inviable meiotic products.

The behavior of this extra pair during cell division is of interest. The incidence of fragments within chromosome complements has been reported, both in nature and in experiments, by several workers. In experiments, ionizing irradiation has been employed to effect fragmentation of chromosomes. The broken ends of the fragments may then either heal, rejoin by restitution, or rejoin with broken ends of other chromosomes (Lea, 1946; Hair, 1952; Giles, 1954). If restitution is to occur, it occurs immediately after the breakage and is dependent on oxidative enzyme metabolism (Wolff & Luippold, 1955). The extra pair of chromosomes (fragments) in *U. altissima* has healed broken ends in somatic cells and hence behaves as a normal autosomal pair during mitosis. During meiosis, however, the ends either remain healed and the pair forms a bivalent of its own, which becomes excluded during polar movement, or the broken ends become reactivated and thereby the pair associates with other chromosome pairs. Such a behavior has not been reported earlier. Rees (1958), however, working on *Scilla*, reported the behavior of chromosome fragments in pollen mother cells. In *Scilla*, the fragments become attached either to their parent autosomes or to any other chromosomes, depending on the relative distance of the fragments to one or the other. The attachment may be synchronous or asynchronous. Synchronous attachment must take place within a sticky matrix. As no sticky matrix was found in *U. altissima*, there was no evidence to suggest that the association of the extra pair with the second large autosomal pair was anything but synchronous. Hence the situation in *U. altissima* differs from that of *Scilla* in that it shows clear evidence of a genetically controlled mechanism of association, thereby stabilizing the resultant genetic system to ensure a high percentage fertility of sexual reproduction. This is in keeping with the suggestions of Blackwood (1956) and Rutishauser (1956).

It will be interesting to find out what initiates the mechanism of healing and reactivation of the broken ends of the fragments and the second large autosomal pair during mitosis and meiosis. It is likely that the stage of development at which the dissociation occurs is the interphase between the end of spore formation and the beginning of spore development, while the reactivation of the broken ends would take place at the onset of meiosis in the sporocyte. Since flowering and sexual reproduction are generally controlled hormonally, these events are likely to be part of the effects of the hormonal control, which in itself is genetic. This allows repetition of this event whenever necessary.

In this case, the extra pair of chromosomes should be regarded as fragments that are genically essential to the survival and success of the genetic system of the plant species. By this fragmentation, an otherwise somatic number of $2n = 20$ has become $2n = 22$. This $2n = 22$ should, however, be seen as $2n = 20 + 2$ ff.

The evolution of this new number may be connected with the morphological differentiation and differential ecological preference that have led to the recognition of *U. altissima* sensu stricto from its relatives *U. gigantea* and U. *viridula* Baker in the *U. altissima* complex (Oyewole, 1975a).

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CYTOTAXONOMIC STUDIES IN THE GENUS *URGINEA* STEIN IN WEST AFRICA. III. THE CASE OF *URGINEA INDICA* (ROXB.) KUNTH IN NIGERIA[1]

S. O. Oyewole[2]

Abstract

Urginea indica (Roxb.) Kunth is a morphologically variable species of wide distribution in the Old World. In West Tropical Africa, it has been considered to consist of a large form and a dwarf form. The large form was investigated morphologically in the field and in the laboratory, as well as karyotypically. Four morphological variants were encountered in the field. They differ in both vegetative and floral morphology, were found in different populations, and showed differences in ecological preferences. Biometrical analysis of vegetative and floral morphology showed that the four variants are distinct and separate but not immediately recognizable taxa. Preliminary karyotype analysis showed that they are similar but not identical in karyomorphology. Artificial crosses between them failed to produce viable seeds. It is concluded that *U. indica* is an incipient polyspecies or species complex.

Urginea indica (Roxb.) Kunth is one of the four species of *Urginea* recognized in the latest revision of Liliaceae in Flora of West Tropical Africa (Hepper, 1968). It is distinguished from the other species by its globose capsule. It is widespread in the Old World tropics, inhabiting savanna vegetation of tropical and subtropical areas of Africa, southern India and further east (Thiselton-Dyer, 1898). In Nigeria, it is widespread in the central segment of the country, occurring between latitudes 7°N and 10°N. It occurs in open, heavy soil with a top layer of humus or in clay soil of seasonally flooded plains.

It occurs in different ecological niches in various soil types within the savanna region and shows a variety of morphological forms. Hepper (1968) observed this morphological variation and contended that there are at least two different forms of this variable species: a large form and a dwarf form. These two are easily distinguishable in the field. The large form has light green leaves whose undersurface, immediately out of the bulb, is pinkish; the reproductive shoot is also pinkish, 45–150 cm tall, with not less than 15 flowers in the lax, racemose inflorescence. The tepal is also pinkish with a greenish keel. Leaves and flowers are never borne together. The dwarf form, on the other hand, has dark green leaves; the reproductive shoot is green, generally less than 40 cm tall, with flowers usually ranging between one and 12; the tepals are yellowish green with a green keel. Leaves and flowers are never borne together. Field studies of this taxon during vegetative growth and flowering revealed that Hepper's contention was a rather conservative estimate. The present paper therefore aims at establishing the taxonomic status of *U. indica* through morphological studies, starting with the large form.

Materials and Methods

Natural populations of the large form were studied morphologically during several field trips. Representative samples were collected and brought into cultivation in nurseries first at the University of Ibadan (southwestern Nigeria), then at Ahmadu Bello University, Zaria (northcentral Nigeria) and later at the University of Ilorin (westcentral Nigeria). Each collection site was visited at least twice—during the vegetative growth period (May to August) and during the flowering and fruiting period (November to March). Altogether about 200 bulbs were brought into cultivation. Four morphological variants were identified from different populations during collection. Titled A–D, they were grown on adjacent nursery beds. No intermediate forms were encountered, even where the variants grew together or in contiguous sites. Records of morphological features were kept and carefully followed in order to identify any environmentally induced features. These collections have been in cultivation since 1972/73.

Each bulb is normally not more than 3–4 inches

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deep in the soil. Soil samples were usually taken along with each bulb, and both texture and composition of the soil were determined later in the laboratory. The type of vegetation in which the population was found was also noted.

Morphological characteristics were divided into qualitative and quantitative features. The qualitative features are bulb shape, shoot color, inflorescence color, leaf form, perianth color, ovary shape, ovary color, filament, style, and anther color. These were assessed visually. The quantitative features are shoot and inflorescence height, number of flowers in the inflorescence, pedicel length, tepal length and width, length of ovary, style and stigma, anther, filament, and leaf, and leaf width. The leaf length-to-width ratio, called leaf ratio (l/w), was calculated for each leaf measured. Measurements were taken with a meter-rule graduated in millimeters and centimeters or with millimeter graph paper. The shoot was measured from its base at bulb surface to its tip, while the inflorescence height was taken from the base of the first flower to the tip of the shoot. Both measurements were taken after the last (youngest and apical) flower had either opened or withered to ensure that the reproductive shoot had stopped elongating. Floral parts from newly opened flowers were dissected out for measurements.

Transverse sections of mature leaves were made in order to investigate leaf cuticular surface pattern, leaf margin, number of veins, structure of veins, stomatal structure, and the general pattern of tissue distribution in the leaf.

Chromosome number and karyomorphology were studied using root tip squashes. Root tips were harvested at about 8 A.M., pretreated for one hour in saturated aqueous solution of p-dichlorobenzene, fixed in fresh 1 : 3 acetic alcohol (glacial acetic acid and absolute ethanol) and stored for at least 30 minutes at about −4°C before hydrolysis. Hydrolyzed root tips were squashed in 2% acetic orcein.

RESULTS

The major collection areas are indicated in Figure 1. Except for Groups B and D, which were found growing together in a wide expanse of land, different groups were found in different populations and in different ecological niches. All the populations encountered were found growing either in large numbers or as a few individuals dispersed in open savanna, with very light grass and forb cover and a few short, scattered trees and shrubs. The soil was heavy clay with or without stones and/or pebbles. The top layer was dark humus. All the populations were found in flood plains with little organic topsoil during the rains. In the dry season, the soil was hot, dry, hard and cakey.

Figure 2 illustrates the vegetative morphology of the four groups, while Table 1 contains a summary of all the morphological features investigated. Leaves are produced from the onset of the rains, and the plants remain vegetative for most of the rainy season. The leaves dry up towards the end of the rains. The early annual savanna fire of October to November burns the dry leaves, and reproductive shoots may be produced any time from two weeks after the burning. The mature flower opens into a bell shape; the pedicel curves back to carry the flower face downwards at anthesis and until after pollination, after which the pedicel straightens up. The flower withers if not fertilized. When fertilization occurs, however, the young fruit enlarges while the fading tepals close over it and shrivel into a little cap on top of the fruit by the time of maturation.

Groups B and D are most similar, being distinguished by shoot and inflorescence height, leaf length and form, and number of flowers per inflorescence only. D is distinguished from C by the lengths of tepal, style and stigma, filament and anther, filament color, bulb shape, shoot and inflorescence color, and ovary shape and color. B differs from A in shoot height and color, inflorescence height, lengths of pedicel, style and stigma, filament, anther, ovary shape, and filament color. A and C are distinguished by shoot height, inflorescence height and color, number of flowers, lengths of pedicel, tepal, anther and leaf, leaf width, and ovary shape. A and D differ in shoot and inflorescence height, number of flowers, lengths of tepal, style and stigma, filament and leaf, filament color, leaf form and width, ovary shape, and bulb shape.

Figure 3 illustrates variations in leaf surface patterns, leaf margin, vein structure, and the pattern of distribution of palisade and spongy tissues of the leaf mesophyll. Each of the groups is distinctly different from the others in each of the features exhibited.

The leaf surface pattern is similar in all, showing minute crenation, which is most noticeable in variant D but less so in variants C, A, and B, respectively (see Fig. 3: A_1, B_1, C_1, and D_1). A and D have similar epidermal cell size, type, and arrangement as well as palisade cell size, form,

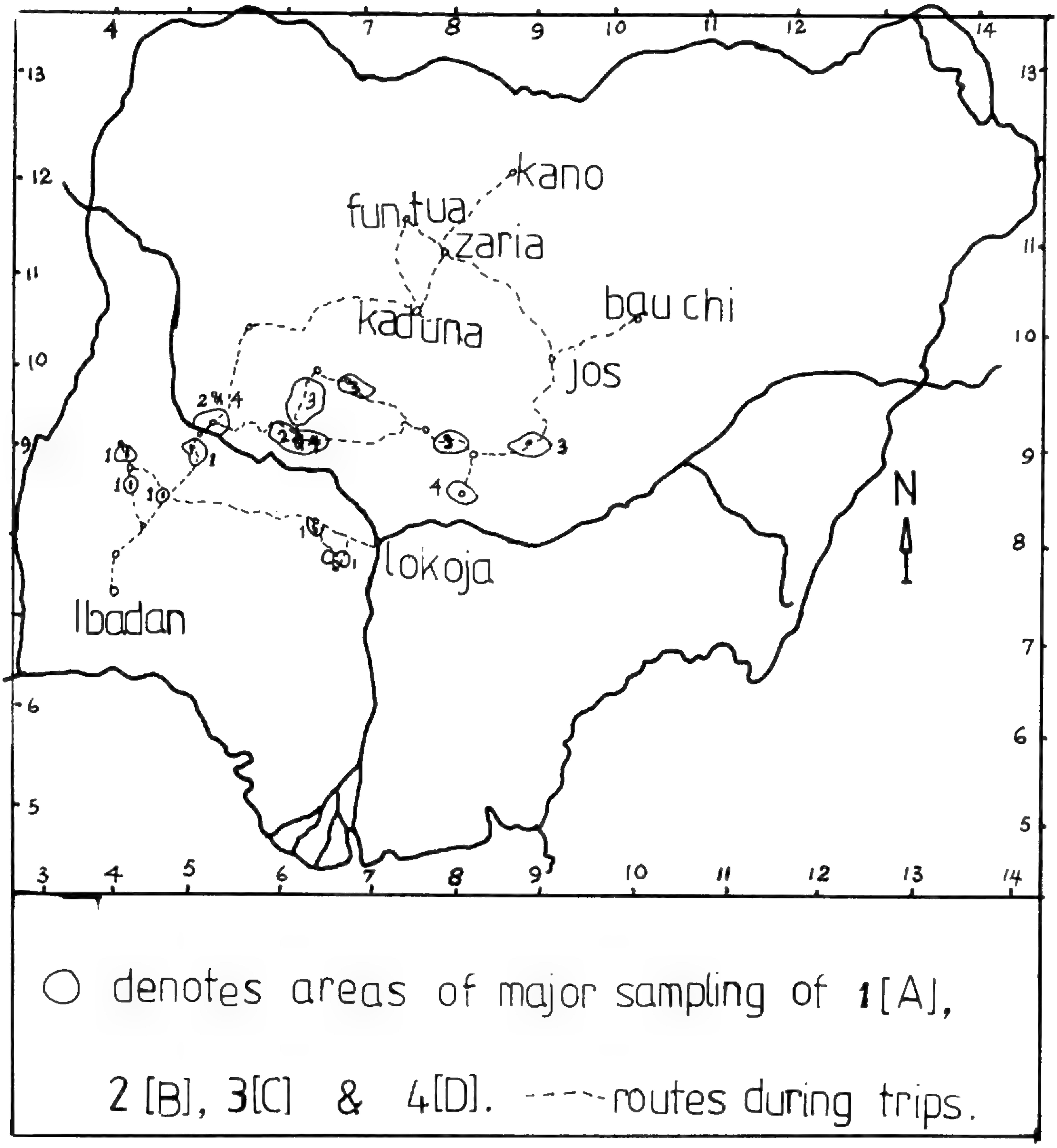


FIGURE 1. Map of Nigeria showing areas of major sampling of the large form of *U. indica*.

and arrangement. They differ in leaf margin, being short and acute in A, the adaxial and abaxial epidermal layers being separated to the margin by the palisade, which aborts on a marginal epidermal cell, while leaf margin in D is projected with both epidermal layers coming together outside the palisade and terminating with a marginal epidermal cell. They also differ in the distribution of phloem tissue in the vein, being bicollateral in A but only collateral in D. In B and C, the epidermal cells are short and isodiametrical, the palisade cells are also short and less tightly arranged, and the veins have large xylem vessels with conspicuous bicollateral phloem tissue. The leaf margin shows progressive elongation, being long and more acute in B than in A. In B, both epidermal layers do not close completely beyond the palisade before terminating in a marginal epidermal cell; in C, leaf margin is projected with rounded tip as in D and the epidermal layers barely close up beyond the palisade before terminating in a single marginal cell. Finally, the arrangement of the large metaxylem vessels is similar in A, B and D but differs in C.

TABLE 1. Data on morphological features.

	Taxa			
Characters	A	B	C	D
Bulb shape	Small, spherical	Medium, spherical	Medium, ovoid	Large, spherical
Shoot color	Green	Pink	Light green	Pink
Inflorescence color	Pink	Pink	Yellowish cream	Pink
Leaf form	Short, coiled	Short, reflexed	Long, coiled	Long, straight
Perianth color	Pinkish brown with green keel	Pink with yellowish green keel	Pinkish brown with green keel	Pink with yellowish keel
Ovary shape	Pyramidal	Globose	Pyramidal	Globose
Ovary color	Green	Green	Green	Light green
Filament color	Pink	Yellowish	Pinkish	Yellowish
Style color	Pink	Pink	Pink	Pink
Undehisced anther color	Dirty white	Dirty white	Dirty cream	Creamy white
Shoot height (cm)	45–60; 52.9	70–90; 76.9	100–140; 123.8	100–140; 119.9
Inflorescence height (cm)	15–20; 17.6	24–30; 27.0	50–60; 54.7	50–70; 59.5
Number of flowers	15–20; 17	15–20; 17	20–30; 24	20–30; 25
Pedicel length (mm)	22–23; 22.6	35–40; 37.1	30–40; 33.9	*(30–) 50–70; 60.3
Tepal length (mm)	12–14; 12.8	12–13; 12.6	15–16; 15.5	11–13; 12.1
Tepal width (mm)	4–4.5; 4.2	4–6; 5.2	3.5–4.5; 4.0	4.5; 4.5
Ovary length (mm)	4.5–5.5; 4.9	5–6; 5.3	4.5–5.0; 4.9	5–6; 5.5
Style + stigma (mm)	6.5–7.5; 7.0	5–6; 5.3	*(6.5–)7.0; 7.0	5–6; 5.5
Filament length (mm)	8.5–9.5; 9.0	5; 5.0	*(8.5–)9.0; 9.0	5–6; 5.6
Anther length (mm)	2; 2.0	2.5–3.5; 3.0	2.5; 2.5	3; 3.0
Leaf length (cm)	20–25; 22.7	25–35; 31.2	50–80; 67.3	50–70; 61.1
Leaf width (cm)	0.8–1.3; 1.0	0.8–1.3; 1.1	1.4–2.6; 2.1	1.0–2.4; 1.6
Leaf index (l/w)	17–31; 23.6	24–43; 29.8	22–52; 32.6	26–56; 39.5

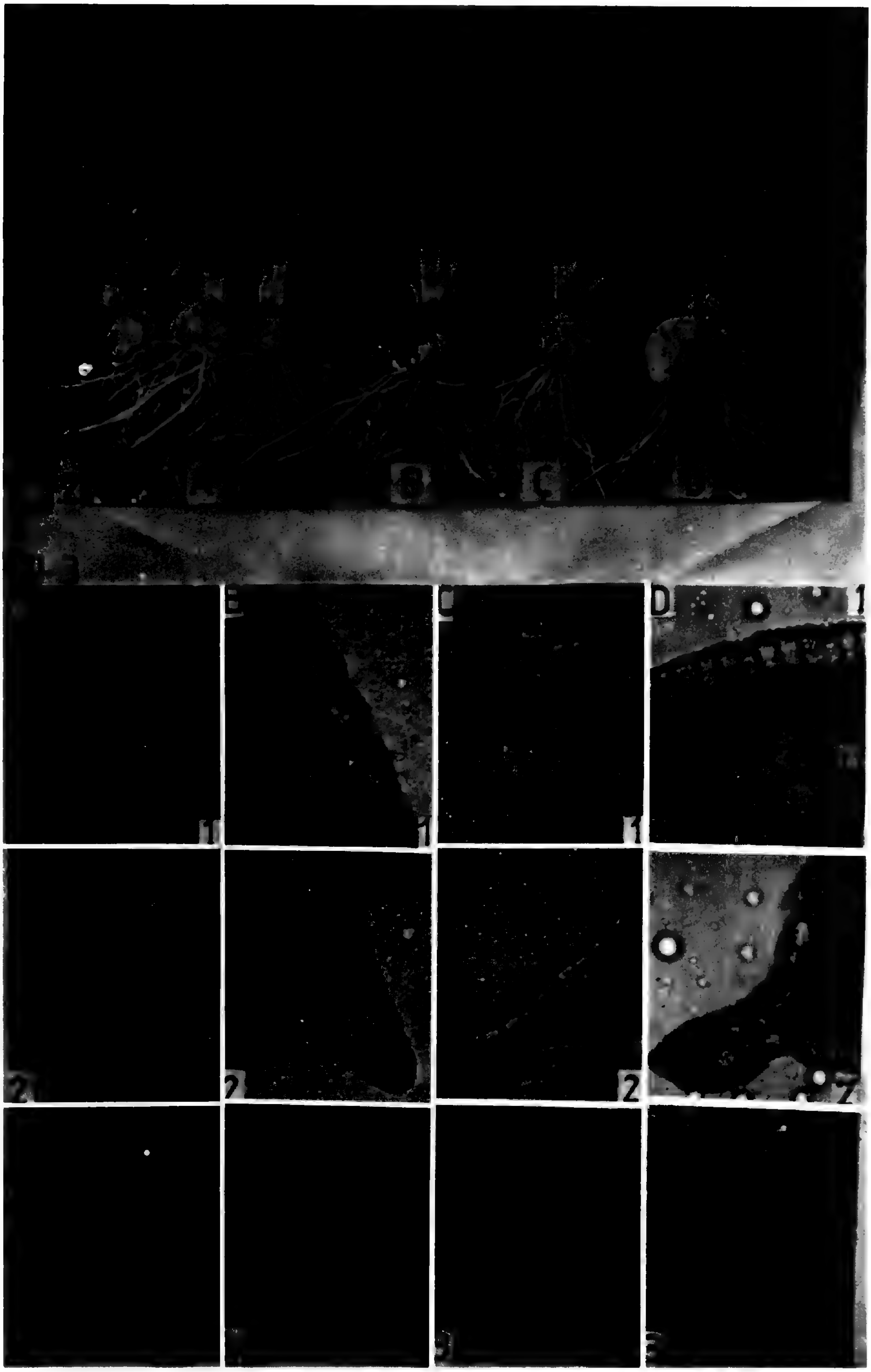
* Indicates infrequent deviating measurements.

All four groups have a somatic chromosome number of $2n = 20$. They have similar but not identical karyomorphology. An analysis of the karyotypes is the subject matter of a separate report (Oyewole, 1986). Artificial crossing between the four groups failed to produce any hybrid fruits.

DISCUSSION

Urginea indica has been described as a variable species (Hepper, 1968; Morton, 1961). Morphological variation was maintained even under uniform cultivation, suggesting that the variation is genetically based. Furthermore, morphological variations are correlated within the variants and with ecological preference rather than being ubiquitous in all populations, as would be expected if the variations were due to polygenic effects (Dobzhansky, 1951; Huxley, 1942; Mather, 1943). In *U. indica,* two distinct forms, B and D, were found together in the same population area without intermediates, indicating that the differences between them are not environmentally induced, while each group has a distinct karyotype (Oyewole, 1986). Hence variation in this case is not just a case of polymorphism.

The correlation between the external morphological variations and the leaf epidermal and mesophyll features strongly supports the idea that this taxon is not just a single species. These anatomical features are genetically controlled and, under the same environmental conditions, still maintain their differences. The importance of such anatomical features in species delimitation has been amply emphasized by Carlquist (1959) and Metcalfe (1963) and exhaustively demonstrated in many other works (for example, Prat, 1932; Church, 1949; Sørensen, 1953; Borrill, 1959, 1961; Oyewole, 1971; Adeyemi, 1981).



FIGURES 2, 3.—2. Vegetative morphology of the four groups (A–D) of the large form of *U. indica.* Horizontal bar represents 4 cm.—3. Leaf surface patterns: 1—Leaf surface, epidermal cell structure and the palisade layer; 2—leaf margin; and 3—Leaf vein structure. Diagonal bar represents 25 μm.

Speciation, in the words of Dobzhansky (1951), is "that stage of evolutionary process at which the once actually or potentially interbreeding array of forms becomes segregated in two or more separate arrays which are physiologically incapable of interbreeding." Recent views on speciation emphasize the relationship of the organism and the environment as the controlling factor (Hutchinson, 1959; Lewis, 1969). Thus adaptive radiations often occur when a species enters an unoccupied habitat with diverse open niches or when a population acquires a new complex of adaptive characters that enables it to exploit available environment more efficiently (Stebbins, 1971), as recorded for the *Axonopus compressus* complex (Gledhill, 1966). Hence it is clear that *U. indica,* in which there are four morphologically distinct, genetically isolated forms even within the so-called large form, is not simply one phenotypically plastic genotype. It is significant that these forms exist side-by-side in nature or at least within the same geographical location and climatic condition while maintaining their identity both reproductively and morphologically. Obviously their karyotypes resemble one another. However, they are biological entities. It is untenable to regard the hitherto *U. indica* as a single species (Lewis, 1969); rather it must be recognized as a species complex. The evolutionary history of *U. indica* may possibly be similar to that of *Albuca nigritana* and the *U. altissima* complex in the same family (Gledhill & Oyewole, 1972; Oyewole, 1975, respectively).

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CYTOTAXONOMIC STUDIES IN THE GENUS *URGINEA* STEIN IN WEST AFRICA. IV. POPULATION DIFFERENTIATION AND KARYOTYPE VARIATION IN *URGINEA INDICA* (ROXB.) KUNTH[1]

S. O. Oyewole[2]

Abstract

Qualitative and quantitative studies of karyotypes of over 250 individual plants of the variable species *Urginea indica* (Roxb.) Kunth were carried out. The plants were sampled from 23 collection sites representing seven distinguishable phenotypes. Root tips were used for mitotic preparations. Ten karyotypes were recognized, four of which represented the first phenotype while the remaining six represented each of the other phenotypes. The species is aggressive in its exploitation of various ecological niches. Small, homogeneous, genetically distinct populations have evolved a response to the demands of each ecological niche and a device to isolate the individual gene pools.

Morphological variability is an undisputed attribute of a species composed of sexually reproducing individuals in a large panmictic population. However, the assumption that continuous populations were spatially fluid, panmictic, and genetically homogeneous has been assailed by the results of extensive works on both plants and animals (Epling & Dobzhansky, 1942; Selander et al., 1969; Bradshaw, 1972; Jones, 1973; Schaal, 1975). This assumption has now been largely replaced by the theory that, particularly in plants, many extensive populations consist of numerous semi-isolated demes. This, according to Linhart et al. (1981), may be due to the effect of diversifying selection in heterogeneous environments and/or highly restricted gene flow as a result of spatial isolation. There is abundant evidence in support of each of these two phenomena in the process of speciation. Evidence of restricted gene flow has led to the assumption that, within continuous populations, there exist small clusters of genetically related individuals (Bradshaw, 1972; Levin & Kerster, 1974). In spite of this, the existence of distinct correlated discontinuities in the phenotypic characteristics of a continuous population, which thereby render the population morphologically heterogeneous, would subsume the existence of distinct segmentation in the genetic structure of the population (cf. Oyewole, 1971). Such segmentation can be maintained only by a number of factors, chief among which is an intrinsic isolation mechanism.

The present work analyzes the results of studies of the genetic structure of morphological variants of the variable species or species complex, *Urginea indica* (Roxb.) Kunth. The morphological differentiation among the large form is the subject of the third in a series of studies of the genus (Oyewole, 1986).

Materials and Methods

Populations were sampled in the wild, and plants were cultivated in experimental sites (Oyewole, 1986). Collection sites are illustrated in Figure 1. The distribution of the species, between latitudes 7°N and 10°N, spans the deciduous woodland and savanna of the Southern Guinea Savanna vegetation zone. Over 250 plants were collected from 23 sites in 17 sampling areas. Plants from distinct populations were grown together under the same experimental conditions; seven distinct morphological groups were recognized. Four of the forms (A, B, C and D) represent the large form, while E, F and G belong to the dwarf form.

Root tips were harvested between 8 and 9 A.M., pretreated for one hour in sat. aq. 1,4-dichlorobenzene, fixed, and treated for mitotic squash preparations following the conventional methods (Darlington & LaCour, 1969). Chromosome counts were taken at random from every preparation. Chromosome measurements were taken from not less than 100 cells, at full mitotic meta-

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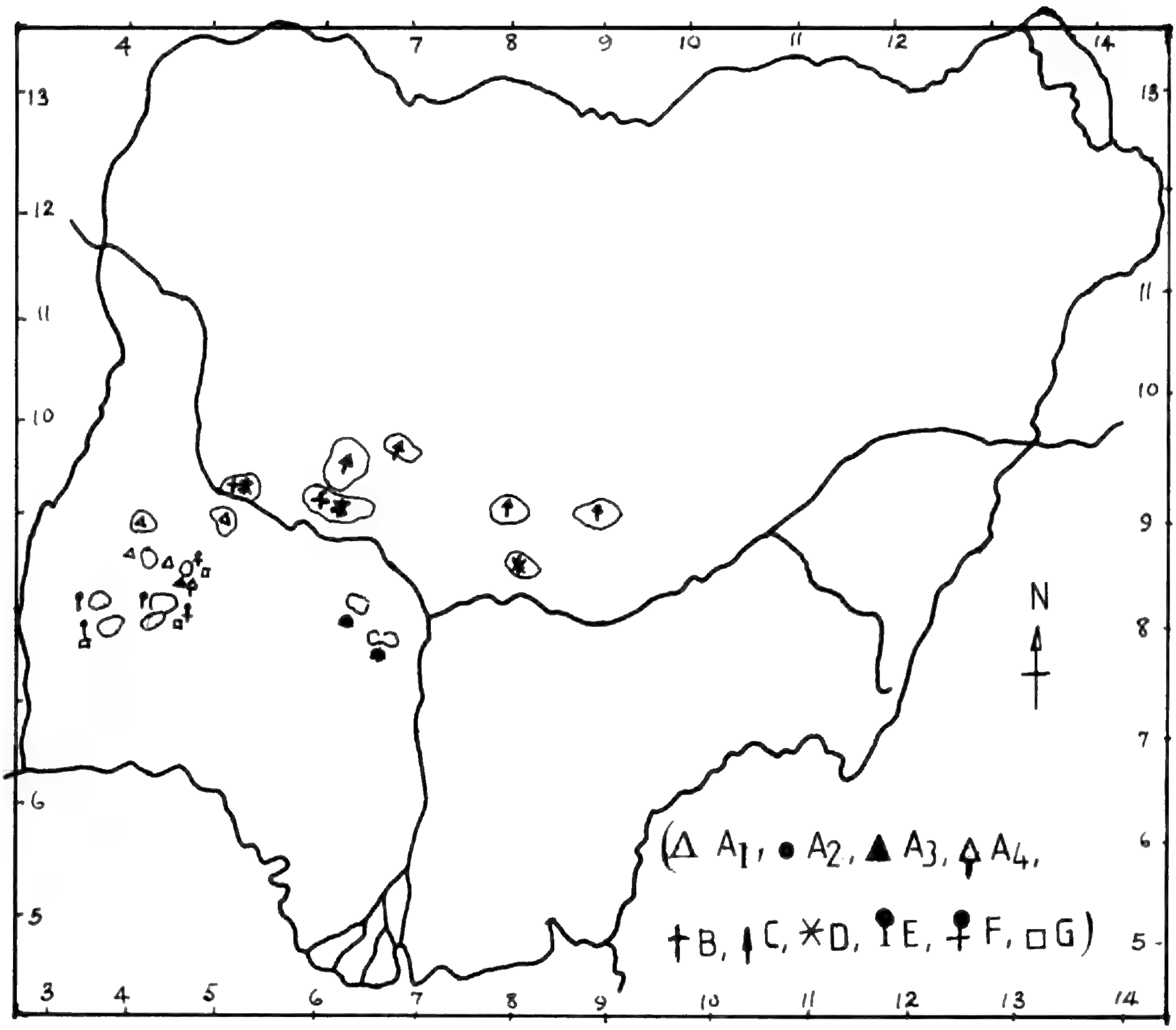

FIGURE 1. Map of Nigeria showing areas of major sampling sites.

phase, in each morphological group. Homologous chromosomes were easily identified in each set of measurements from comparative chromosome lengths and the relative lengths of chromosome arms. Measurements were recorded in order of magnitude for the haploid set. Data were pooled for each group, from which average chromosome length, the relative chromosome-arm length, and the position of the centromere were determined.

Flower buds of appropriate age were collected between 7 and 10 A.M., immediately incised and fixed, and the anthers squashed and stained. As many inflorescences as were available in each group were sampled, and meiotic stages from pachynema to telophase II were examined in not less than 100 pollen mother cells (PMCs) in those groups that flowered (not all the groups have flowered in cultivation).

RESULTS

Figure 2 contains somatic metaphase complements of the various groups. All the groups have $2n = 20$. Karyotype data is summarized in Table 1. Each morphological group is represented by a different karyotype. The total length of chromatin material, at metaphase, of each karyotype differs from the others. The karyomorphology is similar, although intrinsic differences abound (Fig. 3). Chromosome classification, using the chromosome index (ratio of long arm to short arm), is according to Levan et al. (1964). The chromosomes in each complement were classified as long (6.0 μm and above), medium (4.0–5.9 μm) and short (below 4.0 μm). Details of the meiotic study will be presented in a subsequent part of this series.

Group A. This group is represented by four

TABLE 1. Summary of karyotype data (*Urginea indica*).

Homologues		A_1	A_2	A_3	A_4	B	C	D	E	F	G
1	Chromatin length	11.0	10.56	7.5	7.5	9.5	13.1	9.82	13.5	12.05	12.33
	r value	10.0	9.06	6.5	6.5	8.5	11.25	9.67	11.5	11.05	8.25
	Centromere location	t	t	st	st	t	t	t	t	t	t
2	Chromatin length	10.0	9.88	7.25	6.88	8.5	11.75	8.5	11.5	9.35	11.33
	r value	9.0	8.88	8.67	17.3	10.3	10.75	7.5	10.5	8.8	12.6
	Centromere location	t	t	t	t	t	t	t	t	t	t
3	Chromatin length	8.0	7.5	4.88	5.0	6.13	9.56	7.16	9.25	8.63	8.81
	r value	9.67	7.0	8.75	9.0	7.2	8.56	7.6	11.33	7.85	10.9
	Centromere location	t	st	t	t	t	t	t	t	t	t
4	Chromatin length	5.5	5.5	4.75	4.0	5.75	7.13	5.0	7.0	7.8	6.82
	r value	6.0	4.5	5.33	5.6	6.67	7.14	9.0	6.0	7.67	7.74
	Centromere location	st	st	st	st	st	t	t	st	t	t
5	Chromatin length	5.0	4.75	3.5	4.0	4.75	6.0	4.5	5.63	5.65	5.69
	r value	9.0	6.6	6.0	7.0	8.5	5.86	5.0	6.5	6.5	5.4
	Centromere location	t	st	st	st	t	st	st	st	st	st
6	Chromatin length	4.5	4.63	3.5	3.5	4.5	5.92	4.17	5.25	5.43	5.4
	r value	8.0	8.25	6.0	6.0	5.0	7.88	8.07	6.0	6.0	5.59
	Centromere location	t	t	st	st	st	t	t	st	st	st
7	Chromatin length	4.0	4.31	3.0	3.0	3.88	5.5	3.92	5.25	5.28	4.96
	r value	7.0	3.31	3.6	1.0	4.2	5.29	4.88	6.0	6.3	5.36
	Centromere location	st	st	st	m	st	st	st	st	st	st
8	Chromatin length	4.0	4.06	3.0	3.0	3.67	5.25	3.92	5.13	5.15	4.71
	r value	5.0	4.41	3.2	5.0	7.74	5.0	4.88	7.2	5.0	5.63
	Centromere location	st	st	st	st	t	st	st	t	st	st
9	Chromatin length	4.0	3.68	2.75	3.0	3.5	5.13	3.75	4.5	4.55	4.45
	r value	7.0	6.36	2.5	5.0	5.14	7.2	4.0	5.0	6.6	5.29
	Centromere location	st	st	sm	st	st	t	st	st	st	st
10	Chromatin length	3.67	3.31	2.5	2.5	3.0	4.88	3.5	4.25	4.10	4.14
	r value	4.5	4.91	2.6	4.0	5.0	8.75	6.0	4.67	6.9	3.93
	Centromere location	st	st	sm	st	st	t	st	st	st	st
Total chromatin length/complement		119.34	116.36	85.26	84.76	106.36	148.44	108.48	142.52	135.97	137.28
Mean chromatin length/chromosome		5.97	5.82	4.26	4.24	5.32	7.42	5.42	7.13	6.80	6.86

t = terminal; st = subterminal; m = median; sm = submedian.

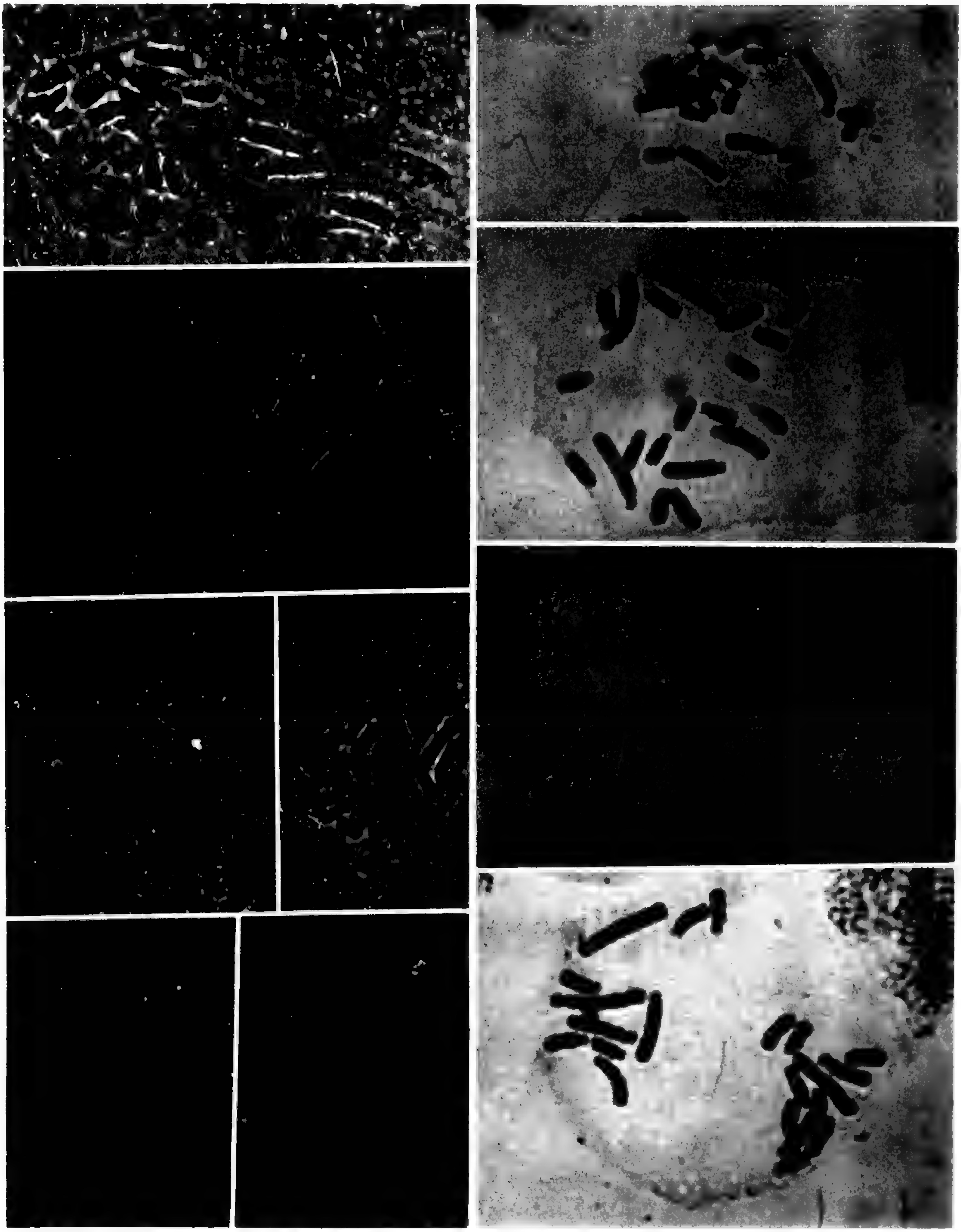

FIGURE 2. Somatic metaphase complements of the various groups. Bar represents 10 μm.

karyotypes (A_1–A_4) that fall into two sets. A_1 and A_2 are similar, forming one set; A_3 and A_4 are similar, forming the other set (Fig. 3, Table 1). Type A_1 represents plants of four contiguous sampling sites; A_2 represents plants of another two contiguous sampling sites about 400 km to the east of A_1. A_3 and A_4 represent separately each of the only two individual plants collected in one sampling site about 80 km to the east of A_1.

A_1 karyotype consists of chromosomes whose average lengths vary between 3.67 μm and 11.0 μm, with an average total chromatin length of 119.34 μm per complement. The complement consists of three long, six medium, and one short pairs of chromosomes, all with terminal and subterminal centromeres. Endomitosis frequently occurs in the root cells. Meiosis is normal, and 10 bivalents are regularly formed.

Even though each complement of A_2, A_3 and A_4 could be resolved into pairs of similar chromosomes, members of such pairs are by no means identical. None of the individuals of these three karyotypes has flowered since they were brought into cultivation; hence these hypothetical pairings could not be verified in actual meiotic pairing.

A_2 consists of chromosomes whose average lengths range from 3.31 μm to 10.56 μm, with an average chromatin length of 116.36 μm per complement. The complement consists of six long, 10 medium, and four short chromosomes, all with subterminal–terminal centromeres. The longest two of the chromosomes have a centric region as wide as the short chromosome arm length.

A_3 chromosomes range in average length from 2.5 μm to 7.5 μm, with an average chromatin length of 85.26 μm per somatic complement. There are five long chromosomes in the complement, four of which resolve into two pairs while the fifth is associable with a shorter chromosome. This long chromosome has a conspicuous secondary constriction (arrowed in Fig. 2, A_3). The whole complement consists of five long, four medium, and 11 short chromosomes, all of which have their centromeres in the subterminal–terminal region, except the smallest two pairs which have submedian centromeres.

A_4 chromosomes vary in average length from 2.5 μm to 7.5 μm. They have an average chromatin length of 84.76 μm per somatic complement. The complement consists of four long, six medium, and 10 short chromosomes, all with subterminal–terminal centromeres except a short pair with median centromere.

Group B. This is represented by only one karyotype. Chromosomes vary in average length from 3.0 μm to 9.5 μm, with an average chromatin length of 106.36 μm per somatic complement. The complement consists of three long, three medium, and four short pairs. All the chromosomes have subterminal–terminal centromeres. The longest pair has a wide centric region. Meiosis is normal except for the infrequent early separation of members of a small pair.

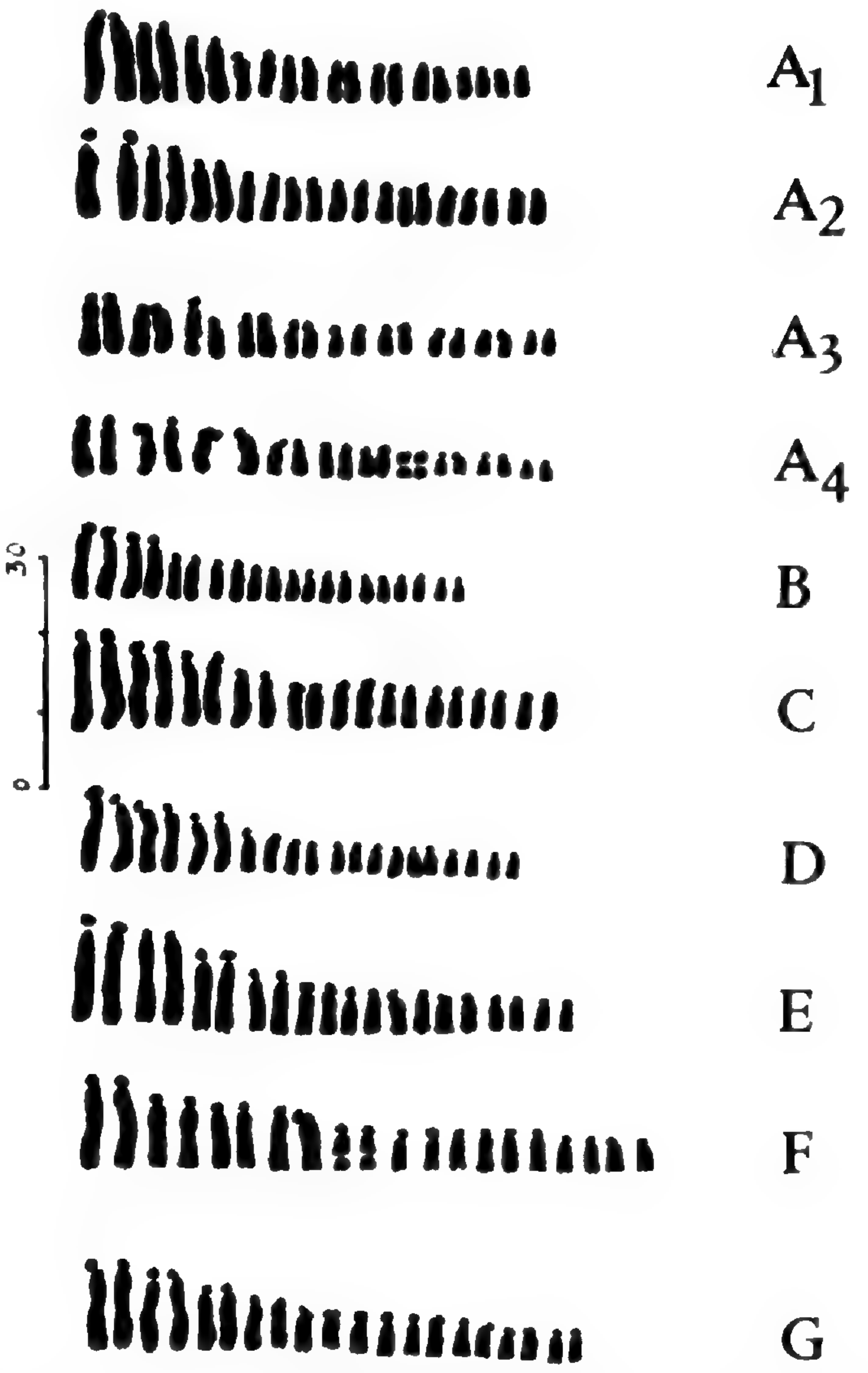

FIGURE 3. Idiograms of the various karyotypes represented by the groups. Horizontal bar represents 30 μm.

Group C. Chromosome length varies from an average of 4.88 μm to 13.1 μm, with an average chromatin length of 148.44 μm per somatic complement. There are five long and five medium pairs of chromosomes in the complement. All the chromosomes have subterminal–terminal centromeres. The longest pair has a centric region as wide as its short arm. Multivalents are frequently formed during meiosis.

Group D. Populations of this group are sympatric with those of Group B. The karyotype consists of chromosomes with subterminal–terminal centromeres. The average chromosome length varies from 3.5 μm to 9.82 μm, with an average chromatin length of 108.48 μm per somatic complement. There are three long, three medium, and four short pairs of chromosomes. The two longest pairs have a wide centric region. Meiosis is regular.

Group E. The karyotype of this group consists of chromosomes with subterminal–terminal centromeres. Chromosomes vary in length from 4.25 μm to 13.5 μm and have an average chromatin length of 142.52 μm per somatic complement. There are four long and six medium pairs of chromosomes. The first and third long pairs have a wide centric region. Meiosis is regular.

Group F. The karyotype consists of chromosomes that vary in length from 4.1 μm to 12.05 μm, with an average chromatin length of 135.97 μm per somatic complement. The complement is made up of four long and six medium pairs, all with subterminal–terminal centromeres. The fifth pair has a secondary constriction on the long arm. Meiosis is regular.

Group G. The karyotype consists of chromosomes whose average lengths vary between 4.14 μm and 12.33 μm, with an average chromatin length of 137.28 μm per somatic complement. The complement consists of four long and six medium pairs, all with subterminal–terminal centromeres. Meiosis is regular.

DISCUSSION

The similarity in the morphology of the karyotypes is obvious. The differences in the karyomorphology of the different populations seem minute, but they are basic and do underlie the differences in the external morphology of each population. Even under cultivation for several years, these morphological differences are still retained. It is, however, evident that changes have occurred (or are occurring) in this taxon that may be correlated with the morphological differentiation of the populations. The recognition of different karyotypes that correspond to different morphological forms is noteworthy; the presence of more than one karyotype in an otherwise morphologically uniform unit raises interesting questions about evolutionary phenomena. This morphologically uniform unit, Group A, is interesting. Karyomorphological segmentation is not accompanied by external morphological differentiation, but it is partly correlated by habitat preferences; the A_2, A_3 and A_4 complements clearly demonstrate lack of homology in the morphology of the chromosomes. There is therefore enough evidence to suspect that these three complements represent natural hybrid swarms that introgressively identify with A_1, which is likely to be one of the putative parents. The different karyotypes are correlated with differences in external morphology and ecological preferences. Those forms that inhabit different ecological niches may have differentiated in response to differences in ecological demands, while those which inhabit same or similar ecologic niches must be fundamentally different genetically in order to retain their individual identities morphologically. In both cases, karyotype differentiation seems to have resulted in reproductive isolation by which the different forms are maintained in nature.

The differences in the amount of chromatin material may have resulted from (or led to) karyotype differentiation. Difference in the chromatin material is correlated with both morphological differentiation and ecological preferences (note A_3 and A_4, B and D are in the same niches; A_1 and A_2, and E, F, and G are in similar niches; and C and E are in different niches).

The morphological variability of this species has long been recognized, but no prior attempts have been made to distinguish the different forms beyond the arbitrary categorization of "large" and "dwarf." This is probably due to the fact that no field collection ever contains both floral and vegetative features together, as well as to the wide east–west distribution of the species. The aggressive exploitation of different niches by different biotypes has resulted in the differentiation of the morphological forms within the species' broad areas of distribution. The isolation of specific biotypes, forming small clusters of individuals, in such ecological niches probably led to the accumulation of favored genes and/or modest chromosomal changes and eventually to the specific karyotypes that are associated with specific morphological forms as well as with specific ecologic niches (Wright, 1940; Bush et al., 1977; Bengtsson, 1980). There is no doubt that morphological differentiation in these populations is more obvious than differentiation in chromosome morphology, suggesting that chromosome repatterning may have been mild and might have involved only small segments in gene/gene block rearrangement. Hence this species seems to comprise a stable polymorphism in which the different forms have attained reproductive isolation and genetic stability, and hence each form has retained its morphological identity. This case is therefore different from that of *Agrostis tenuis*

(Bradshaw, 1959) or *Elymus rechingeri* (Heneen & Runemark, 1962) but seems to be similar to that of the diploid neospecies of *Clarkia* (Lewis, 1973).

Flower formation and fruit development are a common feature with most of the morphological forms, especially in nature. Preliminary studies of meiotic behavior have shown regularity of pollen formation in most of them under cultivation. However, this apparent sexual reproduction is coupled with vigorous vegetative propagation by axillary bulb formation in varying degrees in all forms. It is therefore necessary to have a closer look at the reproductive biology of the entire species in order to ascertain the extent of actual sexual reproduction and the mechanism of pollination in each form. Hybridization experiments between the different forms, which will hopefully shed light on their genetic divergence, are in progress. Thus far, preliminary results of such experiments show successful artificial crossing between only two forms, A_1 and E.

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NEW TAXA OF *OENOTHERA* L. SECT. *OENOTHERA* (ONAGRACEAE)[1]

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ABSTRACT

Several new taxa are described in advance of a complete monograph of *Oenothera* sect. *Oenothera* subsect. *Raimannia*. The populations previously assigned by Munz to *O. laciniata* subsp. *pubescens* are here treated as a species in the new subsect. *Nutantigemma*, which is characterized by nodding buds and a distinct geographical range in montane sites from the western United States south to South America. It forms sterile artificial hybrids with members of subsect. *Raimannia* sensu stricto, which has erect buds and which ranges at low elevations from the central and eastern United States through the plains to eastern Colorado and Texas. Two new outcrossing species, *O. breedlovei* and *O. tamrae*, are differentiated from the permanent structural heterozygote *O. pubescens*, for a total of three species assigned to subsect. *Nutantigemma*.

Subsection *Raimannia* is here divided into two series: series *Candela*, established for the species with densely flowered spikes bearing two or more flowers opening per day, inflorescences without lateral branches, acute to rounded petals, and straight floral tubes (*O. rhombipetala*, *O. heterophylla*, *O. clelandii*, *O. bifrons*, and *O. curtissii*); and series *Raimannia* is restricted to plants with loose inflorescences usually interrupted by lateral branches, usually only one flower opening per day, truncate to emarginate petals, and floral tubes curved upward prior to anthesis (*O. grandis*, *O. falfurriae*, *O. mexicana*, *O. laciniata*, *O. drummondii*, and *O. humifusa*). The new species *Oenothera falfurriae* is described for relictual populations in southeastern Texas that are autogamous but form seven bivalents in meiosis I. It has a unique plastome differentiated from its presumed ancestor *O. grandis* and from the morphologically similar and sympatric *O. laciniata*. The new combination *O. drummondii* subsp. *thalassaphila* is made for the populations in Baja California previously treated as *O. thalassaphila*.

Over 20 years of cultivation of nearly 150 strains for experimental hybridizations, cytological examination, study of breeding systems, and extensive study of herbarium materials, has led to revision of the species referred to subg. *Raimannia* (Rose ex Britton & A. Brown) Munz by Munz (1935, 1965). Extensive analysis of crossing relations has resulted in realignment of a group of 75 species into sect. *Oenothera*, which includes the species referred by Munz to his subg. *Oenothera* and subg. *Raimannia* (Stubbe & Raven, 1979). In turn, this large group of basically intercrossable species was further subdivided into five smaller crossing groups that form highly fertile hybrids and usually have compatible plastids. The first of these groups comprises the South American species, which Dietrich (1977) placed into subsect. *Munzia* W. Dietrich (45 species). The second, subsect. *Oenothera* (13 spp.), was outlined by Raven et al. (1979). The third and most primitive group is subsect. *Emersonia* (Munz) W. Dietrich, Raven & W. L. Wagner (four spp.), revised in 1985 by Dietrich et al. The fourth and fifth groups, subsect. *Raimannia* and the new subsect. *Nutantigemma* described in this paper, will be the subject of an upcoming detailed revision. Prior to publication of the revision, the present paper makes the new subsection and species available for regional floras and concurrent work on *Oenothera*, including DNA restriction mapping and studies of flavonoids, pollen, and seed anatomy.

SUBSECTION *NUTANTIGEMMA*

Populations occurring in montane sites from the western United States south to South America, referred by Munz (1935, 1965) to a variety or subspecies of *Oenothera laciniata* Hill, are morphologically and genetically distinct from *O. laciniata*. This widespread entity is a permanent translocation heterozygote treated by us as *O. pubescens* Willd. ex Spreng.

Two new Mexican species, closely related to *Oenothera pubescens*, one from the cape region of Baja California and one in the southern Sierra Madre Occidental, were detected during the study of herbarium specimens and cultivation of numerous strains in the experimental gardens (Stubbe & Raven, 1979). They are described here as *O. breedlovei* (bivalent-forming) and *O. tam-*

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rae (presumably bivalent-forming). *Oenothera tamrae* is known only from the type collection and has not been grown in the experimental garden. All three species are placed into the new subsect. *Nutantigemma.*

Oenothera L. sect. **Oenothera** subsect. **Nutantigemma** W. Dietrich & W. L. Wagner, subsect. nov. TYPE: *O. pubescens* Willd. ex Spreng.

Oenothera sect. *Onagra* sensu Ser. ex DC., Prodr. 4: 46. 1828, pro parte.

Anogra sensu Wooton & Standley, Contr. U.S. Natl. Herb. 16: 150. 1913, pro parte.

Raimannia sensu Rose, Contr. U.S. Natl. Herb. 8: 330. 1905, pro parte; sensu Sprague & Riley, Bull. Misc. Inform. 200. 1921, pro parte.

Oenothera subg. *Raimannia* sensu (Rose ex Britton & A. Brown) Munz, Amer. J. Bot. 22: 645. 1935, pro parte.

Oenothera sect. *Anogra* sensu Tidestrom, Fl. Ariz. & N. Mex. 273. 1941, pro parte.

Oenothera subg. *Raimannia* sect. *Raimannia* sensu (Rose ex Britton & A. Brown) Munz, N. Amer. Fl. II. 5: 105. 1965, pro parte.

Oenothera sect. *Oenothera* subsect. *Raimannia* sensu (Rose ex Britton & A. Brown) W. Dietrich, Ann. Missouri Bot. Gard. 64: 612. 1977 [1978], pro parte.

Herbae annuae vel probaliter biennes, erectae, rosulatae, simplices vel caules principales ramosi ramis arcuatis e rosula adscendentibus. Folia rosulae anguste oblanceolata, profunde partita vel quasi integra, acuta; folia caulina angustissime elliptica vel elliptica, anguste oblanceolata vel oblanceolata vel lanceolata vel anguste oblonga, profunde partita vel quasi integra, acuta, folia strigillosa vel villosa, raro glanduloso-pubescentia. Inflorescentiae simplices vel interruptae ramis lateralibus, apice nutantes, gemmae juvenes erectae, vetiores nutantes, maturae demo erectae, flos unus efflorescet per diem per spicam. Tubi florales 1.5–5 cm longi, plerumque rubri illimiti, strigillosi vel villosi et glanduloso-pubescentes. Sepala flavida, saepe rubra illimita vel rubra fasciata ad margines, interdum rubra maculata; pubescentia tubi floralis similis; apices sepalorum 0.1–1 mm longi. Petala late vel latissime obovata, raro rotunda, apice truncata vel retusa, 0.5–3.5 cm longa, 0.6–4 cm lata, flava, rubescentia vel aurantiaca post anthesin. Styli 2–6.5 cm longi, stigmate sub anthesi supra antheras elevato vel antheris circumdato. Capsulae cylindricae, 1.8–4.6 cm longae. Semina ambito elliptica vel rotundata, brunnea vel atrobrunnea, saepe atromaculata, 0.9–1.6 mm longa, 0.6–1 mm crassa. Planta homozygotica et autocompatibilis vel structuraliter chromosomatice heterozygotica complexa. Numerus gameticus chromosomaticus, $n = 7$.

The principal reason for according these three species (*O. pubescens*-group of Stubbe & Raven, 1979) subsectional status is the sterility of hybrids in crosses between subsections *Raimannia* and *Nutantigemma.* They range from western Texas west to Arizona and southeastern California, south to Mexico and Guatemala, and one species extends to the Andes of Colombia, Ecuador, and Peru south to the province of Junín. The nodding flower buds on the species of subsect. *Nutantigemma* clearly differentiate them from those of subsect. *Munzia* and subsect. *Raimannia.* This feature is shared with the white-flowered sect. *Kleinia* Munz, sect. *Anogra* (Spach) Endl., sect. *Ravenia* W. L. Wagner, occasionally with *Oenothera caespitosa* Nutt. subsp. *navajoensis* W. L. Wagner, Stockhouse & Klein [sect. *Pachylophus* (Spach) Endl.], and with the yellow-flowered sect. *Eremia* W. L. Wagner. In *Oenothera fruticosa* L. [sect. *Kneiffia* (Spach) Endl.], which has yellow flowers, the shoot apices, but not the flower buds, are bent downward; a similar condition occurs in *O. speciosa* Nutt. [sect. *Xylopleurum* (Spach) Endl.]. Nodding buds appear to represent, at least for the most part, plesiomorphy rather than convergence.

Another important argument for considering this group a subsection is that these three species are distributed completely allopatrically from subsect. *Raimannia.* The species of series *Nutantigemma* grow exclusively in montane habitats, from 3,900 m down to approximately 1,500 m, while the species of subsect. *Raimannia* grow only at lower elevations. *Oenothera breedlovei* is self-compatible and bivalent-forming; *O. pubescens* is a permanent translocation heterozygote forming a ring of 14 chromosomes in meiosis I and with 40–70% pollen fertility; *O. tamrae* is probably an outcrossing bivalent-former, based on 90–100% fertile pollen in the type collection.

KEY TO THE SPECIES OF SUBSECT. *NUTANTIGEMMA*

1a. Stigma elevated above the anthers at anthesis; pollen ca. 90–100% fertile; Laguna Mts., Baja California, Mexico, and Nayarit, Mexico.
  2a. Lower leaves deeply parted almost to the midrib; mature buds up to 5 mm in diameter; Laguna Mts., Baja California, Mexico .... *O. breedlovei*
  2b. Lower leaves not parted to the midrib; mature buds 5–7 mm in diameter; Nayarit, Mexico .... *O. tamrae*
1b. Stigma surrounded by the anthers; pollen ca. 40–70% fertile; Arizona, Texas, Mexico (except Baja California), Guatemala, Colombia to Peru .... *O. pubescens*

Oenothera breedlovei W. Dietrich & W. L. Wagner, sp. nov. TYPE: Mexico. Baja California: granitic slopes surrounding long interior valley, [La Laguna], south of Pico La Aguja, Sierra La Laguna, 6,300–6,700 ft., 22 Oct. 1977, *D. E. Breedlove 43362* (holotype, MO-2695034).

Herbae annuae vel biennes, erectae, rosulatae, 2–3 dm altae. Folia profunde partita vel remote vadoseque dentata. Gemmae vetustiores nutantes. Tubi florales 2.4–4 cm longi. Sepala 1.2–2.2 cm longa, saepe rubromaculata, villosa et glanduloso-pubescentia; apices sepalorum 0.5–1 mm longi. Petala 1.6–3.5 cm longa, flava. Capsulae 1.8–4.6 cm longae, strigillosae. Semina 1.2–1.6 mm longa, 0.6–0.7 mm crassa, saepe maculata. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice structuraliter homozygotica, autocompatibilis.

Erect annual or probably biennial herbs, forming rosettes; stems 2–3(–5) dm long, simple or with a branched main stem and arcuating lateral branches arising from the rosette, usually flushed with red, densely strigillose, sometimes also scattered villous. Rosette leaves narrowly oblanceolate, 4–12 cm long, 0.5–2 cm wide, pinnately parted to remotely and shallowly dentate, the apex acute, gradually narrowed to the petiole; cauline leaves very narrowly elliptic to lanceolate, 2–5 cm long, 0.5–2 cm wide, usually pinnately parted, the apex acute, the base narrowly cuneate, short-petiolate to sessile; bracts lanceolate to narrowly ovate, 1.5–3 cm long, 0.5–1.5 cm wide, deeply parted to remotely shallowly dentate, the apex acute, the base broadly cuneate to narrowly cuneate; leaves and bracts densely strigillose and sparsely villous. Inflorescence usually with lateral branches, the young buds erect, the older ones nodding, becoming erect just before opening. Flowers usually 1 per spike opening near sunset each day. Floral tube flushed with red, 2.4–4 cm long, ca. 1 mm diam., sparsely to densely strigillose, villous, and glandular puberulent. Mature buds oblong, 3–5 mm diam. at the base. Sepals yellowish, often flushed with red, also red maculate and striped at the margins, scattered to densely villous and scattered to densely glandular puberulent, 1.2–2.2 cm long, the free tips 0.5–1 mm long, erect and appressed in bud, strigillose to villous. Petals yellow, broadly obovate to very broadly obovate, retuse, 1.6–3.5 cm long, 1.6–3.7 cm wide. Filaments 1.1–2 cm long; anthers 4–12 mm long; pollen ca. 90–100% fertile. Ovary 1–2.5 cm long, ca. 1.5 mm diam., densely strigillose; style 4–6.5 cm long, the visible part 1.7–2.5 cm long; stigma elevated above the anthers at anthesis, the lobes 3–6 mm long. Capsule cylindrical, 1.8–4.6 cm long, 3–3.5 mm diam., densely strigillose. Seeds ellipsoid to broadly ellipsoid, brown to dark brown, often with darker flecks, 1.2–1.6 mm long, 0.6–0.7 mm diam., the surface pitted. Self-compatible but modally outcrossing. Gametic chromosome number, $n = 7$ (7_{II} at meiotic metaphase I).

This new species, known only from Laguna Mts., southern Baja California, Mexico, is named in honor of Dennis E. Breedlove (California Academy of Sciences), who has added greatly to our knowledge of Mexico through his extensive and excellent collections and to whom we are indebted for collecting material of this and many other Mexican *Oenothera* species for cultivation at the Botanical Institute of the University of Düsseldorf and at the Missouri Botanical Garden.

Oenothera tamrae W. Dietrich & W. L. Wagner, sp. nov. TYPE: Mexico. Nayarit: Sierra Madre, near Santa Teresa, territory of Tepic, 8 Aug. 1897, *J. N. Rose 2133* (holotype, US-301038; isotypes, NY, UC).

Herbae annuae vel biennes, erectae, rosulatae, 2–4 dm altae. Folia partita seu remote obtuseque dentata vel quasi integra. Gemmae vetustiores nutantes. Tubi florales 3.5–4.2 cm longi, villosi et glandoloso-pubescentes. Sepala 1.8–2.5 cm longa, rubro complana et rubro-fasciata ad margines; apices sepalorum 0.5 mm longi. Petala 2–3.5 cm longa, flava. Capsulae 4–4.5 cm longae, strigillosae et villosae. Semina 1–1.1 mm longa, 0.7 mm crassa.

Erect annual or biennial herbs, probably forming rosettes; stems 2–4 dm long, simple or with obliquely ascending lateral branches arising from the rosette, densely strigillose and sparsely to densely villous. Cauline leaves narrowly elliptic or narrowly lanceolate to lanceolate, 4–8 cm long, 0.8–1.8 cm wide, pinnately parted or remotely and bluntly dentate to subentire, the apex acute, the base narrowly cuneate, sessile; bracts narrowly lanceolate to lanceolate, 3–4.5 cm long, 0.7–1.5 cm wide, remotely and bluntly dentate, the apex acute, the base narrowly cuneate, sessile; leaves and bracts strigillose. Inflorescence simple or with lateral branches, nodding. Usually 1 flower per spike opening probably near sunset each day. Floral tube flushed with red, 3.5–4.2 cm long, 1.5–2 mm diam., sparsely villous and sparsely glandular puberulent. Mature buds cylindrical to narrowly ovoid, 5–7 mm diam. at the base, nodding before anthesis. Sepals yellowish, often flushed with red and striped red at the margins, the pubescence as on floral tube, 1.8–2.5 cm long, the sepal tips ca. 0.5 mm long, erect in bud, strigillose. Petals yellow, very broadly obovate, retuse, 2–3.5 cm long, 3–4 cm wide. Filaments 1.5–1.7 cm long; anthers 6–9 mm long; pollen ca. 90–100% fertile. Ovary 1.8–2.6 cm long, ca. 2 mm diam., densely strigillose and densely villous, the apex also glandular puberulent. Style 5.3–6.4 cm long, the visible part 1.8–2.2 cm long; stigma elevated above the anthers at anthesis, the lobes 5–8 mm long. Capsule cylindrical, 4–4.5 cm long, 3–4 mm diam., the pubescence as on ovary but less dense. Seeds broadly ellipsoid, brown with dark red flecks, 1–1.1 mm long, ca. 0.7 mm diam., pitted. Chromosome number unknown.

This rare new species, known only from the type locality, near Santa Teresa in the Sierra Madra, Nayarit, Mexico, is named in honor of Tamra Engelhorn Raven, botanist and wife of Peter H. Raven. The description is based entirely on the type collection made by J. N. Rose in 1897.

SUBSECTION *RAIMANNIA*

The yellow-flowered species assigned by Munz (1935, 1965) to his subg. *Raimannia* from the central and eastern United States are now considered to comprise subsect. *Raimannia.* Stubbe and Raven (1979), when considering the realignment of sect. *Oenothera,* included *O. grandis* (Britton) Smyth, *O. laciniata* Hill, *O. drummondii* Hook., *O. humifusa* Nutt., *O. heterophylla* Spach, and *O. rhombipetala* Nutt. ex Torrey & A. Gray in subsect. *Raimannia.* Work toward the overall revision of the subsection has led to the recognition of two series within it.

Oenothera sect. **Oenothera** subsect. **Raimannia** (Rose ex Britton & A. Brown) W. Dietrich series **Candela** W. Dietrich & W. L. Wagner, series nov. TYPE: *O. rhombipetala* Nutt. ex Torrey & A. Gray.

Oenothera sect. III Spach, Nouv. Ann. Mus. Hist. Nat. 4: 347. 1835, pro parte.
Oenothera § *Euoenothera* sensu S. Watson, Proc. Amer. Acad. Arts 8: 574. 1873, pro parte.
Oenothera sensu Small, Bull. Torrey Bot. Club 23: 172. 1896, pro parte.
Raimannia sensu Rose, Contr. U.S. Natl. Herb. 8: 330. 1905, pro parte.
Oenothera subg. *Raimannia* sensu Munz, Amer. J. Bot. 22: 645. 1935, pro parte; sensu Sprague & Riley, Bull. Misc. Inform. 200. 1921, pro parte.
Oenothera subg. *Raimannia* sect. *Raimannia* sensu Munz, N. Amer. Fl. II. 5: 105. 1965, pro parte.

Herbae annuae vel biennes, probaliter breviter perennes, erectae, rosulatae, simplices vel caules principales ramosi ramis oblique e rosula adscendentibus, 2.5–10 dm altae. Inflorescentiae densae vel laxae, simplices, non interruptae ramis lateralibus; efflorescunt flores 2 vel complures per diem per spicam. Tubi florales 1.5–4.7 cm longi. Capsulae versus apicem ± angustatae, 1–3.3 cm longae, 2–4 mm crassae. Semina anguste elliptica vel late elliptica, 1.1–1.9 mm longa, 0.4–0.8 mm crassa, plerumque atromaculata.

Series *Candela* comprises a clearly defined group of five closely related species that occur in sandy soil in open places such as fields, prairies, roadsides, and open woods, from southern South Dakota, Minnesota, and Michigan south to Texas and southeastern New Mexico and east to Louisiana, Alabama, northern Florida, and southern Georgia. They all have the presumably derived characters of relatively densely flowered spikes on which two or more flowers open every evening, unlike the species of series *Raimannia,* which nearly always produce only one flower per branch each day, a plesiomorphic characteristic. The spikes of series *Candela* never have lateral shoots, as is often the case in series *Raimannia.* The fully grown buds of series *Candela* are narrowly oblong, whereas those of series *Raimannia* are lanceoloid in the large-flowered structural homozygote species and oblong to ellipsoid in the small-flowered heterozygote species. In series *Raimannia,* the older buds are curved upward until very shortly before flowering; those of series *Candela* are straight. The shapes of the petals also clearly differentiate series *Candela* from series *Raimannia*; those of series *Candela* are acute to rounded at the apex, in contrast with those of series *Raimannia* which are truncate to emarginate. Further, the capsules of series *Candela* are relatively short and thicker toward the base, while those of series *Raimannia* are on average longer and nearly cylindrical. All species of series *Candela* appear to be biennials. In contrast to this specialized habit, the species of series *Raimannia* have evolved an annual habit except *O. drummondii* and *O. humifusa,* which inhabit sand dunes and have retained the generalized perennial habit.

Three of the species, *Oenothera heterophylla, O. bifrons* D. Don, and *O. rhombipetala,* are self-incompatible bivalent-formers, and *O. clelandii* W. Dietrich, Raven & W. L. Wagner and *O.*

curtissii (Rose) Small are complex structural heterozygote species, presumably derived from an ancestor similar to *O. rhombipetala*.

Oenothera sect. **Oenothera** subsect. **Raimannia** (Rose ex Britton & A. Brown) W. Dietrich series **Raimannia** (Rose ex Britton & A. Brown) W. Dietrich & W. L. Wagner, comb. & stat. nov. Based on *Raimannia* Rose, Contr. U.S. Natl. Herb. 8: 330. 1905, ex Britton & A. Brown, Ill. Fl. N. U.S., 2nd edition, 2: 596. 1913. *Oenothera* subg. *Raimannia* (Rose ex Britton & A. Brown) Munz, Amer. J. Bot. 22: 645. 1935. *Oenothera* subg. *Raimannia* sect. *Raimannia* (Rose ex Britton & A. Brown) Munz, N. Amer. Fl. II. 5: 105. 1965. *Oenothera* sect. *Oenothera* subsect. *Raimannia* (Rose ex Britton & A. Brown) W. Dietrich, Ann. Missouri Bot. Gard. 64: 612. 1977 [1978]. TYPE: *O. laciniata* Hill.

Onagra sensu Moench, Methodus 1: 675. 1974, pro parte.
Oenothera sect. *Onagra* sensu Ser. ex DC., Prodr. 4: 46. 1828, pro parte.
Oenothera sect. *Allochroa* sensu Fischer & Meyer, Index Sem. Hort. Petrop. 2: 44. 1835, pro parte.
Oenothera sect. I Spach, Hist. Nat. Vég. 4: 353. 1835, pro parte.
Oenothera sect. III & IV sensu Spach, Nouv. Ann. Mus. Hist. Nat. 4: 347. 1835, pro parte.
Oenothera § *Euoenothera* sensu S. Watson, Proc. Amer. Acad. Arts 8: 574. 1873, pro parte.
Oenothera sensu Raimann, Nat. Pflanzenfam. III. 7: 214. 1893, pro parte; sensu Small, Bull. Torrey Bot. Club 23: 172. 1896, pro parte.
Oenothera sect. *Oenothera* sensu Tidestrom, Fl. Ariz. & N. Mex. 272. 1941, pro parte.

Erect to procumbent, annual or perennial herbs ± forming rosettes; stems green or flushed with red, simple or much-branched, strigillose or strigillose and villous, sometimes also glandular puberulent especially in the region of the inflorescence. Rosette leaves very narrowly oblanceolate to oblanceolate or lanceolate, parted to dentate, acute; cauline leaves narrowly oblanceolate to oblanceolate, narrowly elliptic, elliptic, narrowly obovate or narrowly oblong, parted to subentire, the lobes ± dentate, the apex acute, the base narrowly cuneate to acute to almost sessile; all leaves strigillose or strigillose and villous, sometimes also glandular puberulent. Inflorescence lax, often with lateral branches, usually only 1 flower per spike opening near sunset each day. Floral tube 1.5–5 cm long, yellowish, often flushed with red, rarely also red-flecked, strigillose or glandular puberulent, or villous and glandular puberulent, usually curved upward. Sepals greenish to yellowish, often flushed with red or red-striped at the margins, sometimes red-flecked, the pubescence usually as on floral tube, the sepal tips 0.3–5 mm long, erect and appressed or spreading in bud, sometimes separated. Petals very broadly obovate, truncate to emarginate at apex, 0.5–4.5 cm long, 0.5–5.5 cm wide, yellow, sometimes pale yellow, fading red to orange after anthesis. Style 2–7.5 cm long; stigma elevated above the anthers at anthesis or surrounded by the anthers and pollen shed directly onto it. Capsule cylindrical, 2–5.5 cm long, 2–5 mm diam. Seeds ellipsoid to subglobose, brown, sometimes with darker flecks (*O. drummondii, O. humifusa*), 0.8–2 mm long, 0.3–0.9 mm diam. Self-incompatible (1 sp.) or self-compatible and modally outcrossing (1 sp.) to modally autogamous (2 spp.), or permanent structural heterozygotes (2 spp.). Gametic chromosome number, $n = 7$ (7_{II}, $\odot 14$ or intermediate chromosome configurations at meiotic metaphase I).

Series *Raimannia* of subsect. *Raimannia* is comprised of six species occurring in open, sandy, and disturbed places, sometimes on dunes, from North Dakota south to Texas and east to the Atlantic Coast, in Mexico along the Gulf Coast, and disjunct in southern Baja California. The species exhibit considerable variation; among them, however, only *Oenothera drummondii* can be subdivided into two geographically separated subspecies. Typical of the species of series *Raimannia* are loose inflorescences, which often have lateral branches, and upward-curving flower buds. Comparisons with series *Candela* were made in the discussion of that series.

The distribution of series *Raimannia* is essentially the same as that of series *Candela* but extends farther east, to the Atlantic Coast, and extends south to the state of Campeche, Mexico, along the coast of the Gulf of Mexico. *Oenothera drummondii* Hook. subsp. *thalassaphila* (Brandegee), comb. nov. is disjunct, occurring along the Pacific Coast at the southern tip of Baja California, Mexico.

Oenothera grandis (Britton) Smyth, *O. falfurriae* (described as new below), *O. mexicana* Spach, and *O. drummondii* form bivalents, whereas *O. laciniata* Hill and *O. humifusa* Nutt. are permanent structural heterozygotes. In this section only *O. grandis* is self-incompatible; all other species, both bivalent-formers and complex structural heterozygotes, are self-compatible and largely autogamous.

Oenothera falfurriae W. Dietrich & W. L. Wagner, sp. nov. TYPE: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 2 July 1981, cult. no. 81-115 from seeds collected in U.S.A. Texas: Brooks Co., 13.3 mi. S of junction of Highways 281 and 285 in Falfurrias, 10 May 1978, *K. Allred & R. Shaw 2021* (holotype, MO-3332203; isotypes, DUSS, M, MO).

Herbae annuae, erectae vel parum decumbentes, rosulae foliis paucis, 1–4 dm altae. Folia partita vel breviter dentata vel quasi integra. Gemmae erectae. Tubi florales 2.5–4 cm longi, villosi et glanduloso-pubescentes. Sepala 1–2.2 cm longa, viridi-flava, immaculata vel rubromaculata; apices sepalorum minuti, 0.5–2 mm longi. Petala 1.3–2.5 cm longa, flava vel pallide flava. Capsulae 2–4.5 cm longae, 2–2.5 mm crassae, strigillosae, villosae et glanduloso-pubescentes. Semina 0.8–1.4 mm longa, 0.3–0.6 mm crassa. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice structuraliter homozygotica, autocompatibilis.

Erect to decumbent annual herbs, forming a rosette with only a few leaves; stems 1–4 dm long, usually simple, densely to sparsely strigillose, villous and sometimes also glandular puberulent. Rosette leaves oblanceolate, 5–12 cm long, 1.3–3.5 cm wide, dentate to pinnatifid or sometimes subentire, the apex acute, gradually narrowed to a short petiole; cauline leaves narrowly oblanceolate to elliptic or narrowly lanceolate, 2–8.5 cm long, 1–3 cm wide, usually dentate, occasionally pinnatifid or subentire, the apex acute, gradually narrowed to subsessile base; bracts elliptic, narrowly ovate to lanceolate, 2–4.5 cm long, 0.5–2.5 cm wide, dentate or subentire to pinnately lobed, narrowed to the base, subsessile; all leaves densely to sparsely villous and glandular puberulent, especially on the midrib of the lower surface and along the margin, usually also sparsely to moderately strigillose. Inflorescence lax, simple or with lateral branches, usually only 1 flower per spike opening near sunset each day, erect at anthesis. Floral tube 2.5–4 cm long, densely to sparsely villous and glandular puberulent. Mature buds lanceoloid to narrowly ovoid or oblong-ovoid, 0.4–0.6 cm diam. at the base. Sepals green to greenish yellow, sometimes with red spots, the pubescence as on the floral tube, 1–2.2 cm long, the sepal tips 0.5–2 mm long, erect in bud, strigillose and villous. Petals yellow, broadly obovate, 1.3–2.5 cm long, 1.4–2.7 cm wide, the apex truncate to slightly retuse. Filaments 10–17 mm long; anthers 4–5 mm long; pollen ca. 90–100% fertile. Ovary 1–1.7 cm long, ca. 1.5 mm diam., densely villous, strigillose and glandular puberulent; style 3.5–5 cm long, the visible part 1.2–3 cm long; stigma usually elevated above the anthers at anthesis, the lobes 3–7 mm long. Capsule cylindrical, 2–4.5 cm long, 2–2.5 mm diam., the surface pitted. Seeds brown, ellipsoid, 0.8–1.4 mm long, 0.3–0.6 mm diam. Self-compatible, modally autogamous. Gametic chromosome number, $n = 7$ (7_{II} at meiotic metaphase I).

Oenothera falfurriae, named after Falfurrias, Brooks County, Texas, where the type was collected, is endemic to open sandy sites in southeastern Texas. Its range is nearly the same as those of *O. bifrons* and *O. mexicana.* When Dietrich first detected the species, the specimens were treated as hybrids between *O. grandis* and *O. laciniata* since they were somewhat intermediate between these species. Seed samples collected by K. Allred and R. Shaw made it possible to cultivate this species at the Botanical Institute in Düsseldorf, and it soon became obvious that the plants were by no means hybrids, but instead represented an undescribed bivalent-forming species. All plants examined formed 7_{II} in meiosis, and no individuals grown from seed resembled either *O. laciniata* or *O. grandis.* The individual collection numbers of Allred and Shaw represent population samples of several plants from which seeds were taken and sowed separately: *2016, 2020,* and *2021* contained *O. falfurriae* and *O. laciniata*; *2018* contained *O. falfurriae* and *O. mexicana.* Seeds taken from plants of *O. falfurriae* produced only *O. falfurriae* and those of *O. laciniata* produced only *O. laciniata.*

Oenothera falfurriae differs from *O. grandis* in its self-compatibility and smaller petals, which are intermediate in size between those of *O. laciniata* and those of *O. grandis.* Stigmas in the closed mature buds are only slightly raised above the anthers, suggesting that self-pollination is common in *O. falfurriae.* Also, the shape of the buds is more or less oblong, in contrast with the lanceoloid buds of *O. grandis,* and the sepals in *O. falfurriae* are very delicate and pressed together in bud, whereas in *O. grandis* they are often spreading, longer, and thicker.

Oenothera falfurriae is narrowly distributed and presumably relictual. It appears to maintain itself distinct from the other species of series *Raimannia* with which it grows sympatrically—*O. grandis, O. laciniata,* and *O. mexicana*—by possessing a unique plastome. Artificial crosses made by Dr. Behn at the Botanical Institute in Düsseldorf showed that crosses between *O. drummondii* or *O. humifusa* and *O. falfurriae* as the staminate parent produced pale seedlings that failed to grow beyond the cotyledon stage. Similarly, the seeds of crosses between *O. grandis* and *O. falfurriae* did not germinate at all (Behn, pers. comm.). Also, since crosses between *O. drummondii, O. humifusa,* or *O. grandis* and *O. laciniata* produce completely green and viable offspring, we can assume that similar crossing barriers exist between *O. falfurriae* and *O. laciniata,* based on the pattern of such relationship in *Oenothera* sect. *Oenothera* generally.

Oenothera drummondii Hook. subsp. **thalassaphila** (Brandegee) W. Dietrich & W. L. Wagner, comb. nov. Based on *Oenothera thalassaphila* Brandegee, Univ. Calif. Publ. Bot. 10: 185. 1922. *Oenothera drummondii* Hook. var. *thalassaphila* (Brandegee) Munz, Amer. J. Bot. 22: 651. 1935. TYPE: Mexico. Baja California Sur: San José del Cabo, 12 Mar. 1892, *T. S. Brandegee 218* (lectotype, UC-107674; see Munz, Amer. J. Bot. 22: 651. 1935).

The separation of *Oenothera drummondii* subsp. *thalassaphila,* which is restricted to dunes of coastal southern Baja California del Sur, Mexico, from subsp. *drummondii* depends on a combination of characters since no single morphological feature separates them clearly. *Oenothera drummondii* subsp. *thalassaphila* always grows for several years, as is demonstrated by the consistent presence of nonflowering shoots and large taproots on the older plants. By contrast, *O. drummondii* subsp. *drummondii* is basically an annual, seldom overwintering for a second season; it usually has only a few nonflowering shoots or none, and the development of its taproot is considerably weaker than in subsp. *thalassaphila.* In general, the habit of subsp. *drummondii* is more upright than that of subsp. *thallassaphila,* which has prostrate to ascending stems. In addition, the calyx of subsp. *thalassaphila* often has red spots and lacks glandular hairs, whereas the calyx of subsp. *drummondii* only rarely has reddish spots and is often glandular puberulent. The sizes of the capsules and seeds are also modally distinct: in subsp. *thalassaphila* the capsules are 2–4 cm long and 2.5–5 mm in diameter, and the seeds are 1.5–2 mm long and 0.7–0.9 mm in diameter; in subsp. *drummondii* the capsules are 2.5–5.5 cm long and 2–3 mm in diameter, and the seeds are 1.1–1.7 mm long and 0.5–0.8 mm in diameter.

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A NEW COMBINATION AND NEW SUBSPECIES IN *OENOTHERA ELATA* KUNTH (ONAGRACEAE)[1]

Werner Dietrich[2] and Warren L. Wagner[3]

Abstract

The new combination of *Oenothera elata* Kunth subsp. *hookeri* (Torrey & A. Gray) W. Dietrich & W. L. Wagner is made for plants of moist coastal or slightly inland sandy and bluff sites from Marin County south to San Diego County, California, previously known as *O. hookeri* subsp. *hookeri* and subsp. *montereyensis.* Also, *O. elata* subsp. *texensis* subsp. nov. is described from Brazos County, Texas. It appears to be a rare relictual entity most closely related to *O. elata* subsp. *hirsutissima* which occurs disjunctly some 680 km to the west of subsp. *texensis.*

These names are made available in anticipation of their use in regional floras and concurrent studies of flavonoids, cytology, and pollen morphology in advance of a detailed revision of *Oenothera* subsect. *Oenothera* (Dietrich & Wagner, in prep.). Detailed presentation of data and discussions will be given in the revision.

Munz (1949, 1965) divided the large-flowered, bivalent-forming, outcrossing populations of sect. *Oenothera* subsect. *Oenothera* from the western United States south to Panama into two species, *O. hookeri* Torrey & A. Gray and *O. elata* Kunth. During the past ten years we have reevaluated the variation pattern of these plants by a detailed study of a large number of herbarium specimens, fieldwork, and study of plants cultivated in the experimental gardens at Düsseldorf. These studies have shown that the two entities are extremely similar and differ only in bract shape, capsule diameter, and modally in several other features. It was therefore suggested by Raven et al. (1979), in an outline of the systematics of *Oenothera* sect. *Oenothera* subsect. *Oenothera* (formerly *Euoenothera*), that they should be considered conspecific.

Oenothera elata can be subdivided into four subspecies: subsp. *elata* with a scattered distribution from Guanajuato, Mexico, to Costa Rica and Panama in Central America; subsp. *hirsutissima* (A. Gray ex S. Watson) W. Dietrich, which occurs in the western United States from Washington and Oregon south to northern Baja California and Durango, Mexico, and in Kansas, Oklahoma, and western Texas (Dietrich in Wagner, 1983); subsp. *texensis* subsp. nov., known only from one collection in Brazos County, Texas; and subsp. *hookeri* (Torrey & A. Gray) comb. et stat. nov. occurring in moist coastal and slightly inland sandy and bluff sites in California from Marin County south to San Diego County.

The four subspecies of *Oenothera elata* can be distinguished with the following key.

KEY TO THE SUBSPECIES OF *OENOTHERA ELATA*

1a. Stem, leaves, and ovary (capsule) exclusively appressed pubescent (strigillose); stem rarely with scattered pustulate hairs (muricate).
  2a. Stem flushed with red; the free tips of the capsule distinct .... subsp. *hirsutissima*
  2b. Stem usually green; the free tips of the capsule indistinct.
    3a. Mature buds (excl. floral tube) narrowly lanceolate in outline, 3.5–5 cm long; sepal tips 2–3 mm long; petals 4.5–5.5 cm long; capsule 5–6.5 cm long; bracts undulate; leaves membranous; plant in cultivation up to 20 dm tall .... subsp. *texensis*
    3b. Mature buds (excl. floral tube) lanceolate in outline, 2–3 cm long; sepal tips 1–2 mm long; petals 2.5–3.5 cm long; capsule 2.5–4 cm long; bracts plane, leaves somewhat leathery; plant in cultivation not more than 10 dm tall .... subsp. *elata*
1b. Stem and ovary (capsule) predominantly with erect pubescence (short and long villous), stem usually with pustulate hairs (muricate) and in the region of the inflorescence with glandular hairs (glandular puberulent).
  4a. Stem in the region of the inflorescence without glandular hairs .... subsp. *hirsutissima*
  4b. Stem in the region of the inflorescence with glandular hairs.
    5a. Sepals green or flushed with red, without or with indistinct pustulate hairs, sparsely to scattered villous;

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plant in cultivation more than 10 dm tall .... subsp. *hirsutissima*
5b. Sepals always flushed with red, with distinct red pustulate hairs, usually densely long villous; plant in cultivation not more than 8 dm tall .... subsp. *hookeri*

The plants described here as *O. elata* subsp. *texensis* are known only from a single herbarium specimen and from material cultivated at Düsseldorf. In 1981 Dietrich collected a seed of an unusual *Oenothera* from a TRT herbarium specimen. From the large flowers it appeared to represent *O. grandiflora* L'Hér., but when plants were grown in Düsseldorf they clearly represented *O. elata*. Further, based on its strigillose pubescence it appeared to be subsp. *hirsutissima*; however, other characters clearly separated it from both strigillose pubescent subspecies of *O. elata*, subspp. *elata* and *hirsutissima*. The stems of the Brazos County plants are always green, the capsules are 5–6.5 cm long, the buds are narrowly lanceolate, and the leaves are membranous. These plants grow tall in cultivation, to 2 m or more.

Oenothera elata Kunth subsp. **texensis** W. Dietrich & W. L. Wagner, subsp. nov. TYPE: Grown from seeds taken from herbarium specimen TRT-205991 and cultivated at the Botanical Garden of the University of Düsseldorf, 12 Sept. 1984, cult. no. *Stubbe 84-204*; original source, U.S.A. Texas: Brazos Co., ca. 17 km NW of Navasota River bridge on Hwy. 6 in vicinity of Peach Creek cutoff, 25 Oct. 1978, *P. M. Catling & K. L. Intosh* (holotype, MO-3332204; isotypes, DUSS, M).

Herbae biennes, erectae, in culturam usque ad 20 dm altae. Caules virides, strigillosi. Folia undulata. Gemmae maturae (excl. tubus floralis) anguste lanceolatae, 3.5–5 cm longae. Sepala viridia, strigillosa. Petala flava, 4.5–5.5 cm longa. Stylus longus, stigmate sub anthesi supra antheras elevato. Capsulae 5–6.5 cm longae, strigillosae. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice homozygotica (7 bivalenta in metaphasium primum meiosis), autocompatibilis.

Munz (1949, 1965) recognized two subspecies of his *Oenothera hookeri* from moist coastal or slightly inland sites in California: subsp. *hookeri* and subsp. *montereyensis*. He referred plants with a bushy habit, blunt buds, free sepal tips 1–2.5 mm long, and sepals usually 2–2.5 cm long to subsp. *montereyensis*, whereas plants with a less branched habit, attenuate buds, free sepal tips 2–4 mm long, and sepals 3–3.5 cm long were referred to subsp. *hookeri*. Our studies have shown that these characters represent intra- and inter-populational variation and, further, appear to vary independently. The bushier habit of some coastal plants appears to be an adaptation to wind and salt spray. All of these populations are here treated as members of one coastal subspecies of *Oenothera elata* distinguished from the other three subspecies of *O. elata* primarily by its densely glandular puberulent and long-villous buds.

Oenothera elata Kunth subsp. **hookeri** (Torrey & A. Gray) W. Dietrich & W. L. Wagner, comb. et stat. nov.

Oenothera hookeri Torrey & A. Gray, Fl. N. Amer. 1: 493. 1840. TYPE: California [without specific locality] *Douglas s.n.* (holotype, GH).

Oenothera hookeri Torr. & A. Gray subsp. *montereyensis* Munz, Aliso 2: 14. 1949. TYPE: United States. California: Monterey Co., 0.2 mi. S of mouth of Alder Creek, 6 Nov. 1934, *C. B. Wolf 6223* (RSA-12778, holotype (not seen); isotypes, GH, NY, POM).

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A REVISION OF *MEZILAURUS* (LAURACEAE)[1]

HENK VAN DER WERFF[2]

ABSTRACT

The neotropical genus *Mezilaurus* (Lauraceae), which consists of 18 species and is best represented in the drainage area of the Amazon, is revised. *Clinostemon*, a genus of two species recently separated from *Licaria* and reinstated on its own, is included here in *Mezilaurus*. Eight species, *Mezilaurus caatingae* van der Werff, *M. duckei* van der Werff, *M. glaucophylla* van der Werff, *M. micrantha* van der Werff, *M. opaca* Kubitzki & van der Werff, *M. palcazuensis* van der Werff, *M. pyriflora* van der Werff, and *M. quadrilocellata* van der Werff are described as new. One new name, *M. thoroflora* van der Werff, and a new combination, *M. mahuba* (Sampaio) van der Werff, are published.

Mezilaurus comprises 18 species, occurring from Costa Rica to southern Brazil. The majority of the species are found in the drainage area of the Amazon River and adjacent Guayana. The type species, *M. navalium*, is restricted to the Atlantic rain forests of southern Brazil; two species (of which one remains undescribed due to insufficient material) are shrubs from the cerrado vegetation. Fourteen species are Amazonian and have been reported from a variety of habitats. Ten Amazonian species, ranging from shrubs to tall trees, occur in terra firme vegetation, frequently in xeromorphic forests on white sand. One species, *M. mahuba*, is restricted to flooded forest. Three species are known to occur in secondary vegetation (*M. thoroflora, M. synandra* and *M. lindaviana*), although it is not clear whether these are typical of secondary vegetation or were left standing when the primary forest was cut. When cutting primary forest throughout the Neotropics, the local people tend to leave some economically useful species intact for future harvesting. Lauraceae, widely used for timber, are therefore frequently found as isolated trees in pastures or similarly disturbed habitats. No habitat information is available for the Colombian species, which is only known from Chigorodó in northern Antioquia. The Costa Rican species occurs in wet lowland forest near the Pacific Coast.

Most species of *Mezilaurus* are collected infrequently, and I have seen more than ten collections for only two species (*M. itauba* and *M. lindaviana*). That many *Mezilaurus* species are large or middle-size trees and all have small, greenish flowers usually less than 2 mm long no doubt explains the paucity of collections. The genus is greatly undercollected and much more material is needed for a better taxonomic understanding.

The main use of *Mezilaurus* is for timber. The species are locally well known and their hard wood is much used for boat building and construction. Mez (1889) mentioned that the fruits of *M. itauba* are edible. On the label of *Fróes 12152* (*Mezilaurus pyriflora*) it is stated that the wood causes injuries to the skin, presumably a kind of dermatitis.

The present revision was undertaken because it became clear that the genus *Clinostemon* should be merged with *Mezilaurus*. This led to a closer look at recent collections, during which several undescribed species were found. I now recognize 18 species in *Mezilaurus*, which more than doubles the number of species recognized by Kostermans (1938).

MATERIALS

This study is based both on older collections, already cited by Kostermans (1938), and recent collections personally selected during visits to major American and European herbaria or received on loan with other unidentified Lauraceae. In my experience the genus was unrecognized in many herbaria. Unfortunately, I have not yet had the opportunity to visit the leading Brazilian herbaria. I fully expect that such visits will yield additional taxa, not only from the Amazonian forests, but also from the cerrado vegetation and possibly the Atlantic rain forests. Although this study is therefore incomplete, I hope it will kindle the interest of neotropical botanists in this group of small-flowered Lauraceae.

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TAXONOMIC HISTORY

The first species of *Mezilaurus* was published by Allemão (1848) as *Silvia navalium.* Meissner (1864) recognized that *Silvia* Allemão was a later homonym of *Silvia* Vellozo and proposed the new name *Silvaea.* Unfortunately, *Silvaea* Meissner is a later homonym of *Silvaea* Phillipi. O. Kuntze (1891) proposed another new name, *Mezia,* to replace *Silvia* Allemão, but the name *Mezia* O. Kuntze was predated by *Mezia* Schwacke, a genus of Malpighiaceae. Finally, Taubert (1892) proposed the name *Mezilaurus,* which Mez (1892) accepted. He included seven species in the genus. Pax (1897), overlooking the publication of *Mezilaurus,* proposed *Neosilvia* as a new name for *Silvia* Allemão. *Neosilvia* is therefore a superfluous name. The name *Mezilaurus* was not universally accepted at first. Even Mez (1904, 1920, 1924) used the name *Silvia* again. Ducke (1930, 1935) published several new species under the generic name *Silvia.* Kostermans's revision (1938) definitively established the use of *Mezilaurus* Taubert.

During the nineteenth century, several species now placed in *Mezilaurus* were described in other genera, mostly in genera now included in *Licaria.* Meissner (1864) described three species in *Acrodiclidium* and one in *Oreodaphne* (a synonym of *Ocotea*). Bentham in Hooker (1878) transferred two of these to *Misanteca* (a synonym of *Licaria*) and Bentham and Hooker (1880) placed the other two (including the type species of *Mezilaurus*) in *Endiandra,* an Old World genus. Mez (1889) recognized six species in *Mezilaurus* (as *Silvia*), the type species, the four species described by Meissner (1864), and a sixth species now included in *Licaria.* Kostermans (1938) accepted eight species of *Mezilaurus,* four of Mez's species and four described since 1889 by Mez and Ducke. Allen (1964) described two new species of *Mezilaurus* from Venezuela.

Kuhlmann and Sampaio (1928) published the monotypic genus *Clinostemon* based on *Acrodiclidium mahuba* Samp. Kostermans (1938) did not accept this genus and placed it in *Licaria.* Later Allen (1948) described a new species closely related to *Licaria mahuba* and noted the resemblance to *Mezilaurus.* Recent investigations (Kubitzki et al., 1979) have shown that these two species do not belong in *Licaria* and are more closely related to or congeneric with *Mezilaurus.* In this paper both are included in *Mezilaurus.*

The eight species recognized in Kostermans's monograph are all maintained in this publication. The increase in the number of *Mezilaurus* species is partly due to the inclusion of *Clinostemon* in *Mezilaurus* and partly due to recent collections that represent undescribed species.

GENERIC RELATIONSHIPS

One of the main taxonomic difficulties in Lauraceae is that many of the genera are poorly defined. This is reflected in the various infrafamilial classification schemes and the frequency with which species are transferred between various genera. During the last 30 years generic relationships within the Lauraceae have been discussed in three papers (Kostermans, 1957; Hutchinson, 1964; and Richter, 1981).

Kostermans (1957) attached much importance to the fruit (with or without cupule) and less importance to the number of anther cells; he placed *Mezilaurus* in the subtribe Beilschmiediinae of the tribe Perseeae, close to *Endiandra,* and noted, as did Bentham and Hooker (1880), a similarity to *Endiandra.* He also stated that *Endiandra* and *Mezilaurus* differ in anther shape and the positions of their leaves. Additional differences are the very fine reticulation of the leaves and the large, spreading tepals in many species of *Endiandra* (comparable to tepals in *Nectandra*), which are very unlike the small, erect, scale-like tepals in *Mezilaurus.* These differences greatly outweigh the similarities between *Endiandra* and *Mezilaurus* (number of fertile stamens, number of anther cells, fruit more or less without cupule) and *Endiandra* is probably not a close relative of *Mezilaurus.*

Hutchinson (1964) considered the number of anther cells more important than the development of the cupule. He placed *Mezilaurus* next to *Misanteca,* but the distribution data given under *Misanteca* strongly suggest that Hutchinson, as did Bentham and Hooker (1880), included in his *Misanteca* two Brazilian species here included in *Mezilaurus.*

As can be seen from the taxonomic history of *Mezilaurus,* its species frequently have been placed in *Licaria* (or its synonyms *Acrodiclidium* and *Misanteca*). These two genera have in common that they are the only neotropical Lauraceae with three fertile, two-celled stamens. The general flower shape of species belonging to these two genera can be quite similar and a generic separation based solely on flowers can be very difficult. Fortunately, other characters readily identify the genera: *Mezilaurus* has the leaves always clustered at the tips of the branches, *Licaria* never; in *Mezilaurus* the cupule consists of a small, platelike disk, in *Licaria* it grows into a rather large, double-rimmed cup, and the inflorescence of *Mezilaurus* is a double raceme (Figs. 3, 8C), an inflorescence type never found in *Licaria.* Kubitzki et al. (1979) partly enumerated these differences and discussed the placement of *Licaria mahuba* (Samp.) Kostermans and *L. maguireana* Allen. They concluded that these species did not belong in *Licaria* and resurrected the generic name *Clinostemon* to accommodate them. *Clinostemon* was considered a close relative of *Mezilaurus,* the only difference being the presence of staminodia in *Clinostemon* and their absence in *Mezilaurus.* The two *Clinostemon* species also share large, obovate leaves with an abruptly rounded base.

The taxonomic importance of absence/presence of staminodia in defining genera of Lauraceae is open to discussion. In some genera staminodia are consistently present (*Persea, Phoebe*); in others they may be present or absent (*Aiouea, Aniba, Licaria, Ocotea*). This suggests that a generic separation based only on presence/absence of staminodia is weak, especially because the staminodia are small, ca. 0.5 mm, and not easy to find. The discovery of two undescribed species in Colombia and Costa Rica with the leaf shape and size of a *Mezilaurus,* but with staminodia like *Clinostemon,* is another reason to place *Clinostemon* in synonymy under *Mezilaurus.*

Richter (1981) amply discussed the wood and bark anatomy of the Lauraceae. He found that within the Lauraceae, *Mezilaurus* occupied an isolated position and was easily recognized both on wood and bark characters. He also found that the wood (bark was not available) of the two *Clinostemon* species was either undistinguishable or very similar to *Mezilaurus* and suggested that *Clinostemon* should be placed very close to *Mezilaurus,* or merged with it, a conclusion he published earlier in Kubitzki et al. (1979). The great similarity in wood anatomy plus the isolated position of *Mezilaurus/Clinostemon* in the Lauraceae is the second reason to merge these two genera. Richter (1981) also found that *Licaria* and *Endiandra* are, as far as wood anatomy is concerned, not closely related to *Mezilaurus.* The genus most closely related to *Mezilaurus* by wood characters is *Anaueria,* a monotypic genus incompletely known from a few collections in Brazil and Peru. Kostermans (1952) and Hutchinson (1964) both placed *Anaueria* in *Beilschmiedia*; Kostermans mentioned, without giving details, that he did so as a result of studying additional herbarium material from Rio de Janeiro. Neither *Anaueria* nor *Beilschmiedia* is likely to be confused with *Mezilaurus,* since they have flowers with six or nine fertile stamens and never have clustered leaves.

Two species described in this paper merit additional comments. *Mezilaurus quadrilocellata* and *M. glaucophylla* have an unusual distribution, being only known from northern Colombia and Costa Rica. All other *Mezilaurus* species occur in the Amazonian forests or other parts of Brazil. Secondly, *M. quadrilocellata* and *M. glaucophylla* have staminodia (as do the species formerly placed in *Clinostemon*) and the leaf shape of *Mezilaurus* species (quite unlike the species formerly included in *Clinostemon*). Thus, they link *Mezilaurus* with *Clinostemon.* Moreover, they are the only species in the genus with four anther cells on each stamen. Given the importance frequently attached to the number of anther cells and the number of fertile stamens, the presence of three four-celled anthers (not found in any other New World Lauraceae) could be sufficient for the recognition of a new genus. However several other genera include species with two-celled and four-celled anthers, and because other characters (leaves clustered at branch tip, shape of the inflorescence) point toward *Mezilaurus,* I include these species in *Mezilaurus.*

As a result of the transfer of *Clinostemon* and the inclusion of *Mezilaurus quadrilocellata* and *M. glaucophylla,* my concept of *Mezilaurus* is wider than has been used by previous authors. I regard as diagnostic characters the leaf position (clustered at the tips of branches), the small, platelike cupule (but fruits from most species are not yet known), the type of inflorescence (a double raceme), and the presence of three fertile stamens. Richter (1981) discussed diagnostic wood and bark characters.

In conclusion, *Mezilaurus* shows in floral characters a strong resemblance to *Licaria.* However, these two genera differ in wood anatomy, cupule shape, leaf position, and inflorescence type. Wood anatomy suggests a close relationship between *Mezilaurus* and *Anaueria,* but these two genera differ in characters of leaf position, inflorescence type, and number of fertile anthers. A close relationship between *Mezilaurus* and *Endiandra* is very unlikely. Currently available information indicates that *Mezilaurus,* including *Clinoste-*

mon, is endemic to the Neotropics, and that it occupies an isolated position in the family.

MORPHOLOGY AND TAXONOMIC CHARACTERS

Mezilaurus species range from small trees or shrubs (the cerrado species) to tall forest trees much valued for their timber. The twigs are generally thick, show conspicuous leaf scars, and are often covered with a thick bark layer.

Leaves. The leaves in all species are pinnately veined. The lateral veins frequently arch upward and become connected with the more distal lateral vein. The texture of the leaves is variable; most species have chartaceous leaves, but a few have coriaceous leaves in which secondary and tertiary venation is poorly visible. Conspicuous gland dots in the leaves occur rarely. The leaves generally turn dark upon drying.

Characteristic for the genus is the fact that the leaves are always clustered at the tips of the branches. Young shoots grow initially rapidly without developing leaves; after this elongating period, leaves are formed at the tip of the young branch. Such branches may have several clusters of leaves, representing different growing seasons. I will call this growth pattern long shoot–short shoot. Under unfavorable conditions (several *Mezilaurus* species are reported from white sand forests or caatinga forests) the difference between the long shoots and short shoots becomes less pronounced and the growth pattern may seem a succession of short shoots, with only one cluster of leaves at the tip of the branches. However, I think the difference between long shoot–short shoot or short shoot growth pattern is quantitative, not qualitative.

Species with clustered leaves of the long shoot–short shoot pattern occur regularly, but not frequently, in several other neotropical genera of Lauraceae (*Aniba, Endlicheria, Nectandra, Ocotea, Phoebe,* and *Pleurothyrium*). However, only in *Mezilaurus* is this clustered leaf pattern characterisitic or dominant. The non-*Mezilaurus* species with clustered leaves are rarely confused with *Mezilaurus*; even in vegetative state they are readily separated by conspicuous pubescence or leaf color differences. Only one species, *Ocotea rubra,* very closely resembles *Mezilaurus* in sterile state. However, its flowers with nine four-celled stamens and fruit with a large cupule make identification easy.

Nearly all species of *Mezilaurus* have elliptic to obovate leaves. The base of the leaves, however, offers some useful characters. Four species, *Mezilaurus mahuba, M. pyriflora, M. thoroflora,* and *M. duckei,* have large leaves (to 60 cm long) which become gradually narrowed toward the base; at the base the leaves are abruptly narrowed, becoming rounded or even cordate. Three species, *M. subcordata, M. quadrilocellata,* and *M. glaucophylla,* have an obtuse or rounded leaf base with a distinct petiole, 2–6 cm long. In these three species the leaf shape is slightly obovate or ovate. In all other species (with the exception of *M. crassiramea*), the leaf base is gradually attenuate or decurrent on the petiole. Most of these species have a petiole. Three species, however, *M. caatingae, M. crassiramea* and *M. decurrens,* have sessile leaves or nearly so. In some collections of *M. crassiramea* the leaf base is gradually narrowed, in others it is rather abruptly narrowed. In this species the petioles, if present, are less than 1 cm long.

Pubescence. There is not much variation in pubescence within *Mezilaurus.* Two species, *M. crassiramea* and *M. lindaviana,* have erect pubescence on the lower surface of the leaves; this can be quite sparse in *M. lindaviana,* however. The other species have varying amounts of appressed pubescence on leaves, stems, terminal buds, and inflorescences. These varying amounts of pubescence have little diagnostic value.

Inflorescence. The inflorescence of *Mezilaurus* consists of a compound raceme (dibothryum, see Weberling, 1981, 1985). This inflorescence type is present without modifications in *M. crassiramea, M. lindaviana, M. mahuba, M. pyriflora, M. thoroflora,* and *M. duckei.* Short tertiary axes are sometimes present in *M. glaucophylla* and *M. quadrilocellata.* In the other species the inflorescences are smaller and the flowers are not evenly distributed along the lateral branchlets of the inflorescence, but are clustered at the tips of these branchlets. The occasional occurrence of flowers along the branchlets suggests that the clustered flowers are a derived condition. It is worth noting that the species with a well-developed dibothryum have larger (often much larger) inflorescences and have usually smaller flowers than the species with clustered flowers. A dibothryum is a rare inflorescence type among other neotropical Lauraceae (if it ever occurs outside of *Mezilaurus*).

The inflorescence type of one *Mezilaurus* species, *M. decurrens,* is not known due to the fragmentary nature of the single available specimen.

Flowers. In the following discussion I consider only mature flowers. Because it is difficult to tell whether a flower is mature or not in *Mezilaurus,* I define a mature flower as one with opened anther cells. In buds or young flowers diagnostic characters are often difficult to see.

The flowers of *Mezilaurus* are unusually difficult to dissect. In addition to their small size, the floral tube contains much mucilage, which has usually hardened during drying. Softening the flowers requires boiling for at least one hour. After softening, the mucilage becomes viscid and sticky and the dissected floral parts frequently stick tightly to the floral tube. Therefore, I have rarely relied on characters of the floral parts to separate taxa, especially because other characters are available.

Dimensions given for flowers and their parts should be accepted with some reservation. In order to dissect the flowers, it is necessary to boil them. During the boiling the flowers swell; the degree of size increase depends on the duration of boiling. I have recorded flowers that measured 1.3 mm dry as swelling to 1.7 mm after boiling. Similar increases in size were found for the stamens as well. Only rarely have I used flower sizes in the key and, in these cases, flower sizes are taken from dry flowers. The tepals are generally small and equal. The exceptions are *M. glaucophylla* and *M. quadrilocellata,* in which the outer three tepals are smaller than the inner three.

With the exception of three species (*Mezilaurus caatingae, M. palcazuensis,* and *M. mahuba*), all species have clearly pedicellate flowers. Staminodia (which are not easy to find due to their small size) are present in six species (*M. duckei, M. glaucophylla, M. mahuba, M. pyriflora, M. quadrilocellata,* and *M. thoroflora*), and only *M. mahuba* has glands at the base of the fertile stamens.

The most interesting variation of floral structures is found in the shapes and positions of anthers. In most neotropical Lauraceae the anthers have the shape of erect stalked plates with the anther cells on the inner or outer surface (for instance, in *Persea, Phoebe, Nectandra,* and *Ocotea*). In several of the genera with two-celled anthers the plate shape of the anthers is less pronounced or lost and the anther cells are situated at or near the tip of the anthers (*Aniba, Licaria*). In several species of *Licaria* the stamens are shaped like columns with the anther cells situated near the apex and here the difference between filament and anther has disappeared. In a few species of *Mezilaurus* (*M. duckei, M. glaucophylla, M. pyriflora,* and *M. quadrilocellata*) a similar arrangement is found. Here the stamens remain included in the erect tepals and the anther cells are situated at the tips of the stamens. In *M. glaucophylla* and *M. quadrilocellata,* the only species with four anther cells on each stamen, the tips of the stamens are flattened and form a small platform on which the anther cells are situated. Thus, by looking from the outside in the flowers, one sees the 12 anther cells as small pores. In these four species the anther cells are situated apically and also open apically; that is, the flaps open upward.

Mezilaurus subcordata is the only species with the anther cells situated introrse or introrse-lateral; in all remaining species the anther cells are extrorse, situated on the outer face of the stamen. Here the anther cells are more or less exserted, tend to be relatively large, and, most interesting, the stamens develop a dorsal ridge on which the anther cells are situated. The ridge is usually about as long as the anther cells and appears as an outward-facing hump near the tip of the stamen. The anther cells open towards the crest of the ridge, where the flaps are situated back-to-back. Such anther cells have been described as opening "laterally" in the literature, but in order to avoid confusion with laterally situated anther cells (which occur, for instance, in *Pleurothyrium*), I will call this type of opening "back-to-back."

In *M. decurrens* the dorsal ridges are not strongly developed and the anther cells are hardly exserted. In the remaining species the anther cells are clearly exserted.

The most extreme development is found in *M. mahuba,* where the dorsal ridges with the anther cells are exserted as downward curved hooks. The sequence from immersed anther cells to greatly exserted anther cells does not correspond with variation in other characters. In fact, the extremes (*M. pyriflora* with immersed anther cells, *M. mahuba* with greatly exserted anther cells) are very similar in other characters such as leaf shape, leaf size, and type of inflorescence.

In a few species (*M. crassiramea, M. lindaviana, M. palcazuensis, M. sprucei, M. subcordata,* and *M. synandra*) the filaments of the stamens are fused in a ring or a short tube. This is a useful character, but because it is hard to recognize, I have not used it in the key. It is most easily seen on young fruits. When the filaments are free, they are visible at the base of the fruit;

when the filaments are united, they are visible as a small cap on top of the fruit.

REPRODUCTIVE BIOLOGY

In a study of the reproductive biology of some neotropical Lauraceae, Kurz (1983) and Kubitzki and Kurz (1984) reported that a *Clinostemon* species here described as *Mezilaurus duckei* showed synchronized dichogamy with a pronounced protogyny.

In this system, two flowering morphs are found. In the A morph, flowers open in the morning and expose the receptive stigmas. During this phase, no pollen is released. Around midday, the stigma wilts and is no longer receptive. The male phase, when the anthers shed the pollen, takes place in the afternoon. An individual flower thus lasts only one day. In the B morph, flowers open in the afternoon, when the stigmas are receptive. Pollen is released during the morning of the following day.

During the fieldwork, Kurz was able to observe only two flowering *Mezilaurus* trees and these turned out to be both A morphs. However, he studied A and B morphs of other Lauraceae species and found that for fertilization, cross-pollination between A and B morphs was necessary. Selfing of A or B morphs did not result in seed set. It is likely that these findings apply to *Mezilaurus* as well.

The *Mezilaurus* flowers observed by Kurz were visited by four species of small (2–3 mm) *Trigona* bees (Meliponinae). *Mezilaurus* flowers are not known to produce nectar and it is likely that pollen is the only reward for their pollinators.

TAXONOMIC TREATMENT

Mezilaurus Taubert, Bot. Centralbl. 50: 21. 1892. TYPE: *M. navalium* (Allemão) Taubert.

Silvia Allemão, Dissertatio, Rio de Janeiro. 1848, non Vell. Conc. *Silvaea* Meissner, DC. Prodr. 15: 84. 1864, non Phillipi; *Mezia* Kuntze, Revis. Gen. Pl. 2: 573. 1891, non Schwacke. *Neosilvia* Pax, Natürlichen Pflanzenfamilien, Nachtrag zu Teil II–IV. 1897, nom. superfl.

Clinostemon Kuhlm. & Samp., Bol. Mus. Nac. Rio de Janeiro 4(2): 57. 1928. TYPE: *C. mahuba* (Samp.) Kuhlm. & Samp.

Shrubs to tall trees, mostly South American, but with one species in Costa Rica. Leaves alternate, usually congested at the apex of the twigs, entire. Petioles often swollen at base. Inflorescences axillary, sometimes seemingly terminal, few- to many-flowered, forming a compound raceme (dibothryum); flowers clustered at the tips of the inflorescence branchlets in several species. Bracts and bracteoles deciduous. Tepals 6, equal or nearly so, small, scalelike, usually erect. Fertile stamens 3, representing the third whorl, 2-celled (in two species 4-celled). Staminodia present or absent. Staminal glands present in one species. Filaments free or connate; anther cells usually extrorse and exserted, situated on a dorsal ridge. Ovary ellipsoid to ovoid, included in the flower tube. Fruit ellipsoid, situated on a small, platelike cupule.

KEY TO *MEZILAURUS*

1a. Stamens 4-celled; N. Colombia and Costa Rica 2
  2a. Inflorescence and pedicels rufous tomentellous; tertiary venation on upper leaf surface immersed; N. Colombia .... *M. quadrilocellata*
  2b. Inflorescence gray strigose; pedicels glabrous or with few basal hairs; tertiary venation on upper leaf surface raised; Costa Rica .... *M. glaucophylla*
1b. Stamens 2-celled; S. America E. of the Andes 3
  3a. Leaves gradually narrowed toward base, usually abruptly rounded there, generally large, exceeding 25 cm 4
    4a. Flowers sessile; anthers exserted as little hooks; only known from flooded forests in Amazon basin .... *M. mahuba*
    4b. Flowers pedicellate; anthers not hooklike exserted; not occurring in flooded forest 5
      5a. Leaves elliptic or slightly obovate, rounded at tip; anthers not exserted at anthesis .... *M. duckei*
      5b. Leaves strongly obovate, acute or acuminate at tip; anthers exserted or not 6
        6a. Anthers exserted at anthesis; pedicels 4–8 mm long .... *M. thoroflora*
        6b. Anthers included at anthesis; pedicels 1.5–2 mm long .... *M. pyriflora*
  3b. Leaves decurrent or obtuse at base, generally small, rarely exceeding 20 cm 7
    7a. Leaves pubescent below; twigs visibly pubescent 8
      8a. Flowers pubescent; shrub or small tree in cerrado vegetation .... *M. crassiramea*
      8b. Flowers glabrous; tree in rain forest .... *M. lindaviana*
    7b. Leaves glabrous below; twigs not visibly pubescent 9
      9a. Leaf tip acute (in *M. micrantha* apex is blunt, but present) 10
      9b. Leaf tip rounded 12

10a. Flowers sessile; Peru .... *M. palcazuensis*
10b. Flowers pedicellate; Brazil or Peru 11
11a. Leaves coriaceous; pedicels ca. 2 mm long .... *M. micrantha*
11b. Leaves chartaceous; pedicels (5)10–15 mm long .... *M. sprucei*
12a. Flowers glabrous 13
13a. Flowers sessile; caatinga forests along Rio Negro .... *M. caatingae*
13b. Flowers pedicellate; rain forests of S. Brazil .... *M. navalium*
12b. Flowers pubescent 14
14a. Leaf base obtuse or rounded; anther cells (lateral) introrse .... *M. subcordata*
14b. Leaf base gradually narrowed into petiole; anther cells extrorse 15
15a. Tepals erect; flower tube not constricted at apex; flowers cup-shaped 16
16a. Leaves sessile or nearly so; anthers scarcely exserted at anthesis, the filaments connate .... *M. decurrens*
16b. Leaves with petioles at least 1 cm long; anthers clearly exserted at anthesis, the filaments free .... *M. itauba*
15b. Tepals incurved; flower tube constricted at apex; flowers depressed globose 17
17a. Flowers 2 × 2 mm; upper leaf surface shiny and with raised reticulation .... *M. synandra*
17b. Flowers 1.5 × 1.5 mm; upper leaf surface opaque, the reticulation not raised .... *M. opaca*

Mezilaurus caatingae van der Werff, sp. nov. TYPE: Brazil. Amazonas: Rio Negro, São Felipe, caatinga on sandy soil, tree, 15 m, 27 Sept. 1952, *Frôes 28761* (holotype, MO). Figures 1, A & B; 2.

Arbor, 15 m. Ramuli teretes, glabri. Folia coriacea, conferta ad apices ramulorum, glabra, margine involuta, apice rotundata, basi attenuata, obovata, 10–15 × 4–5 cm, super laevia nitidaque, subtus opaca costa elevata nervis lateralibus et venatione immersa. Petioli ca. 1 cm longi. Inflorescentia axillaris, minute adpresse pubescens (basis inflorescentia tantum adest). Flores glabri vel basi leviter minute adpresse pubescentes, obconici, sessiles, conferti ad apices ramulorum inflorescentiae, 2.2 mm longi. Tepala 6, aequalia, erecta, parva (0.2 mm). Stamina 3, per anthesim exserta, 1 mm longa, antheris bilocellatis, extrorsis, lateraliter dehiscentibus. Filamenta libra, pubescentia, antheris aequantia latitudine. Tubus floralis glaber. Ovarium glabrum, globosum, 0.5 mm. Stylus 0.6 mm longus, per anthesim exsertus. Fructus ignoti.

Tree, 15 m. Twigs terete, glabrous. Leaves clustered at the tips of branches, glabrous, coriaceous, obovate, 10–15 × 4–5 cm, the tip rounded, the base gradually narrowed to the short petiole, the margin inrolled, the upper surface smooth, slightly lustrous, the lower surface with a raised midvein; lateral veins (8–12) and reticulation ± immersed; petioles ca. 1 cm, the lamina decurrent as two narrow ridges. Inflorescence axillary, minutely appressed pubescent, paniculately branched, broken on the specimen seen. Flowers glabrous or with some minute pubescence at the base, sessile, clustered at the tips of the inflorescence branchlets, 2.2 mm long, obconic. Tepals 6, very small, 0.2 mm long, equal, erect. Stamens 3, exserted at anthesis, 1 mm long, the anthers 2-celled, extrorse, opening back-to-back; filaments free, as wide as anthers, pubescent. Floral tube glabrous. Ovary globose, glabrous, 0.5 mm. Style slender, 0.6 mm long, exserted at anthesis. Fruit unknown.

In leaf shape *Mezilaurus caatingae* resembles *M. itauba* and *M. decurrens.* The sessile flowers separate it immediately from these species, however. Vegetatively, the recurved leaf margin is diagnostic. This character also occurs in *M. micrantha,* but this species has a bluntly acute leaf apex, never rounded as in *M. caatingae.*

Mezilaurus crassiramea (Meissner) Taubert ex Mez, Arbeiten Königl. Bot. Gart. Breslau 1: 112. 1892. *Oreodaphne crassiramea* Meissner, DC. Prodr. 15(1): 117. 1864. *Silvia crassiramea* (Meissner) Mez, Jahrb. Königl. Bot. Gart. Berlin 5: 106. 1889. *Mezia crassiramea* (Meissner) Kuntze, Revis. Gen. Pl. 2: 574. 1891. TYPE: Brazil. Goiás: Serra d'Ourada, *Pohl 1463* (W, K, G-DC, U—this the only specimen seen). Figures 1, C & D; 2.

Small trees, to 6 m tall. Twigs terete, thick, the older ones with a thick and conspicuous cork layer, the young tips with a dense, light brown tomentum. Leaves clustered at the tips of the twigs, almost sessile (petioles to 3 mm long), ovate or slightly obovate, the tip rounded, the base

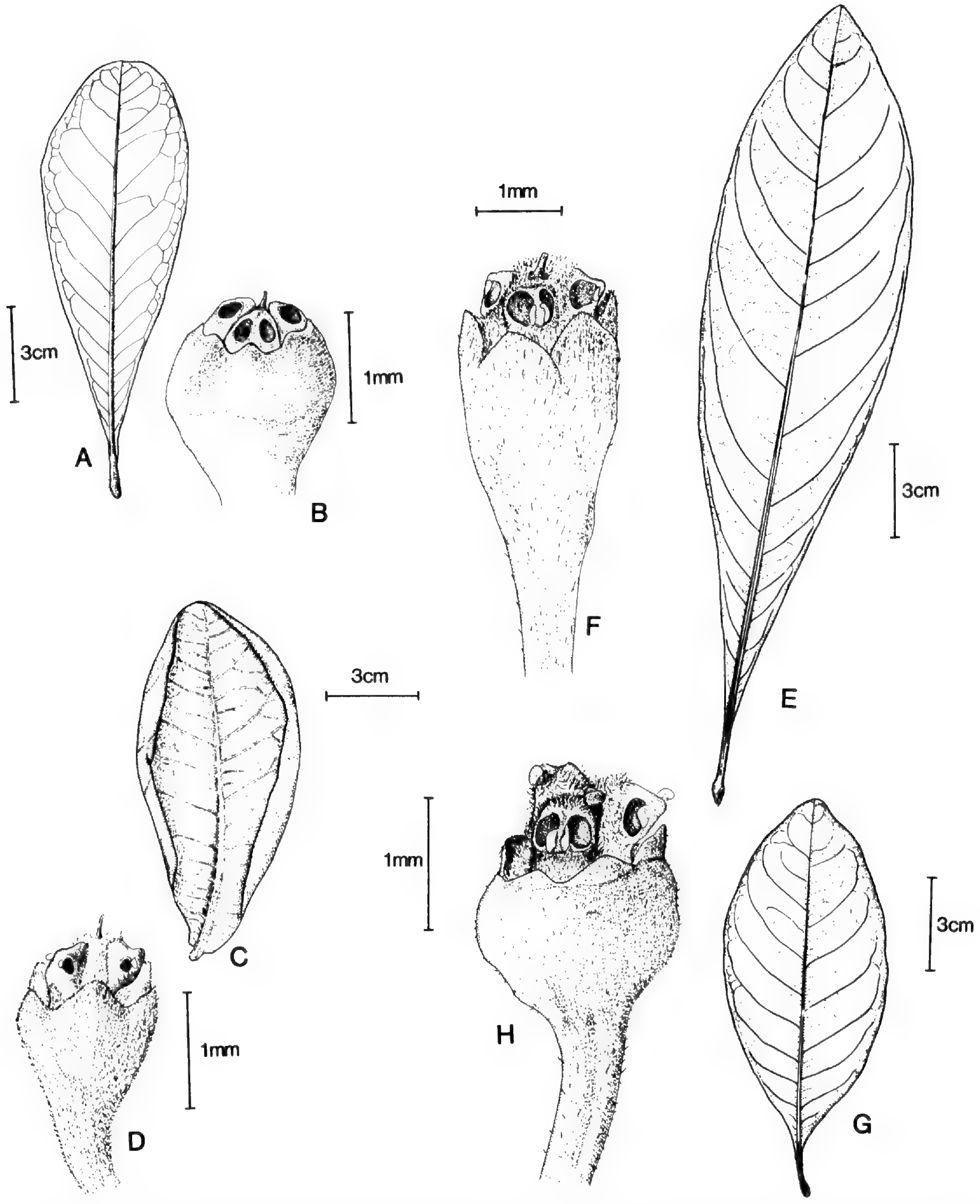

FIGURE 1. A–B. *Mezilaurus caatingae.*—A. Leaf.—B. Flower. C–D. *M. crassiramea.*—C. Leaf.—D. Flower. E–F. *M. decurrens.*—E. Leaf.—F. Flower. G–H. *M. itauba.*—G. Leaf.—H. Flower.

rounded or gradually narrowed and abruptly rounded, with margins frequently recurved, 10 × 5 cm, the upper surface pubescent, but becoming glabrous with age, the lower surface rather densely pubescent with pale brown hairs; lateral veins 10–15 pairs, leaving the midvein under almost 90°; veins and the final reticulation immersed on upper surface, raised on lower surface. Inflores-

FIGURE 2. Distribution of *Mezilaurus caatingae* (●), *M. crassiramea* (●), *M. decurrens* (▲), and *M. duckei* (■).

cences in the axils of small bracts, seemingly terminal, 7–12 cm long, about as long as leaves, pedicellate, puberulous or with very short pubescence, the flowers arranged spicately along the lateral branchlets; branchlets and flowers subtended by puberulous, ovate bracts, these ca. 0.1 mm long, the flowers brown puberulous, ca. 2 mm long; pedicel ca. 2 mm. Tepals 6, equal, ca. 0.8 mm long, erect, ovate. Stamens 3, exserted; anthers 2-celled, the cells small, on dorsal ridge of anthers, opening back-to-back; filaments fused into a tube. Ovary ovoid, ca. 1 mm, the style gradually narrowed, ca. 1 mm, exserted beyond anthers. Staminal glands and staminodia lacking. Young fruit globose, 6 mm diam., seated on swollen pedicel, the tepals persisting.

Vernacular name. *Cumbuquinha* (fide Ratter).

Additional specimens examined. BRAZIL. GOIÁS: Serra Dourada, *Anderson 10003* (F, NY, MO, US). MATO GROSSO: 7 km SW of Xavantina, *Ratter et al. 805* (MO); ca. 270 km N of Xavantina, *Ratter 1293* (MO).

Mezilaurus crassiramea is a well-defined species known from a few collections in cerrado vegetation. Diagnostic characters are the thick corky twigs, the pubescent leaves, and puberulous flowers. It can, as many cerrado species, withstand fire; the Ratter collections come from trees with charred or fire-blackened trunks.

Mezilaurus decurrens (Ducke) Kosterm., Meded. Bot. Mus. Herb. Rijks Univ. Utrecht 25: 40. 1936. *Silvia decurrens* Ducke, Trop. Woods 42: 19. 1935. TYPE: Brazil. Amazonas: Rio Negro, mouth of Rio Curicuriary, non-inundated forest. *Ducke RB 23669 = Yale No. 20999* (lectotype, RB, not seen; isolectotype F, fragm. U). Figures 1, E & F; 2.

Large tree. Twigs minutely puberulous toward apex, the terminal bud with yellowish, appressed pubescence. Leaves clustered at the tips of branches, glabrous on both surfaces, elliptic or narrowly elliptic, 15–25 × 5–7.5 cm, the tip rounded, the base gradually decurrent onto the petiole, this 1–2 cm long; laminae coriaceous, opaque, the reticulation not raised, rather lax. Lateral veins not strongly developed, 7–12 pairs, immersed above, slightly raised below. Midrib thick, dark, raised above, more conspicuously so on lower surface. Inflorescences axillary, subterminal, pyramidal, 10–18 cm long (fide Kostermans), appressed pilose. Flowers subglobose or obconical, ca. 2–2.5 mm long, 2 mm wide, appressed pubescent. Tepals 6, equal, erect, triangular, wider than long. Fertile stamens 3, 2-celled, 1–1.5 mm long, slightly exserted, pubescent; filaments connate, wider than anthers; anther cells extrorse, opening back-to-back. Ovary subglobose, densely pubescent (except base), ca. 1 mm long, the style slender and briefly exserted. Fruit unknown.

Mezilaurus decurrens is rare and known to me with certainty only from the type collection. At first glance it appears quite similar to *M. itauba,* but differs in several subtle characters. The leaves of *Mezilaurus decurrens* do not have the raised reticulation and minute gland dots of *M. itauba,* and their leaf bases taper more gradually into the petioles. Better differences are found in the flowers: in *M. decurrens* the anthers are scarcely exserted and the filaments are connate, whereas in *M. itauba* the anthers are greatly exserted and the filaments free.

A few collections that I place in *Mezilaurus itauba* are close to *M. decurrens* in leaf outline (*Ducke 681, Foldats 3613*), but I attach more diagnostic value to the raised reticulation and the greatly exserted anthers.

Mezilaurus duckei van der Werff, sp. nov. TYPE: Brazil. Amazonas: Reserva Florestal Ducke, *Aleusio 98* (holotype, US). Figures 2, 3.

Arbor, 20 m alta. Ramuli crassi, cicatribus conspicuis foliorum delapsorum notati, apicibus dense minuteque puberulis, glabrecentibus. Gemmam terminalem non vidi. Folia conferta ad apices ramulorum, chartacea, elliptica vel leviter obovata, apice rotundata, basi abrupte angustata, 30 × 10 cm, glabra praeter costam et nervos secundarios puberulos. Costa et nervii secundarii super immersi, subtus elevati. Reticulatio super obscura, subtus elevata. Petioli crassi, ca. 1 cm longi, dense minuteque puberuli. Inflorescentiae axillares, subterminales, 20–25 cm longae, minute puberulae, anguste pyramidales, bractis bracteolisque persistentibus et puberulis. Flores spicatim secus ramulos inflorescentiae dispositi, frequenter reflexi, turbinati, ca. 1 mm longi. Pedicelli ca. 2 mm longi, glabri vel pubescentia laxa ad basim. Tepala 6, aequalia, erecta, ca. 0.3 mm longa. Stamina fertilia 3, ca. 0.5 mm longa, filamentis pubescentibus, liberis, latioribus quam antheris glabris 2-locellatisque. Staminodia 6, parva, ca. 0.2 mm longa. Ovarium conicum, glabrum, ca. 0.4 mm longum, stylo ca. 0.7 mm longo. Fructus ignoti.

Tree, 20 m. Twigs thick, 1 cm diam. 5 cm below the tip, with conspicuous leaf scars, the tip very finely brown tomentellous. Leaves clustered at the tips of branches, slightly obovate, 25–30 × 8–10 cm, the tip rounded, gradually narrowed toward the base, the base abruptly narrowed; upper surface glabrous, opaque, venation immersed, the tertiary venation scarcely visible; lower surface minutely puberulous when young, glabrescent with age, the indument persisting on the main veins, 10–12 pairs of lateral veins, the secondary and tertiary venation raised, the midrib strongly raised and thick; petioles 0.5 cm thick, ca. 1 cm long, minutely puberulous. Inflorescences axillary, ca. 20–25 cm long, paniculately branched, the branchlets 3–4 cm long, the upper ones slightly shorter than the lower ones, minutely brown puberulous. Bracts and bractlets pilose, persisting at anthesis, the bracts 1.5 mm long, bractlets ca. 0.7 mm long. Flowers pedicellate, pedicels ca. 2 mm long, glabrous. Flowers glabrous, cup-shaped, 1 mm long, tepals 6, small, 0.3 mm long, erect. Fertile stamens 3, ca. 0.5 mm long, the filaments free, pubescent, wider than the glabrous, 2-celled anthers. Staminodia 6, ca. 0.2 mm long. Ovary conical, glabrous, ca. 0.4 mm long, the style ca. 0.7 mm long. Fruit unknown.

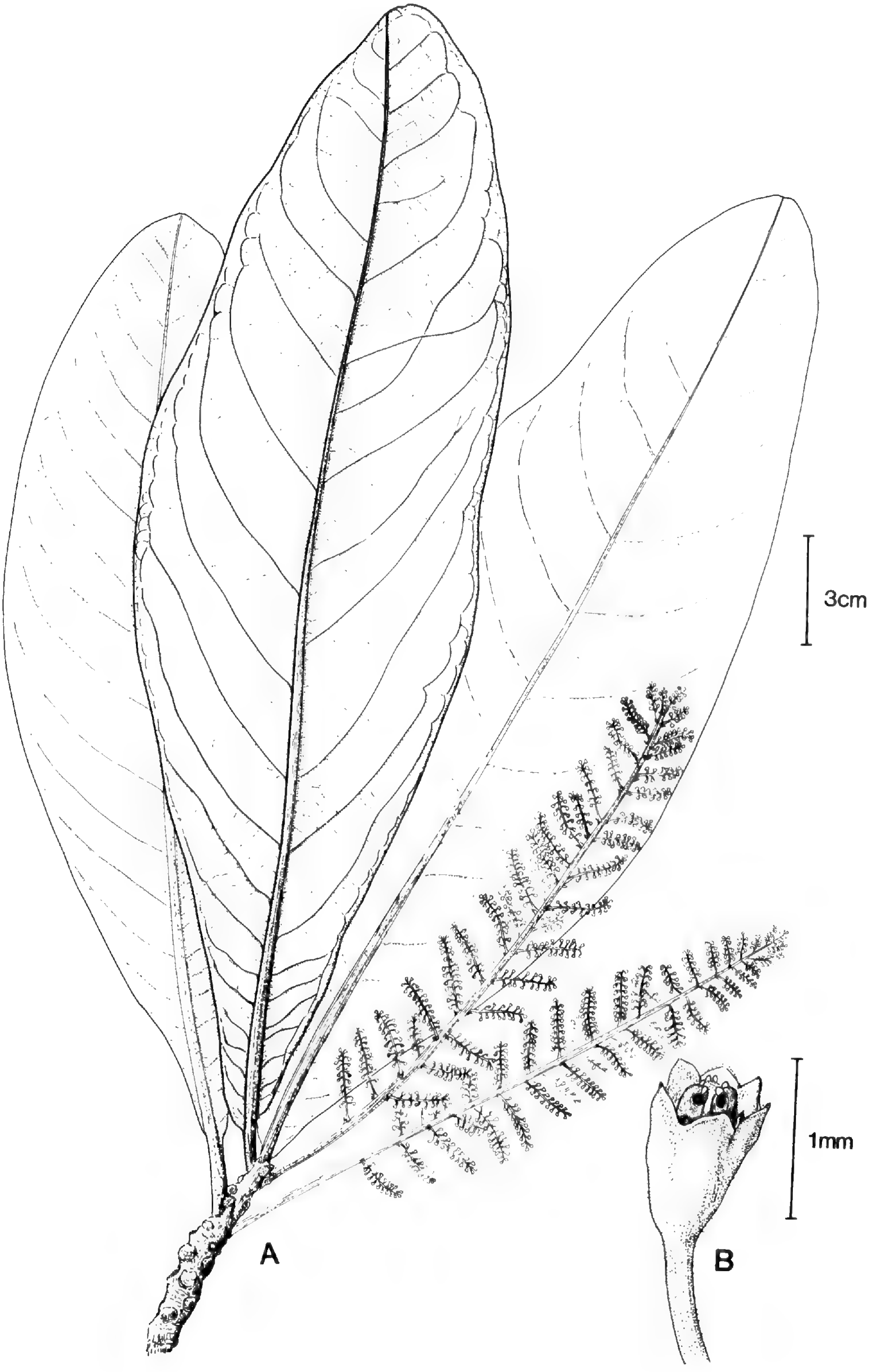

FIGURE 3. *Mezilaurus duckei.*—A. Habit.—B. Flower.

Common name. *Itauba abacate.*

Paratype. BRAZIL. AMAZONAS: Reserva Florestal Ducke, tree nr. 116, *Rodrigues 8203* (NY).

This species is named after Adolpho Ducke, an outstanding botanist and collector who made numerous excellent collections of Lauraceae in Amazonian Brazil. It is fitting that this new species is only known from the forest reserve dedicated to Ducke.

Mezilaurus glaucophylla van der Werff, sp. nov. TYPE: Costa Rica. Prov. San José: Zapatón de Puriscal, tree, 9 m, *Zamora & Poveda 1014* (holotype, MO; isotypes, F, CR). Figure 4.

Arbor, 20 m. Ramuli teretes, cicatribus insignibus foliorum muniti, minute pubescentes; gemma terminalis adpresse leuco-pubescens; cortex ramulorum veterum lenis desquamansque. Petioli inflatis fundis, leviter canaliculati vel triangulares, cinereo-pubescentes, ad 6 cm longi. Folia ad apices ramulorum conferta, obovata, chartacea, subtus glauca, apicibus basibusque obtusis vel acutis, super costis et nervis immersis, venatione leviter elevata, praeter puberulas costas glabra; subtus costis nervisque elevatis, venatione leviter elevata; nervi 10–14-jugi; laminae subtus parce minuteque puberulae. Inflorescentiae ad 15 cm longae, axillares, pyramidatae, cinereo-strigosae. Pedicelli ad 1.5 mm longi, glabri vel basim aliquot pilis. Flores glabri, cupuliformes, in sicco ca. 1 mm longi et lati. Tepala 6, per anthesin erecta vel paullo incurvata; inaequalia, 3 exteriora interioribus breviora, late deltoidea. Stamina 3, 4-locellata, filamentis latitudine antheris aequantibus, ca. 1 mm longa, ca. 0.7 mm lata, tepalis exterioribus opposita. Staminodia 3, ca. 0.5 mm longa, strigosa, lanceolata, tepalis interioribus opposita. Tubus floralis vadosus, intus glaber. Ovarium glabrum, ellipsoideum, sensim in stylo attenuatum, ovarium stylusque ca. 1 mm longus. Fructus ignotus.

Tree, to 20 m tall. Twigs terete, with conspicuous leaf scars, minutely pubescent, the terminal bud white appressed pubescent; bark on older twigs soft and flaking. Leaves clustered at the tips of the branches, alternate, obovate, chartaceous, glaucous and laxly and minutely puberulous below, the tip rounded or acute, the base obtuse or acute, 15–25 × 8–12 cm, the midrib and lateral veins immersed, but the tertiary venation slightly raised above, glabrous except for the puberulous midrib; midrib and lateral vein raised below, the tertiary venation much less so; lateral veins 10–14 pairs; petioles with swollen bases, shallowly canaliculate to triangular in cross section, grayish puberulent, to 6 cm long. Inflorescences axillary, pyramidate, to 15 cm long, gray strigose. Pedicels ca. 1.5 mm long, glabrous or with few gray, appressed hairs at the base, subtended by 2 small, deltoid, strigose bracts, ca. 0.2 mm long. Flowers glabrous, more or less cup-shaped, ca. 1 mm long and wide when dry. Tepals 6, at anthesis more or less erect, the outer three smaller than the inner three, broadly deltoid. Stamens 3, all 4-celled, the filaments as wide as the anthers; glabrous or with a few hairs at the base, ca. 1 mm long, 0.7 mm wide, situated opposite the outer tepals; tips of the stamens curved inward; anther cells positioned on the upper part. Inner tepals pushed apart at anthesis and exposing anther cells in their sinuses. Staminodia 3, alternating with stamens, lanceolate, strigose, ca. 0.5 mm long. Ovary glabrous, ellipsoid, gradually narrowed into style, ovary and style ca. 1 mm long. Floral tube shallow, glabrous inside. Fruit unknown.

Paratypes. COSTA RICA. PUNTARENAS: Osa Peninsula, in forest W. of Rincón, *Hammel et al. 15214* (MO; duplicates to be distributed).

There is no doubt that *Mezilaurus glaucophylla* and *M. quadrilocellata* are closely related. They differ from the other *Mezilaurus* species in the following characters: distribution (the only species north of the Andes); presence of four-celled anthers; leaves more or less glaucous below; unequal tepals; and the inflorescence not strictly a dibothryum, but sometimes with short tertiary axes. These two species could be regarded as forming a new genus, based on their four-celled stamens and unequal tepals, but it should be mentioned that several other *Mezilaurus* species have small tepals that one cannot very well judge to be equal or not. If additional differences separating *M. glaucophylla* and *M. quadrilocellata* from the other *Mezilaurus* species are found (in cupule shape, for instance), it might be better to treat them as a separate genus, but for the time being, I prefer to include them in *Mezilaurus.*

In addition to the differences mentioned in Table 1, the few available collections also suggest that *Mezilaurus glaucophylla* has larger, thinner leaves and larger inflorescences than *M. quadrilocellata.*

Mezilaurus itauba (Meissner) Taubert ex Mez, Arbeiten Königl. Bot. Gart. Breslau 1: 112. 1892. *Acrodiclidium itauba* Meissner, DC. Prodr. 15(1): 86. 1864. *Endiandra itauba* (Meissner) Benth. & Hook., Gen. Pl. 3: 154. 1880. *Silvia itauba* (Meissner) Pax, Natürlichen Pflanzenfamilien 3(2): 123. 1889.

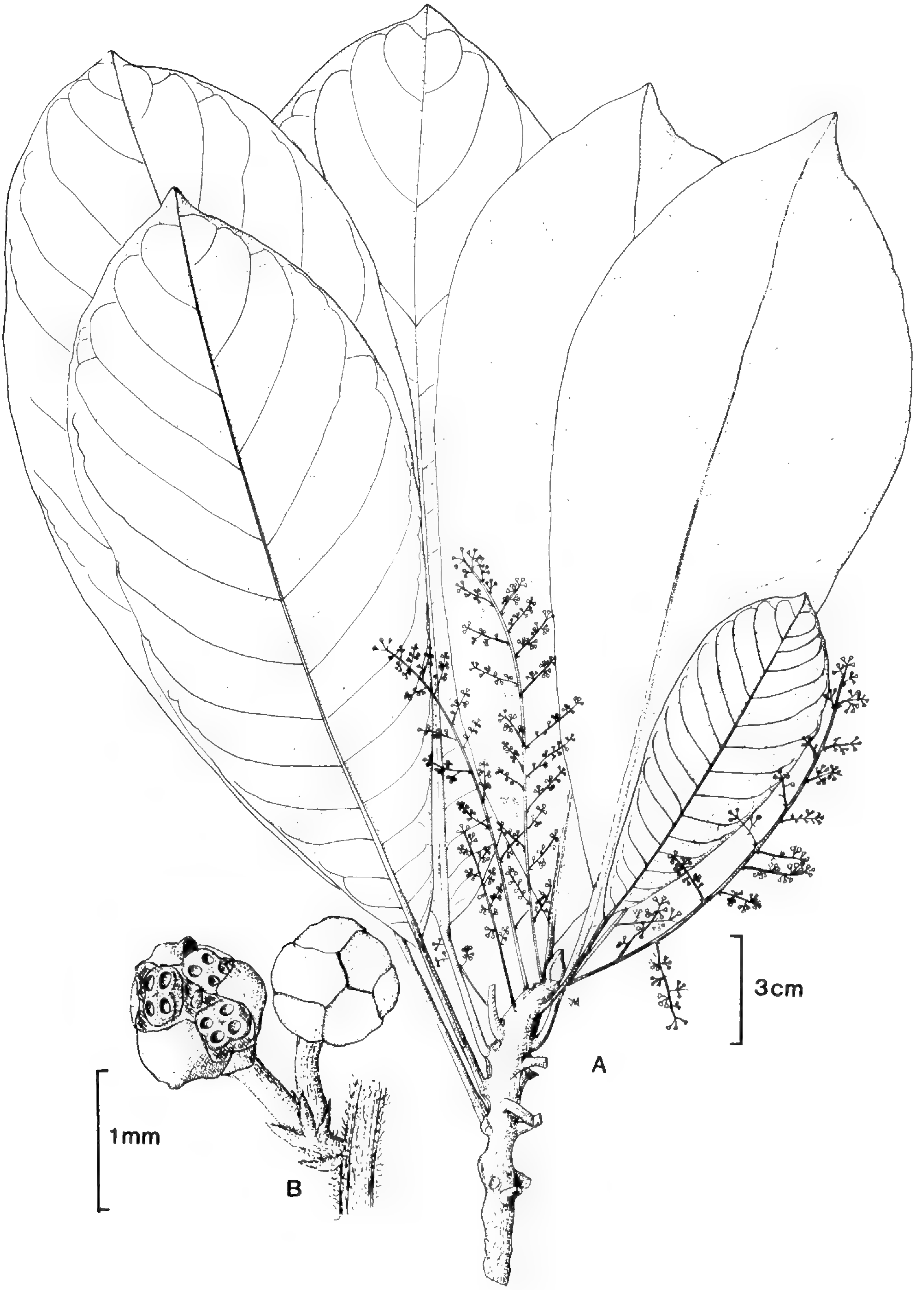

FIGURE 4. *Mezilaurus glaucophylla.*—A. Habit.—B. Flower and bud seen from above.

Mezia itauba (Meissner) Kuntze, Rev. Gen. Pl. 2: 574. 1891. TYPE: Brazil. Pará: Santarem, *Spruce 643* (lectotype, K, fide Kostermans, BM, C, fragm. F). Figures 1, G & H; 5.

Acrodiclidium itauba Meissner var. *amarella* Meissner, DC. Prodr. 15(1): 86. 1864. TYPE: Brazil. Pará: Santarem, *Spruce 646* (lectotype not chosen, BM, C).

Oreodaphne hookeriana Meissner, DC. Prodr. 15(1):

TABLE 1. Comparison of *Mezilaurus glaucophylla* with *M. quadrilocellata*.

	M. glaucophylla	*M. quadrilocellata*
Inflorescence	gray strigose	rufous tomentellous
Pedicels	few basal hairs, otherwise glabrous	rufous tomentellous
Tertiary venation on upper leaf surface	raised	immersed
Terminal bud	densely gray pubescent	brown tomentellous

131. 1864. TYPE: Brazil. Pará: Santarem, *Spruce 669* (not seen.)

Mezilaurus anacardioides (Meissner) Taubert ex Mez, Arb. Bot. Garten Breslau 1: 112. 1892. *Acrodiclidium anacardioides* Meissner, DC. Prodr. 15(1): 86. 1864. *Misanteca anacardioides* (Meissner) Benth. & Hook., Gen. Pl. 3(2): 155. 1880. *Silvia anacardioides* (Meissner) Mez, Jahrb. Bot. Gart. Berlin 5: 108. 1889. *Mezia anacardioides* (Meissner) Kuntze, Revis. Gen. Pl. 2: 574. 1891. TYPE: Venezuela. Amazonas: San Carlos de Río Negro, *Spruce 2961* (lectotype not chosen, BM, G).

Silvia polyantha Mez, Bull. Herb. Boiss. 2ᵉ sér. V: 233. 1905. TYPE: Brazil. Amazonas: Moura, Rio Negro, *Ule 6055* (holotype, B, not seen, isotype, G).

Silvia rondonii Mez et Hoehne, Bot. Archiv VI: 230. 1924. TYPE: Brazil. Mato Grosso: near Tres Buritys, *Kuhlmann 1976* (K, not seen).

Large trees to 35 m tall, rarely shrubs. Twigs terete, glabrous or nearly so, the terminal bud appressed pubescent, the bark rather thin and flaking. Leaves clustered at the tips of branches, firmly chartaceous or coriaceous, glabrous at maturity, elliptic or slightly obovate, ca. 15 × 5 cm, the base gradually narrowed into petioles, the tip rounded, the reticulation on both surfaces slightly raised, the midrib and lateral veins (7–12 pairs) immersed above, raised on lower surface, the lateral veins arching upward and fading near the margin. Lower leaf surface densely and minutely gland dotted; petioles glabrous, with swollen bases, 1–2.5 cm long. Inflorescences axillary, subterminal, narrowly pyramidate, 5–10 cm long, laxly appressed pubescent. Flowers subumbellately arranged at tips of lateral branchlets, laxly and minutely appressed pubescent. Pedicels minutely appressed pubescent, 2–4 mm long. Bracts and bractlets deciduous. Flowers hemispherical, 1.5–2 mm long, the 6 equal tepals erect (rarely spreading), wider than long, the anthers exserted. Fertile stamens 3, 2-celled, ovate-elliptical, ca. 1–1.2 mm long, the filaments free, pubescent, the anther cells glabrous, situated on a dorsal ridge, the cells large, opening back-to-back. Ovary ellipsoid, pubescent, the style exserted. Flower tube pubescent. Staminal glands and staminodia lacking. Fruit an ellipsoid berry, ca. 2 × 1 cm, subtended by a small, platelike cupule.

Selected additional specimens examined. SURINAM. Boschreservaat, sectio O, tree No. 760, *Boschwezen 3088* (NY). BRAZIL. PARÁ: Rio Tapajos, Villa Braga, *Ducke RB 17537* (G, US). PARÁ: Serra dos Carajas, *M. G. Silva 2909* (MO); Rio Jari, Monte Dourado, *N. T. Silva 1041* (NY). PERU. MADRE DE DIOS: Tahuamanú, *Diaz 17 53-96* (MO). BOLIVIA: San Francisco, 50 km from Pto. Rica Pando, *E. Menesk 626* (MO).

Mezilaurus itauba is the most frequently collected and widest ranging species of the genus. In addition to the countries listed, it has been reported from French Guiana, based on a Mélinon collection I have not seen. Although there is some variation in degree of pubescence and leaf shape throughout its range, *M. itauba* is adequately characterized by free staminal filaments, pubescent flowers, and glabrous leaves rounded at the tip and gradually narrowed basally. The anthers, with large cells, are also long exserted for their size. The numerous gland dots on the lower leaf surface are best seen on rather young leaves; on mature, more coriaceous leaves they are often scarcely visible.

Alencar 55 (MO) is included in *M. itauba* with hesitation; it differs somewhat in leaf shape, but in the absence of floral differences I regard it as *M. itauba.* However, when more collections are available, it might turn out to be a new species.

The wood of *Mezilaurus itauba* is hard and much used for construction. Mez (1889) reported that the berries are edible.

Mezilaurus lindaviana Schwacke et Mez, Arb. Bot. Garten Breslau 1: 112. 1892. TYPE: Brazil. Amazonas: Rio Branco, *Schwacke 7080* (lectotype, chosen by Kostermans, B, not seen). Figures 6, A & B; 7.

Misanteca duckei Samp., Commissão Linhas Telegr. Estrat. Matto Grosso Amazonas, Publ. 56 (Annexo 5, Bot. Part X): 15. 1917. *Silvia duckei* (Samp.) Samp., Bol. Mus. Nac. Rio de Janeiro 4: 39. 1928. TYPE: Brazil. Amazonas: Montealegra, *Ducke RB 17540 = MG 16032,* not seen.

Mezilaurus wurdackiana C. K. Allen, Mem. New York Bot. Garden 10: 56. 1963. TYPE: Venezuela. Bolívar: Hato La Vergareña, *Wurdack & Guppy 91* (holotype, NY, isotype, US).

FIGURE 5. Distribution of *Mezilaurus itauba.*

Tree, to 25 m. Twigs thick, round, with a rather thick corky layer, the tips with brown velutinous pubescence. Leaves alternate, clustered at the tips of the branches, chartaceous or coriaceous, obovate, 8–17 × 4–8 cm, the tip rounded or very shortly acute, the base cuneate or abruptly rounded; young leaves hirsute, becoming glabrous above (except on midrib and primary veins) at maturity; venation impressed above, the midrib, secondary and tertiary venation raised below; secondary veins about 10 pairs; petioles short, thick, brown-tomentose, 5–8 mm long. Inflorescences axillary, mostly subterminal on branches, pyramidal, tomentellous, about as long as the leaves; branchlets patent, 1–3 cm long, the flowers spicately arranged and often somewhat recurved. Flowers white or yellow-green, fragrant, glabrous, 1.2 mm long. Tepals 6, equal, triangular, ca. 0.2 mm long, 0.4 mm wide. Fertile stamens 3, 1 mm long; filaments (ca. 0.5 mm) connate, narrower than anthers, pubescent; anthers shortly exserted, 2-celled, 0.5 mm long, the cells situated on a dorsal ridge, opening back-to-back. Ovary ellipsoid, 0.8 mm long, with slender

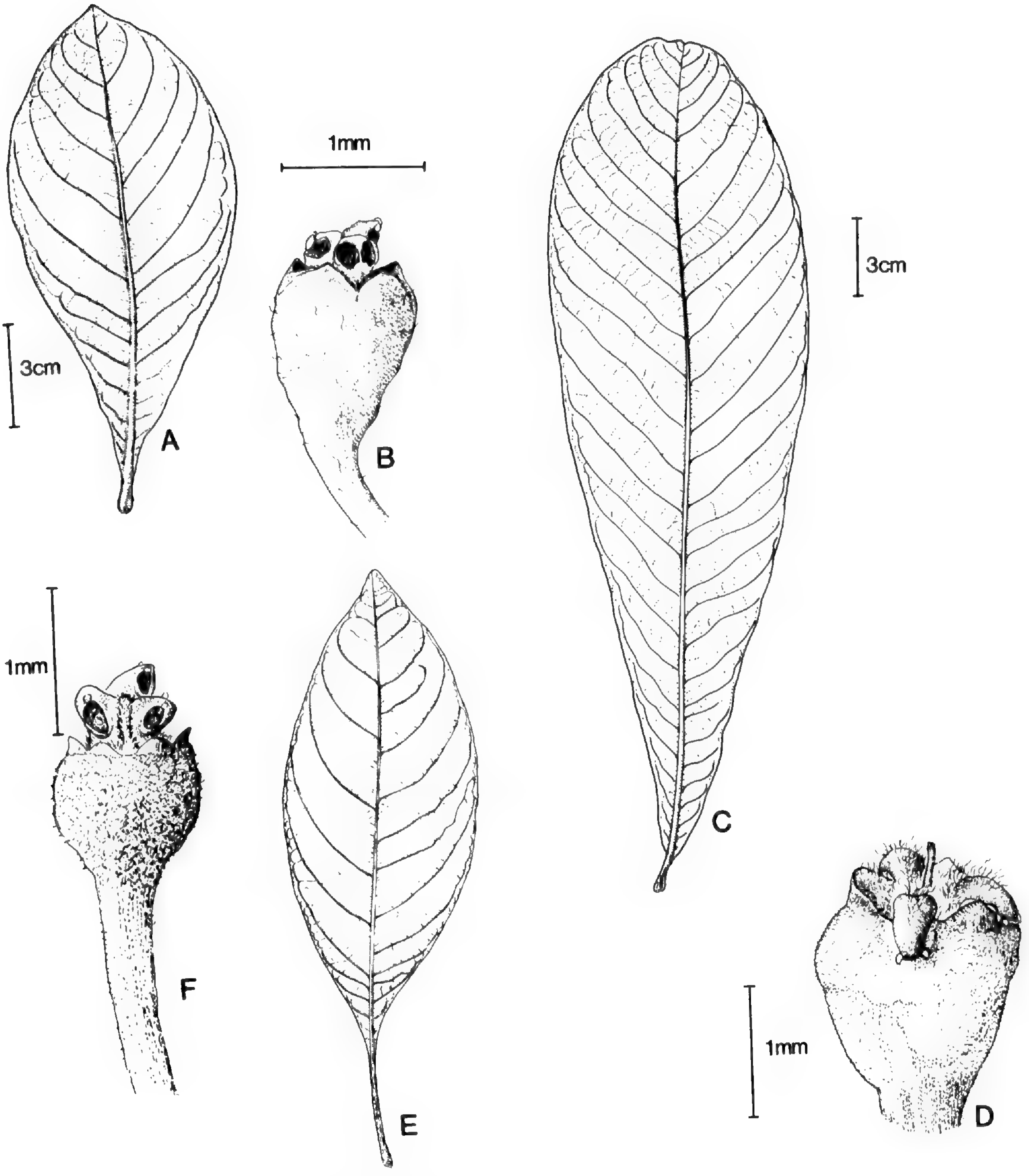

Figure 6. A–B. *Mezilaurus lindaviana.*—A. Leaf.—B. Flower. C–D. *M. mahuba.*—C. Leaf.—D. Flower. E–F. *M. micrantha.*—E. Leaf.—F. Flower.

style exceeding the anthers. Stamens without basal glands. Staminodia lacking. Fruit ellipsoid, 2 × 1.2 cm, subtended by a small platelike cupule (ca. 3 mm diam.).

Selected additional specimens examined. Guyana: Kanuku Mountains, *For. Dept. Brit. Guyana 5804* (NY), same location, *Smith 3208* (F, MO, US). Brazil. amazonas: Rio Branco, Boa Vista, *Ducke 1336* (F, NY, US). amapá: surrounding of Macapa, *Fróes & Black 27453* (NY). pará: Planalto de Santarem, *Fróes 30976* (NY, US); Rio Jarí, Monte Dourado, *E. Oliveira 4749* (NY), same location, *N. T. Silva 996* (NY, US).

Mezilaurus lindaviana is somewhat variable in leaf shape but is clearly characterized by the combination of pubescent leaves and glabrous flowers. *Mezilaurus crassiramea,* a similar species with pubescent leaves, has pubescent flowers and is known only as a shrub or a small tree in cerrado vegetation.

FIGURE 7. Distribution of *Mezilaurus lindaviana* (●), *M. mahuba* (▲), and *M. micrantha* (■).

Silva 2403 (NY, 2 sheets, MO) is included in *M. lindaviana* as an aberrant collection; it differs from other collections of that species in having sparse appressed pubescence. Other characters (leaf shape, size, flowers) point to *M. lindaviana* and I feel that a single collection with unusual pubescence need not be given taxonomic status.

Kostermans (1938) cited as type of *M. lindaviana Schwacke 7080 = Glaziou 19798* and gave Serra d'Antonio Pereira in Minas Gerais as the type locality. Schwacke and Mez (Mez, 1892) cited only *Schwacke 7080* as type collection and gave as type locality "in campis ad Rio Branco." It is likely that Glaziou distributed duplicates of the Schwacke collection under his own name with incorrect locality data, as he did with other collections (Wurdack, 1970). Therefore, I ignore the reference of *M. lindaviana* as occurring in Minas Gerais, as cited by Glaziou (1905–1913) and Kostermans (1938).

Mezilaurus mahuba (Samp.) van der Werff, comb. nov. Basionym: *Acrodiclidium mahuba* Samp., Commissão Linhas Telegr. Estrat.

Matto Grosso Amazonas, Publ. 56 (Annexo 5, Bot. Parte X): 14. 1917. *Clinostemon mahuba* (Samp.) Kuhlm. & Samp., Bol. Mus. Nac. Rio de Jan. 4(2): 57. 1928. *Licaria mahuba* (Samp.) Kosterm., Rec. Trav. Bot. Neérl. 35: 123. 1938. *Misanteca mahuba* (Samp.) Lundell, Wrightia 4: 100. 1969. TYPE: Brazil. Pará: Gurupa, Varzea do Rio Amazonas, *Ducke MG 16538 = RB 17582* (isotype, U). Figures 6, C & D; 7.

Large trees. Twigs thick, glabrescent, with dense brown tomentum when young. Leaves large, 20–40 × 12–15 cm, obovate, clustered at the tips of branches, glabrous above with the exception of the puberulous midrib, softly pubescent below, the apex rounded, the base cuneate; venation immersed on upper surface; midrib, lateral veins (15–23 pairs) and tertiary venation raised below; petioles thick, 5 mm diam., 2–3 cm long, densely and minutely tomentose. Inflorescences subterminal, densely puberulous, large (20–35 cm long), the flowers arranged in clusters on the lateral branches. Flowers sessile, brown-puberulous, more or less globose, ca. 1.8 mm long. Tepals 6, minute, incurved. Fertile stamens 3, all 2-celled; filaments densely strigose, with 2 glands attached a little above the base; anthers glabrous, strongly curved outside the flower tube. Staminodes 9, ca. 0.5 mm long, lanceolate, strigose. Ovary glabrous, globose, ca. 0.5 mm long, the style ca. 1 mm long, curved at the tip. Fruit ellipsoid, 3.5 cm long, seated on a small, glabrous disk.

Additional specimens examined. BRAZIL. AMAPÁ: Rio Juruxi-Mazagão, *B. V. Rabelo 2715* (MO). PARÁ: Belem, *Ducke RB 17583* (U, US), *Ducke 1234* (NY, MO, US); Trapiche Hypolito, *Krukoff 5870* (BR, NY, MO); Ilha de Pará, *Mori et al. 16510* (MO); Belem, *Murça Pires 1488* (NY).

Mezilaurus mahuba is very distinctive because of its peculiar anthers. When sterile, it is rather similar to *M. thoroflora*. The latter, however, has shorter petioles and a fine and closely appressed pubescence on young twigs and leaves, whereas in *M. mahuba* the petioles are longer and the pubescence consists of spreading hairs. *Mezilaurus mahuba* is a species known only from seasonally inundated forest in the states of Pará and Amapá.

The few available collections of *Mezilaurus mahuba* clearly show two phases in the floral development, probably corresponding with the male and female phase as described by Kubitzki and Kurz (1984) for several other species of Lauraceae. The three sheets of *Krukoff 5870* all have flowers with the anthers recurved and tightly pressed against the flower, almost hiding the anther cells (female phase), while the three sheets of *Ducke 1234* have only flowers with the anthers spreading and free of the flower, fully exposing the anther cells (male phase). The inflorescences of these specimens are large, and it is interesting that the flowers on an inflorescence all appeared to be in the same phase of development, quite unlike what I have seen in species of *Ocotea* and *Nectandra* with large inflorescences.

Mezilaurus micrantha van der Werff, sp. nov. TYPE: Brazil. Amazonas: Manáos, Reserva Florestal Ducke, *Rodrigues & Coelho 7555* (holotype, NY). Figures 6, E & F; 7.

Arbor, 20 m alta. Ramuli teretes, glabri vel prope apicem adpresse pubescentes; gemma terminalis sericea. Folia conferta ad apices ramulorum, coriacea, adulta glabra, juvenalia adpresse pubescentia, elliptica, 10–15 × 3.5–5 cm (sine petiolo), basi attenuata, apice acuta acumine obtuso, marginibus revolutis, in sicco atra. Venatio super immersa, subtus costa et nervi laterales (5–8) elevati. Petioli ad 2 cm longi, juvenales adpresse pubescentes, adulti glabri. Inflorescentiae axillares, subterminales, ad 5 cm longae, paniculatae, leviter adpresse pubescentes. Flores parvi, 1–1.1 mm longi, fasciculati ad apices ramulorum inflorescentiarum, cyathiformes, leviter adpresse pubescentes. Pedicelli ad 2 mm longi, leviter adpresse pubescentes. Bracteae bracteolaeque deciduae. Tepala 6, aequalia, triangularia, erecta vel leviter patentia. Stamina 3, ca. 0.6 mm longa, per anthesin 0.3 mm exserta, filamentis liberis, dense pubescentibus. Antherae 2-locellatae, locellis extrorsis, latere ventrali staminis omnino pubescenti. Ovarium glabrum, sensim in stylo attenuatum, ovarium stylusque 1 mm longus. Fructus ignoti.

Tree, 20 m tall. Twigs terete, glabrous or, near the apex, with some appressed pubescence, the terminal bud sericeous; the bark rather thick. Leaves clustered at the tips of the branches, coriaceous, drying blackish, glabrous at maturity, but when young with some appressed pubescence, elliptic, ca. 10–15 × 3.5–5 cm (exclusive of petiole), the base gradually narrowed attenuately into the petiole, the tip blunt but not rounded, the margins revolute; veins and reticulation not or scarcely raised on upper surface; midvein and main lateral veins (5–8 pairs) raised on lower surface, but reticulation not obvious. Petioles to 2 cm long, glabrous at maturity. Inflorescences axillary, subterminal, to 5 cm long, pyramidate, with some appressed pubescence. Flowers arranged subumbellately at the ends of the lateral branches, appressed pubescent. Pedicels minutely appressed pubescent, ca. 2 mm long at anthesis. Bracts and bractlets deciduous. Flowers cup-shaped, 1–1.1 mm long. Tepals 6, equal, triangular, erect. Stamens 3, 0.6 mm long, exserted 0.3 mm at anthesis, the filaments free, densely pubescent; anthers 2-celled, glabrous, the cells extrorse, opening back-to-back; ventral side of the anther entirely pubescent. Floral tube pubescent. Staminal glands and staminodia lacking. Ovary glabrous, gradually narrowed into style, the ovary and style ca. 1 mm long, the style exserted at anthesis. Fruit unknown.

Paratypes. BRAZIL. AMAZONAS: Manáos, Reserva Florestal Ducke, *W. Rodrigues 8190* (NY); AM-1, Km 74, *W. Rodrigues 7066* (NY).

Mezilaurus micrantha is rather similar to *M. itauba*; it differs in having smaller flowers, blunt but not rounded leaf tips, lack of gland dots on the leaves, slightly revolute leaf margins, and nearly black dried leaves. These characters are not strong individually, but taken together they allow identification of flowering as well as sterile collections. The flowers of this species are among the smallest I have seen in the genus, hence its specific epithet.

Mezilaurus navalium (Allemão) Taubert ex Mez, Arbeiten Königl. Bot. Gart. Breslau 1: 112. 1892. *Silvia navalium* Allemão, Dissertatio, Rio de Janeiro. 1848. *Silvaea navalium* (Allemão) Meissner, DC. Prodr. 15(1): 84. 1864. *Endiandra navalium* (Allemão) Benth. & Hook., Gen. Pl. 3: 154. 1880. *Mezia navalium* (Allemão) Kuntze, Revis. Gen. Pl. 2: 574. 1891. TYPE: Brazil, Rio de Janeiro, *Allemão, s.n.* (holotype, R, not seen). Figures 8, A & B, 9.

Tall trees, to 25 m. Branches terete, glabrous, the tips with appressed, short hairs, the terminal bud densely gray strigose. Leaves clustered at branch tips, narrowly elliptic, 10–12 × 3–3.5 cm, somewhat coriaceous, glabrous on both surfaces or with few appressed hairs along the midrib, the tip rounded, the base sharply acute, lateral veins not strongly developed, 10–15 pairs, the upper surface dull, smooth, lower surface with slightly elevated reticulation; petioles ca. 1 cm long. Inflorescences axillary, glabrous or with few scattered hairs, 3–5 cm long, the flowers clustered at the ends of the lateral branches. Flowers glabrous, ca. 2 mm long. Pedicels 2–3 mm long, glabrous. Bracts deciduous. Tepals 6, equal, erect, scalelike, ca. 0.3 mm long. Stamens 3, ca. 1.5 mm long; filaments free, strigose; anthers exserted, glabrous, the 2 large cells positioned on a dorsal ridge, opening back-to-back, slightly divergent, exposing the exserted stigma. Ovary ellipsoid, glabrous, ca. 2 mm long, including the exserted stigma. Staminal glands and staminodia lacking. Immature fruits subtended by the small tepals, occasionally the stamens visible at the base of the young fruit.

Additional specimens examined. BRAZIL. RIO DE JANEIRO: Theresopolis, *Glaziou 11470* (C, G, U), *Glaziou 11473* (C); Petropolis, *Glaziou 12124* (C, G), *Glaziou 12125* (C, G, MO, U, US).

Mezilaurus navalium is the only *Mezilaurus* species known from the Atlantic rain forests in southern Brazil. The wood is hard and much used for naval construction. Diagnostic characters, in addition to its distribution, are the glabrous flowers and leaves with rounded or blunt apices.

Mezilaurus opaca Kubitzki & van der Werff, sp. nov. TYPE: Peru. Depto. Loreto: Prov. Requena, Distr. Jenaro Herrera, trocha al Río Yaveri, cerca al Arboretum de Jenaro Herrera, 15 m tree in low forest, flowers greenish yellow, 20 Aug. 1976, *Revilla 1226* (holotype, MO; isotype, HBG). Figures 8, C & D; 12.

Arbor, 20 m. Ramuli glabri, sed apicibus foliiferis sericeis, cicatricibus conspicuis munitis. Folia alterna, conferta ad apices ramulorum, glabra (juvenalia adpresse pubescentia), chartacea, apice rotundo vel obtuse acuto, basi petiolo attenuato, elliptica, ca. 20 × 9 cm. Laminae super opacae, costa elevata, venatione secundaria leviter elevata, venatione tertia immersa; subtus opacae, venatione magis elevata. Petioli 3–4 cm longi, peranguste alati laminis decurrentibus. Inflorescentiae axillares, parvae longiores quam petiolis. Flores conferti ad apices ramulorum inflorescentiarum, minute appresse pubescentes, depresse globosi. Tepala 6, aequalia, parva, ca. 0.4 × 0.2 mm, minute adpresse pubescentia. Stamina 3, exserta, filamentis connatis pubescentibus, antheris glabris, exsertis per anthesim, 2-loculatis. Ovarium glabrum, ovoideum, sensim in stylo attenuatum. Fructus ignoti.

Tree, 15 m. Twigs glabrous, rather thick (5–7 mm diam. immediately below the leaves), with conspicuous leaf scars, the bark gray. Tips of branches with dense, brown, sericeous pubescence. Leaves alternate, clustered at tips of branches, ca. 20 × 9 cm, young ones with some appressed pubescence, glabrous at maturity, chartaceous, elliptic, the tip rounded or bluntly

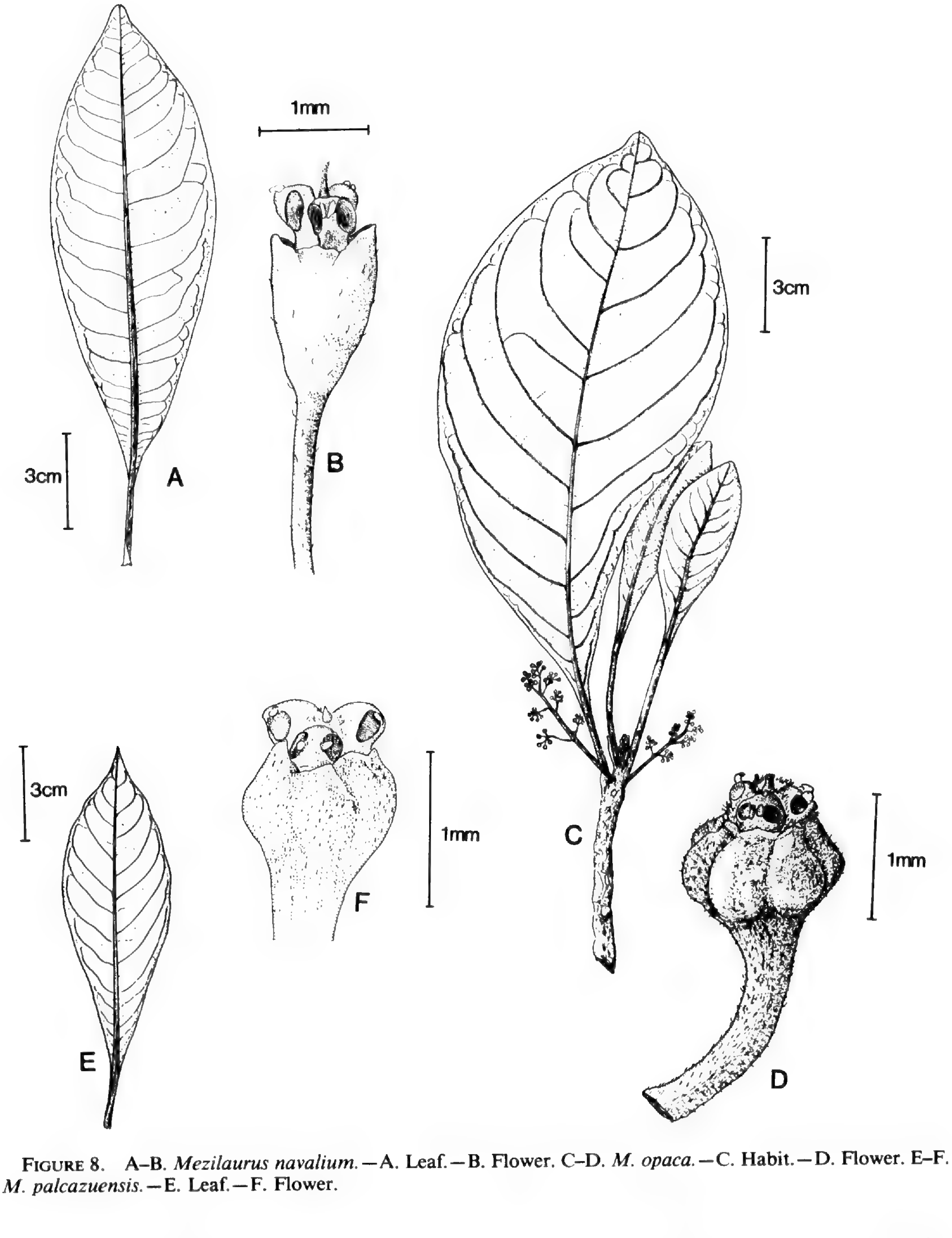

Figure 8. A–B. *Mezilaurus navalium.*—A. Leaf.—B. Flower. C–D. *M. opaca.*—C. Habit.—D. Flower. E–F. *M. palcazuensis.*—E. Leaf.—F. Flower.

acute, the base gradually narrowed onto the petiole, green, opaque above, the midvein elevated, the secondary veins slightly elevated, the tertiary venation more or less immersed, not easily visible; lower surface also opaque but with the venation more elevated; petioles 3–4 cm long, with narrow wings of the decurrent laminae. Inflorescences compound racemes in the axils of deciduous bracts, slightly longer than the petioles, when young rather densely appressed pubescent, at anthesis less so. Bracts and bracteoles deciduous. Flowers clustered at the tips of inflorescence branchlets, with some appressed pubescence, depressed globose, constricted at the apex, ca. 1.5 ×

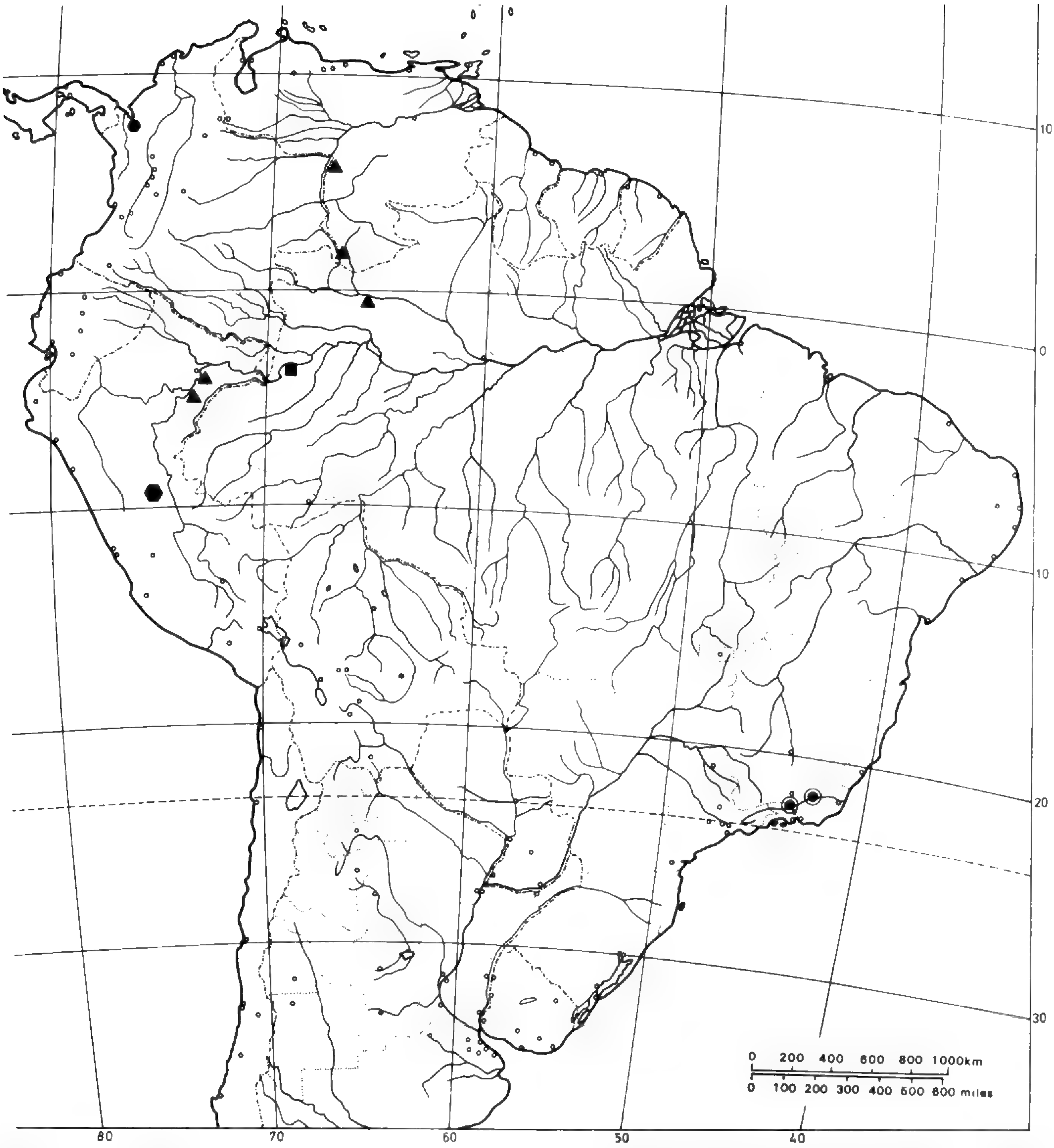

FIGURE 9. Distribution of *Mezilaurus palcazuensis* (●), *M. pyriflora* (■), *M. quadrilocellata* (●), *M. sprucei* (▲), and *M. navalium* (⊙).

1.5 mm (including the exserted stamens). Tepals 6, equal, pointing inwards, wider than long, ca. 0.4 mm wide, ca. 0.2 mm long, with some appressed pubescence. Floral tube short, ca. 0.5 mm long, with a pubescent ring in the upper part. Stamens 3, 2-celled, ca. 1 mm long, the anthers glabrous, exserted at anthesis, the cells on a dorsal ridge, the valves opening back-to-back; filaments broad, connate, pubescent, ca. 0.6 mm long. Ovary glabrous, ovoid, gradually narrowed into the style; style exserted beyond stamens; stigma a small plate. Fruit unknown.

Mezilaurus opaca is rather similar to *M. synandra,* but differs from that species by its smaller flowers and the leaf characters mentioned in the key. Béguin et al. (1985) reported *M. synandra* from the Jenaro Herrera Arboretum. It is possible that this specimen represents *M. opaca,* but I have not seen it.

Mezilaurus palcazuensis van der Werff, sp. nov. TYPE: Peru. Cerro de Pasco: Selva Central, Palcazu Valley, elev. 300–600 m, 7 Dec.

1984, *Hartshorn, Quijano & Mateo 2691* (holotype, MO). Figures 8, E & F; 9.

Arbor, 25 m. Ramuli teretes, glabri vel prope apicem adpresse pubescentes, cicaticibus foliarum conspicuis munitis. Gemma terminalis sericea. Folia chartacea, conferta ad apices ramulorum, adulta glabra, juvenalia adpresse pubescentia, obovata vel anguste obovata, apice acuta, basi attenuata, 10–15 × 3–4 cm. Costa elevata; nervi laterales et venatio immersa, haud conspicua. Petioli ca. 1 cm longi. Inflorescentia axillaris, minute adpresseque pubescens, paniculata, 4 cm longa, floribus congestis ad apices ramulorum inflorescentiae, sessilibus vel quasi sessilibus. Flores minuti adpresseque pubescentes, obconici, ca. 1.5 mm longi. Tepala 6, erecta, parva, 0.3 mm longa. Stamina 3, 0.8 mm longa, per anthesin exserta. Antherae 2-locellatae, glabrae, extrorsae. Filamenta connata, glabra praeter aream parvam pubescentem in superficie ventrale. Ovarium globosum, glabrum. Fructus ignoti.

Tree, 25 m. Twigs terete, glabrous or with some appressed pubescence near tip, with conspicuous leaf scars. Terminal bud sericeous. Leaves chartaceous, clustered at the tips of branches, with some appressed pubescence when immature, glabrous when mature, obovate or narrowly obovate, the tip acute, the base gradually narrowed into the petiole, 10–15 × 3–4 cm; costa raised on both surfaces; secondary veins and reticulation immersed, not obvious; petioles ca. 1 cm long. Inflorescence axillary, 4 cm long, paniculate, minutely appressed pubescent, the flowers clustered at the tips of the lateral branches, sessile or nearly so. Flowers minutely appressed pubescent, sessile, ca. 1.5 mm long. Tepals 6, erect, 0.3 mm long. Fertile stamens 3, 2-celled, exserted at anthesis; anthers extrorse, situated on a dorsal ridge, opening back-to-back; filaments united, glabrous. Staminal glands and staminodia lacking. Fruit unknown.

Mezilaurus palcazuensis is only known from the holotype, consisting of a small twig with few leaves and one inflorescence. It is therefore quite likely that the description does not embrace the morphological variation of this species. Noteworthy features are the acute leaf tips and the sessile flowers, both unusual characters in the genus. The leaves are also thinner than in other species of *Mezilaurus,* but with only one specimen available, it is not certain whether this is a distinguishing character.

Similar sessile flowers occur also in *M. caatingae,* known from caatinga forest along the Rio Negro, which differs in having larger flowers and coriaceous, rounded leaves with inrolled margins.

Mezilaurus pyriflora van der Werff, sp. nov. TYPE: Brazil. Amazonas: São Paulo de Olivença, basin of creek Belem, 26 Oct.–11 Dec. 1936, *Krukoff 8711* (holotype, NY; isotype, MO, GH). Figures 10, A & B; 9.

Arbor, 25 m alta. Ramuli crassi, ad 1 cm diametro, teretes, cicatricibus conspicuis foliorum delapsorum notati, apicibus dense adpresseque puberulis, glabrescentibus. Gemma apicalis dense pubescens. Folia conferta ad apices ramulorum, chartacea, obovata, in dimidio inferiore persensim dilatata, in dimidio superiore abrupte dilata, 40–60 × 14–18 cm, apice acuta, basi abrupte angustata, rotunda vel subcordata. Costa super et subtus elevata; nervi secundarii 20–25, super immersi, subtus elevati; nervatio tertia super obscura, subtus elevata. Lamina glabra praeter costam basimque laminae adpresse puberulam. Petioli 1 cm longi, 5 mm diametro, adpresse puberuli, cristis duabus lateralibus. Inflorescentia axillaris, subterminalis, anguste pyramidalis, ramulis basalibus perlongioribus quam terminalibus, adpresse pubescens. Flores parvi (0.9 mm × 0.9 mm), glabri, pyriformes. Pedicelli pubescentes, 1.5–2 mm longi. Stamina fertilia 3, inclusa, 0.8 mm longa, 2-locellata. Filamenta libera, pubescentia. Locelli parvi, terminales, aperientes ad apicem. Ovarium depresse globosum, glabrum, 1.2 mm latum, 1 mm longum. Staminodia 6. Glandulae filamentorum nullae. Fructus ignoti.

Tree, to 25 m tall. Twigs thick (diam. 1 cm 4–5 cm below tip), terete, with conspicuous leaf scars, the tip with gray, minute and appressed pubescence, becoming glabrous with age. Terminal bud densely gray pubescent. Leaves clustered at tips of branches, firmly chartaceous, obovate, the basal half of the lamina widening very gradually, the apical half rather abruptly widened, large (40–60 × 14–18 cm at maturity), the tips acute, gradually narrowed towards the base, but the base abruptly narrowed, rounded or almost subcordate, mostly glabrous, with some appressed pubescence on midrib or near base, the midrib thick (5 mm wide), raised on both surfaces, the main lateral veins (20–25 pairs) immersed above and elevated below, the tertiary venation scarcely visible above, raised below; petioles ca. 1 cm long, 5 mm thick, densely appressed pubescent, the lamina decurrent as two narrow ridges. Inflorescences axillary, subterminal, pyramidal, the basal branchlets much longer than the terminal branches (the longest ca. 10 cm long, decreasing to ca. 1 cm), the main axis and branchlets with appressed pubescence; bracts and bracteoles pubescent. Flowers arranged spicately along branchlets, glabrous, often reflexed, pear-shaped, ca. 0.9 mm long, 0.9 mm wide. Pedicels pubescent, especially near the base, 1.5–2 mm long at anthesis. Fertile stamens 3, ca.

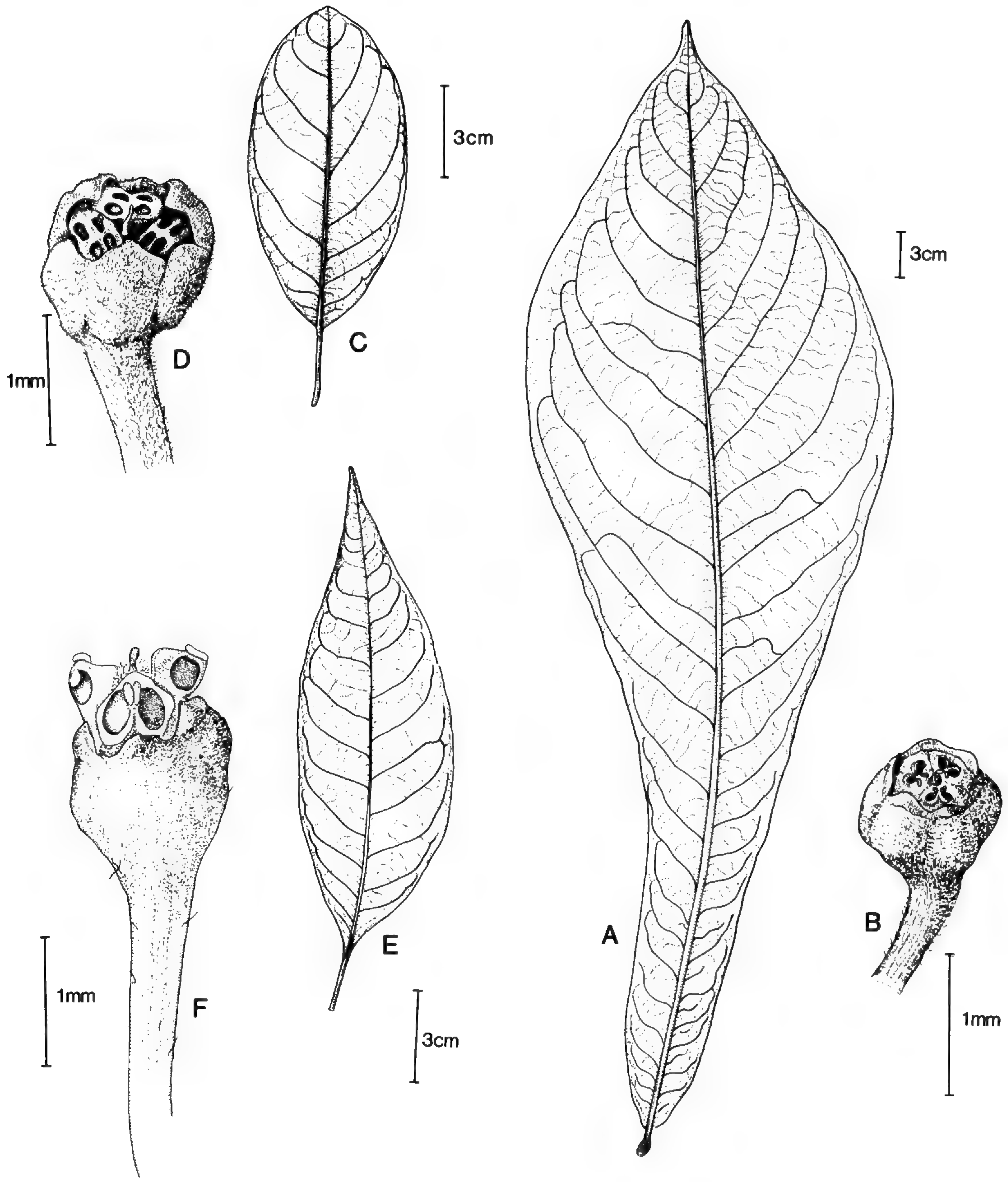

FIGURE 10. A–B. *Mezilaurus pyriflora*.—A. Leaf.—B. Flower. C–D. *M. quadrilocellata*.—C. Leaf.—D. Flower. E–F. *M. sprucei*.—E. Leaf.—F. Flower.

0.8 mm long, included; filaments free, pubescent; anther cells minute, terminal, opening towards the tip. Ovary depressed globose, glabrous, ca. 1.2 mm wide, ca. 1 mm long. Staminodia 6, representing the outer 6 stamens, pubescent, ca. 0.5 mm long. Staminal glands lacking. Fruit unknown.

Paratype. BRAZIL. AMAZONAS: *Fróes 12152* (NY).

Mezilaurus pyriflora is known only from two collections from the vicinity of São Paulo de Olivença. Leaf shape, the short, pubescent pedicels, the included, short anthers and the pear-shaped flowers (with the apical valves of the anthers mimicking the dried crown of a pear) separate this species from *M. mahuba* and *M. thoroflora.* The Fróes collection in NY bears the annotation "wood causes injury to the skin."

The two collections of *Mezilaurus pyriflora* had been annotated as Euphorbiaceae and Ochnaceae; because Krukoff's collections were widely distributed, it is possible that duplicates of *M. pyriflora* are misidentified in additional herbaria.

Mezilaurus quadrilocellata van der Werff, sp. nov. TYPE: Colombia. Antioquia: Chigorodó. Tree, 20 m. Flowers white. 100–200 m, *M. Garcia Barriga 17626* (holotype, GH; isotypes, AAU, US). Figures 10, C & D; 9.

Arbor, 20 m. Ramuli crassi, 4–5 mm diametro, teretes, glabri apicibus foliiferis tomentellis. Folia conferta ad apices ramulorum, glabra, elliptica vel leviter obovata, chartacea, basi cuneata, apice rotundata, ca. 15 × 8 cm, petiolis 2–4 cm longis, tomentellis, margine cartilaginea, leviter incrassata. Venatio super immersa, subtus tomentella costa manifeste elevata, nervis lateralibus (6–8) elevatis, nervis basalibus marginem attingentibus. Inflorescentiae axillares, foliis breviores, anguste pyramidatae, 6–9 cm longae, tomentellae. Flores parvi, ca. 1.5 mm longi, pedicellis 2–3 mm longis, tomentellis. Tepala 6, 3 interioria 3 exterioribus duplo longiora, erecta, apicibus incurvatis, tepala exteriora ovata, ca. 0.6 mm longa, interiora ovata, ca. 1.2 mm longa, omnia glabra. Stamina 3, ca. 1.0 mm longa, filamentis pubescentibus, sine glandulis, antheris quadrilocellatis glabris, apicibus antherarum incurvatis. Staminodia 3, parva, ca. 0.5 mm longa, dense pubescentia. Ovarium ellipsoideum, glabrum, 1 mm longum, sensim in stylum attenuatum. Fructus ignoti.

Tree, 20 m tall. Twigs thick, 4–5 mm diam. immediately below the leaves, terete, glabrous except for the rufous tomentellous leaf-bearing apex. Leaves clustered at tips of branches, glabrous, elliptic or slightly obovate, ca. 15 × 8 cm, the base cuneate, the apex rounded, the margins cartilaginous and slightly thickened, the venation immersed above, the midrib prominently raised and tomentellous on lower surface, the lateral veins (6–8) less prominently raised, the basal ones reaching the margin, the upper ones arcuate and not reaching the margin; tertiary venation slightly raised, petioles 2–4 cm long, rufous tomentellous. Inflorescences axillary, shorter than the leaves, narrowly pyramidate, 6–9 cm long, tomentellous. Flowers small, ca. 1.5 mm long; pedicels 2–3 mm long, tomentellous; flower tube and tepals glabrous outside. Tepals 6, the outer ones half as long as the inner ones, erect, with tips curved inward; outer tepals ca. 0.6 mm long, ovate, inner ones ca. 1.2 mm long, ovate, glabrous. Ovary ellipsoid, gradually narrowed into the style, 1 mm long, glabrous. Fertile anthers 3, ca. 1 mm long; filaments rather densely pubescent; anthers 4-celled, glabrous, the tips bent inward, forming a flat shield exposed at anthesis; anther cells situated on this shield. Fertile anthers alternating with 3 small (ca. 0.5 mm), slender, densely pubescent staminodia. Fruit unknown.

Mezilaurus quadrilocellata is known only from the type collection in northern Colombia, not far from the Panamanian border and the Caribbean. Further discussion is given under *M. glaucophylla.*

Mezilaurus sprucei (Meissner) Taubert ex Mez, Arbeiten Königl. Bot. Gart. Breslau 1: 112. 1892. *Acrodiclidium sprucei* Meissner, DC. Prodr. 15(1): 86. 1864. *Silvia sprucei* (Meissner) Mez, Jahrb. Königl. Bot. Gart. Berlin 5: 119. 1889. *Mezia sprucei* (Meissner) Kuntze, Revis. Gen. Pl. 2: 574. 1891. TYPE: Brazil. Amazonas: San Gabriel de Cachoeira, Rio Negro, May 1852, *Spruce 2323* (lectotype, chosen by Kostermans, K; isotypes BM, C, NY, U). Figures 10, E & F; 9.

Mezilaurus maguireana C. K. Allen, Mem. New York Bot. Garden 10: 58. 1963. TYPE: Venezuela. Amazonas: Río Guainía, Maroa, *Maguire et al. 41698* (holotype, NY; isotype, GH).

Small tree, to 10 m tall. Twigs terete, glabrous, the terminal bud densely yellowish strigose. Leaves clustered at the tips of branches, papyraceous, glabrous, elliptic, 12 × 5(20 × 9) cm, the base acute, the apex acute or acuminate; lateral veins 10–15 pairs, slightly elevated or immersed on upper face, raised on lower surface, the reticulation slightly raised on both surfaces; petioles to 3 cm long, flat, bordered by a narrow ridge, the very base of the petiole round and thickened. Inflorescences 5 or 6, terminal, glabrous, slender, paniculate, shorter than or exceeding leaves, to 15 cm long; branchlets subtended by strigose bracts 1.5 mm long; floral bracts also strigose, but shorter. Flowers glabrous, ± umbellately arranged at the tips of the branchlets, ca. 2 mm long, the pedicels to 1.5 cm long. Tepals 6, equal, erect, ca. 0.5 mm long. Stamens 3, ca. 1.2 mm long, exserted; anthers free and somewhat divergent, 2-celled, the cells large, opening back-to-back; filaments pubescent, connate. Ovary ellipsoid, ca. 0.8 mm long, abruptly narrowed into the slender, ca. 1 mm long, style. Flower tube pubescent within. No staminal glands or staminodia. Fruits not seen.

Additional specimens examined. VENEZUELA: 30 km N of Puerto Ayachucho, *Guanchez 255* (TFAV). AMAZONAS: San Carlos de Río Negro, *Clark & Maguirino 7784* (MO), *8091* (MO); Cerro Neblina base camp, *Gentry & Stein 46836* (MO); BRAZIL. AMAZONAS: Río Negro above Camanaus, *Prance et al. 16042* (NY). PERU. LORETO: Iquitos, near Picuruyacu, *Revilla 106* (G, MO); Requena, Jenaro Herrera, *Vasquez & Jaramillo 984* (MO).

Mezilaurus sprucei can be recognized easily by its glabrous, acute or acuminate leaves, lax inflorescences, and especially by the flowers with long pedicels. The Revilla collection from Peru has short pedicels (5 mm long) but agrees in other characters with *Mezilaurus sprucei.*

I tentatively place *Mezilaurus maguireana* in synonymy under *M. sprucei.* The type does not agree completely with the typical *M. sprucei*; the inflorescences are stiffer, the flowers have pedicels only 5 mm long, the reticulation is less raised on the upper leaf surface, and the leaf apices are less acuminate. These differences are only of degree and the few collections of *M. sprucei* at hand probably do not show the full range of variation in the species. In what I consider important characters (acute leaves, long petioles, glabrous, subumbellately arranged flowers, and connate filaments), *M. maguireana* agrees with *M. sprucei.*

I found that in old flowers the anthers become divergent, although the filaments remain connate.

Mezilaurus subcordata (Ducke) Kosterm., Meded. Bot. Mus. Herb. Rijks Univ. Utrecht 25: 40. 1936. *Silvia subcordata* Ducke, Arch. Jard. Bot. Rio de Janeiro 5: 115. 1930. TYPE: Brazil. Pará: dry upland forest of Jumanda River, *Ducke RB 19974* (holotype, RB; not seen; isotype, U). Figures 11, 12.

Medium-sized tree to 20 m. Twigs terete, with conspicuous leaf scars, the terminal bud densely and minutely appressed pubescent, this disappearing rapidly as twig matures. Leaves clustered near apices of branches, rarely few leaves persisting on older twigs, the leaves glabrous, coriaceous, slightly ovate or elliptic, ca. 15 × 7 cm, the base rounded, the apex obtuse; midrib, secondary veins (8–12 pairs), and ultimate reticulation slightly raised above, more prominently below; petioles 3–5 cm, rarely only 1 cm long. Inflorescences axillary near tips of twigs, pyramidal, rather laxly flowered, appressed tomentellous, 5–12 cm long; branchlets slender, distant, to 1.5 cm long, the flowers clustered near their tips. Bracts and bracteoles deciduous. Pedicels slender, tomentellous, 1–1.5 mm long. Flowers globose, puberulous, ca. 1.5 mm long. Tepals 6, equal, erect, ca. 0.6 mm long. Stamens 3; ca. 1 mm long; filaments ca. 0.7 mm, pubescent, connate; the 2-celled anthers exserted like small horns from the flower tube, glabrous; anther cells large, lateral-introrse, opening toward the tip. Ovary glabrous, ca. 1 mm long; style exserted, the stigma minute. Staminal glands and staminodia lacking. Fruit (fide Kostermans, 1938) ellipsoid, 2.5–3 cm long, 1.5 cm diam., subtended by a small, platelike cupule (4–5 mm diam.) with subpersistent tepals.

Additional specimens examined. PERU. MADRE DE DIOS: Tambopata, *Gentry et al. 46116, 45952* (MO).

Mezilaurus subcordata is collected rarely and known to me only from an isotype and two recent collections in Peru. Very possibly it is not a true disjunct—it may also occur in the intervening area, since a tree with green flowers 1.5 mm long can easily be overlooked. The Peruvian collections come from a tree plot in which every tree was sampled, regardless of whether it was fertile or not.

The description is based on the U isotype. The Peruvian specimens differ in having glabrous flowers and slightly thinner leaves. I find these differences too weak for recognition of a new taxon, but additional collections may show the Peruvian plants to be distinct.

Mezilaurus subcordata can be recognized readily by its long petioles and rounded leaf bases; it is also the only species in the genus with lateral-introrse anther cells.

Mezilaurus synandra (Mez) Kosterm., Meded. Bot. Mus. Herb. Rijks Univ. Utrecht 25: 40. 1936. *Silvia synandra* Mez, Feddes Repert. 16: 306. 1920. TYPE: Brazil. Amazonas: Manáos, dry upland forest near Pensados, *Ule 8835* (lectotype, B, fide Kostermans, not seen; isolectotype, L). Figures 13, A & B; 12.

Tree, to 15 m tall. Twigs terete, glabrous, often with conspicuous leaf scars, the terminal buds yellowish strigose-sericeous. Leaves clustered at tips of branches, glabrous, elliptic or slightly obovate, 8–20 × 4–10 cm, the base cuneate or acute, the tip rounded, lateral veins 10–15 pairs, ± immersed above, slightly raised below, the tertiary

FIGURE 11. *Mezilaurus subcordata.*—A. Habit.—B. Flower.

venation reticulate and slightly raised on both surfaces, the midvein raised below, triangular in diameter; petioles conspicuous, 3–5 cm long, glabrous, flat or with 2 narrow ridges on upper side. Inflorescences subterminal, much shorter than leaves, ca. 3 cm long, the flowers in small (4–5 flowered) clusters at the ends of few lateral branchlets, minutely strigose. Bracts and bractlets early deciduous, not seen. Flowers sparsely and minutely strigose, depressed globose, as wide as long or wider than long, the flower tube narrowed toward the tip (ca. 2 mm wide and 1.7 mm long on unpressed flowers). Tepals 6, equal, erect, scalelike, ca. 0.4 mm long, ca. 0.8 mm wide. Stamens 3, ca. 1.9 mm long, exserted, the anthers glabrous, 2-celled, the cells opening lateral-apically or apically; filaments connate, pubescent. Ovary pubescent, ca. 1–2 mm long; style ca. 0.3 mm long. Staminal glands and staminodia lacking. Fruit ovoid, ca. 2 cm long, 1 cm wide, subtended by a small, platelike cupule.

Additional specimens examined. BRAZIL. AMAZONAS: Manáos, Igarape da Cachoeira, Baixa do Tarumã, *Chagas s.n. = MG 21.108* (NY); Manáos, Parque 10 de Novembre, *Coelho s.n. = INPA 3934* (NY); Manáos, Pensador, *Ducke 233* (F, NY), *Ducke 233, second collection* (US); Manáos, *Ducke RB 23964* (G, US); Manáos, Pensador, *Ducke RB 25092* (US); Manáos, Cachoeira, Alta do Tarumã, *Rodrigues & Lima 3047* (NY). Reported by Béguin et al. (1985) from the Arborétum Jenaro Herrera, Loreto, Peru.

FIGURE 12. Distribution of *Mezilaurus opaca* (●), *M. subcordata* (▼), *M. synandra* (■), and *M. thoroflora* (●).

Mezilaurus synandra is only known from dry, low forest on terra firme, near Manaus and one collection in Peru. Several collections indicate that it occurs in secondary vegetation. When flowering, *M. synandra* can be recognized easily by its short inflorescences and broad, depressed-globose flowers, which otherwise occur only in *M. opaca.* Fruiting or sterile collections are rather similar to *M. itauba,* which has, however, a larger inflorescence, generally smaller leaves, and the upper leaf surface dull, not shiny, with less prominently raised reticulation.

Mezilaurus thoroflora van der Werff, nom. nov. Basionym: *Licaria maguireana* Allen, Bull. Torrey Bot. Club 75: 315. 1948. *Misanteca maguireana* (Allen) Lundell, Wrightia 4: 100. 1969. *Clinostemon maguireanum* (Allen) Kurz, J. Arnold Arbor. 60: 520. 1979. TYPE: Guyana: Mazaruni Station, *Forestry Dept. Brit. Guiana 2956* (*F220*) (holotype, NY; isotype, K). Figures 13, C & D; 12.

Tree, ca. 25 m tall. Twigs thick, terete, the tip densely and minutely appressed pubescent, be-

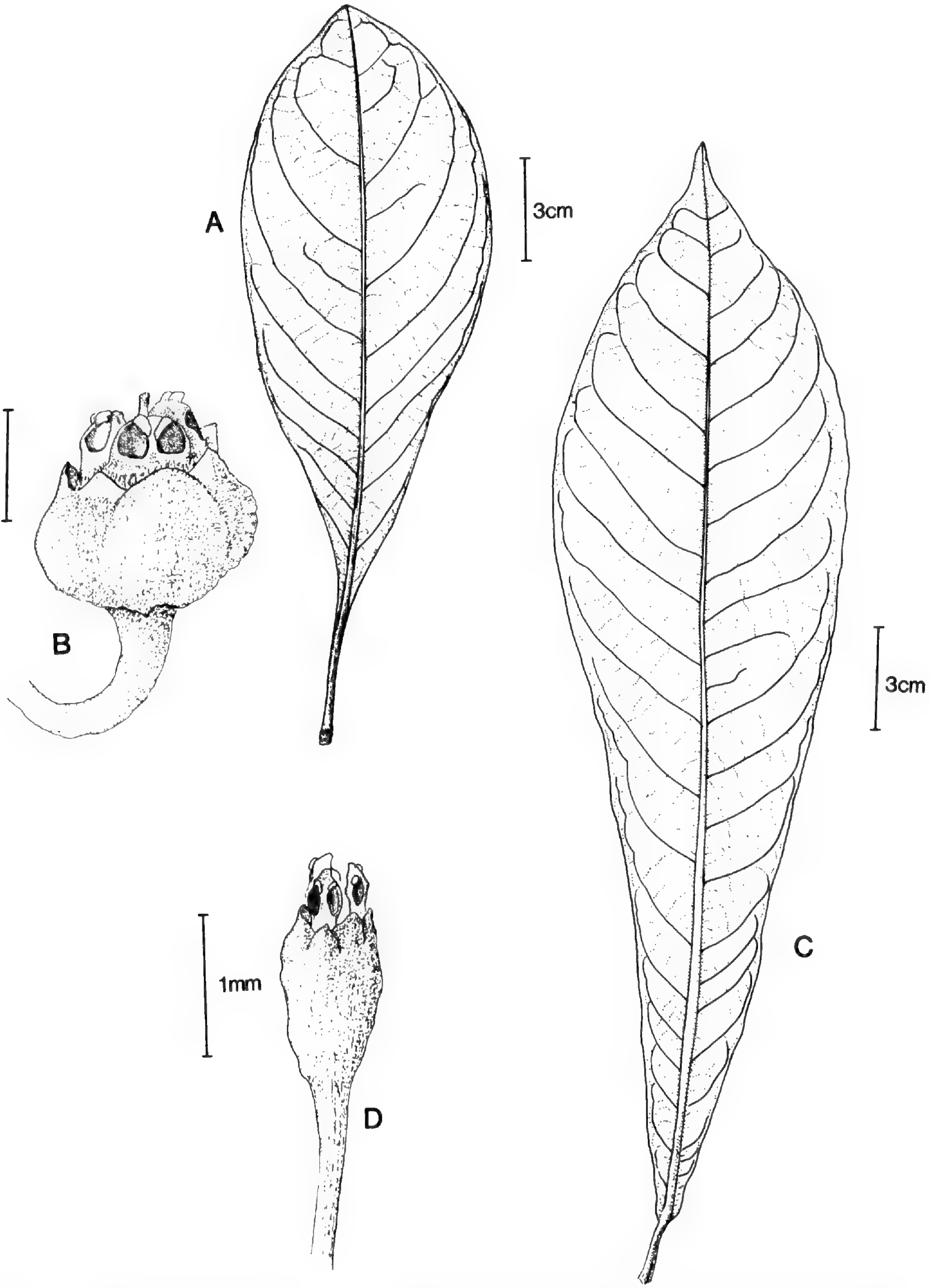

FIGURE 13. A—B. *Mezilaurus synandra.*—A. Leaf.—B. Flower. C–D. *M. thoroflora.*—C. Leaf.—D. Flower.

coming glabrous with age. Terminal bud yellowish pubescent. Leaves clustered at the tips of branches, coriaceous, obovate, gradually narrowed toward base, the base abruptly rounded, the apex acute or shortly acuminate, 30–60 × 12–18 cm, pinnately veined, 15–25 pairs of lateral veins, these immersed above, but elevated below. Midrib thick, ca. 7 mm wide, raised on both surfaces. Tertiary venation not visible above, but raised below. Lamina glabrous above, except along midrib, sparsely appressed pubescent below, especially near the base and along midrib. Inflorescences in axils of aborted leaves, subterminal, appressed gray-pubescent when young, with few hairs at anthesis, 30–50 cm long, lateral branchlets 2–3 cm long over the entire length of cylindrical inflorescence, these with scattered hairs, bracts and bractlets, strigose, persisting at anthesis. Flowers clustered toward the tips of branchlets, glabrous, ellipsoid, ca. 1.5 mm long, 1 mm wide, the anthers ca. 0.5 mm exserted, pedicels 4–8 mm long. Tepals 6, equal, erect, scalelike. Fertile stamens 3, ca. 1 mm long, the filaments free, pubescent, ca. 0.5 mm long, the 2-celled anthers glabrous, exserted, the large cells extrorse and opening apically. Ovary glabrous, ellipsoid, ca. 0.8 mm long, abruptly narrowed into the equally long style. Staminodia 9, pubescent, the outer six slightly sagittate, the inner three lanceolate. Infructescence ca. 60 cm long, the fruit ellipsoid, ca. 1.7 × 1 cm, subtended by a thin platelike cupule, ca. 0.6 cm diam.

Paratype. Guyana, Mazaruni Station, *Forest Dept. Brit. Guiana 2704* (K).

Mezilaurus thoroflora is known only from a few collections in Guyana. Diagnostic for this species are the long-pedicelled flowers, the large exserted anthers, and the uniform, short, lateral branchlets of the inflorescence. Vegetatively, *M. thoroflora* closely resembles *M. pyriflora,* which has leaves with long and narrow basal parts; they rather abruptly widen at the middle of the lamina, not gradually as in *M. thoroflora.*

The illustration in Kubitzki et al. (1979) of *M. thoroflora* (as *Clinostemon maguireanum*) is not representative of material I have seen. The two collections from the Forest Department of British Guiana do not have such pronounced cordate leaf bases and do not have the lower branchlets of the inflorescences much longer than the upper ones, as shown in Kubitzki et al. (1979).

Kostermans (1938) cited two collections (*Monteiro Costa 323, Kaufmann 605,* both in F) under *M. lindaviana.* In my opinion these specimens belong to *M. thoroflora* or are very close to it. They have considerably smaller leaves than the type of *M. thoroflora,* but leaf shape is quite similar. *Monteiro Costa 323,* a flowering specimen, shows exserted anthers and staminodia, and this clearly indicates *M. thoroflora.* Pedicels are shorter and leaves smaller than in *M. thoroflora,* but it is likely that the few available collections do not show the full range of vegetative variation.

Because the combination *Mezilaurus maguireana* already exists, it was necessary to create a new epithet for *Licaria maguireana.* The new epithet *thoroflora* is derived from the Greek "thoros," semen, and "flos," flower, in reference to resemblance between the small, long-pedicelled flowers and spermatozoa.

IMPERFECTLY KNOWN SPECIES

Mezilaurus sp. A.

A collection made by J. da Silva Costa (*RB 180796*) in the State Mato Grosso, Brazil, probably represents an undescribed species. The locality data suggest it was collected in cerrado vegetation as a 9 m tree. The most distinguishing characters are found in the leaves, which are densely gland-dotted on the upper surface, chartaceous, and have a few appressed hairs on the lower surface. The young flower buds are glabrous. This is clearly not the other cerrado species, *M. crassiramea,* which has pubescent leaves, and the gland-dotted upper leaf surface has not been found in other *Mezilaurus* species. I prefer to wait with a formal description until flowering material is available.

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Cover illustration. *Peperomia gentryi* Steyermark.

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VASCULAR EPIPHYTISM: TAXONOMIC PARTICIPATION AND ADAPTIVE DIVERSITY[1]

DAVID H. BENZING[2]

ABSTRACT

Vascular epiphytes share few qualities beyond occurrence in tree crowns that identify them as a single ecological type, primarily because their phylogenetic origins and life styles in forest canopies are diverse. Mineral ion procurement by epiphytes is sometimes novel, often requiring trophic mutualism and unusual substrata. Patterns of moisture and nutrient use are, on the whole, not unlike those of terrestrials native to comparably arid or infertile sites. Moisture supply, more than any other feature, determines where a particular type of epiphyte will survive. Epiphytes constitute about 10% of all vascular species; the group is dominated by higher ferns and relatively few angiosperm taxa. Factors that probably predisposed ancestors of such modern clades as ferns, bromeliads, and orchids for epiphytism are identified. Reasons for the disproportional representation of certain dicot families in tree crowns are less clear, but some possibilities are offered. Constraints centered on water relations and, indirectly, mineral nutrition may explain why epiphytism has rarely, if ever, preceded branch parasitism.

EPIPHYTISM: DEFINITION AND BREADTH

Epiphytes are plants that spend much or all of their lives attached to other plants. Qualifying forms range from microbes to angiosperms; both aquatic and terrestrial vegetation provide mechanical support. Interaction with phorophytes can range from incidental to physiologically intimate; primarily rain-fed "atmospheric" bromeliads and orchids (Figs. 3, 4) are anchored by a few roots (sometimes only one), whereas contact is almost complete for the largely endophytic dwarf mistletoes. (The designation "epiphyte" is here reserved for free-living vascular species; it does not include hemiparasites.) This report has two purposes: to describe taxonomic participation in epiphytism and to explore the extraordinary proliferation in arboreal habitats by some families and higher taxa. First, epiphytes are examined in terms of basic characteristics and important biological distinctions.

Plants considered to represent a specific ecological category usually share key qualities that

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ANN. MISSOURI BOT. GARD. 74: 183–204. 1987.

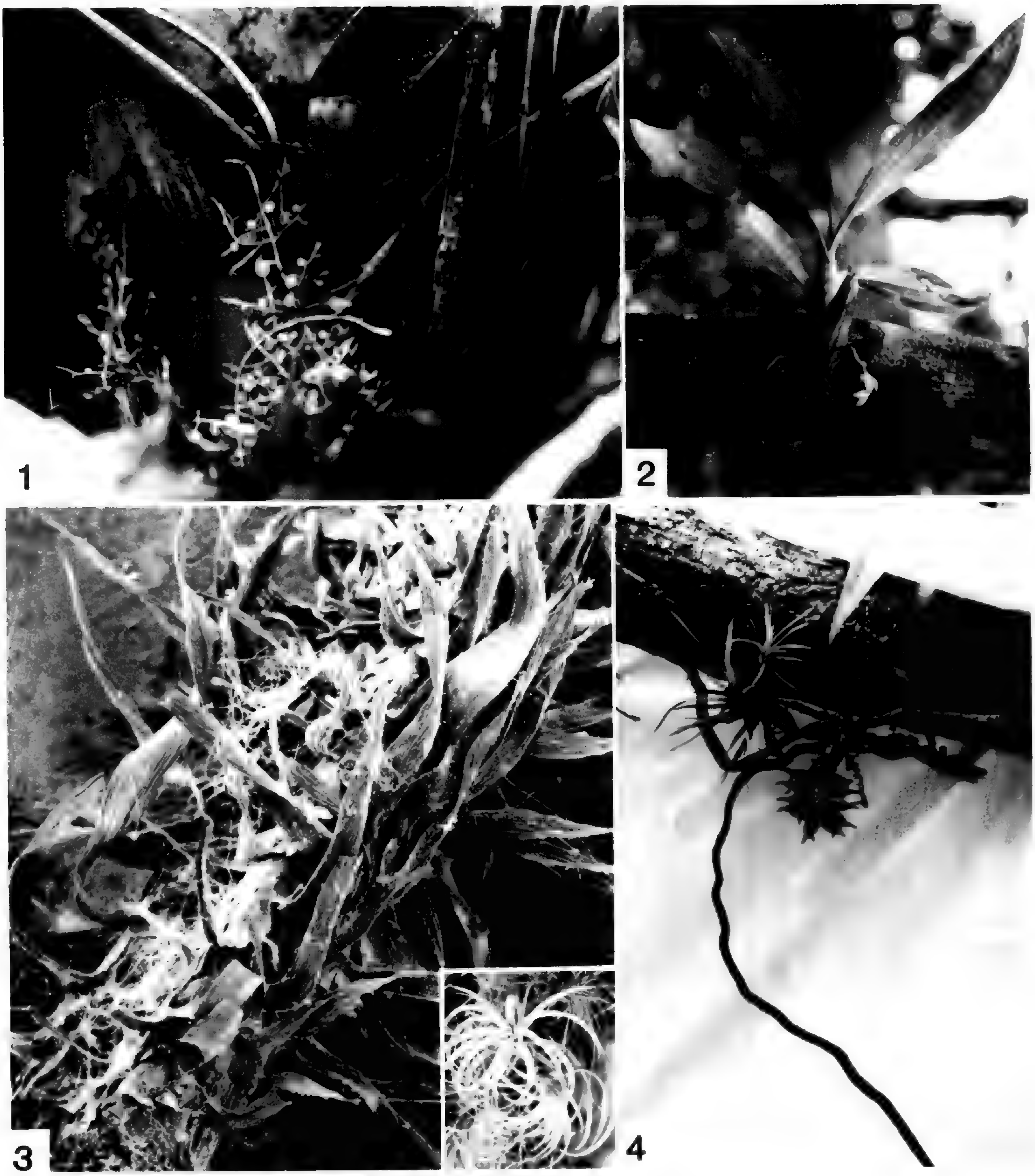
set them apart from other vegetation. Occurrence on the same general type of substratum and, more importantly, utilization of comparable resource bases by similar mechanisms require considerable, often conspicuous, convergence. All botanical carnivores possess traps designed to attract and process fauna for food; all lianas feature slender habit and novel vascular anatomy; all vernal ephemerals from temperate deciduous forests generate simplified shoots bearing heliophilic, short-lived foliage. In contrast, anchorage in tree crowns—sometimes even inability to survive terrestrially—exhibited by so many of the approximately 25,000 epiphytic species appears to have little unifying basis. No growth form, seed type, identity of pollen vector, water/carbon balance regimen, source of nutrient ions, nor resource procurement mode is shared by all mechanically-dependent species. Moreover, characteristics of epiphytic and soil-based flora overlap broadly, as do important aspects of their habitats.

Growing conditions for epiphytes, as indicated by rooting media, microclimate, and stability and dispersion of substrata, are diverse and similar to those for much terrestrial vegetation. Like soils, which range from equable to dry and infertile, canopies of everwet to microphyllous to cactus forests impose mild to severe stress on resident flora. Problems of anchorage and dispersal in tree crowns are probably similar to those experienced by cliff dwellers and plants native to other precipitous sites. A naked bark surface must complicate water and mineral balance just as do thin soils and rock faces. At the other extreme, however, the everwet forest's rotting trunks or branches (Fig. 2), debris-filled knotholes, and ant nests (Fig. 7) probably offer to certain humiphilous epiphytes resources equal to those available at humid, fertile, terrestrial sites. In effect, heterogeneity and similarity to other habitats complicate definition of the epiphytic biotope and thwart attempts to understand why tree crowns offer the only recourse to such a variety of vascular plants. From another vantage point, canopy-dependent species seem to be no more versatile than soil-rooted plants; most will survive only under narrowly proscribed circumstances (e.g., rigid confinement to twigs rather than larger axes, humus as opposed to "unconditioned" bark, dark instead of better-illuminated sites).

Many taxonomies have been formulated to classify mechanical dependence. Criteria most often used are extent of arboreal presence (facultative vs. obligate forms), nature of dependency on supporting vegetation (mistletoes vs. epiphytes), exposure requirement (heliophiles vs. sciophytes), habit (e.g., tank forms, myrmecophytes), and type of substratum (e.g., humiphobes, ant-nest forms). A further criterion recognizes two types in a special group that normally taps soil part of the time—the hemiepiphytes. Primary hemiepiphytes, a group which includes stranglers, begin life on bark and later produce soil roots; secondary hemiepiphytes (Fig. 11) germinate on the ground and then become canopy-dependent as older roots and basal stems of vining shoots decay. Features more directly reflecting peculiarities of vegetative function associated with epiphytic life (e.g., presence of absorptive trichomes, carbon fixation pathway) have not generally been employed to distinguish epiphytic vegetation despite their utility for explaining type of microsite and how existence in that kind of space is sustained.

One criterion above all others may prove meaningful to those concerned with the mechanics of epiphytism: temporal access to moisture. While adequate mineral nutrition and exposure are no less critical than are suitable water relations to long-term survival of an epiphyte, avoiding drought injury is the more immediate challenge. Constant adjustment to rapidly changing moisture supply must be accomplished via appropriate stomatal and photosynthetic responses. There are just two types in this new taxonomy: continuously-supplied (CS) and pulse-supplied (PS) forms. Moisture supplies are steady for CS species tapping deep, absorbent media (Figs. 2, 5) or catchments created by the plant itself (Figs. 8, 9). The most self-contained members of the canopy-dependent flora (PS epiphytes) draw water from relatively nonabsorbent substrata or other sources subject to quick drying (Figs. 3, 4).

Epiphyte life history has been influenced by many selective forces, including substratum distribution and stability. Patchiness in the epiphytic biotope ranges from gross patterns due to hyperdispersion of tropical-forest trees to finer-grained discontinuity in the scattered arrays of suitable bark within individual hosting crowns. Mortality continues to be high during and following seedling establishment. Disturbance is lethal when supporting bark fragments exfoliate, inhabited twigs fall, infested trees collapse, and (less common but broader in extent) natural dis-



FIGURES 1–4.—1. Partially dissected shoot of the bromeliad *Brocchinia tatei* on Cerro Neblina, Venezuela, exposing rhizomes bearing traps of *Utricularia humboldtii*, a tank bromeliad endemic.—2. Young specimen of *Catasetum* sp. rooting in a rotting branch in Amazonas, Venezuela.—3. Scanning electron micrograph of the indumentum of *Tillandsia tectorum*, an atmospheric bromeliad. Inset illustrates habit.—4. Fruiting specimen of *Campylocentrum pachyrrhizum* and two small bromeliads growing on a small branch in south Florida.

asters ravage whole communities. Effective patch life (patch duration relative to the interval needed for a resident plant to reproduce) must be especially short for a multitude of epiphytes whose fecundity is limited by drought and poor nutrient sources. It is this group that possesses an unusual combination of stress and r-selected characters (Benzing, 1978). In contrast, CS species, with their relatively regular resource supplies, should exhibit less emphasis on shortening the life cycle and channeling scarce commodities into reproductive rather than vegetative tissue.

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Adaptive Variety in Canopy Dependents

Some adjustments to conditions in tree crowns are predictable and obvious—viz. capacities for aerial dispersal and holdfast—but others are more cryptic and varied. Depending on taxon and habitat, epiphytes exhibit various mechanisms for carbon fixation and procurement of moisture and nutrients. Essential elements are drawn from remarkably diverse sources, including several not normally available to plants. A survey in some Indian forests (Sengupta et al., 1981) revealed greater nitrogenase activity in the phyllosphere of epiphytes than of terrestrials, including hosting trees. Impoundments built of roots or shoots provide access to nutrients via intercepted canopy fluids and litter (Figs. 8, 9) and the necessary detritivores and saprophytes these catchments attract (Benzing, 1986a). Carnivory is rare in the epiphyte synusia (Fig. 1), while trophic myrmecophily (Fig. 12) is common and may, in fact, be entirely restricted to canopy habitats (Thompson, 1981; Givnish et al., 1984). Where substrata are deeply penetrable and moist, absorptive organs and nutrient supplies are more conventional. It is not known whether epiphytes possess special permeabilities to match the character of the media (organic and acidic) they so often exploit.

Water/carbon balance is also assured by considerable mechanistic variety. At one extreme, some canopy-dependent pteridophytes alternate between wet-active and dry-inactive states as microclimate dictates. Quite the opposite, impoundments provide continuous drought relief for hundreds of species of bromeliads (Fig. 8), fewer orchids, some other monocots (Fig. 9), and ferns. Turnover of the entire leaf surface cued by impending seasonal drought is exemplified by members of several orchid genera (Fig. 2). Crassulacean acid metabolism (CAM) may be better represented in the forest canopy than in any other habitat type; stable carbon and hydrogen isotope data as well as more direct measurements of fixation pathway indicate that every known variation on this mechanism exists in epiphyte flora. Occasional subjects—the shootless orchids, for instance—exhibit novel machinery for gas exchange (Cockburn et al., 1985). Unusual osmotic qualities and related stomatal sensitivities appear to rank among the most unique of the functional peculiarities of epiphytism (Benzing, 1986a). Survival is often predicated on extensive storage capacity, economical water use, and ability to rebound rapidly from drought-imposed stress. Water balance is aided by special absorptive tissues that prolong contact with transitory fluids via mini-impoundment (e.g., the velamen of orchid roots; Fig. 10; Benzing & Pridgeon, 1983). Like other stress-tolerant plants, PS epiphytes grow slowly, a characteristic which moderates resource requirements but heightens vulnerability to habitat patchiness, disturbance, and other phenomena that oblige heightened fecundity.

Habits of epiphytes are often specialized in ways other than those associated with impoundment and myrmecophily. Abbreviation and merger of functions is common in the especially xerophytic forms, particularly the PS epiphytes; the most spectacular reductions occur in Bromeliaceae and Orchidaceae (Benzing & Ott, 1981). Within *Tillandsia/Vriesea,* root development has been almost completely suppressed and paralleled by complementary shoot modification. Just about every intermediate condition between profuse and very sparse rooting exists throughout the complex of more than 500 species. Corresponding shoot changes center on a progressively diminished impoundment capacity and an indumentum elaborated to the point where, among atmospheric forms, absorbent trichomes densely cover all foliar and most stem surfaces (Fig. 3). At this stage of specialization, no other organs are needed for uptake function. Orchidaceae (subtribe Sarcanthinae) exhibit a comparable progression except that here a telescoped, leafless shoot now supports production of green roots and the periodic axillary scape (Fig. 4).

The loss of axial differentiation seen exclusively in PS epiphytes may not be coincidental. Species that grow attached to impenetrable media or hang free in the atmosphere occupy habitats as uniform as those colonized by prevas-

←

Figures 5–8.—5. A mixed colony of angiospermous epiphytes rooted in deep humus on a palm on Cerro Neblina, Venezuela.—6. A dense growth of bryophytes supporting shade-tolerant hymenophyllaceous ferns at the base of a tree in undisturbed lowland rain forest in Amazonas, Venezuela.—7. Seedlings of epiphytes rooted in ant-nest carton in lowland Venezuelan rain forest.—8. *Tillandsia utriculata,* a tank bromeliad, in south Florida.

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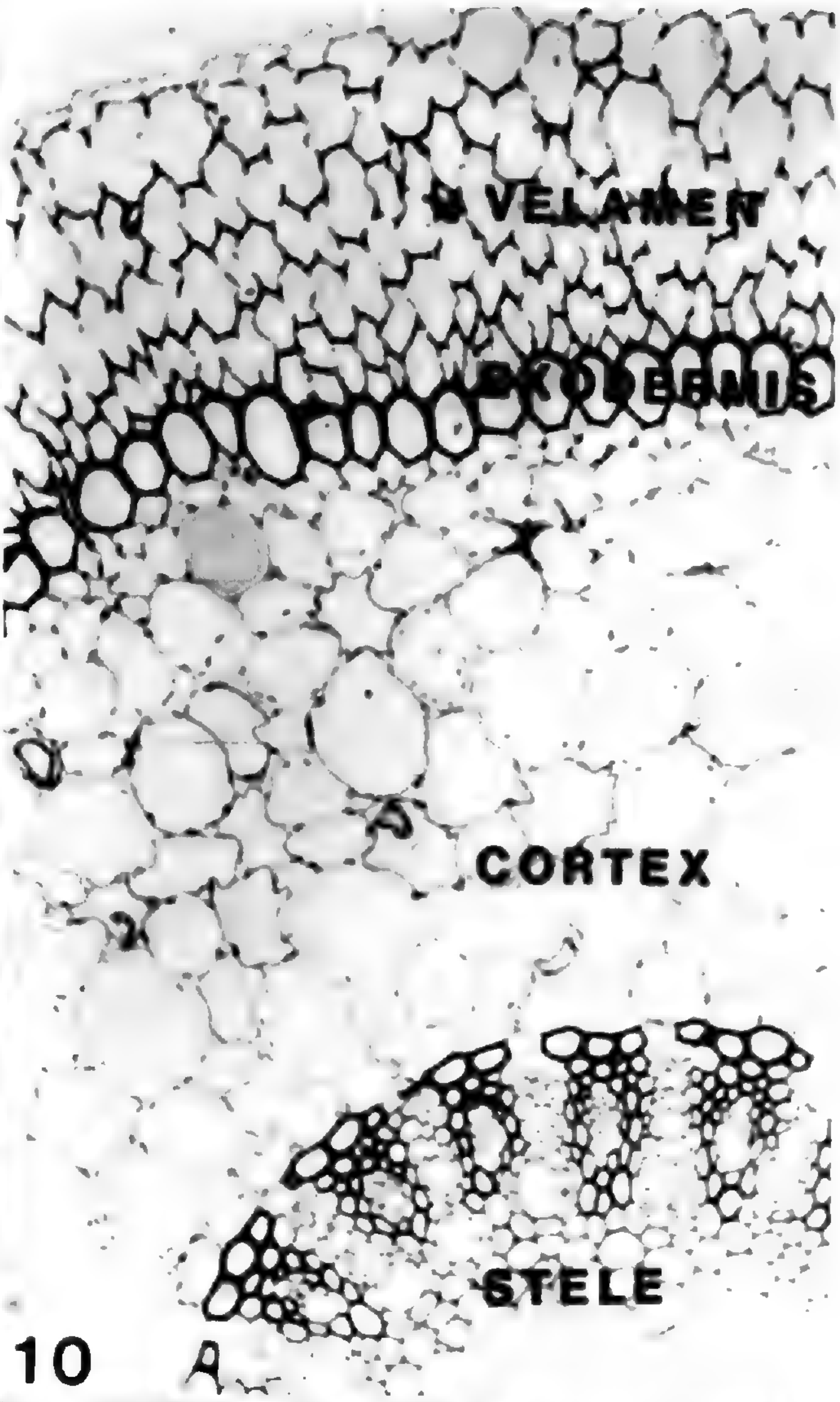

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cular plants or modern aquatics. In such an environment, PS epiphytes need not maintain the division of labor between shoot and root that would be required for life on soil and, in fact, may sacrifice fitness by retaining a body plan inherited from terrestrial ancestors. Material and energy economy accompanying amalgamation of vegetative function in a single organ system while other parts are lost may promote fitness where stress and high mortality place a premium on fecundity. Complex functional tradeoffs obliged by extreme habit reduction in Bromeliaceae and Orchidaceae have been described elsewhere (Benzing & Ott, 1981; Benzing et al., 1983). Somewhat less spectacular abbreviations leading to single-leaf ramets parallel increased exposure and stress tolerance in additional, predominantly epiphytic, orchid lines (e.g., *Dendrobium, Epidendrum*).

Although extensive studies have been made of orchid pollination, seed germination, and seedling nutrition, and some work has been done on mistletoes (e.g., Bernhardt, 1983), bromeliads (Smith & Downs, 1974), and a few other epiphytes, life history characteristics of canopy-dependent vegetation as a whole remain obscure. What data are available indicate that nonuniformity is the rule once again. An exception is the usual pattern of extended iteroparity; only a few *Tillandsia* and *Vriesea* species flower just once. Pollinators include all the common vectors except wind. Because air turbulence is adequate to disperse most epiphyte seeds despite their greater mass compared with pollen, absence of wind pollination must relate to other factors, most likely to the expense of required reproductive material or hyperdispersion of populations. Syndromes featuring specialized animals or unusual foraging activities are more common here than in other tropical synusiae. Breeding systems vary from those obliging strict outcrossing via trapliners to autogamy. Some minor patterns may be emerging, however. Orchids seem to be predominantly allogamous, while many ant-nest inhabitants and Marcgraviaceae are selfers (Gentry & Dodson, 1987). The widely-held view that, on average, epiphyte populations are more fragmented than those of terrestrials and hence subject to special genetic structuring and propensity for cladogenesis needs to be verified. If they are not, neither a uniform nor unique reproductive pattern should be expected.

Seed is dispersed by various agencies. Among families, the vectors are most often animals (via fleshy fruits), but when species are counted, anemochory ranks first owing to the immensity of the Orchidaceae. Among wind-borne species (more than 80% of the total), seeds bearing elaborate appendages are uncommon. Attempts to relate seed form and mass to mobility in aerial habitats can be complicated because disparate agents sometimes provide service for the same species. *Dischidia* seeds bear a plumose coma but also an oily eliasome to attract ants (short-range vectors; Docters van Leeuwen, 1954). Nest-inhabiting *Codonanthe* has a fleshy berry containing myrmecochorous seeds. Other subtleties of epiphytic reproduction are just as easily overlooked—one flat side on otherwise fusiform *Hydnophytum* seeds reduces vulnerability to dislodgement by stemflow (pers. obs.). Seed size differential between terrestrial and epiphytic relatives is not consistent. Madison (1977) reported more massive seeds in soil-based compared with canopy-based Araceae and Cactaceae, but epiphytic gesneriads definitely do not produce lighter seeds than do numerous terrestrial relatives (H. Wiehler, pers. comm.). Surprisingly, microsperms of terrestrial orchids are more buoyant than those of test epiphytes (Stoutamire, 1974). Rockwood's survey (1985) of 365 species in eight families from diverse communities in Costa Rica, Panama, and Peru yielded additional, unexpected results. Average seed mass of 59 epiphytes (orchids excluded) was lighter than that of tree seeds but heavier than that of terrestrial herbs and shrubs.

Table 1 tabulates angiosperm families containing more than 50 epiphytic species and lists characteristics that contribute to their success in tree crowns. Figure 13 summarizes adaptive diversity within free-living, canopy-dependent, vascular flora relative to local moisture supply. Species with character states assigned to the far

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FIGURES 9–12.—9. A "trash basket" *Anthurium* in lowland rain forest in Amazonas, Venezuela.—10. Cross section through the root of *Epidendrum radicans* illustrating the major tissues, ×250.—11. Hemiepiphytic aroid in rain forest at Río Palenque, Ecuador.—12. *Hydnophytum formicarium* illustrating ant-accommodating cavities within the swollen hypocotyl.

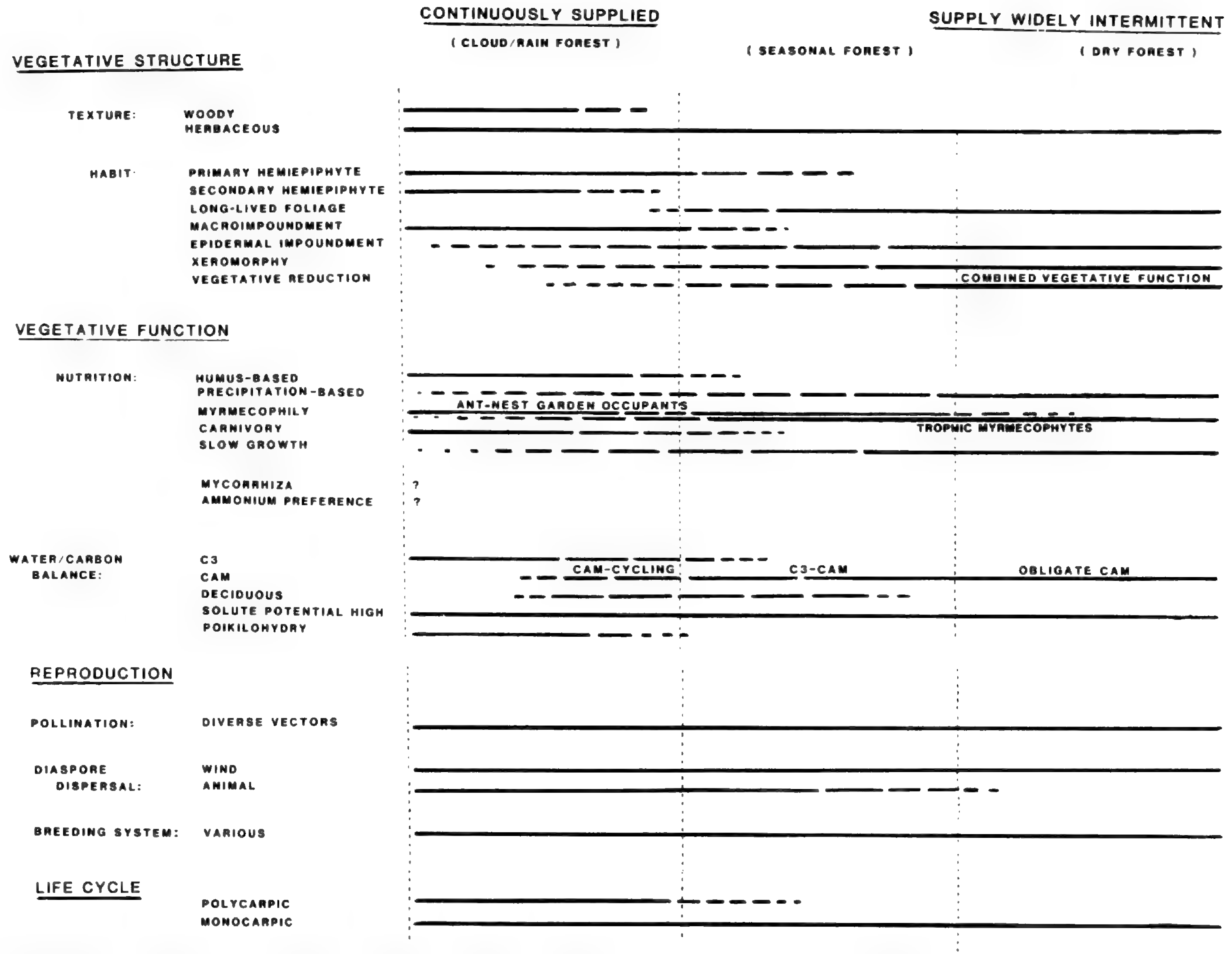

FIGURE 13. Occurrence of character states of vascular epiphytes according to moisture availability in microhabitats. See text for details.

right of the grid (indicated by lines) are usually PS types. Those on the extreme left experience continuous supply punctuated only by the uncommon, normally brief, drought. Epiphytes bearing character states assigned predominantly to the left or right of Figure 13 can occur together. Pulse-supplied and CS forms inhabit humid sites, although only PS epiphytes occupy tree crowns in drier locations. Twig and free-hanging "mist" types in rain forests, for instance, receive moisture and nutrients exclusively via periodic flow, so their supply is intermittent. A nearby tank or humus epiphyte experiences considerably less discontinuity between rain events. Species situated on highly exposed sites in humid forests or on most anchorages in arid woodlands exhibit slow growth, long-lived photosynthetic organs, and foliar or root surfaces modified to prolong contact with passing fluids (i.e., thick velamina or absorbing trichomes). Vegetative bodies are often much abbreviated, another means of improving economy. Woodiness seems to be sustainable only where moisture is abundant.

Features associated with regular resource supply are diverse. Hemiepiphytes are continuously supplied, at least while rooted in soil; habits may be woody or herbaceous. Nutrient ions are drawn from various types of humus by roots and absorptive leaves of various CS forms. Carnivory is possible for the tank former. Ant-nest gardens are scarcer in the drier forests, but trophic myrmecophily is widely available. Too little is known about mycorrhizae and nitrogen nutrition in the mechanically-dependent synusia to posit their incidence in Figure 13, although humidity promotes microbial activity elsewhere. The C_3 photosynthetic pathway, first supplemented with CAM-cycling and then ever greater reliance on nocturnal fixation, seems to play a diminishing role from left to right. Precise ordering of CAM variations in Figure 13 and the proposed significance of CAM-cycling as a mechanism that "poises" the plant for drought (Ting, 1985) should be considered provisional at this time. Poikilohydry is feasible only on relatively humid sites for reasons described below. Deciduousness (e.g., *Catasetum*; Fig. 2) occupies an intermediate position, occurring where drought is predictable (seasonal) and not too severe. High solute potential has been documented among CS and PS epiphytes (Harris, 1918; Spanner, 1939; Sinclair, 1983) although its effect on stomatal sensitivity has not been examined extensively. Vegetative features seem to have no bearing on type of pollinator used. Dispersal syndromes correlate only weakly with habitat humidity or resource procurement mechanisms. Anemochory is found everywhere, but a pulse-supplied nature increases the probability that an angiosperm will be wind-dispersed. Propagules that pass safely through a bird's gut are generally larger (more expensive) than the smaller anemochores, a relationship that may help explain why wind-dispersed *Tillandsia* and Orchidaceae dominate the most stressful epiphytic habitats. Without small seeds, low productivity would probably result in low generative capacity for the PS epiphyte. The few monocarpic bromeliads are relatively well-provisioned impounders rather than stress-tolerant atmospherics; the latter's resource procurement capability is probably inadequate to support semelparity (Benzing & Davidson, 1979).

In summary, epiphytes engage in a broadly similar rather than a narrowly proscribed way of life. Many other ecological groups are better defined because members subjected to less varied environmental constraints conform to more coherent adaptive syndromes. Inconsistency in the epiphyte synusia is a function of habitat breadth (numerous possibilities for adaptive specialization) and the multiple phylogenetic origins of tree crown occupants. More than one character combination can be associated with specific types of rooting media and climates, and no single key feature or suite of features is evident. Vegetative phenomena that seem to be proportionately better represented in canopy- than in soil-dependent floras include various types of nutritional symbioses, creation of soil substitutes, slow growth, evergreenness, CAM, special absorptive tissues, and abbreviated habits. Most specialized of the epiphytes are the PS species because they are most vulnerable to drought and substratum patchiness and disturbance. Modes of pollen and seed conveyance are also various among epiphytic plants, with few, if any, characters unique to these taxa. Indeed, most features of canopy-dependent plants occur among terrestrial flora as well, although not necessarily in the same combinations.

SYSTEMATIC OCCURRENCE AND THE MULTIPLE ORIGINS OF EPIPHYTISM

Approximately 10% of all vascular plant species are at least occasionally epiphytic, but distribution among higher taxa is uneven (Gentry & Dodson, 1987). Broad involvement is particu-

TABLE 1. Preliminary tabulation of predominantly vegetative features underlying the epiphytic habit in angiospermous families containing more than 50 canopy-dependent species. Common and less frequent strategies for canopy life are also included.

Group or Family	Habitat Humidity	Most Pervasive Adaptive Features	Less Pervasive Adaptive Features	Common Ecological Types	Minority Ecological Types
Ferns	Wet to moderately dry	Dust-size propagules; poikilohydrous tendency; shade tolerance; diverse habits	Macroimpoundment: brood chambers for ants; CAM; pronounced resurrection capacity; absorbing foliar trichomes	General humus-rooted, sciophytic epiphytes	Trophic myrmecophytes: resurrection forms; drought-enduring, CAM forms, trash-basket epiphytes
Araceae	Wet	Vining habit; macroimpoundment; microimpoundment (velamen); plastic foliar form	Deciduousness	Secondary hemiepiphytes; trash-basket and general humus-rooted epiphytes	Nest-garden epiphytes
Bromeliaceae	Wet to dry	Macroimpoundment; microimpoundment (foliar trichomes); CAM; vegetative reduction; xeromorphy	Carnivory; brood chambers for ants; deciduousness	Tank epiphytes; PS epiphytes (atmospherics)	Nest-garden and general humus-rooted epiphytes; trophic myrmecophytes; drought avoiders
Orchidaceae	Wet to dry	Microimpoundment (velamen); CAM; vegetative reduction; microsperms; xeromorphy; fungus-assisted juvenile nutrition; mycorrhizae (?); diverse habits	Macroimpoundment; brood chambers for ants; deciduousness	General humus-rooted epiphytes; PS epiphytes (drought-enduring CAM forms)	Trophic myrmecophytes; nest-garden epiphytes; drought avoiders
Araliaceae	Wet	Versatile root growth and function		Woody hemiepiphytes	General humus-rooted, shrubby epiphytes
Asclepiadaceae	Wet	Vining habit; CAM; xeromorphy; various ant associations		Vining, often humus-rooted epiphytes	Trophic myrmecophytes
Cactaceae	Wet to dry	CAM; xeromorphy		Secondary hemiepiphytes; general humus-rooted epiphytes	
Clusiaceae	Wet	Versatile root growth and function	CAM; xeromorphy	Woody, primary hemiepiphytism, occasionally stranglers	General humus-rooted, shrubby epiphytes

TABLE 1. Continued.

Group or Family	Habitat Humidity	Most Pervasive Adaptive Features	Less Pervasive Adaptive Features	Common Ecological Types	Minority Ecological Types
Ericaceae	Wet	Mycorrhizae (?); preference for acid, organic, oligotrophic substrata (?)		General humus-rooted, shrubby epiphytes	
Gesneriaceae	Wet to moderately dry	CAM; xeromorphy; various ant associations; diverse habits		General humus-rooted epiphytes	Ant-nest epiphytes
Marcgraviaceae	Wet	Vining habit; plastic foliar form		Secondary hemiepiphytism	
Melastomataceae	Wet	Preference for acid, organic, oligotrophic substrata (?)		General humus-rooted, shrubby epiphytes	Hemiepiphytes
Moraceae	Wet to moderately dry	Versatile root growth and function; strangling habit		Stranglers	
Piperaceae	Wet	CAM; xeromorphy; small size		General humus-rooted epiphytes	
Rubiaceae	Wet	CAM; xeromorphy; brood chambers for ants		Myrmecophytes; humus-rooted epiphytes	

larly apparent at the higher taxonomic levels. Fully 44% of all vascular plant orders and 16% of families (sensu Cronquist, 1968) contain one or more tree-crown populations. Arboreal monocots far outnumber dicots, even exceeding Filiopsida (44 vs. 27%) for proportional occurrence in forest canopies. Of the two large lycopod genera, *Lycopodium* is about one-third epiphytic (143 spp.) while *Selaginella*—a considerably larger, heterosporous group—contains only five such species (Beitel, 1979). A majority of Psilotophyta regularly inhabit tree crowns. Gymnosperms, on the other hand, are largely confined to soil, in part no doubt because of their heavy seeds and costly wind pollination. Orchidaceae have been more successful than any other lineage in canopy habitats. Two out of three epiphyte species are orchids; about 70% of the family is canopy-dependent. Two other large monocot groups with a pronounced epiphytic bias are Araceae, especially *Anthurium, Philodendron,* and *Rhaphidophora,* and Bromeliaceae, more than half of which anchor on bark. Canopy-dwelling dicots are disproportionally represented by Cactaceae, Ericaceae, Gesneriaceae, Melastomataceae, Moraceae, Piperaceae (specifically *Peperomia*), and Rubiaceae. Versatility within participating clades is not consistent. Component taxa may be diverse or uniform in the mechanisms that foster habitation in tree crowns (Table 1).

In all, about 80 vascular families contain at least one canopy-dependent member, but there are conspicuous, occasionally puzzling, omissions. Some very large, ecologically diverse groups with numerous tropical members are little represented in, or even absent from, canopy floras. Leguminosae may be constrained by fruit and seed types that offer little potential for aerial dispersal. Poaceae (and all Cyperales) may be almost entirely terrestrial owing to consistent wind pollination and the graminoid habit, which does not lend itself to evergreen drought endurance. Plausible reasons for the paucity of epiphytes within the immense Asteraceae are not so obvious; both CAM-assisted xerophytism and wind-dispersed seeds are well developed in parts of this family. These exceptions notwithstanding, angiospermous epiphytes are concentrated in the more advanced taxa. The same is true of ferns, but again, there are exceptions. Two members of the primitive order Ophioglossales root in humus impounded by persistent palm leaf bases and *Platycerium* fronds. If *Psilotum* and *Tmesipteris* of the bigeneric Psilotophyta are indeed sole remnants of the Silurian/Devonian psilophyte complex, epiphytism is possible for the most primitive vascular relics.

Epiphytism has probably evolved independently from terrestrial stock in every participating family of seed plants and most families of ferns. It has arisen more than once in most of those spermatophyte taxa containing canopy-dependent species on different continents (Gentry & Dodson, 1987), indicating that propensity for arboreal life is rather fundamental in some major clades. Most diverse of the epiphyte types, phylogenetically speaking, are the humiphiles whose drought liability obliges access to moist organic debris such as that covering older bark exposures in everwet forests. Virtually every family containing epiphytes includes at least one such species; most contain no other type. Where more exacting conditions (e.g., exposed bark and twig surfaces) prevail, few families are represented, although these are sometimes speciose (Benzing, 1978). Neotropical ant nests provide specialized substrata for a small myrmecochorous flora which often offers extrafloral nectar. Perhaps additional traits as yet unrecognized that might affect capacity to root in cartons are mostly limited to Araceae, Bromeliaceae (specifically subfamily Bromelioideae), Cactaceae, Gesneriaceae, Marcgraviaceae, Orchidaceae, and Piperaceae. Some Asclepiadaceae, Melastomataceae, and Rubiaceae are part of similar but less well-defined symbioses in Australasia (Janzen, 1974). Those trophic myrmecophytes that exhibit unequivocal modifications for ant occupancy all belong to Asclepiadaceae, Bromeliaceae, Melastomataceae, Orchidaceae, Polypodiaceae, and Rubiaceae (Huxley, 1980). Rubiaceae seem to be most specialized for the relationship (Fig. 12). Stranglers—about 300 in all—come from just eleven families of dicots, most notably Moraceae (*Ficus*). Secondary hemiepiphytes have vining habits, and indeed the majority belong to groups with a scandent tendency (e.g., Araceae, Cyclanthaceae, Marcgraviaceae). Bromeliaceae largely account for the tank formers (Fig. 8). Trash-basket habits (Fig. 9) are present in a modest number of families; the numerous PS epiphytes are almost exclusive to Bromeliaceae (mostly *Tillandsia*) and Orchidaceae (many subtribes).

Both parallelism and convergence have fostered much redundancy in the rise of epiphytism. Parallelism is illustrated by CAM, which features a key mechanism (incorporation of CO_2 via β-carboxylation) fundamental to regulation of ionic and osmotic balance through metabolism of malate and perhaps other organic ions (via a biochemical pH-stat). Heightened enzyme activity, appropriate malic acid mobility and storage capacity, phase-shifted stomatal behavior, and other associated characters enabling high water use efficiency have emerged in close to 30 families and more than once among some of those containing epiphytes—Bromeliaceae and Orchidaceae, for instance. Inherently slow relative growth rates, great longevity of whole plants and their individual parts, along with underlying oligotrophic physiology in canopy- and soil-based vegetation alike, probably also reflect common potential realized under similar selective impetus. Somewhat more unique features based less on homology than on novel design opportunity are, among others, devices to effect impoundment and/or accommodate ant occupancy. On balance, mechanisms governing resource use appear to be based on relatively few, widely available, genetic foundations, while functions and structures effecting resource procurement have more numerous and varied origins, likely based on convergence.

Predisposition and Adaptive Canalization

Compared with vertebrates, vascular plants exhibit great adaptive fluidity. While mammalian radiation has conformed to body plans and dietary patterns established early in the group's history, botanical taxa of comparable rank exhibit varied habits, tolerances, and life histories. Quite commonly, natives of disparate habitats even belong to the same genus. Difference in evolutionary pattern partly reflects the higher plant's greater physiological plasticity aided by continuous turnover of both vegetative and reproductive organs. Selection may occur among ramets—perhaps even tissues within individual organs—during the life of a single clone (Walbot & Cullis, 1985). Evolutionary tempo is rapid enough to effect speciation in as little as 10^4–10^5 years—or perhaps a few decades!—in Orchidaceae (Gentry & Dodson, 1987). Reputedly, only a small number of genes need to be involved to alter structure, function, and ecological tolerance (Gottlieb, 1984; but see Coyne & Lande, 1985). Some angiosperm lineages are quite conservative, however, as if for them, too, entry into certain adaptive zones restricts access to others.

Cases of evolutionary canalization abound in Magnoliophyta. Somatic conservatism is frequent within genera and an invariant adaptive mode can typify entire, albeit small, specialized families (e.g., Sarraceniaceae, Lemnaceae). More impressive evidence for constraints on direction but not speciation in plant evolution is provided by greater redundancy in other families. Examples include halophytism in Chenopodiaceae, ruderalism in Brassicaceae, drought-enduring xerophytism in Cactaceae and, of course, epiphytism in Orchidaceae. No single life style characterizes the entire clade in any of these examples, but particular themes turn up too often to deny underlying family-wide dispositions. Success in a particular environment is predicated on a novel set of features that imparts ability to counter major external constraints. Once the essential components were perfected and integrated, whether by serendipity or some optimizing mechanism, each ancestral stock became better equipped to enter one, and less so another, adaptive zone. Since accessible space was widely available in each case, considerable cladogenesis followed, sometimes through agencies unrelated to vegetative performance, hence native substratum. Orchidaceae achieved unequalled speciation in humid, neotropical forest canopies because of behavior peculiar to male euglossine bees.

Adaptive syndromes are comprised of structural, functional, and phenological components which can be identified through consistent occurrence in participating species. Ruderals succeed through their capacity to create seed mass rapidly, because time is the major constraint affecting success in resource-rich, disturbed habitats. Components of this well-defined syndrome are: habits incorporating minimal mechanical and root tissue; vigorous photosynthetic machinery; small, long-lived, often light-sensitive, propagules; and self-compatibility. Here, such traits as low shoot/root ratios, woodiness, and extensive succulence are never found because they are inconsistent with ephemeral life histories. Although the habits of vascular halophytes range from large trees (mangroves) to succulent terrestrial and submerged herbs, certain physiological phenomena are common to all because potential for desiccation is always one of the predominant problems in saline media. Osmotic compensation and compartmentation of specific solutes provide the only means for maintaining water relations in hyperionic habitats. In every case, potentially toxic ions, taken in from the environment to lower tissue water potential, must be sequestered in vacuoles at concentrations above those encountered in glycophytes, and they must be balanced across the tonoplast by osmotica of plant origin. Salt balance can be fine-tuned further by taxon-specific features. Chenopod halophytism is aided in salty surroundings by multicelled vesicular hairs which excrete excess Na^+ and Cl^-; succulence provides for ion dilution. The presence of organic solutes, including proline, in other salt-tolerant taxa instead of the betaines found in Chenopodiaceae reveals that physiological convergence among natives of saline environments is not complete. Likewise, the abundant malic acid synthesized by all CAM plants at night for subsequent daytime generation of an internal CO_2 supply is usually decarboxylated through only one of the three existing reactions: mediation by NAD- or NADP-dependent malic enzyme or PEP carboxykinase.

On balance, floristic variety generally reflects the equability and heterogeneity of a particular adaptive zone, all other variables being equal. Fertile, moist soils and abundant light have fostered wide convergence—ruderals are a good example. Weeds in crop fields belong to many families, reflecting easy access to a collection of required character states. Tropical forest canopies have been similarly colonized but only to a certain degree. Whereas many lineages have evolved traits that allow growth on the organic arboreal "soils" of everwet forests, few have invaded more demanding zones, as demonstrated by narrower taxonomic participation in PS epiphytism (Benzing, 1978).

Inherited—in effect, phyletic—constraints determined which ancestors of modern families could generate epiphytic derivatives. Inherent barriers are complex and little understood, but their existence in plants is becoming recognizable (e.g., Kochmer & Handel, 1986; Hodgson & MacKey, 1986). Potential to express key components of an adaptive syndrome was not sufficient to assure its establishment. Universal occurrence of CAM-like function, for instance, did not guarantee adoption of CAM by all xerophytes nor by all aquatic macrophytes in the softwater lakes where nocturnal fixation is favored by limited carbon supply (Keeley, 1981; Richardson et al., 1984). Moreover, each character of a syndrome must be free of pleiotropic and linkage relationships with maladaptive or internally incompatible traits. Biomechanical compatibility is essential; for instance, plants with vigorous cambia may rarely employ CAM, probably because costly woodiness is not sustainable without greater capacity for carbon gain.

Little is known at this point about inertia in the genetic, epigenetic, and biomechanical interplay among phenomena responsible for salt balance in halophytes, resource uptake and processing in short-lived eutrophs, or water economy in CAM plants. But occurrence among related genomes does demonstrate that some characters affecting vegetative performance and thereby suitability in particular habitats—e.g., sites of nitrate reduction (shoot as opposed to root), ability to adjust osmotically under various degrees of stress, and presence of particular ion pumps and channels—can be more or less readily gained, modified, or lost. More narrowly restricted throughout Magnoliophyta, often to a single family or order, are features such as capacity to form a particular type of mycorrhiza, nodulate with *Rhizobium,* synthesize cardiac glycosides or betaines rather than anthocyanin pigments, and utilize sorbitol rather than sucrose for phloem transport.

Access to vital characters during plant evolution has been affected by related impacts on photon, water, and nitrogen use efficiency (Raven, 1985a). Constraints on evolutionary opportunity have been strongest where drought, shade, or infertile substrata accentuate premiums on water, energy, and nutrient economy respectively. Type of nitrogen source, for instance, imposes different demands, depending on where (in which organ) processing takes place, how much water and energy is needed per unit of product, and the environmental context (is light or moisture scarce or abundant?). Calculation of comparative costs must extend beyond inputs for chemical synthesis to include transport and pH regulation. Excess protons must be eliminated by users of NH_4^+ and N_2, while excess OH^- is consumed or excreted by NO_3^- assimilators. Although the ammonium-to-protein pathway is least expensive in terms of energy consumption, overriding factors may still dictate another choice even where NH_4^+ is in greatest environmental supply. Soil is the usual sink for H^+ generated by NH_4^+ use.

Indeed, owing to the immobility of protons in phloem, terrestrial plants process most of their acquired NH_4^+ in roots, a potential limitation with special relevance for epiphytism. If this is the universal rule, then what compensation, if any, accompanied root system reduction in advanced Bromeliaceae? Evidence indicates that NH_4^+ is the predominant form of nitrogen in at least some tropical-forest canopies (e.g., Curtis, 1946). Conceivably, the absence of similar morphological diminution in nonbromeliad lineages is in part related to their less flexible nitrogen metabolism, although the role bromeliad foliar trichomes have played in obviating absorption by roots cannot be ignored in such comparisons. Perhaps slow-growing plants like the atmospheric bromeliads metabolize N at such low rates that complications are avoided. Either the internal biochemical pH-stat is adequate for disposal or excess protons are dumped from trichomes when shoots are wetted.

Similarly, land plants have evolved several mechanisms to effect osmotic balance. Here, cost escalates with deployment of inorganic (e.g., Na^+, Cl^-), then organic nonnitrogenous, and finally nitrogenous solutes, especially on infertile media. Again, nitrogen is an important currency but perhaps no less so than the energy and water spent for its acquisition and processing. In a somewhat different vein, fungal biomass has to be supported by the mycorrhizal plant; but returns in phosphorus, and sometimes water and other nutritive ions, justify the investment in all but the most fertile habitats. Comprehensive cost accounting, through knowledge of functional incompatibilities and the hereditary and epigenetic phenomena controlling access to key traits, is necessary to interpret patterns of radiation. It is at these levels of plant performance that many of the tradeoffs, economies, and accommodations underlying the evolutionarily-stable strategy occur.

HISTORICAL BASIS FOR CANOPY DEPENDENCE

It is currently impossible to explain fully why one particular lineage developed canopy dependence while another did not. But partial answers are available in some cases; several of the more notable ones are discussed below. Four questions provide focus: Why are proportionally more ferns than seed plants epiphytic? Why do so many monocots, particularly orchids, dwell in canopies? Why have several families of dicots with no obvious advantage by basic habit or water balance profile succeeded so widely there? Finally, why is branch parasitism relatively uncommon?

Ferns. Homosporous pteridophytes are successful in tree crowns, where they usually occupy lower strata, because of small diaspores. A second, less obvious, factor is a capacity to tolerate substantial drying and deep shade. Poikilohydry is pronounced in exceptional taxa (*Polypodium polypodioides*), but many other filicaleans exhibit desiccation tolerance superior to that possessed by most seed plants. A fern's pattern of drought resistance, unlike that of most CAM plants, is particularly compatible with occurrence deep in the forest. For instance, ultrathin fronds of Hymenophyllaceae (Fig. 6) probably photosaturate at very low fractions of full insolation and they can survive considerable desiccation. Greater exposure might be tolerable, and upper as well as lower strata heavily colonized, but for the tradeoff associated with poikilohydry. Resurrection is adequate for countering the occasional brief drought every humid forest experiences now and then, but frequent dehydration is another matter. A regulated water economy based on thick (expensive, opaque) epidermal barriers and greater diffusive control is critical on markedly arid sites because photosynthesis is more likely than is respiration to be curtailed by severe water deficits. Should moisture supply be too intermittent and poikilohydrous foliage dry too often, carbon balance tends to become negative (Benzing, 1986a). Raven (1985b) cited rates of physiological processes, including photosynthesis and transpiration at the low end of the ranges reported for tracheophytes, as a reason why ferns are so well equipped to inhabit shady, drought-prone locations.

Nevertheless, a modest invasion of drier locations has been possible for higher ferns. One enabling mechanism here is drought avoidance via seasonally deciduous foliage (e.g., *Phlebodium aureum*). Occurrence in some stressful Australasian sites is possible for evergreen *Pyrrosia* and its equally coriaceous relatives through an odd juxtaposition of structural and physiological characters. There are reports of CAM in *Drymoglossum piloselloides, Pyrrosia longifolia,* and *P. angustata* (Wong & Hew, 1976; Sinclair, 1983; Hew, 1984) along with drying characteristics more reminiscent of a resurrection plant than a typical desiccation-resistant xerophyte. A thorough examination of ferns with regard to microclimates, substrata, and water and carbon relations in both gametophyte and sporophyte stages will be necessary to place discussion of the evolution of pteridophytic epiphytism on a firmer foundation.

Liliopsida as a whole. Orchids account in large measure for the immense numbers of epiphytic species, but monocots would be disproportionately common in tree crown habitats even without them. Bromeliaceae and Araceae rank second and third. The ratio of monocot to dicot species in tree crowns is 5 : 1, but it is 1 : 4 overall. Although Araceae, Bromeliaceae, and Orchidaceae are the most successful families in forest canopy habitats, there is no common adaptive theme. Two photosynthetic pathways in many variations, tank and trash-basket impoundments, myrmecophytism, foliar trichomes, velamentous roots, and virtually all the dispersal modes enabling arboreal existence occur in epiphytic monocots. A peculiar body plan, shared to some extent with the higher ferns but less so with dicots, may have offered special class-wide opportunity.

Monocots in particular, but dicots as well, are often sectoralized in the sense that individual shoots operate as collections of relatively independent, serially aligned, physiological units (IPUs; sensu Watson & Casper, 1984). Tracer studies have shown that meristems may receive fixed carbon mainly from nearby leaves, sometimes only those attached at the subtending nodes. Longitudinal segmentation seems to be more characteristic of dicots, and may also help explain why several different habits and associated ecological tendencies have been emphasized in one or the other of the two classes. Partitionment into vertical compartments is evidenced by movement of labeled photosynthate among leaves and associated buds along a single orthostichy. Xylem supply is similarly restricted. Secondary thickening may eventually obliterate conductive barriers to lateral flux imposed by the dicot primary body, particularly where eustelic stem vasculature is "open"—i.e., composed of discrete series of interconnected leaf traces (sympodia). But, as previously noted, woodiness imposes another set of limitations, especially in arid habitats. Monocots with their more reticulate "atactostele," best known today in palms (a group portraying the "Raphis Principle"; Tomlinson, 1984), appear to possess unique capacity for functional integration on one hand and, on the other, habits that permit extensive vegetative renewal in mimimal space. Perhaps especially fortuitous is the unusual ability to coordinate remote sources and sinks, and a related capacity to localize effects of damage and maintain vascular supply to organs that a more rigid system might be forced to abandon or underutilize. This kind of flexibility was illustrated by some experiments with grasses when mature ramets, returned to sink status by shading or defoliation (e.g., Callaghan, 1984; Welker et al., 1985), remained alive rather than self-pruned, as commonly occurs in forest trees. Historically, integration of this sort may have fostered extraordinary architectural plasticity with special implications for novel evolution. Recall that several large epiphytic monocot lineages have undergone major vegetative reorganization unequaled in dicot counterparts.

The exceptionally well-developed horizontal segmentation just described was undoubtedly important in the evolution of stress-tolerant epiphytic monocots, perhaps ferns as well. The advantages of a rhizomatous sympodial habit and potential physiological autonomy of the single phyton (a morphological unit composed of a leaf and associated adventitious root(s), bud(s), and subtending stem segment) were most accentuated during orchid phylogeny. Sequential production of reduced shoots (in effect, shoots composed largely of single expanded phytons in extreme cases) is a recurrent theme in this family. Adult shoots of *Dendrobium ultissimum* consist of nothing more than strings of stubby, closely placed, leafless pseudobulbs. The broader suitability of architecture based on serial renewal via determinate shoots generated from closely-placed meristems is illustrated by occurrence beyond the monocots. Somewhat less condensed versions of the same general arrangement exist among mechanically-dependent dicots (e.g., some Gesneriaceae) and *Lycopodium.* Differentiation of roots into feeder and holdfast types (Fig. 9), a useful division of labor for the vine or epiphyte, seems to be more common in monocots than elsewhere.

Nonorchid monocots. Bromeliaceae, with far fewer species and almost exclusively neotropical distribution, nevertheless rival Orchidaceae for variety of epiphytic life styles. Tank habits have evolved independently in two subfamilies, and in all three if *Brocchinia* is correctly assigned to Pitcairnioideae (Benzing et al., 1985). A rosulate shoot was required for each transference of absorptive role from root to shoot. Ancestry was apparently mesic in both Tillandsioideae and Pitcairnioideae; tank shoots are associated with C_3 photosynthesis in each subfamily. Bromelioideae, with about 500 species capable of creating soil substitutes in leaf bases, are fundamentally CAM plants. Specialization for PS epiphytism, in effect for greater stress tolerance, has proceeded farthest in Tillandsioideae by way of the derived atmospheric forms (Benzing et al., 1985). Here, absorbing trichomes (Fig. 3) are perfected to the highest degree whilst the vegetative apparatus is reduced to simplest form.

Epiphytic Bromeliaceae, more than most, were clearly adapted to endure rigorous conditions by the presence of a suitable epidermal appendage and habit in precursors. Here, epiphytism is based on a modified shoot (Fig. 8) with the foliar trichome as its keystone feature (Table 1). Absorptive function might be possible in glabrous leaf bases when long-term contact with moist, nutritive tank fluids is maintained, but the rapid uptake required to sustain a rootless, nonimpounding PS bromeliad would be impossible without an extraordinary foliar indumentum. Myrmecophytism, and perhaps a single case of carnivory (*Catopsis berteroniana*; Givnish et al., 1984), are also associated with specialized trichomes and inflated leaf bases (Benzing, 1970). Hypotheses concerning how the bromeliad foliar epidermis may have acquired its current function and importance are described elsewhere (Pittendrigh, 1948; Benzing et al., 1985). (Briefly: contrary to Pittendrigh's proposition that absorptive function would only emerge under drought selection, Benzing et al. posited a mesic, infertile, ancestral habitat where the foliar epidermis evolved primarily to promote acquisition of nutrient ions from impounded humus or perhaps animal prey.) Bromeliad seeds are disseminated by birds (Bromelioideae) or wind (Pitcairnioideae and Tillandsioideae). Pollination syndromes are diverse and apparently not associated with either tank or atmospheric habit.

Aroid, by comparison with bromelioid or orchidoid, epiphytism is neither as advanced nor as versatile. There are no reports of CAM here, and overlapping foliage that might mitigate drought lacks the water-tight quality possessed by inflated bromeliad leaf bases. Trash-basket catchments (Fig. 9) sometimes trap falling litter but little moisture. Roots fail to produce velamina as elaborate as those serving the most drought-tolerant Orchidaceae, nor is there any indication that these organs can match foliage in photosynthetic vigor. Seasonally deciduous leaves on green or tuberous stems occur in *Philodendron* and *Remusatia* respectively, but these are minor themes with few participating species. Arboreal existence in Araceae is based predominantly on two mechanisms, both humus-based: impoundment, seen in short-stemmed *Anthurium* and some *Philodendron* (Fig. 9); and secondary hemiepiphytism (Fig. 11), a more widespread phenomenon most often encountered in *Philodendron*. Velamentous roots, and rosulate and vining habits incorporating progressive dieoff of proximal stem regions, appear to be the central vegetative features responsible for aroid expansion in canopy habitats (Table 1). Both sympodial (e.g., *Philodendron*) and monopodial (*Pothos*) habits are found in the hemiepiphytes. Ant nests are utilized by some *Anthurium* and *Philodendron*. Water and nutritional relations exhibit no obvious unusual modifications for arboreal life, but neither have been examined closely. Baccate fruits are an integral part of the syndrome, but they occur throughout the family without habitat restriction. Pollinators range from beetles to euglossines. Specialized pollen vectors may have encouraged enlargement of *Anthurium* and possibly other genera. Cyclanthaceae, the only other nonorchid monocot family with a sizable epiphyte contingent (about 66% of *Asplundia*), mostly penetrate the forest canopy as rooted climbers and secondary hemiepiphytes. True epiphytism occurs in *Sphaeradenia* and *Stelestylis* (G. Wilder, pers. comm.). Stems and internodes are shorter than those of related hemiepiphytes.

Orchid monocots. Orchidaceae owe their numerical superiority among epiphytes to an exceptionally propitious set of vegetative and reproductive features and to extraordinary cladogenesis promoted by specialized pollination syndromes (Benzing & Atwood, 1984). Vegetative mechanisms vary tremendously according to the taxon's native substratum and ecoclimatic conditions. But there are several important attributes common to all canopy-dependent family members that, in some form, predisposed early stock for arboreal life. For example, epiphytic Orchidaceae possess specialized roots varying in photosynthetic performance and water relations, depending on structure and metabolism; uptake is enhanced in all cases by a nonliving velamen which imbibes precipitation and contained solutes for subsequent sorption through transfer cells in an underlying exodermis (Benzing et al., 1983; Benzing & Pridgeon, 1983; Fig. 10). This same mantle effectively retards desiccation injury from both short-term and extreme drought (Benzing, 1986a). Velamina simply embolize air in order to break the hydraulic continuum that, if left intact, would allow matric forces in adjacent drying substrata to dehydrate living epiphyte tissue. A green cortex supplements shoot photosynthesis and is the major site of carbon gain for the plant in exceptional cases (Fig. 4). Hyperovulate gynoecia and aggregated pollen characterize most of the family. Microspermy—up to millions of tiny, lightly provisioned seeds per capsule—requires fungal intervention for germination. High-fidelity, long range, but often inefficient pollinators promote ethological isolation leading to plant speciation (Benzing & Atwood, 1984).

Pre-epiphytic orchid stock probably possessed structurally modified, locally suberized epidermis/hypodermis layers as do most extant terrestrial family members and some other monocots (e.g., *Zea, Allium, Amaryllis*). Similar root specialization is less known in dicots. Microspermy and associated mycotrophic nutrition were probably also acquired in a terrestrial context, as suggested by the current habitats in which all other such heterotrophic plant symbioses occur (e.g., Monotropaceae, achlorophyllous Gentianaceae). Production of numerous tiny diaspores, subsistence on transitory resource supplies, and maintenance of high water and nutrient use efficiencies set the stage for migration to forest canopies, including many uninhabitable by less stress-tolerant epiphytes. Evolution of pheromonelike fragrances and specialized floral morphology tightened relationships with specific hymenopterans and dipterans, and assured extensive proliferation of several clades that happened to be canopy-dependent. Large clusters of related species among taxa relying on smaller, short-range vectors with no known propensity for exclusive foraging suggest that substratum-specific factors have also been important. As in a number of other diverse communities of sessile organisms, coexistence of densely packed epiphyte populations may be favored on substrata subject to intermediate disturbance (Connell, 1978; Benzing, 1981, 1986b). Radiation in other speciose, canopy-dependent taxa visited by opportunistic or sedentary pollinators (e.g., *Anthurium, Peperomia*) may be due to similar phenomena.

Dicots. Magnoliopsida are, on the whole, poorly disposed to epiphytism—just 2% of species are involved—but there are exceptional taxa (Gentry & Dodson, 1987). Success in a clade is often predicated on a single theme and no other family incorporates the diverse resource procurement mechanisms or stress tolerances exhibited by epiphytic Bromeliaceae and Orchidaceae. Except in Marcgraviaceae, dicot terrestrials always outnumber confamilial epiphytes. In tree crowns, *Peperomia* ranks first in size among successful dicot genera and even families, a statistic fostered by pantropical distribution, the presence of CAM variations (Sipes & Ting, 1985), and high-volume production of small adhesive fruits. Habits range from shrubby to minute and creeping. Moraceae also owe much of their major epiphytic presence to a single genus (*Ficus*) with a similar broad range; here the strangler habit provides the vegetative basis for success. Rampant speciation within a relatively narrow adaptive profile has again been encouraged by circumtropic range and host-specific pollinators—in this case, the fig wasps. According to Ramirez (1977), the moraceous strangling habit evolved "as a response to lack of light at the forest level." Necessary attributes for success included presence of viscid hyaline coats on seeds that would germinate only on moist humus, long aerial roots, water-use-efficient seedlings, and dispersal by winged vertebrates. Marcgraviaceae and Clusiaceae are additional single-strategy families, emphasizing secondary and primary hemiepiphytism respectively. Stranglers also occur in *Schefflera* (Araliaceae), *Posoqueria* (Rubiaceae), *Metrosideros* (Myrtaceae), and elsewhere, but they are atypical among confamilial canopy-based taxa.

Most epiphytic Asclepiadaceae belong to closely related, succulent, vining *Dischidia* and *Hoya*. Flasklike leaves of *D. rafflesiana* and several other species enclose nests; ants provide dispersal service for many more. Forms with less specialized foliage regularly root in or grow against ant debris, providing clues as to how ant-fed relatives evolved. Dome-shaped leaves of *D. collyris* grow tightly pressed against bark, providing shelter for *Iridomyrmex* colonies (Huxley, 1980). Photosynthesis involves CAM and/or CAM-cycling (Kluge & Ting, 1978). Cactaceae became equipped for the canopy-dependent synusia through drought selection in terrestrial habitats. Fleshy, small-seeded fruits and climbing habit would eventually favor life in canopies. Movement into tree crowns appears to have involved some reversals. Originally aphyllous, stems of the most advanced epiphytic forms (which happen to be natives of humid forests—e.g., *Zygocactus, Ripsalis*) have lost their armature and become much flattened, or narrowed if still terete (e.g., *Hatiora*), presumably to improve performance in shade. Family-wide CAM is probably present in relatively muted form as well. Response to the resulting elevated moisture demands requires uptake by long-lived roots from more or less continuous supplies in tree fissures or soil (the secondary hemiepiphytes). Despite the extreme drought tolerance of many terrestrial relatives (e.g., *Maxillaria, Ferrocactus*), epiphytic Cactaceae seemingly never colonize the most demanding bark and twig exposures.

Less obvious is the basis for high epiphyte success in Ericaceae, Gesneriaceae, Melastomataceae, and nonmyrmecophytic Rubiaceae. Most canopy-dependent members in all four families grow exclusively on humus mats in humid forests. Woody habits and sclerophyllous foliage, sometimes complemented by storage tubers, characterize Ericaceae and Melastomataceae. About one-half of the rubiaceous epiphytes (*Hydnophytum, Myrmecodia*) supplement mineral nutrition and store moisture via ant-inhabited, swollen hypocotyls (Fig. 12). Basically herbaceous Gesneriaceae feature broader growth-form variety, and several genera contain CAM plants. Like some *Peperomia,* these gesneriads exhibit trilayered mesophyll that may signal unusual photosynthesis. Substrata are more diverse in this family, ranging from ant-carton to less specialized humus. *Codonanthe* and related genera, along with some hemiepiphytic cacti, are probably the best drought-insulated of the dicot epiphytes. Baccate fruits provide seed mobility in most cases, although *Rhododendron,* a few gesneriad genera, and large proportions of Melastomataceae and Rubiaceae ripen wind-borne seeds. Ant-associated species are myrmecochorous.

Representation in canopy habitats varies among these families, ranging from 4% to 35% of all genera in Rubiaceae and Ericaceae respectively (Madison, 1977). The ericad statistic is all the more impressive considering the family's size and numerous temperate taxa. The other three families are larger and nearly or exclusively moist-tropical, hence have had greater access to arboreal habitats. Breadth and depth of specialization for canopy dependence is further indicated by comparing the total of exclusively epiphytic genera containing two or more species with the number which include soil-based species as well. Gesneriaceae are most canopy-adapted by this measure with 13 genera meeting each criterion, while Ericaceae is least so with only four terrestrial-free genera out of 22 containing epiphytes; the largest of the four contains only eight species. *Vaccinium* is especially noteworthy for its wide range throughout Old and New World boreal to equatorial zones and diverse habitat assignments. Epiphytic only : mixed genera ratios for Melastomataceae and Rubiaceae are 8 : 12 and 5 : 14.

The influence of geography in determining which families would contribute the most species to the forest canopy flora (Gentry & Dodson, 1987) is apparent in Magnoliopsida. Epiphytic Gesneriaceae are centered in the neotropics where tribe Episcieae and particularly genera like *Drymonia, Columnea, Dalbergaria,* and *Trichantha* have radiated extensively in tree crowns. Speciation here, as in epiphytic Liliopsida (Araceae, Bromeliaceae, Orchidaceae), appears to involve specialized American pollinators (hummingbirds and euglossines). Paleotropical counterparts are far fewer but still number more than 100 species. Canopy-dependent ericads are also disproportionally neotropical and ornithophilous. All but a small fraction of the peperomias are American, although little is known about the group's reproductive biology. Because 73% of Costa Rica's large fern flora roots in tree crowns (Wagner & Gómez, 1983), it appears that neotropical epiphytism is not all pollinator-related. Wide availability of moist montane forest in the northern Andes and Central America, which is reputedly amenable to fine niche partitionment (Gentry & Dodson, 1987), has also been important for expansion of American forms. Melastomataceae and Rubiaceae number among the few heavily epiphytic pantropical families that failed to generate more New than Old World epiphytes. Scrutiny of reproductive systems and pertinent vegetative characters might help explain why mechanically-dependent New World portions of these two families have failed to undergo as much cladogenesis as have many co-occurring epiphytic pteridophytic and angiospermous groups.

Chemical peculiarities of substrata or unusual mycorrhizae may be responsible for uneven epiphyte development among higher monocot and dicot taxa. Ericaceae, Melastomataceae, and Orchidaceae exhibit family-wide affinity for acidic, often humid and organic, infertile soils. Little is known about the physiochemical details of canopy surfaces, but available nutrient ions are probably often scarce. Substrata in everwet forest where most epiphytes live tend to be sodden, at least moderately acid, and certainly organic. Use of NH_4^+ rather than oxidized nitrogen by plants native to such substrata may have been a predisposing character for epiphytism. Ericads are notably deficient in nitrogen reductase, a sign of long dependence on reduced nitrogen. Ericaceae were perhaps especially well positioned for canopy invasion through formation of mycorrhizae of a type seen in some extant terrestrials that mobilize nitrogen and phosphorus from sterile, organic soil (Stribley & Read, 1975; St. John et al., 1985). Terrestrial Orchidaceae are also strongly mycorrhizal, but the advantages, if any, that fungi provide canopy-dependent adults remain little studied and controversial (Hadley & Williamson, 1972; Sanford, 1974; Benzing & Friedman, 1981). Broad surveys of epiphyte roots and nitrogen-cycle microbes in canopy substrata could prove rewarding. A general work-up of tree-crown media as nutrient sources is much needed.

Mistletoes. Restricted taxonomic participation in branch parasitism is made all the more intriguing by the widespread abundance of mistletoes, some of which range farther north than any vascular epiphyte. Virtually the entire complement—about 1,300 species—belongs to Santalales. Why many thousands of plants from so many other higher taxa root nowhere but on bark yet never invade host vasculature is puzzling. Occurrence in Santalales of terrestrials with haustoria, including primitive Loranthaceae, but no epiphytes suggests that branch parasitism arose from root parasitism. Perhaps more direct aerial transitions were precluded by biomechanical constraints. Mistletoes transpire profusely even during drought in order to acquire sufficient nitrogen from host xylem (Ehleringer et al., 1985). This is the antithesis of an epiphyte's usual conservative water use pattern. Failure by so many epiphytic lineages to achieve parasite status simply because invasive organs are difficult to acquire seems unlikely in light of the diverse soil-based species that tap any nearby roots. More plausible is the theory that continuous function during a historical crossover between the high solute potential/low maximum turgor/sensitive stomata pattern of the epiphyte and the three to five times more concentrated osmotica (Harris & Lawrence, 1916; Harris, 1918) and correlated foliar conductance patterns of the parasite would require buffering, which is less available in canopy than in terrestrial habitats. Most of the root hemiparasite's absorptive apparatus continues to function in the conventional manner, drawing upon soil moisture and thus reducing the liability to water loss of transitional forms.

SUMMARY

Epiphytes do not constitute a narrowly defined group of plants on either taxonomic or functional grounds, nor is their habitat usually unique in its important physical characteristics. Growing conditions in both humid and arid forest canopies overlap with those at ground level, as do adaptive mechanisms in canopy- and soil-dependent flora. Substrata exhibiting the most unique and powerful constraints on plant success occur in the driest exposures. Circumvention of dependence on soil by epiphytes is varied. Modes of moisture and nutrient acquisition are the most unusual, especially among PS forms. Ways in which resources are conserved and deployed are often variations on, and perhaps sometimes identical to, patterns present in terrestrial relatives. No single key feature—like CAM, impoundment habit, or animal dispersal—nor combination of key characters underlies epiphytism. Solutions are many, a condition favoring broad taxonomic composition of mechanically-dependent synusiae. In contrast, failure of a large tropical group to evolve epiphytic members may relate to the presence of a few well-entrenched, maladaptive features. Evolutionary inertia probably also reflects little-understood genetic constraints and functional incompatibilities that block emergence of enabling syndromes even though some of their mechanistic components are already well established.

Cladogenesis and adaptive radiation for life on varied substrata have been more closely allied in some epiphytic taxa than in others. Most families, even some containing hundreds of epi-

phytic species, have entered forest canopies through a single vegetative theme. Propitious relationships with pollinators, intermediate disturbance, and narrowly circumscribed substratum requirements are among the agencies that have promoted astounding speciation in several heavily canopy-dependent taxa. Speciation sometimes required no accompanying displacement of nonfloral characters. Bromeliaceae and Orchidaceae are exceptional for their diverse vegetative mechanisms. These two families do well under equable conditions, but they are especially dominant in stressful environments because they can maintain enough generative power to compensate for mortality imposed by habitat patchiness and disturbance.

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DIVERSITY AND BIOGEOGRAPHY OF NEOTROPICAL VASCULAR EPIPHYTES[1]

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In his classic work Schimper (1888), emphasizing the taxonomic diversity of epiphytes, listed 33 families and 232 genera of epiphytes. Until very recently, subsequent authors have generally accepted Schimper's figures (Richards, 1957; Johansson, 1974). However, epiphytism (here used in a broad sense to include hemiepiphytes, see Kress, 1986) was recently reported to exist in 65 different vascular plant families (56 families excluding ferns), 38 of these with epiphytes in the Neotropics (Madison, 1977). Our own data (Appendix 1) and additional records compiled by Kress (1986) now record 83 vascular plant families with epiphytic species.[3] At least 876 genera include at least one epiphytic species and there are perhaps 29,000 epiphytic species, ca. 10% of all vascular plants (Table 1). Thus at first sight epiphytism seems a very widespread and successful life-style, which very many unrelated taxa have evolved.

However, a closer examination suggests that even though there are both many species and higher taxa of epiphytes, few of the higher taxa account for most of the species. Burger (1985), for example, emphasized that relatively few lineages have been able to enter the epiphytic niche, presumably because of the complex suite of adaptations needed. Thus even though it is true that the evolution of an epiphytic habit has been a relatively common feature of vascular plant evolution, it is equally true that very few of the taxa that have evolved an epiphytic habit have radiated successfully to produce other epiphytic species (Table 2). In most of the epiphyte-containing families, epiphytism is a rather insignificant anomaly. Indeed, eliminating a mere 85 such "oddball" species from the roster of the world's epiphytes removes 31 families from the epiphytic ranks. Only 32 seed plant families have as many as five or more epiphytic species, 26 of these with epiphytes in the Neotropics. It is on the 42 families (Table 3) that contain epiphytes in the Neotropics that this paper will focus.

Even though this analysis of epiphyte diversity and distribution is largely focused on the Neotropics, a few comparisons with the Paleotropics are instructive. There are actually slightly more families with epiphytes in the Paleotropics (43) than in the Neotropics (42), with all of the paleotropical epiphytic families having epiphytic representatives in Australasia but only 15 in Africa and Madagascar. If only the 32 seed plant families with five or more epiphytic species are considered, there are also roughly equal representations of epiphyte-containing families in the Neotropics (26) and Australasia (25) but only about half as many in Africa (14).

At the species level the story is very different. There are many more epiphytes in the Neotropics, at least half again as many as in Australasia and six times as many as in Africa. Although similar numbers of genera and families evolved epiphytism in the different regions, subsequent speciation as epiphytes was dramatically greater in the Neotropics. A major objective of this paper, then, will be to try to explain why there is so much epiphyte diversity in the Neotropics.

EPIPHYTE FAMILIES

One approach to an overview of neotropical epiphyte diversity is a taxonomic one. Table 3 summarizes the neotropical epiphytic seed plant flora by family. Of the 42 families represented by at least one habitually epiphytic species in the Neotropics, the Orchidaceae are by far the most important with ten times as many epiphytic neo-

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[3] The data set used in this paper was derived independently from that of Kress (1986) and is mostly based on Madison's figures as modified in Appendix 1.

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TABLE 1. Taxonomic distribution of vascular epiphytes (modified from Madison, 1977 and Kress, 1986).

	Families with Epiphytes	Genera with Epiphytes	Species of Epiphytes
Pteridophytes	13	92	2,593
Gymnosperms	2	2	4
Monocots			
Without orchids		80	2,657
Orchids (fide Madison)		500	20,000
Orchids (compiled from Dressler, 1981)		460	15,000
Orchids (fide Kress, 1986)		440	13,951
Total (fide Kress, 1986)	17	520	16,608
Total (our estimate)	17	540	22,657[1]
Dicots	51	262	4,251
Total	83	896	29,505

[1] Includes Madison's orchid figure (see text).

tropical species as runners-up Araceae and Bromeliaceae. All three of these most speciose neotropical epiphyte families are monocots. One other monocot family, Cyclanthaceae, also has a significant number of epiphytes. Commelinaceae, Rapateaceae, and Philesiaceae, although with few species, have an exclusively epiphytic genus (respectively, *Cochliostemon, Epidryos, Luzuriaga,* and (in our experience) *Philesia*). As summarized by Madison (1977), the rest of the epiphytic monocot flora of the Neotropics consists of single species of *Burmannia* and *Yucca* and a few Central American species of *Smilacina.*

Since orchids are so overwhelmingly the most diverse group of epiphytes (about 70% of their species are epiphytic), estimates of orchid diversity are critical to an evaluation of epiphyte diversity. Unfortunately, orchids are amazingly poorly known taxonomically (compare the ca. 12 orchid taxonomists with the ca. 200 systematists specializing in the similar-sized Compositae). Estimates of the number of orchid species range from 12,000 ("some authors" fide Dressler, 1981) or 17,000 (Airy Shaw, 1973) to 30,000 (Madison, 1977) or 35,000 ("some authors" fide Dressler, 1981). In the best available review Dressler (1981) counted almost 20,000 species and suggested 20,000–25,000 as the best estimate of orchid species numbers. Since 70% of the total number of orchid species should approximate the number of species of epiphytic orchid, there should be between ca. 12,000 (from Airy Shaw's estimate) and ca. 20,000 (from Madison's estimate). Unfortunately, the 8,000 species "slop" between these two estimates is as great as the total number of epiphytes in all other families combined! Madison (1977) used the higher figure for his calculations, whereas Dressler (1981) generally opted for more conservative estimates of orchid species numbers. We have mostly taken the higher values since we know of many cases where Dressler's figures for species numbers are significant underestimates but none where he has overestimated. For example, Dressler suggested that there are 830 species in subtribe Epidendrineae, whereas in Ecuador alone there are 500 species in the single genus *Epidendrum* and we think 1,200 species would be a better subtribal estimate.

Moreover, new orchid species are being discovered at an astonishing rate, especially in the northern Andean region, again suggesting that Dressler's estimates of species numbers will have to be adjusted dramatically upward. For example, about 2,315 orchid species are now known from Ecuador, ca. 700 of these described only in the last 15 years. Nevertheless, more than 1,500 additional Ecuadorian orchid "morphospecies" have not been identified with any published name. Even if the 300 unaccounted for names should all prove applicable to the unidentified specimens at hand, it is inevitable that most of the unidentified taxa will prove undescribed and the list of orchids for Ecuador alone will increase to well over 3,000 species.

The neotropical epiphytic dicot flora is more diverse in families but much less diverse in species than the monocots. Twenty-nine dicot families have at least one habitually epiphytic species in the Neotropics. The largest of these are Piperaceae (ca. 500 spp.), Gesneriaceae (483 spp.), Melastomataceae (227 spp.), Ericaceae (ca. 300 spp.), Cactaceae (133 spp.), Guttiferae (ca. 90 spp.), and Marcgraviaceae (87 spp.). In addition there are perhaps 110 neotropical species of Moraceae stranglers in the genera *Ficus* and *Coussapoa.* The only other dicot families with more than 20 epiphytic species in the Neotropics are Araliaceae, Bignoniaceae, Compositae, Rubiaceae, and Solanaceae (Table 3).

In addition, Bombacaceae, though with few

TABLE 2. Largest epiphyte families (in part from Madison, 1977).

Family	No. Genera with Epiphytes	No. Epiphytic Species	Total No. Species	Percent Epiphytes
Orchidaceae	460	20,000 (−13,951[1])	30,000 (−19,128[1])	67 (73)
Bromeliaceae[1]	26	1,144	2,500	46
Araceae	15	1,100[2]	2,500+[2]	42
Polypodiaceae[1]	53	1,023	1,100	93
Piperaceae	2	710	3,000	24
Melastomataceae	33	ca. 647[3]	4,770[3]	14
Gesneriaceae	28	598[4]	3,000[4]	20
Moraceae (incl. stranglers)	3	521	1,400	37
Ericaceae	28	478[5]	4,000	23
Hymenophyllaceae[1]	2	400	600	67
Aspleniaceae[1]	1	400	675	59
Dryopteridaceae[1]	10	292	1,920	15
Rubiaceae	21	217	6,000	4
Lycopodiaceae[1]	1	200	400	50
Davalliaceae[1]	8	139	150	10
Asclepiadaceae	6	135	2,000	7
Cactaceae	25	133	2,000	7
Cyclanthaceae	7	125[6]	205	61
Vittariaceae[1]	9	112	112	100
Guttiferae	6	92	1,000	9
Marcgraviaceae	7	89[7]	117	76
Araliaceae	5	73	700	10

[1] Kress, 1986.
[2] Croat, pers. comm.
[3] Renner, 1986 and pers. comm.
[4] Wiehler, 1983.
[5] Luteyn, pers. comm.
[6] Hammel, pers. comm.
[7] Bedell, pers. comm.

species, has an epiphytic genus (*Spirotheca*). The other 16 epiphytic neotropical dicot families are represented by only occasional epiphytic species of predominantly terrestrial genera.

In addition to these angiosperm families, there are two gymnosperm families with single epiphytic neotropical species in generally terrestrial genera and at least 838 epiphytic fern species belonging to 32 different genera, a common epiphytic *Psilotum,* and some epiphytic species of *Lycopodium.*

Reproductive Biology

A number of salient characteristics that may be critical to success as epiphytes are shared by many different neotropical epiphytic taxa. Madison (1977) nicely summarized many of the features of epiphyte reproductive biology and this discussion is largely based on his. From the viewpoint of dispersal biology, there are three main types of epiphyte propagule. The great majority of epiphyte genera and species have tiny dust-like wind-dispersed sporochores, often with highly sculptured epidermis, to aid in air flotation. Such seeds, representing an extreme in r-selection and a high risk gamble on chance establishment, are found in the two most successful epiphyte groups, orchids and ferns, as well as in such taxa as *Begonia* (although at least one African epiphytic species has a fleshy fruit, pers. obs.), *Utricularia,* Rapateaceae, and perhaps capsular melastomes, although seeds of capsular melastomes may be 1 mm long and are not strictly comparable (Renner, pers. comm.). In closed-canopy tropical forests such seeds are virtually unique to epiphytes. While tiny sporochore seeds are found in some tropical weedy herbs, they are unknown among tropical forest lianas (except mostly hemiepiphytic *Adelobotrys*) and trees (excluding tree ferns), although the pterochore seeds of genera like *Chimarrhis* may not be any larger.

TABLE 3. Epiphytic neotropical seed plant families (in part from Madison, 1977).

Family	Number of Neotropical Epiphytic Species	Neotropical Genera with Epiphytes	Distribution of Epiphytes
Gnetaceae	1	*Gnetum*	also epiphytic in Malaysia
Zamiaceae	1	*Zamia*	Costa Rica, Panama; only in Neotropics
Agavaceae	1	*Yucca*	Mexico; only in Neotropics
Araceae	1,034	*Anthurium, Caladiopsis, Monstera, Rhodospatha, Philodendron, Stenospermation, Syngonium*	also epiphytic in Africa and Asia
Bromeliaceae	1,144 (fide Kress, 1986)	18 genera entirely or predominantly epiphytic; 5 others with some epiphytes	only in Neotropics
Burmanniaceae	1	*Burmannia*	also epiphytic in New Guinea
Commelinaceae	3	*Cochliostemon, Campelia*	only epiphytic in Neotropics
Cyclanthaceae	125	*Asplundia, Dicranopygium, Evodianthus, Ludovia, Sphaeradenia, Stelestylis, Thoracocarpus*	only in Neotropics
Dioscoreaceae	1	*Dioscorea*	Ecuador
Liliaceae	4	*Smilacina*	also epiphytic in Australia, Pacific, and Madagascar
Orchidaceae	11,000 (fide Madison)	ca. 80 genera entirely or predominantly epiphytic	also epiphytic in Africa and Australasia
Philesiaceae	3	*Luzuriaga, Philesia*	also epiphytic in New Zealand
Rapateaceae	6	*Epidryos, Stegolepis*	only in Neotropics
Apocynaceae	1	*Mandevilla*	Costa Rica
Alzateaceae	1	*Alzatea*	Costa Rica-Colombia
Araliaceae	45	*Schefflera, Oreopanax*	also epiphytic in Africa and Australasia
Asclepiadaceae	2	*Cynanchum*	mostly epiphytic in Malaysia
Begoniaceae	25	*Begonia*	also epiphytic in Africa and Asia
Bignoniaceae	29	*Schlegelia, Gibsoniothamnus*	only in Neotropics
Bombacaceae	4	*Spirotheca*	only in Neotropics; mostly Andean
Burseraceae	1	*Bursera*	Costa Rica
Cactaceae	133	25 genera entirely or predominantly epiphytic	*Rhipsalis* also epiphytic in Africa and Ceylon
Campanulaceae	7	*Burmeistera*	neotropical; mostly Andean
Compositae	ca. 30	*Mikania, Nelsoniothamnus, Neomirandea, Pseudogynoxys, Senecio* (*Pentacalia*), *Sinclairia, Tuberostylis*	Central America and Andean; *Senecio* also epiphytic in New Zealand and Madagascar
Crassulaceae	2	*Echeverria*	also few epiphytic in Himalayas and Madagascar
Ericaceae	ca. 300	18 genera entirely or predominantly epiphytic; several with epiphytic species	also epiphytic in Australasia
Gentianaceae	1	*Voyria*	South America
Gesneriaceae	483	12 genera entirely or predominantly epiphytic; 4 other	also epiphytic in Africa and Australasia

TABLE 3. Continued.

Family	Number of Neotropical Epiphytic Species	Neotropical Genera with Epiphytes	Distribution of Epiphytes
		genera with some epiphytic species	
Griseliniaceae	3	*Griselinia*	Chile and Brazil; also epiphytic in New Zealand
Guttiferae	ca. 90	*Clusia, Clusiella, Havetiopsis, Oedematopus, Quapoya, Renggeria*	only epiphytic in Neotropics
Lentibulariaceae	12	*Utricularia*	also 2 epiphytic in Africa and Australasia
Marcgraviaceae	89	all 7 genera entirely or predominantly epiphytic or hemiepiphytic	only in Neotropics
Melastomataceae	227	7 genera entirely or largely epiphytic; 5 others with some epiphytic species	also epiphytic in Africa and Asia
Moraceae	111	*Coussapoa, Ficus* subg. *Urostigma*, and 1 *Pourouma*	*Ficus* stranglers also in Africa and Australasia
Myrsinaceae	ca. 12	*Cybianthus, Grammadenia, Myrsine* (*Rapanea*)	also epiphytic in Africa and Asia
Onagraceae	3	*Fuchsia*	only epiphytic in Neotropics
Piperaceae	ca. 500	*Peperomia, Piper*	also epiphytic in Africa and Asia
Rubiaceae	ca. 57	*Balmea, Coprosma, Cosmibuena, Hillia, Malanea, Manettia, Psychotria, Ravnia, Relbunium, Schradera*	also epiphytic in Australasia
Sapotaceae	1	*Bumelia*	Costa Rica
Saxifragaceae	ca. 3	*Hydrangea, Phyllonoma*	only in Neotropics
Solanaceae	ca. 30	*Juanulloa, Lycianthes, Markea* (+ segregates), *Solanum*	also epiphytic in Malaysia (*Solanum, Lycianthes*)
Urticaceae	ca. 15	*Pilea*	also epiphytic in Indo-Malaysia

The second most prevalent dispersal mode among epiphytes is via birds. Most bird-dispersed epiphytes have indehiscent berry fruits but a few, including *Drymonia* and *Clusia*, have dehiscent capsules with arillate seeds. In either case the seeds tend to be smaller and more numerous than in related nonepiphytic taxa (Madison, 1977). In some families there is a marked change in dispersal mode accompanying the shift to epiphytism. In Bignoniaceae all epiphytic species (with two probably bat-dispersed exceptions) are bird-dispersed but only one nonepiphytic species (*Synapsis ilicifolia*) is (see Gentry, 1983). In Melastomataceae 85% of the epiphytic species have berry fruits as compared with 60% of the nonepiphytic species (Renner, 1986).

The third major diaspore dispersal syndrome in epiphytes is wind-dispersal via winged or plumed seeds (pterochory and pogonochory, respectively). Interestingly, plumed seeds as compared with winged seeds greatly predominate among epiphytes, whereas the opposite holds true for trees and lianas, at least in mature forest species. Some of the important epiphyte taxa with pogonochore diaspores are Bromeliaceae subfamily Tillandsioideae, Asclepiadaceae, Gesneriaceae, and Rubiaceae. In Rubiaceae some epiphytic genera have small winged seeds while others have true pogonochores; the difference between these dispersal modes tends to break down in such groups, with some species having such narrow reduced wings that these effectively approximate large hairs.

Finally there are a few epiphyte taxa with such miscellaneous dispersal syndromes as bat-dispersal (some strangler figs), exozoochory via sticky diaspores (some *Peperomia*), and the not readily classifiable "sloppy corn-on-the-cob" ingestion of some cyclanth fruits by *Callicebus* and other primates (Terborgh, pers. comm.).

In general, epiphyte seeds are smaller and more numerous than those of nonepiphytic relatives. For example, Renner (1986 and pers. comm.) noted that in Melastomataceae mostly epiphytic *Blakea* and *Topobea* have ca. 1,000 seeds per fruit compared with a few dozen seeds per fruit in typical nonepiphytic genera such as *Miconia* and *Clidemia*. Madison (1977) estimated that seeds of epiphytic *Anthurium* are typically ca. 2 mm long as compared with 4–8 mm long in terrestrial *Anthurium* species. There are also exceptions to this pattern. For example, Rockwood (1985) pointed out that in Gesneriaceae epiphytic species actually have significantly larger seeds than do shrubs and herbs. According to Rockwood's (1985) analysis, epiphyte seed size tends to be bimodal; those groups with dust-seeds or other wind-dispersed seeds have the smallest seeds of any habit type while taxa not dispersed by wind have seeds averaging larger than those of herbs, vines, and shrubs, similar to lianas, and only smaller than trees. Nevertheless, since the great majority of epiphytes are wind-dispersed, the epiphyte habit class as a whole is generally characterized by the smallest seeds of any habit class. A dispersal strategy emphasizing many small seeds and chance establishment is typical of the r-selection syndrome often found in weedy species. Epiphytes would seem to be most unusual in being r-selected components of mature forest ecosystems.

POLLINATION

Madison (1977) emphasized animal-pollination as a characteristic trait shared by all angiosperm epiphytes. While true, this is hardly remarkable in a tropical context since, with virtually no exceptions (*Myriocarpon* (pers. obs.), *Trophis* (Bawa et al., 1985), and just possibly *Sorocea* and a few *Chamaedorea* species (fide Bawa et al., 1985)), all lowland tropical forest angiosperms are animal-pollinated. Nevertheless, epiphytes as a whole surely have a more pronounced trend toward highly specific and specialized pollination systems than do nonepiphytes, if for no other reason than that so many epiphytes are orchids. In addition to the well known orchid pollination specializations (e.g., Dodson, 1967; van der Pijl & Dodson, 1966; Williams, this symposium), many aroids have similar Euglossine-attracting scent systems. Five of the largest neotropical orchid genera have specific bee pollinators attracted by specific scents and *Anthurium* is the largest nonorchid genus in the Neotropics. While *Pleurothallis*, the largest neotropical epiphyte genus, does not participate in the presumably speciation-promoting Euglossine-pollination syndrome, it is pollinated by the large and diverse fly genus *Bradesia* (CD, pers. obs.) and similar coevolutionary patterns may be involved; among other small-flowered and inconspicuous but highly diverse orchid genera, *Stelis* and *Lepanthes* are probably pollinated by *Drosophila* and similar flies, and *Telipogon* is pollinated by pseudocopulation with tachinid flies, another very large and diversified insect taxon.

Unique to the Neotropics, hummingbird-pollination is also much more prevalent among epiphytes (and terrestrial herbs) than in trees or free-climbing lianas. Epiphytic taxa among which hummingbird-pollination is prevalent include Ericaceae, Bromeliaceae, Gesneriaceae (especially *Columnea*), Marcgraviaceae (*Norantea*, sensu lato), Rubiaceae (*Ravnia, Manettia*), and Cactaceae (e.g., *Schlumbergera*). The correlation between hummingbird-pollination and epiphytism is well shown by Bignoniaceae. Of the two epiphytic genera of Bignoniaceae, one (*Gibsoniothamnus*) is entirely hummingbird-pollinated and the other (*Schlegelia*) also has several hummingbird-pollinated species; hummingbird-pollination is rare elsewhere in the family. Other specialized pollination systems shown by epiphytes include hawkmoth-pollination in Cactaceae (e.g., *Epiphyllum*) and Rubiaceae (e.g., *Cosmibuena, Hillia*, perhaps *Schradera*), bat-pollination in *Marcgravia* (though most species may be autogamous, Bedell, pers. comm.), and rat-pollination in *Blakea chlorantha* (Lumer, 1980). Perhaps more striking than the diversity of highly specialized pollination systems among neotropical epiphytes is their lack of the small, inconspicuous, generalist-pollinated flowers that characterize the great majority of trees in the wet forests where epiphytes are prevalent. The only epiphytic taxa characterized by such flowers are Araliaceae, Moraceae, Piperaceae, Myrsinaceae, and Urticaceae, the latter two only marginally epiphytic. If hummingbirds, well known as specialist pollinators (Stiles, 1981), are taken as an example, this pattern may be clearly seen at the community level: in lowland tropical forests hummingbird-pollination is almost exclusively confined to herbs and epiphytes.

Another relevant aspect of epiphyte pollination biology is that such phenomena as self-compatibility and autogamy are apparently much more prevalent than typical in tropical lowland taxa. For example seven of seven species of *Blakea, Topobaea,* and *Adelobotrys* tested at Monteverde, Costa Rica were self-compatible (Lumer, 1980; Renner, 1986) vs. 34 of 43 tested terrestrial melastome species in the Manaus area (Renner, 1984). In Marcgraviaceae this is carried to an extreme with all species tested being autogamously pollinated in bud despite the elaborate floral adaptations (Bedell, pers. comm.).

In summary, epiphyte reproductive biology appears to be a unique mix of r-selection and specialization. Unlike other components of mature forest communities, epiphytes share many reputedly r-selected traits with weedy herbs, especially in their dispersal ecology. Yet at the same time most epiphytes have highly specialized pollination systems, strong niche specificity, and many other traits more characteristic of k-selected mature forest species.

DISTRIBUTIONAL PATTERNS

To this point, we may conclude that, although an epiphytic habit has arisen many times during the course of plant evolution, very few higher taxa have been more than marginally successful at speciation and adaptive radiation as epiphytes. However, the few taxa that have successfully radiated as epiphytes have done so very prolifically. Even though remarkably similar numbers of plant families have achieved epiphytism in the Neotropics and Paleotropics, the process of epiphyte speciation would seem to have been much accelerated in the former, to judge from the very many more neotropical species of epiphytes.

We would now like to examine some trends in epiphyte distribution that may help to understand not only neotropical epiphyte biogeography but also some of the continental differences in epiphyte occurrence.

MOISTURE

One of the most striking distributional patterns shown by epiphytes is a tremendous decrease in both numbers of species and individuals in drier habitats. Although this pattern seems obvious, it is by no means well-documented. Indeed Walter (1985: 57) claimed that epiphytes, contrary to such other habit groups as lianas, are found in dry as well as wet tropical forests. At the other extreme, Schimper (1903) suggested that in areas with marked dry seasons epiphytes are either completely wanting or rare and that presence of epiphytes outside the rain forest is always a sign that the dry season is not long or is accompanied by copious dew. Data for 1,000 m^2 samples of western Ecuadorian dry forest (Capeira, 804 mm per year) and moist forest (Jauneche, 1,855 mm) quantify the extent of this difference (Gentry & Dodson, 1987; Table 4, Fig. 1). If our results are indicative, most plants in a wet forest are epiphytes. At Río Palenque such a sample included 4,517 epiphytic plants representing 63% of all individuals sampled. At Capeira a mere ten epiphytic plants were included in a similar sample of dry forest, representing 0.2% of the sampled individuals. The moist forest Jauneche site was intermediate with 116 epiphytes constituting 4% of the individual plants sampled. The difference in epiphyte density between wet and dry forest is almost 500 fold.

Moreover the decrease of epiphyte density in dry forest contrasts greatly with the situation for other habit groups. The number of herbs more than doubles from our moist and wet forest samples to our dry one. Contrary to Walter's assertion (1985: 57), lianas double from wet to dry forest; they are much commoner yet in our moist forest sample, the latter presumably atypical since Jauneche happens to be the most liana-rich site in the Neotropics (of 45 similar samples). Shrub density also increases somewhat from wet to dry forest; unlike lianas, shrubs are only about half as abundant in the intermediate moist forest as in dry and wet forest. In contrast, the number of individual trees ≥10 cm DBH, and thus the apparent density of the forest, changed little (52, 64, and 69 trees ≥10 cm DBH in wet, moist, and dry forest, respectively).

Epiphytes are also important contributors to the species richness of neotropical wet forests. Indeed there are 35 epiphyte species in our 0.1 ha. wet forest sample, accounting for over a third of the sampled species. This compares with only 13 epiphytes (8% of the species) in the comparable moist forest sample and three (2% of the species) in the dry forest one (Fig. 2).

The importance of the epiphytic contribution to species diversity is equally apparent when en-

TABLE 4. Number of species and individuals of different habit types in 1,000 m^2 samples of three forests in western Ecuador. Río Palenque is wet forest, Jauneche is moist forest, Capeira is dry forest (from Gentry & Dodson, 1987).

	Río Palenque				Jauneche				Capeira			
Habit Group	No. Spp.	%	No. Ind.	%	No. Spp.	%	No. Ind.	%	No. Spp.	%	No. Ind.	%
Herbs (incl. palmettos)	50	14	1,220	17	18	11	944	34	50	29	2,854	53
Shrubs	39	11	531	7	16	10	279	10	13	8	742	14
Epiphytes (incl. hemiepiphytes)	127	35	4,517	63	13	8	116	4	3	2	10	.2
Climbers (incl. lianas; excl. hemiepiphytes)	36	10	117	2	58	34	484	17	58	34	895	16
Lianas ≥2.5 cm (excl. herbaceous + hemiepiphyt.)	12	3	28	.4	43	25	124	4	19	11	58	1
Total tree spp. (incl. juven.)	114	31	653[1]	9	64	38	960	34	48	28	927	17
Trees <2.5 cm DBH (= saplings + seedlings)	87	24	559[1]	8	48	28	672	24	38	22	750	14
Trees ≤10 cm, ≥2.5 cm	86	24	217	3	35	21	245	9	32	18	108	2
Trees ≥10 cm DBH	32	9	52	1	30	18	64	2	29	17	69	1
Total herbs (epiphytes + herbs—woody epiphytes)	162		5,525		31		1,060		53		2,864	
Shrub layer (shrubs + saplings)	126		1,090		65		948		51		1,492	
Underlayers (< ca. 3 m) (herbs + shrubs + saplings)	176		2,310		83		1,892		101		4,346	
Total	365		7,210[1]		169		2,783		173		5,428	

[1] Excluding dense patch of 123 *Quararibea asterolepis* seedlings.

tire florulas are compared (Table 5, Fig. 3). Almost one fourth of all the Río Palenque plant species are epiphytes (Dodson & Gentry, 1978). Similarly, in another lowland wet forest at La Selva, Costa Rica, 25% of the species are epiphytes (Hammel, pers. comm.). Even in moist forest sites like Barro Colorado Island, Panama (Croat, 1978) and Jauneche, Ecuador (Dodson et al., 1985), epiphytes constitute 12–16% of the total flora. Only in dry forests are epiphytes relatively insignificant, accounting for 2–4% of the species of Capeira (Dodson & Gentry, 1987) and Santa Rosa National Park, Costa Rica (Janzen & Liesner, 1980).

We conclude, contrary to Walter (1985), that epiphytes decrease more drastically in drier areas than does any other habit group, but contrary to Schimper's (1903: 198) emphasis, a few vascular epiphytes are characteristically present in even the driest neotropical forests (e.g., Capeira with 804 mm of annual precipitation).

Familial makeup of the epiphytic flora also changes with precipitation (Table 6). Many more families have epiphytic representatives in wet forests than in drier ones (Fig. 4), and many epiphytic taxa are confined entirely to wetter forests. In the Neotropics the same families tend to be represented by epiphytes under similar climatic conditions. In the driest forests, the only epiphytes are orchids and bromeliads, perhaps the two most specialized epiphytic families. Ferns, peperomias, and Cactaceae join orchids and bromeliads in slightly moister conditions. The next epiphytic families to appear with increasing humidity are aroids, Moraceae (stranglers), and Gesneriaceae, joining representatives of all the dry forest families, each of whose number of epiphytic species is maintained or increased. The two local florula sites with over 2,500 mm of precipitation, Barro Colorado Island (Croat, 1978) and Río Palenque (Dodson & Gentry, 1978), have remarkably similar epiphytic floras. The same seven epiphytic families are most species rich at both sites, in roughly the same

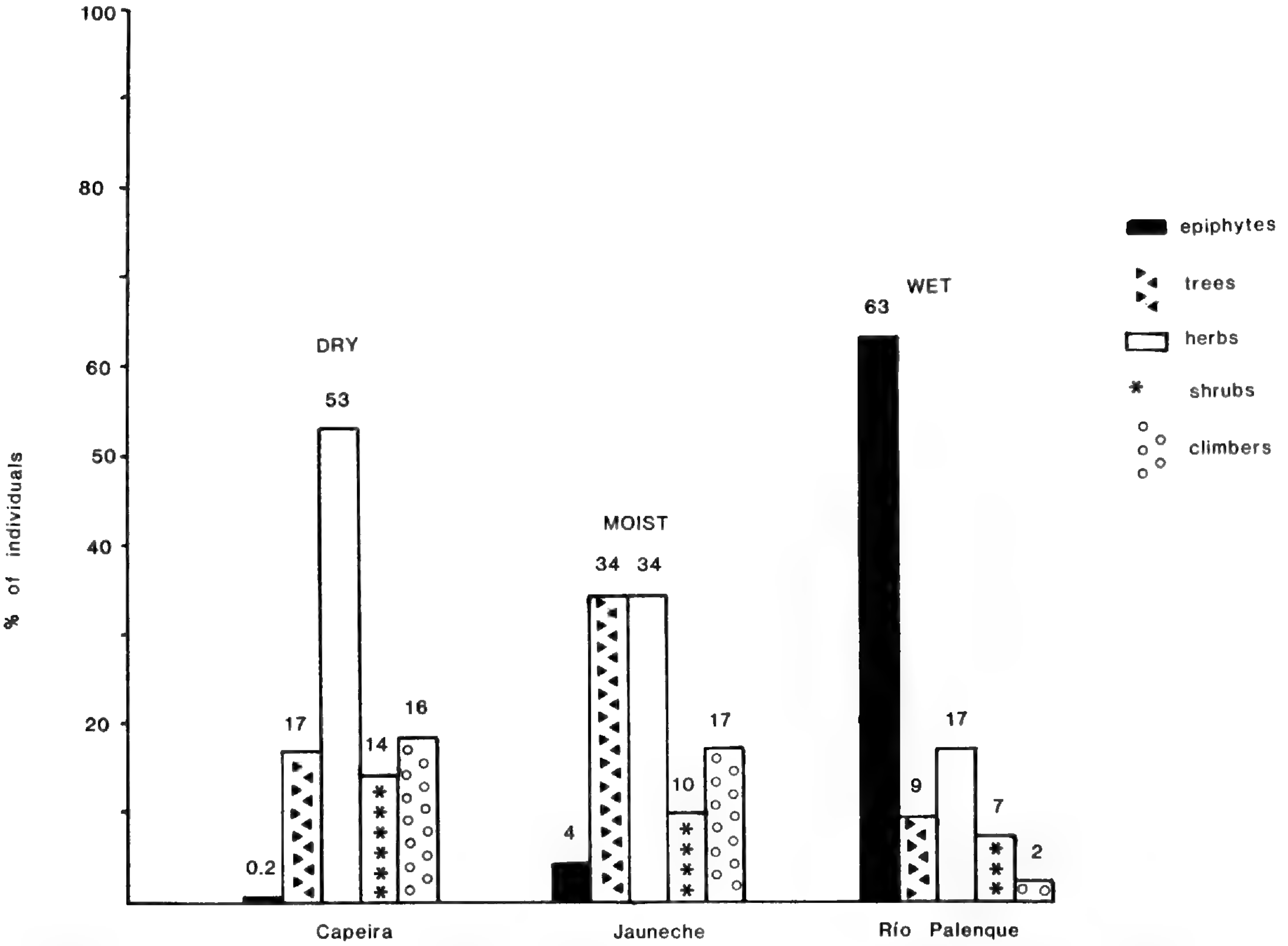


FIGURE 1. Percent of individual plants belonging to different habit groups in 1,000 m² samples of three western Ecuadorian forests.

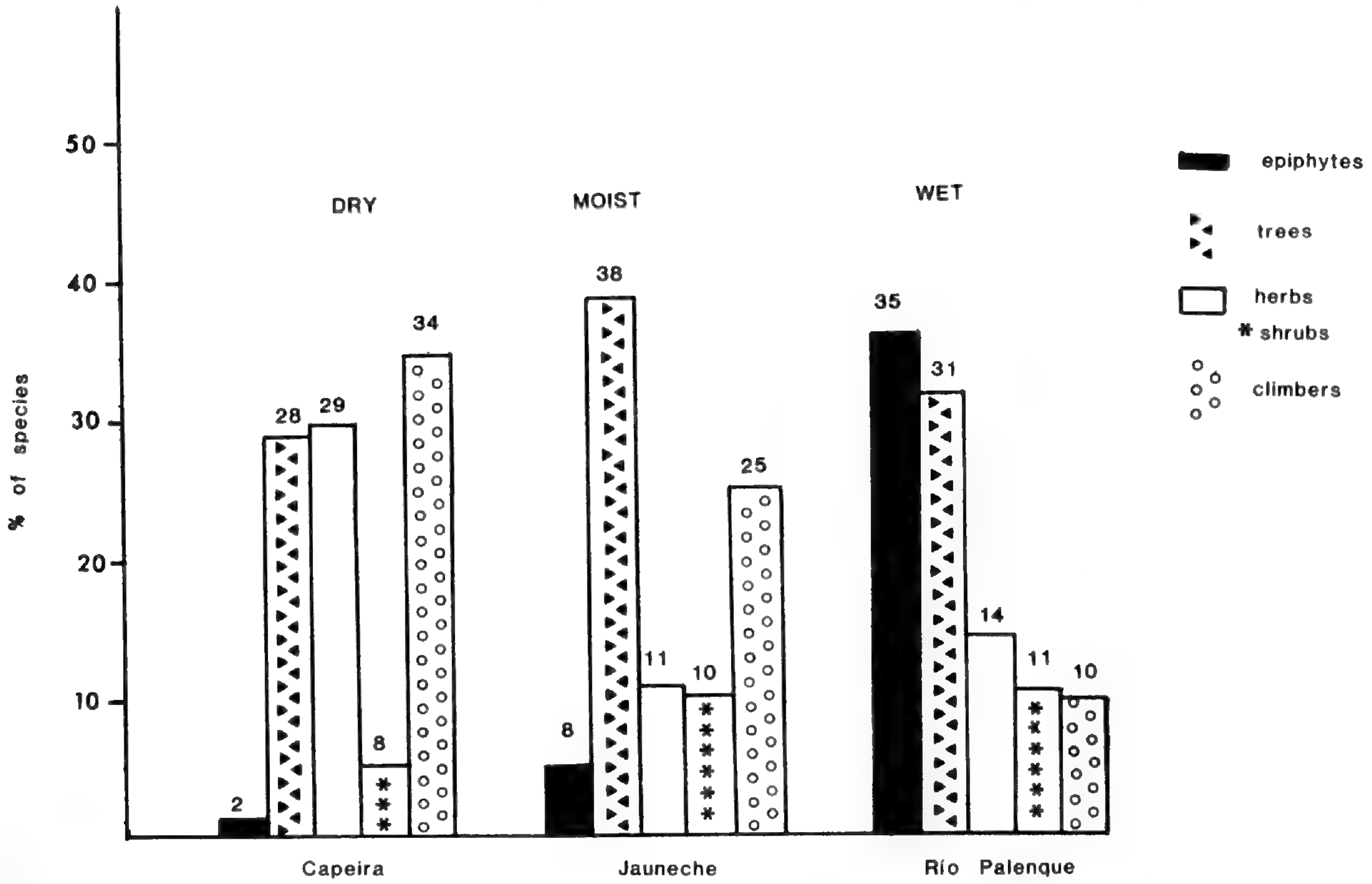


FIGURE 2. Percent of species belonging to different habit groups in 1,000 m² samples of three western Ecuadorian forests.

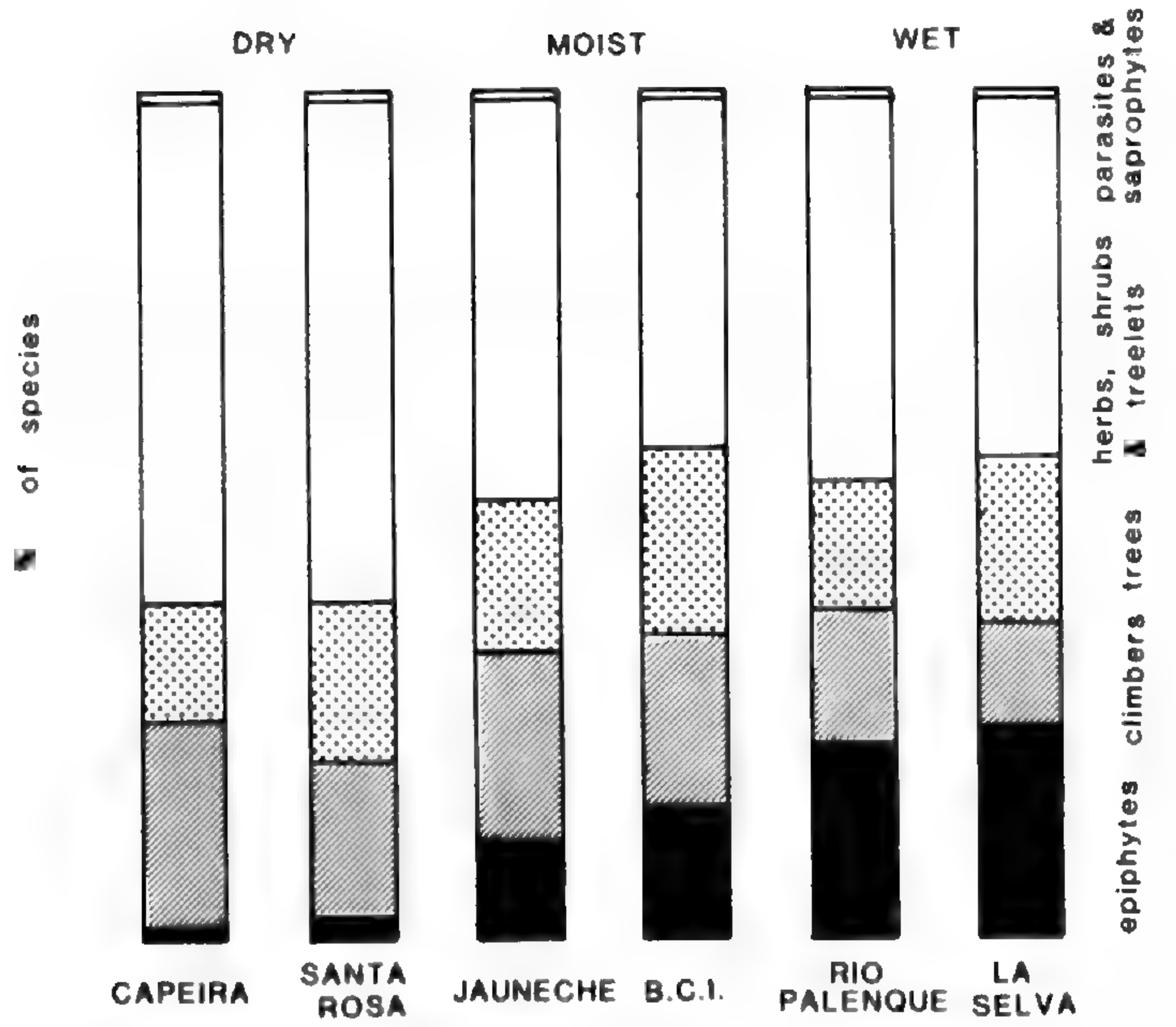


FIGURE 3. Percent of species in local florulas belonging to different habit groups.

order, just as they are in Hammel's unpublished La Selva, Costa Rica, species list. Remarkably, there are 81 epiphytic species of orchids at Río Palenque and 82 at Barro Colorado Island (BCI), 35 epiphytic aroids at Río Palenque vs. 30 at BCI, 18 species of epiphytic Bromeliaceae, and 14 species of epiphytic or strangler Moraceae at both sites. Only epiphytic ferns and fern allies are noticeably better represented at BCI than at Río Palenque and only epiphytic Gesneriaceae and Cyclanthaceae show the reverse pattern. Both sites have three epiphytic cacti and one epiphytic melastome plus one or two epiphytic Araliaceae, Solanaceae, and begonias. Only Rubiaceae and Saxifragaceae have epiphytic members at BCI but not Río Palenque; only Urticaceae, Polemoniaceae, Bignoniaceae, and Ericaceae have epiphytic representatives in the Río Palenque flora but not the Barro Colorado one.

Again, the same epiphyte families predominate at other wet sites in western Ecuador (Table 7). The exact same seven most species rich families at BCI, La Selva, and Río Palenque are the most species rich at Centinela, again in roughly the same order. Even at Tenafuerste (alt. 1,000 m) the five families richest in epiphytes are exactly the same ones that are most species rich at the other Ecuadorian wet forest sites.

At the extreme wet end of the precipitation gradient there are other, as yet unquantified, changes in the epiphytic flora. In the wetter part of Chocó (precipitation > 8,000 mm) berry-fruited epiphytes like Melastomataceae, Araceae, Marcgraviaceae, and Ericaceae, along with arillate-seeded Guttiferae, appear to predominate to a much greater degree than at Río Palenque, while ferns (Sota, 1972) and dust-seeded orchids are more poorly represented. Possibly this change is related to the inability of dust-seeds to establish themselves in the face of such superabundant rainfall.

There is also a noticeable habit change in the epiphytic flora of the wettest sites. Most of the predominant Chocó epiphytic families are actually hemiepiphytic, many of them woody as well. In the same sites with abundant hemiepiphytes, free-climbing lianas become noticeably less prevalent. While the average of climbers ≥ 2.5 cm in diameter for 0.1 ha. samples at two pluvial forest sites in the Colombian Chocó was exactly the same (68) as that for a series of 20 similar samples from neotropical lowland moist and wet forests, half the sampled pluvial forest climbers were hemiepiphytic vs. an average of

TABLE 5. Habit compositions of complete local florulas. Capeira, Ecuador and Santa Rosa National Park, Costa Rica, are dry forest; Jauneche, Ecuador and Barro Colorado Island, Panama, are moist forest; Río Palenque, Ecuador, is wet forest.

	Capeira		Santa Rosa		Jauneche		Barro Colorado		Río Palenque	
Habit Category	No.	%	No.	%	No.	%	No.	%	No.	%
Trees ≥10 cm DBH	69	15	141	21	112	18	290	22	165	16
Small trees + large shrubs	28	6	64	10	60	10	151	11	99	9
Herbs + subshrubs	242	52	317	48	224	37	389	30	376	36
Epiphytes (including stranglers)	9	2	24	4	72	12	216	16	238	23
Parasites and saprophytes	4	1	6	1	4	1	12	1	6	1
Lianas	46	10	52	8	81	13	149	11	87	8
Small vines	66	14	63	9	55	9	109	8	84	8
Total species	464		667		608		1,316		1,055	

TABLE 6. Familial composition of epiphyte floras in lowland forests with different precipitations.

Family	La Selva, Costa Rica[1] 4,000 mm	Río Palenque, Ecuador[2] 2,980 mm	Barro Colorado, Panama[3] 2,750 mm	Jauneche, Ecuador[4] 1,855 mm	Santa Rosa, Costa Rica[5] 1,550 mm	Capeira, Ecuador[6] 804 mm	Makokou, Gabon[7] 1,755 mm
Orchidaceae	109	81	82	33	8	5	21
Araceae	76	35	30	10	—	—	10
Ferns and allies	59	28	43	5	7	—	26
Piperaceae	12	19	10	4	1	1	—
Bromeliaceae	29	18	18	6	3	2	—
Moraceae	13	14	14	9	2	—	7+
Gesneriaceae	16	12	4	2	—	—	—
Cyclanthaceae	11	8	1	—	—	—	—
Marcgraviaceae	8	5	2	—	—	—	—
Guttiferae	11	4	2	—	—	—	—
Cactaceae	6	3	3	3	3	1	1
Ericaceae	2	3	—	—	—	—	—
Araliaceae	2	2	1	—	—	—	1
Bignoniaceae	3	2	—	—	—	—	—
Melastomataceae	2	1	1	—	—	—	—
Polemoniaceae	—	1	—	—	—	—	—
Solanaceae	1	1	2	—	—	—	—
Urticaceae	1	1	—	—	—	—	—
Begoniaceae	2	1	1	—	—	—	—
Rubiaceae	4	—	1	—	—	—	—
Saxifragaceae	—	—	1	—	—	—	—
Commelinaceae	1	—	—	—	—	—	—
Total epiphytes	368	238	216	72	24	9	66+
Percent of flora	24	23	16	12	4	2	6+
No. families with epiphytes	20	18	17	8	6	4	6

[1] B. Hammel, pers. comm.
[2] Dodson & Gentry, 1978.
[3] Croat, 1978.
[4] Dodson et al., 1985.
[5] Janzen & Liesner, 1980.
[6] Dodson & Gentry, 1987.
[7] Hladik & Gentry, in prep.; Florence & Hladik, 1980 and cited references.

2.7 hemiepiphytic climbers sampled at the moist and wet sites (Gentry, 1986). In a sense, hemiepiphytic climbers seem somehow to replace free-climbing lianas in the wettest lowland forests and also in middle elevation cloud forests.

ALTITUDINAL

The epiphytic flora also changes in both diversity and composition on an altitudinal gradient. The general tendency is for epiphytes to be better represented in intermediate elevation cloud forests. In the Andes the peak in epiphyte diversity appears to be between 1,000 m and 2,000 m, but it lies somewhat lower in Costa Rica and Panama. Few data are available, but a comparison of incomplete data sets for several Ecuadorian sites (Table 7) documents this trend for the lower part of the gradient. The sites for which relevant data are available are Centinela (600 m) and Tenafuerste (1,000 m), both on the western slopes of the Central Ecuadorian Andes, and Mera (1,000 m) on the eastern slope. Of the well-documented sites, Centinela has the most species of epiphytes, 337, or 35% of the flora. This compares with 238 epiphyte species accounting for 23% of the flora at nearby Río Palenque (alt. 200 m). The data for the two 1,000 m sites are less complete, with many species remaining to be discovered. Tenafuerste, with much less cloud forest effect than Centinela or Mera, has the poorest epiphyte representation, only 31% of the flora. The extreme is pluvial Mera where few collections have been made as yet. Three

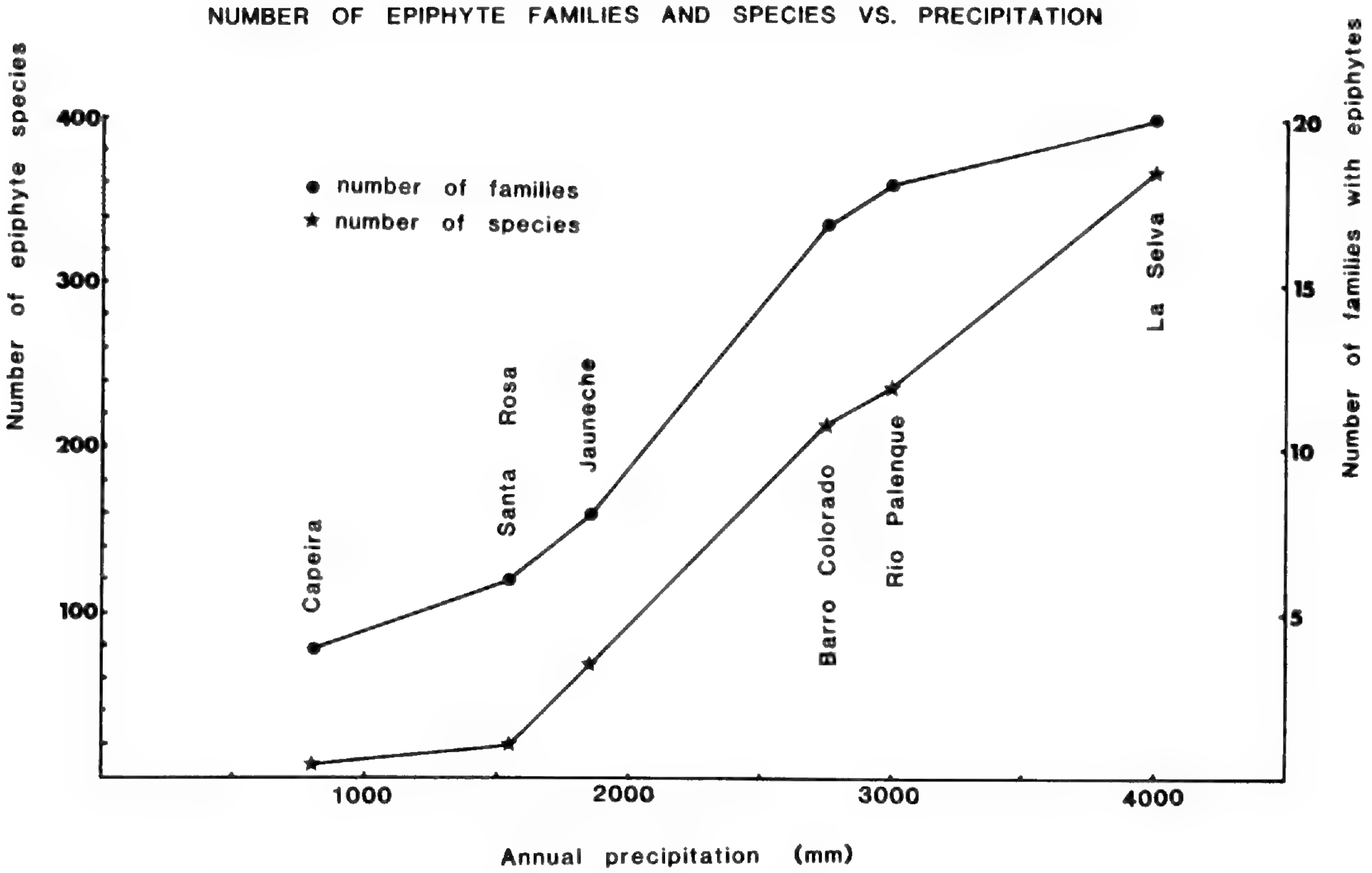


FIGURE 4. Increase in numbers of epiphyte species and families in local florulas as a function of precipitation.

hundred twenty-two orchid species are already known and we expect that there may be as many as 200 additional epiphytes as well.

In contrast, Peru's Huascarán National Park, 3,500–5,000 m in altitude, has only seven epiphytic species, constituting a mere 1% of the park's flora (Smith, pers. comm.).

The differences between Mera and Tenafuerste point out that altitudinal and moisture effects on epiphytes are complexly interrelated. Similarly Gilmartin (1973) showed that the 17 species of Bromeliaceae that occur on both sides of the Ecuadorian Andes occur at lower altitudes on the moister eastern slopes.

Density of epiphytes, although also greatest at intermediate altitudes, does not closely parallel diversity; although unquantified, we feel that epiphyte density in the Andes tends to be greatest around 2,000–2,500 m, again occurring at somewhat lower elevations in Costa Rica and Panama. Due to the high densities, epiphytes are often most conspicuous at these relatively high altitudes, even though relatively few species may be present. In middle elevation cloud forests, epiphytes may make up as much as 30% of the foliar biomass and 45% of the foliar mineral capital of a forest (Nadkarni, 1984).

Contrary to what happens along the moisture gradient, familial composition of the epiphyte flora changes very little along an altitudinal gradient, or at least on that part of it for which we have data. The same families are important in roughly the same order. The seven families with the most epiphyte species at Centinela (600 m) are the same seven that have the most species at Río Palenque (200 m). The five families with the most species at Tenafuerste (1,000 m) are the same five that have the most species at Río Palenque and Centinela. The most noteworthy difference between these sites is the absence of Moraceae stranglers at Tenafuerste; Gesneriaceae are also conspicuously less diverse at the 1,000 m Tenafuerste site but Ericaceae are more diverse (nine species vs. three at Río Palenque). Melastomataceae is another family that has notably more epiphyte diversity at intermediate altitudes (four spp. at Centinela and two at Tenafuerste but only one at Río Palenque; see also Renner, 1986). A few families (e.g., Bignoniaceae) disappear from the middle elevation epiphyte flora and most other families have decreasing numbers of epiphytes at higher elevations.

Our only high altitude data set is for Huascarán National Park, Peru (Smith, pers. comm.), where the seven epiphyte species, all restricted to the lower part of the park between 3,500 and

4,000 m, belong to four families. The four families with epiphytes—Piperaceae, Bromeliaceae, Orchidaceae, and ferns—are all in the top five epiphytic families in the wet Ecuadorian sites. Of the usually prevalent epiphyte families, only Araceae is lacking. Perhaps more interesting, the epiphyte families at Huascarán are exactly the same ones that are represented at Santa Rosa, Costa Rica, except that Cactaceae is missing. Apparently at environmental extremes, either altitudinal or precipitational, only these same families that are otherwise most successful as epiphytes are able to survive.

The very interesting but controversial suggestion has been made that in the tropics diversity is generally greatest at middle elevations along an altitudinal gradient. This has been shown for leaf litter herps (Scott, 1976), insects (Janzen, 1973; Janzen et al., 1976), and suggested for plants. Greater equability is a likely controlling factor for this putative "mid-elevation bulge" in species diversity. However, data for 0.1 ha. samples of plants ≥2.5 cm DBH suggest that plant species diversity decreases more or less uniformly from the most diverse lowland wet forest sites to the least diverse high altitude ones (Gentry, 1982a, 1987c). If a mid-altitude bulge in plant species richness really does occur, it must be due largely to epiphytes. Unfortunately our data sets from middle and upper elevation forests are too incomplete to be definitive. Indeed one of us (CD) thinks that because of the increase in epiphytes there are more plant species at middle elevations than in lowland tropical forest while one of us (AG) thinks that the decrease in species numbers of such other habit groups as lianas and trees with altitude outweighs the increased number of epiphytes. In either case the role of epiphytes in the plant community is presumably greatest in middle elevation forests.

TABLE 7. Familial composition of epiphyte floras in wet forests at different altitudes in Ecuador.

Family	Río Palenque 200 m	Centinela 600 m	Tenafuerste 1,000 m
Orchidaceae	81	133	68
Araceae	35	52	26
Ferns	28	38	28
Piperaceae	19	19	11
Bromeliaceae	18	23	18
Moraceae	14	10	—
Gesneriaceae	12	16	8
Cyclanthaceae	8	5	3
Marcgraviaceae	5	3	2
Guttiferae	4	9	3
Cactaceae	3	2	1
Ericaceae	3	9	9
Araliaceae	2	4	—
Bignoniaceae	2	2	—
Melastomataceae	1	4	2
Polemoniaceae	1	1	—
Solanaceae	1	2	1
Urticaceae	1	1	1
Acanthaceae	—	1	—
Rubiaceae	—	1	—
Total	238	337	181
Percent of flora	23	35	31

SOIL FERTILITY

To our knowledge no attempt to relate epiphyte diversity to soil fertility has been made previously. Indeed one might suppose that since epiphytes are intrinsically "insulated" from direct dependence on soil nutrients they would be relatively unaffected by changes in soil fertility. For example, Janzen (1974a) discussed the symbiotic relationships between several epiphytes and ants in low-diversity poor soil "kerangas" habitats in Borneo, with the implication that epiphytes are unusually well represented in such habitats. Whitmore (1984) also emphasized the frequency of epiphytes in these forests.

It is increasingly well-documented that major changes in the diversity and floristic composition of other components of tropical plant communities are associated with changes in soil fertility (e.g., Ashton, 1976, 1977, 1978; Huston, 1979, 1980; Gentry, 1987b; Gentry & Emmons, 1987). For example, there are generally fewer tree, liana, and terrestrial herb species in neotropical forests on poorer soils (Gentry, 1981; Gentry & Emmons, 1987). We have few data with which to relate epiphyte community composition to soil fertility. One of us (AG) has compiled species lists for a series of sites on different substrates in the Iquitos, Peru, area which share a similar rainfall and climatic regime. Of these, the site with the poorest soil (Mishana, on almost pure white sand) has the fewest epiphytes (31 epiphyte species plus a few "indets." in a relatively intensively inventoried area vs. 38 identified and many unidentified at less intensively studied better-soil Yanamono), suggesting that epiphyte diversity varies with soil fertility as does the diversity of other habit groups. However, to date the sampling of epiphytes at these sites has been much less intensive than at our Ecuadorian local florula sites and is probably too haphazard and incomplete to make these data very meaningful.

Data are also available for understory composition and levels of flowering and fruiting for a broad array of neotropical (and paleotropical) sites (Gentry & Emmons, 1987). If the data for epiphytes are extracted from that data set, a very strong reduction in numbers of fertile species of understory epiphytes on poorer soils is apparent, paralleling the overall trend of decreased numbers of flowering and fruiting understory species on the same gradient. Our data for habit composition of the understory suggest that epiphytes, like terrestrial herbs, are especially sensitive to loss of soil fertility: as soil fertility decreases, terrestrial herbs, epiphytes, understory shrubs, and lianas disappear from the understory in that sequence, leaving virtually only tree saplings and seedlings in the most severely stressed forests (Gentry & Emmons, 1987).

Anecdotal evidence also indicates that epiphytes are much less diverse and abundant on poor soils. We have observed many fewer epiphytes in poor soil parts of Central Amazonian Brazil, southern Venezuela, and elsewhere in the Guiana shield area than in parts of the Neotropics with richer soils. Large-scale biogeographical analysis also indicates that epiphytic taxa are poorly represented in these areas compared with richer soil areas nearer the Andes and in Central America (Gentry, 1982b). In a somewhat different context, Janzen (1977) has suggested that the paucity of epiphytes in dipterocarp forests results from the generally nutrient-poor Southeast Asian soils. Among the evidence for this hypothesis cited by Janzen (1977) is the observation that trees cultivated in Malesia along roads, where dust stirred up by passing vehicles increases the nutrients available to epiphytes in an otherwise unusually poor-soil situation, have relatively large epiphyte loads compared with the native forests.

On balance it seems clear that the epiphytic plant community is very sensitive to soil fertility, with fewer epiphytes and fewer epiphytic species in forests on poorer soils. Indeed epiphyte diversity may be even more sensitive to change in soil fertility than is tree or liana diversity, a suggestion that would accord with the idea (Gentry & Emmons, 1987) that plants (presumably including epiphytes despite their lack of direct contact with the soil) that are barely able to eke out a marginal existence should be more susceptible to the effects of relatively slight decreases in environmental favorability.

LATITUDE

It is well known that the presence of vascular epiphytes is a characteristic of tropical forests as compared with temperate ones. We know of only four vascular epiphytes that occur north of Florida in the temperate United States—*Tillandsia usneoides, T. recurvata* (only in southernmost Arizona), *Epidendrum conopseum,* and *Polypodium polypodioides.* Even *Tillandsia usneoides,* the northernmost vascular epiphyte, does not reach the Mason-Dixon line. The only continental United States epiphyte species that is not widespread in the tropics is *Tillandsia simulata* Sm., endemic to Central Florida but sometimes lumped with *T. bartramii* Ell. (The Mexican range of *Epidendrum conopseum* is also somewhat limited.) Even in very wet areas that would be full of epiphytes in the tropics, only lower plants have adopted the epiphytic habit. In intermediate subtropical areas a gradient of increasing epiphytism at lower altitudes is evident. The decrease in vascular epiphytes with increasing latitude can be clearly seen in Florida where subtropical South Florida (latitude 25°N) has 46+ (= 2.8%) epiphytic species (Long & Lakela, 1971), Central Florida has 41 (= 1.9%) (Wunderlin, 1982), and Florida Caverns State Park in northern Florida (30°50′N latitude) has only two (= 0.4%), *Tillandsia usneoides* and *Polypodium polypodioides* (Mitchell, 1963).

Curiously, the decrease in vascular epiphytes with increasing latitude is not symmetrical on both sides of the equator. A number of epiphytic species and even a few endemic genera of epiphytes occur in south temperate forests. Endemic temperate South American epiphytic genera include the monotypic fern *Synammia,* the monotypic cactus *Pfeiffera,* three monotypic Gesneriaceae genera (*Asteranthera, Sarmienta,* and facultatively epiphytic *Mitraria*), and the Liliaceae (or Philesiaceae) *Luzuriaga* and *Philesia.* In the Australasian region, New Zealand is especially noteworthy for its autochthonous epiphytes including genera like the monotypic fern *Anarthropteris,* the liliaceous *Collospermum* (also reaching Fiji and Samoa), the only epiphytic species of families like Cunoniaceae (with two different genera having epiphytic members), and genera like *Microlaena* (Gramineae) and *Metrosideros* (Myrtaceae). There is even a largely epiphytic south temperate family shared by New

Zealand and Southern Argentina–Chile—Griseliniaceae (sometimes included in Cornaceae). In the north the only noteworthy temperate epiphytes are in the Himalayas where aberrant epiphytic species of otherwise terrestrial genera like *Ilex, Tripogon, Euonymous, Sedum,* and *Thalictrum* occur. This latitudinal asymmetry was already noted by Schimper (1903), who pointed out that north temperate epiphytes are merely range extensions of widespread tropical species, whereas many unusual and distinctive epiphytic taxa occur in the South Temperate region.

At the community level the same trend is apparent. For example, Parque Nacional El Rey in Argentina, at 24°45′S latitude, has a species list (L. Malmierca, pers. comm.) of well over 500 vascular plants including 47 species of epiphytes: 20 ferns, four orchids, three species of *Rhipsalis* and *Peperomia,* and no fewer than 17 bromeliads including 14 tillandsias. In contrast, Florida Caverns State Park at 30°50′N latitude has only two epiphytes in its similar-sized flora of 485 native species (Mitchell, 1963). Even in rather dry south temperate vegetations vascular epiphytes can be extremely prevalent, a situation apparently without parallel in the North Temperate region. For example, in the Valley of Lerma near Salta, Argentina (1,200 m, ca. 700 mm ppt.), there are at least 14 angiosperm epiphytes including at least ten *Tillandsia* species in a flora of over 750 species (Novara, 1984).

Farther south in the Valdivian region of Chile vascular epiphytes, mostly belonging to endemic genera, are conspicuous elements of local floras, ranging from six species (3% of the native flora) at relatively dry Parque Nacional Tolhuaca (38°15′S) (Ramírez, 1978) to 17 species (17% of the native flora) at very wet Fundo de San Martín (39°30′S) (Cárdenas, 1976; Riveros & Ramírez, 1978); even at 41°S there are 15 vascular epiphyte species in Puyehue National Park (Muñoz, 1980). New Zealand forests have even more epiphytes than the Chilean ones; even well south of 40°S, about 30 vascular epiphytes are typically included on local species lists (Dawson, 1980). However, at comparable latitudes in North America there are no vascular epiphytes.

Why there are more, and more distinctive, epiphytes in south temperate than in north temperate forests is unclear but presumably relates to the relatively mesic, more or less oceanic climates that prevail in the Southern Hemisphere. There are more epiphytes at 25°S (47 epiphytes constituting ca. 8.5% of the flora of Parque El Rey, L. Malmierca, pers. comm.) as compared with 25°N (46 epiphytes constituting ca. 2.8% of the South Florida flora, Long & Lakela, 1971). At least in South America, the prevalence of many species of the genus *Tillandsia* in southern forests (e.g., 14 at Parque El Rey), perhaps due purely to biohistorical reasons, is another important factor. A similar pattern occurs with lianas, which are better represented in New Zealand than in north temperate forests (Dawson, 1980).

CONTINENTAL TRENDS

There are several conspicuous differences between the epiphytic floras of different continents. Obviously, predominantly extratropical continents have few vascular epiphytes. However, there are also striking differences within the tropics between the Neotropics, tropical Africa, and tropical Australasia. The African epiphytic flora has been widely noted to be very impoverished compared with the other two regions, presumably reflecting a loss of mesic-adapted species during the dry periods associated with the Pleistocene glacial advances at higher latitudes (Richards, 1973; Madison, 1977). According to Madison there are only ca. 2,400 epiphytic species in Africa, less than a sixth as many as in the Neotropics and a quarter as many as in tropical Australasia. Even though several families and genera with epiphytes in Madagascar were omitted from Madison's (1977) epiphyte summary (see Appendix), their inclusion does not appreciably increase the number of African epiphyte species.

Curiously, the depauperate nature of the African epiphytic flora is not obvious at the community level. For example, the 59 epiphyte species at Makokou, Gabon, constitute 5% of the total Makokou flora (Table 8; compiled from Hladik & Gentry, in prep.; Florence & Hladik, 1980, and included references). While 5% of a moist forest flora might seem fewer epiphytes than would be expected in the Neotropics, Makokou is quite dry, with only 1,785 mm of annual rainfall, and its 66 (6%) epiphytic species (including stranglers) are quite in line with the 72 (12%) epiphytic species at Jauneche and 24 (4%) at Santa Rosa (Table 9). Johansson (1974) studied a relatively moist region in the Nimba mountains of northern Liberia and reported 153 vascular epiphyte species (excluding six filmy ferns and 23 "facultative" epiphytes) in his study area, up to 44 species in a single 750 m plot, and up to 22 species on a single tree. In even wetter areas

TABLE 8. Habit distributions of Makokou, Gabon plant species.

Habit	Ferns	Gymnosperms	Monocots	Dicots	Total
Epiphytes	26	0	31	2	59
Parasites + saprophytes	0	0	3	6	9
Climbers	1	2	8	248	259
Trees	0	0	5	390	395
Herbs, shrubs, and treelets	42	0	125	251	418
Total species	69	2	172	897	1,140

like southwestern Cameroon epiphytes are almost as prevalent as in many similar areas of the Neotropics (AG, pers. obs.).

That tropical Australasia is also floristically impoverished with respect to the Neotropics has only recently been realized (Raven, 1976; Gentry, 1982b). Epiphytes account for much of the overall difference between the two regions with half again as many epiphytes in the Neotropics as in Australasia (15,500 vs. 10,200) according to Madison's (1977) figures. Moreover, at least in those lowland Asian forests we have visited, there also seem to be many fewer epiphytic individuals than in comparable neotropical forests. Richards's (1936) remark is typical: "One of the most striking features of the Sarawak rain forest, especially when compared with that of tropical South America, is the poverty of the epiphytic vegetation both in species and individuals." Madison suggested that the fewer tropical Asian epiphytes might stem simply from lack of the extensive cloud forest habitats of the Neotropics, but that would hardly explain the lower numbers of individuals in comparable lowland forests. Janzen (1974b, 1977) emphasized that many tropical Asian forests tend to have relatively nutrient-poor soils, and, if so, our suggestion of a positive correlation between epiphytes and soil fertility might help explain the relatively low epiphyte diversity and biomass in tropical Asia.

Another important continental level difference in epiphytes is taxonomic. Orchids and ferns are the predominant vascular epiphytes nearly everywhere, but the other elements of the epiphytic flora are often very different on different continents (Table 10). Johansson (1974) generalized that the African epiphytic flora is made up almost entirely of pteridophytes and orchids, whereas these groups are joined by bromeliads and Cactaceae as important epiphytic taxa in South America and by Asclepiadaceae and Rubiaceae in Southeast Asia. Although there are 18 seed plant families with epiphytic species only in Australasia and 15 with epiphytes only in the

TABLE 9. Representation of different habits in local florulas.

	Capeira		Santa Rosa		Jauneche		Barro Colorado		Río Palenque		La Selva[1]		Makokou	
Habit	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Epiphyte (incl. stranglers)	8	2	19	3	72	12	216	16	238	23	368	25	66+	6+
Parasites + saprophytes	4	1	6	1	4	1	12	1	6	1	8	1	9	1
Climbers	112	24	115	18	136	22	258	20	171	16	182	12	259	23
Trees ≥ 10 cm DBH	69	15	142	21	112	19	290	22	165	16	310	21	389	34
Terrestrial herbs, shrubs, treelets	270	58	381	58	280	47	540	41	475	45	622	42	418	37
Total species	463		667		604		1,316		1,055		1,490		1,140	

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

TABLE 10. Taxonomic distribution of epiphytic taxa in some lowland florulas.

	Ferns		Monocots			Dicots			Total	
Site	No. Spp.	%	No. Fam.	No. Spp.	%	No. Fam.	No. Spp.	%	No. Spp.	%
Neotropics										
Capeira, Ecu.	—	—	2	7	88	2	2	22	9	2
Santa Rosa, C.R.	7	29	2	11	46	3	6	25	24	4
Jauneche, Ecu.	5	7	3	49	68	4	18	25	72	12
Barro Colorado, Pan.	43	20	4	131	61	12	42	19	216	16
Río Palenque, Ecu.	28	12	4	142	60	14	69	29	238	23
La Selva, C.R.	59	16	5	226	61	15	83	23	368	25
Africa										
Makokou, Gabon	26	44	2	31	53	3	9+	3	66+	6+
Asia										
Flora of Java	200	24	3	520	63	11	109	13	829	—

Neotropics (in the case of Campanulaceae there are also 11 Hawaiian species), Africa has only one family uniquely epiphytic. That family, Costaceae, is a dubious segregate of Zingiberaceae, the latter with epiphytes in Asia. At least nine seed plant families have epiphytic species in both the Neotropics and Australasia (but not Africa), but not a single one has epiphytes in both the Neotropics and Africa-Madagascar but not Australasia. There are 14 families with epiphytic species in all three of the world's main tropical regions. In total there are 33 (or 34 if Costaceae is segregated) families with epiphytes on only one continent as compared with 23 with epiphytes on more than one continent: clearly most seed plant families have epiphytes on only a single continent.

Many of the "epiphytic" families included in the above analysis are actually terrestrial families with one or two aberrant species adapted to epiphytism. There are only 32 seed plant families with five or more epiphytic species. If the continental representations of these 32 families are compared, seven (Bromeliaceae, Cyclanthaceae, Rapateaceae, Bignoniaceae, Campanulaceae, Marcgraviaceae, and Guttiferae) have epiphytes only in the Neotropics; six (Myrtaceae, Nepenthaceae, Pittosporaceae, Loganiaceae, Balsaminaceae, and Zingiberaceae, sensu stricto) have epiphytes only in Australasia; 14 have epiphytes in all three tropical regions; and five (Asclepiadaceae, Ericaceae, Rubiaceae, Solanaceae, and Urticaceae) have epiphytes only in the Neotropics and Australasia.

Put another way, there are 42 neotropical seed plant families with epiphytes (Table 3) but epiphytism is minimal in 19 of these (one to four epiphytic species in the Neotropics). Of the families with at least five epiphytic species in the Neotropics, seven—Bromeliaceae, Cyclanthaceae, Rapateaceae, Campanulaceae (also in Hawaii), Bignoniaceae, Marcgraviaceae, Guttiferae—are epiphytic exclusively in the Neotropics, and another, Cactaceae, has only one epiphytic species widespread in the Paleotropics. Fourteen of the families with some neotropical epiphytic species have epiphytes in all three tropical regions—Araceae, Orchidaceae, Liliaceae, Araliaceae, Begoniaceae, Compositae, Crassulaceae, Gesneriaceae, Lentibulariaceae, Melastomataceae, Moraceae, Myrsinaceae, Piperaceae (plus, marginally, Cactaceae). In addition to exclusively south temperate Griseliniaceae and Philesiaceae, seven families—Gnetaceae, Burmanniaceae, Asclepiadaceae, Ericaceae, Rubiaceae, Solanaceae, Urticaceae—have epiphytes only in the Neotropics and Australasia.

The sharing of epiphytic taxa between Australasia and the Neotropics but not with Africa is a very different pattern from that normally found in angiosperms, where close floristic relationships between Africa and the Neotropics (reflecting a shared early angiosperm Gondwanan flora, Raven & Axelrod, 1974) or between Africa and tropical Asia (reflecting the relatively direct migration route provided by today's geography) are the general rule.

Even within the same family paleotropical and neotropical epiphytes are often not closely related. For example, the paleotropical epiphytic

Gesneriaceae belong to subfamily Cyrtandroideae while neotropical ones are mostly in the endemic subfamily Gesnerioideae (Wiehler, 1983). Madison (1977) noted that epiphytism has arisen independently in at least three different groups of aroids. Most epiphytic neotropical orchids belong to subtribes Pleurothallidinae, Maxillarinae, and Oncidinae, while most paleotropical ones belong to Dendrobiinae and Bulbophyllinae. The few epiphytic Central American species of *Cynanchum* are quite unrelated to the many paleotropical epiphytic species of Asclepiadaceae. Most epiphytic neotropical Ericaceae belong to subfamily Vaccinioideae, half the paleotropical ones to Rhododendroideae. Most epiphytic neotropical Rubiaceae belong to tribe Cinchoneae (subfamily Cinchonioideae), most paleotropical ones to Psychotrieae (subfamily Rubioideae).

Even when the same genus has epiphytic species in all three continental regions, these may not be closely related to each other. Altogether only 30 epiphyte-containing seed plant genera are found in more than one of the three main tropical regions, and only 14—*Liparis, Malaxis, Vanilla, Polystachya, Bulbophyllum, Schefflera, Begonia, Rhipsalis, Vaccinium, Utricularia, Ficus, Myrsine, Peperomia, Senecio*—are pantropical. Twelve of the genera that occur as epiphytes on more than one continent are large, diverse, terrestrial genera in which epiphytism has arisen occasionally. For example, there are at least two independent origins of epiphytism in *Utricularia* (P. Taylor, fide Madison, 1977). Genera like *Gnetum, Myrsine, Burmannia, Schefflera, Begonia, Senecio, Gaultheria, Vaccinium, Piper, Psychotria, Solanum,* and *Pilea* have independently derived and mostly quite unrelated epiphytic species in Old and New Worlds. There are five exclusively paleotropical genera with epiphytic species in Africa and Asia: predominantly epiphytic *Medinilla* (Melastomataceae) and the orchid genera *Acampe, Oberonia,* and *Taeniophyllum,* and occasionally epiphytic *Embelia* (Myrsinaceae). We are left with only *Schefflera, Rhipsalis, Ficus, Peperomia, Liparis, Malaxis, Vanilla, Polystachya,* and *Bulbophyllum* as genera in which epiphytism is widely prevalent on all three continents. Indeed the only genera in which epiphytism in both the New and Old Worlds seems to represent a true synapomorphy are three south temperate genera (*Luzuriaga, Griselinia,* and *Coprosma*), *Ficus, Rhipsalis,* probably *Peperomia,* and possibly *Schefflera.* The clearest cases of a shared epiphytic ancestor are Cactaceae where long distance dispersal of one species of *Rhipsalis* is responsible for the pattern seen today (Barthlott, 1983), and the peculiar case of *Ficus* where the large successful pantropical subgenus (*Urostigma*) has specialized as stranglers. The five pantropical epiphytic orchid genera likely achieved their present distributions via long-distance dispersal of their dustlike seeds. Predominantly epiphytic *Peperomia* may have been originally epiphytic; it is probably ancient (cf. Burger, 1977) and in many aspects of its biology, in addition to its pantropical distribution, it is anomalous among epiphytes.

Schefflera is predominantly epiphytic in the Neotropics, predominantly terrestrial in the Paleotropics; according to Madison's (1977) estimate only 65 species are epiphytic. Many species grow both as epiphytes and terrestrials; epiphytism, though widespread, does not seem fundamentally intrinsic to *Schefflera* and may have arisen independently in all three regions and probably within a given region as well.

Ferns, notorious for the ease of long-distance dispersal of their dustlike diaspores, contrast with the angiosperms in having most large epiphytic genera preponderately pantropical. There are even exclusively epiphytic pantropical fern genera including *Pleopeltis, Platycerium, Ctenopteris, Xiphopteris, Psilotum, Vittaria,* and (almost) *Polypodium*; there is not a single exclusively epiphytic pantropical seed plant genus. Even in ferns the majority of the epiphytic genera are restricted to one geographical region. Only one epiphytic fern genus is disjunct between the Neotropics and Asia (*Ophioglossum,* a large genus with only two epiphytic species separately arisen on the two continents). Five epiphytic fern genera occur in both tropical Asia and Africa but not the Neotropics, three of them on Madagascar but not continental Africa; again this is a pattern without parallel in the seed plants.

We may conclude that, except for the ferns, strangler figs, *Peperomia, Rhipsalis,* and a few orchid genera, the epiphytic floras of the different tropical regions are independently derived, even in most cases where the same family or genus is involved in different regions.

While certain taxa are preadapted to an epiphytic lifestyle, evolution of an extensive array of epiphytic species in any given taxon depends largely on the peculiarities of that region's evolutionary milieu. Epiphytism has arisen very many times in very many groups. However, certain regions have given rise to many epiphytes; others have not. In this context, the partial explanation offered by Madison (1977) for the greater representation of epiphytes in the Neotropics—that historical accident in the distribution of families like Bromeliaceae, Cactaceae, Marcgraviaceae, and Cyclanthaceae has led to the neotropical predominance in epiphytic species—seems largely irrelevant. Indeed, as many families (and other supraspecific taxa) have evolved epiphytism in the Paleotropics as in the Neotropics; the difference is that in the Neotropics evolutionary experiments with an epiphytic life-style have subsequently led to much more profuse speciation. Madison (1977) also thought that one element in explaining the continental difference of epiphyte diversity is a paucity of paleotropical nonorchid monocot epiphytes. However, our analysis emphasizes that it is not the evolution of epiphytism itself in such taxa that is the critical factor, but rather that there has been little subsequent radiation. Why have epiphytic taxa of Zingiberaceae, Costaceae, Pandanaceae, or Liliaceae not evolved into paleotropical versions of Bromeliaceae or Cyclanthaceae? We will try to analyze why this should be so in the next section.

EVOLUTION OF EPIPHYTE SPECIES DIVERSITY

Why are epiphytes so much better represented in some habitats than in others within the Neotropics? Part of the answer to that question can be adduced from the diversity gradients discussed above. From the patterns documented above we can generalize that epiphytes are most diverse in wet, middle elevation, rich-soil, tropical American forests. With the exception of the somewhat tenuously established trend toward greater diversity at middle elevations, these are exactly the trends shown by angiosperms in general (Gentry, 1982a, 1982b, 1987c). In a previous paper, based on data extrapolated from a large array of published monographs of neotropical taxa, Gentry (1982b) concluded that plant families belonging to different habit groups have fundamentally different distributional patterns. Families composed mostly of canopy trees or lianas have their greatest diversity in Amazonia whereas families made up mostly of epiphytes, shrubs, or palmetto-type herbs are largely extra-Amazonian and are especially concentrated along the lower slopes of the northern Andes and to a lesser extent in southern Central America. For epiphytes this concentration of species diversity could have been predicted from the trends outlined above. But *why* are epiphytes (and some other plants) so much more diverse in these regions?

One reason that epiphytes are especially diverse in wet aseasonal forests is that they are able to achieve a much finer niche partitioning, and thus a higher alpha diversity, there. Western Ecuador provides a good example of how this phenomenon operates. In the evergreen Río Palenque wet forest nearly all of the epiphytes have a characteristic and usually very restricted habitat, occurring only in the understory, the middle story, or the canopy. Altogether 41 species of vascular epiphytes at Río Palenque are understory specialists: 19 species of Araceae, one of Begoniaceae, one of Bignoniaceae, five of Cyclanthaceae, eight of Piperaceae, one of Solanaceae, and six ferns. However, there is not a single understory-specialist epiphyte species in the highly seasonal semideciduous moist forest at Jauneche, only a few tens of kilometers away. The presence of 41 species of understory specialist epiphytes at Río Palenque accounts for much of the difference between its diverse epiphytic flora and the relatively depauperate one at Jauneche. Nonstrangling epiphytic trees like *Clusia*, another specialized habit not occupied by Jauneche epiphytes, account for another five species of the difference. Presumably the more constant environment at Río Palenque favors within-community microhabitat specialization by epiphytes. Thus classical ideas about the greater spatial heterogeneity of everwet tropical forests (e.g., Baker, 1970) are certainly applicable to epiphyte diversity patterns both within the tropics and on a latitudinal gradient.

To some extent niche fine-tuning in constant environments also occurs in nonepiphytes. A good example is provided by *Gasteranthus* at Centinela, Ecuador (see Gentry, 1987b). Six species occur together sympatrically. All are terrestrial herbs and five are strictly endemic. The nonendemic species, *G. oncogastris*, occurs on the lower slopes away from the 600 m ridge top. Another species, *G. crispus*, grows only in sandy creek beds of the north part of the ridge and is not strictly sympatric with the other four species. Of the four strictly sympatric species, one, *G. atratus*, has switched from hummingbird- to bee-pollination and has yellow flowers completely distinct from the orange flowers of the other species. Two of the strictly sympatric species both have large flowers and grow in the deep shade along creek beds, but *G. macrocalyx* blooms in the wet season and *G. pubescens* in the dry season. The final species, *G. carinatus,* is morphologically differentiated by slightly smaller flowers and ecologically by growing only along the ridge top. In *Gasteranthus,* as in the Río Palenque epiphytic flora, very fine niche partitioning in a relatively constant climate seems an important key to maintenance of high species diversity. To the extent that such niche partitioning is related to equable montane cloud forest conditions, it might be expected to be relatively favored in the Neotropics.

A second explanation for the great epiphyte diversity in the Andean area focuses on β-diversity resulting from the greater microsite differentiation typical of mountainous regions. A test of this hypothesis might come from comparing epiphyte diversity in areas with high and low microsite differentiation. The two "nudos" where the eastern and western Andean cordilleras come together briefly at opposite ends of Ecuador provide such a test. The southern Nudo de Loja (or Sabanilla) marks the beginning of the Huancabamba biogeographic discontinuity (cf. Berry, 1982); the northern Nudo de Pasto, mostly across the border in Colombia, marks the point where the three Colombian cordilleras diverge. In both of these areas a tremendous variety of habitats spanning the gauntlet from very wet to very dry occur together in very close proximity due to the unusually broken terrain and very different orientations of adjacent slopes. *Telipogon* (Orchidaceae) provides a good example of how such microsite heterogeneity can multiply epiphyte species diversity. There are 37 *Telipogon* species in Ecuador and five more on the Colombian side of the Nudo de Pasto. There are 14 species on the Nudo de Loja and 16 species on the Nudo de Pasto, as compared with only 14 species in the entire intervening 600 km. More instructive, nine of the *Telipogon* species on Nudo de Loja and five on Nudo de Pasto are locally endemic, each found in a single valley or a single slope. In the much larger intervening area there are only nine endemic species, each restricted to a small area of a few hectares, in several cases representing unusual and restricted microhabitats similar to those around the Nudos. It seems clear that in *Telipogon* diversity is associated with local speciation and microgeographic specialization. Again, epiphytes are not the only group to show such patterns, but they do seem especially prone to this kind of microgeographic speciation. Probably the association of accentuated microgeography with mountainous terrain, which is much more prevalent in the Neotropics, explains some of the intercontinental diversity differences.

A third, not necessarily mutually exclusive, potential explanation for high epiphyte diversity in the northern Andean and southern Central American cloud forests is the "evolutionary explosion" hypothesis advanced by Gentry (1982b) in an attempt to explain why there are so many more neotropical than paleotropical plant species. A relatively small number of genera of epiphytes, understory shrubs, and palmetto-type herbs have speciated profusely in the northern Andean region, in each case giving rise to very many locally endemic and often rather poorly differentiated species. Gentry (1982b: 587) interpreted the high local endemism (cf. Gentry, 1987b) and apparent "species swarms" in such large evolutionarily plastic genera as *Anthurium, Piper,* and *Cavendishia* as reflecting "shifting balance" founder effect phenomena (Wright, 1977; Templeton, 1980) with major genetic reorganizations or genetic transilience (Templeton, 1980) optimized by small and localized populations and by the need for constant recolonization in a habitat partitioned by mountains, local rainshadows, vertically shifting cyclically coalescing vegetational zones, and frequent landslides. If genetic founder effects associated with recolonization of the open areas resulting from landslides or unusually frequent tree falls in these geologically and ecologically dynamic regions are major determinants of speciation events, then much speciation in Andean-centered taxa could well be essentially sympatric and largely random. This model thus differs from the "microgeographic speciation" model in that speciation could take place at a much finer "sympatric" scale, e.g., as colonization of a specific landslide, with many of the resultant species ecologically indistinguishable from each other, rather than each adapted to a specific microsite. Since this scenario is largely dependent upon the extreme ecological dynamism imputed to be associated with tropical mountains it would be expected to be most applicable in the Andean region, by far the most extensive mountain system in the world's tropics.

We have indirect but highly suggestive evidence for speciation associated with genetic tran-

FIGURE 5. *Stanhopea jenishiana* Reichb. f.

silience in founder populations in several genera of epiphytes. *Embrya rodigasiana* (Cogn.) Dodson provides a good example of a founder event. This species is distributed mostly in western Colombia, between 1,000 m and 1,500 m, ranging from west of Medellín to near Buenaventura. There is also a disjunct population in a small area of southern Ecuador near Panguí, at 1,500 m above Bomboiza and Gualaquiza; prior to recent widespread habitat destruction, the species was very common in the disjunct and geographically very limited Ecuadorian part of its range, where it was surely introduced by a long-distance dispersal founder event. *Masdevallia chontalensis* is a similar example. Well known and occurring in a well-known habitat, it ranges from Guatemala to Panama with a small disjunct population near Piñas in southern Ecuador. There are several similar cases of unsuccessful founder events by dust-seeded tropical epiphytes that have temporarily established disjunct populations in Florida, been duly recorded as members of the Florida flora, and then subsequently disappeared. An example is *Leochilus labiatus* which grew for a while near Fackahatchee.

The *Stanhopea jenishiana* complex, well characterized by a suite of distinctive morphological characters, provides an example of the next step in such a process. *Stanhopea jenishiana* Reichb. f. (Fig. 5) ranges from Cali to Popayán in the Cauca Valley of Colombia, with a disjunct population near Piñas in southern Ecuador. There are two other small geographically isolated populations of this complex in western Ecuador, each of them specifically distinct but clearly derived from *S. jenishiana* and each likely resulting from a single long-distance dispersal event—*Stanhopea frymirei* Dodson is endemic to a range of relatively moist hilltops near the coast in Manabí and Guayas provinces and *S. embreei* Dodson occurs only around 1,000 m in the Bolivar-Cañar border area (Fig. 6).

The herbaceous and shrubby taxa that show such patterns have relatively short generation times, providing conditions appropriate for rapid evolutionary diversification. Under either the microgeographic or founder effect hypothesis, epiphytes, as the major herbaceous component of wet tropical forests, might be expected to show unusually rapid "evolutionary explosion" type speciation. Relatively specific pollination systems constitute a second factor suggested by Gentry (1982b) as potentially promoting unusually rapid speciation in "Andean-centered" taxa, with shifts in specific pollinators accompanied by coevolutionary fine-tuning of precise plant-pollinator systems apparently a common evolutionary theme. Again epiphytes, often characterized by high pollinator specificity, should be prime candidates for rapid speciation.

The *Stanhopea jenishiana* complex (see above) is a good example of how founder events and

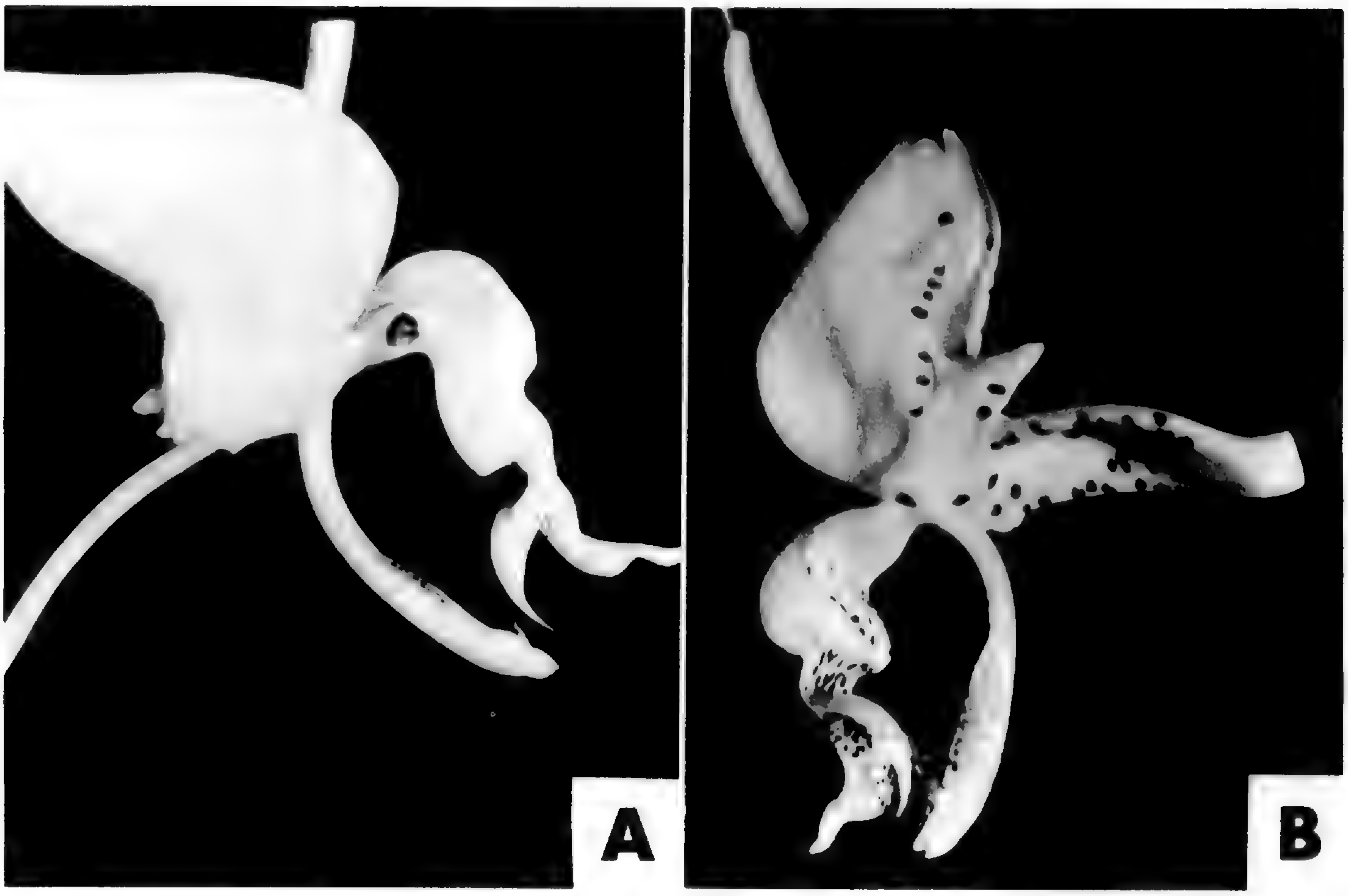


Figure 6. Two localized derivatives of *Stanhopea jenishiana*.—A. *S. embreei* Dodson.—B. *S. frymirei* Dodson.

shifts in pollination syndromes can combine to give rise to new species. The presumed ancestral species, *S. jenishiana*, has orange flowers and is pollinated by bees of the genus *Euglossa* while both of the locally endemic derivative species in central Ecuador have white (*E. embreei*) or straw-colored (*E. frymirei*) flowers and have switched to pollination by *Eulaema bomboides*. All three species have methyl cinnamate as the major scent attractant but each has a different set of scent-modifying compounds. *Eulaema bomboides*, a very effective pollinator that specializes on flowers producing methyl cinnamate, is endemic to central Ecuador. We interpret this situation as reflecting three different instances of long-distance dispersal. In the southern Ecuador Piñas population, outside the range of *E. bomboides*, pollination by *Euglossa* was maintained and no speciation occurred. In the two isolated central Ecuadorian populations speciation to take advantage of *Eulaema bomboides* as a pollinator occurred with essentially the same selection operating in these two different founder populations. Different evolutionary solutions reflected by the two distinct derivative species resulted.

Scelochilus, another epiphytic genus of orchid, provides an even more intriguing indication of how rapid speciation might be in such taxa. *Scelochilus* is a genus of 34 species found mostly epiphytic in guava trees; sparsely represented in natural vegetations, it was apparently ideally preadapted for the special conditions provided by guava plantations. Fifteen species of *Scelochilus* occur in Ecuador. In 1957 one of us (CD) made an intensive study of populations of *Scelochilus* in an extensive guava grove near the edge of wet forest at 1,000 m altitude at km. 94 of the old Guayaquil-Cuenca road in Ecuador. Two undescribed species of *Scelochilus* were present, growing intermixed, both very common, and together averaging about 30 flowering plants per host tree. Vegetatively the two species were indistinguishable, but their flowers, though somewhat variable in each species, were very distinctive with no overlap whatsoever between the two species. Indeed the original study, intended to focus on hybrid introgression, had to be abandoned because the two taxa proved to be so consistently differentiated. These species were described as *S. frymirei* and *S. embreei* (Fig. 7). Fifteen years later, in 1982, a return visit was made to the same guava grove. In the intervening years most of the nearby forest had been cut and converted to pasture. As a result the habitat was very different, with a much dryer aspect and the remaining guava trees rather old and decrepit. *Scelochilus* was much rarer but ca. 50 plants were located in the remaining guavas. Incredibly, neither *S. embreei* nor *S. frymirei* was present in 1982, but rather two *different* new species were found, later described as *S. gentryi* and *S. romansii.* As in 1957, both of these species, vegetatively indistinguishable, were clearly differentiated from each other by floral characters (Fig. 7). Both of the species present in 1982 are closely related to *S. frymirei.* We suspect that they may represent in situ speciation events, at least in the case of *S. romansii* (*S. gentryi* has also been found in several other localities in western Ecuador). If so, natural speciation in *Scelochilus* can occur in as little as 15 years!

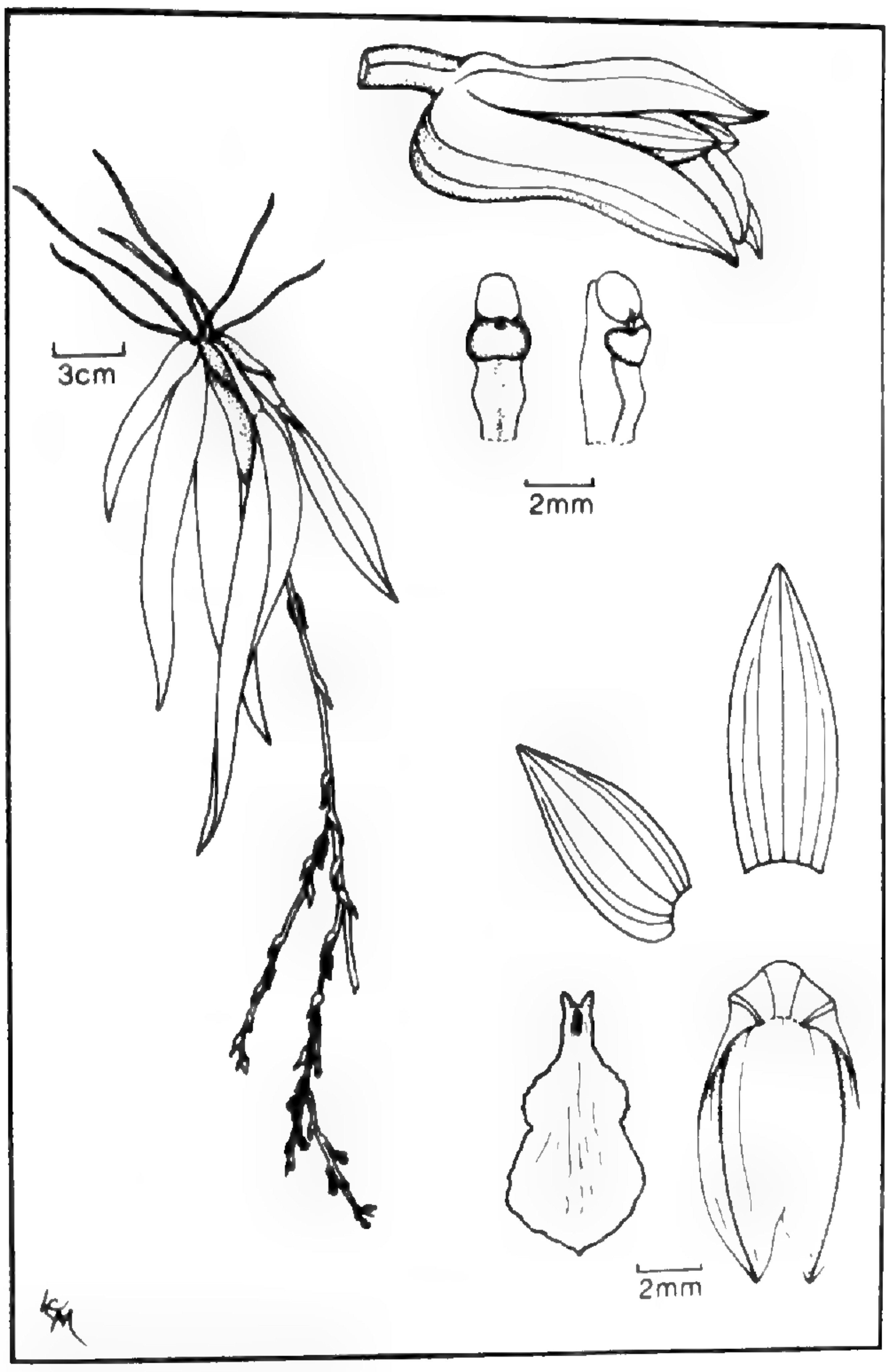
An obvious alternative interpretation is that specific limits in *Scelochilus* are too finely drawn, with *S. gentryi* and *S. romansii* representing part of the intraspecific variability within polytypic *S. frymirei.* However, this possibility seems obviated by the fact that the two co-occurring *Scelochilus* species of 1982 pass the test of sympatry as biologically differentiated populations, even though they are more similar to each other than to their putative ancestor *S. frymirei.* We favor the interpretation that the kind of genetic reorganization that reflects speciation in *Scelochilus,* and presumably other orchids and even some nonorchid epiphytes, is so labile that it can be effected in incredibly short times. If this interpretation is correct, then it is no wonder that many epiphytic taxa have undergone what appears to be truly explosive speciation in the Neotropics. Obviously, it is also possible that *S. gentryi* and *S. romansii* immigrated to the guava grove in question sometime between 1957 and 1982 with *S. frymirei* and *S. embryi* coincidentally becoming locally extinct during the same time interval. But the mere fact that natural speciation in fifteen years seems an equally plausible explanation for these observations is surely significant.

Another line of reasoning also supports the idea that certain neotropical epiphytes have undergone explosive evolution. It is probably safe to assume that, as a general rule and despite many potential exceptions, genera with many species are those which have, on the average, undergone the most rapid speciation. Thus an examination of the largest epiphyte genera might indicate some of the trends, both geographic and ecological, that characterize successful epiphytism. Table 11 lists the 47 largest genera of vascular epiphytes worldwide (those with 90 or more epiphytic species) and provides the data for such an analysis. Again orchids are preeminent. Half (22) of the 47 largest epiphyte genera are orchids. While orchids might appear to be exceptional in their unusual genetic plasticity and highly specific pollination systems, they must unavoidably be regarded as the most successful practitioners of the art of being epiphytic. Biogeographical analysis of the large orchid genera is instructive. Three are pantropical, nine exclusively neotropical, and ten exclusively paleotropical. Even though the number of large neotropical and paleotropical orchid genera is the same, there is a dramatic difference in the number of species that they contain. The nine neotropical genera are far larger, accounting for 5,240 species (average 582 spp. per genus) vs. 2,626 species (average 263) for the ten paleotropical ones.

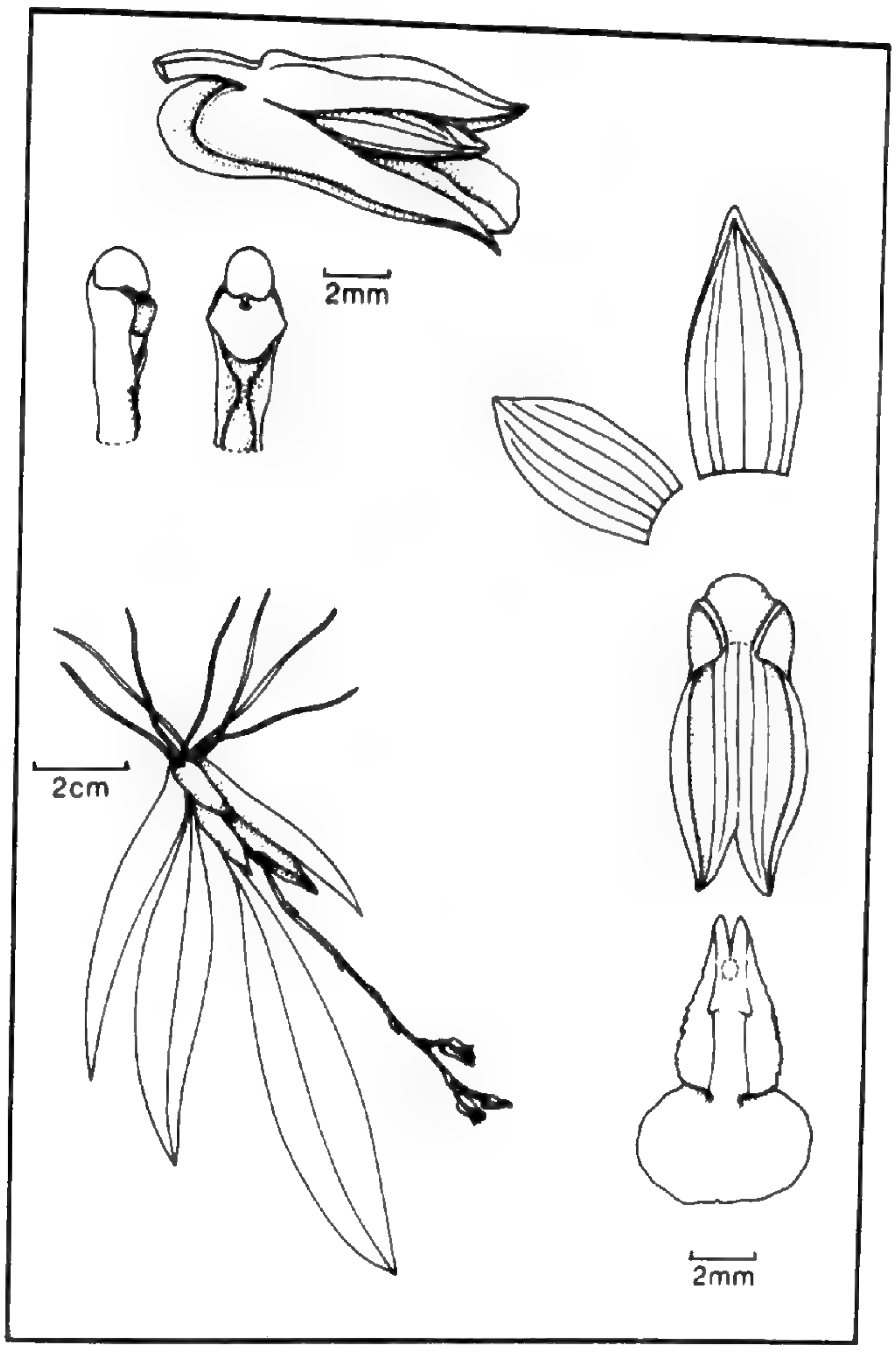
Ferns account for eight of the largest epiphyte genera. Not surprisingly, in view of their diaspore vagility, nearly all of the large epiphytic fern genera are pantropical, showing little evidence of unusually rapid differentiation or speciation in the Neotropics. Only one fern genus, *Pyrrhosia,* is restricted to the Paleotropics, none to the Neotropics.

The remaining 15 of the largest epiphytic genera are split evenly between dicots and monocots. The two largest dicot genera, *Peperomia* and *Ficus,* are pantropical, although the former, at least, is better represented in the Neotropics; the other largest epiphytic dicot genera are two neotropical gesneriads (*Drymonia* and *Columnea,* sensu lato), two ericads (*Rhododendron* and *Cavendishia*), one each epiphytic in Old and New Worlds, and two melastome genera (*Medinilla* and *Blakea*), restricted respectively to the Old and New Worlds (and extremely similar to each other as well as to another large neotropical genus *Topobea*). In general, there seems a reasonable numerical balance between Old and New World representation in the largest dicot epiphyte genera, except in Gesneriaceae. The situation is very different among the nonorchid monocot epiphytes. Six of the seven largest genera—*Anthurium, Tillandsia, Philodendron, Vriesia, Guzmania,* and *Aechmea*—are exclusively neotropical; only *Rhaphidophora* is paleotropical. Thus the very many species that have evolved among certain monocot epiphyte genera seem a peculiarity of the Neotropics.

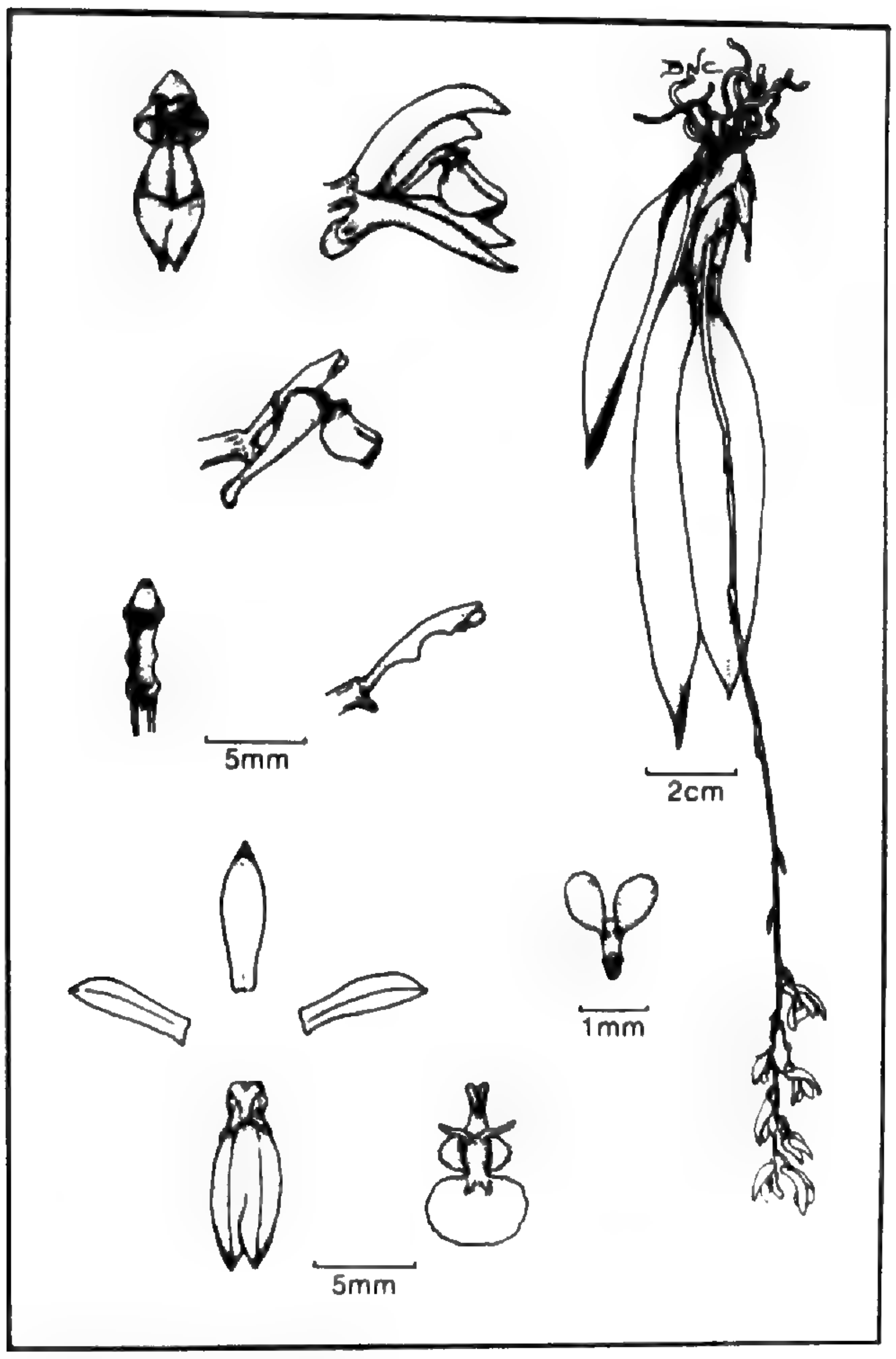
Why have epiphytes been especially suscep-



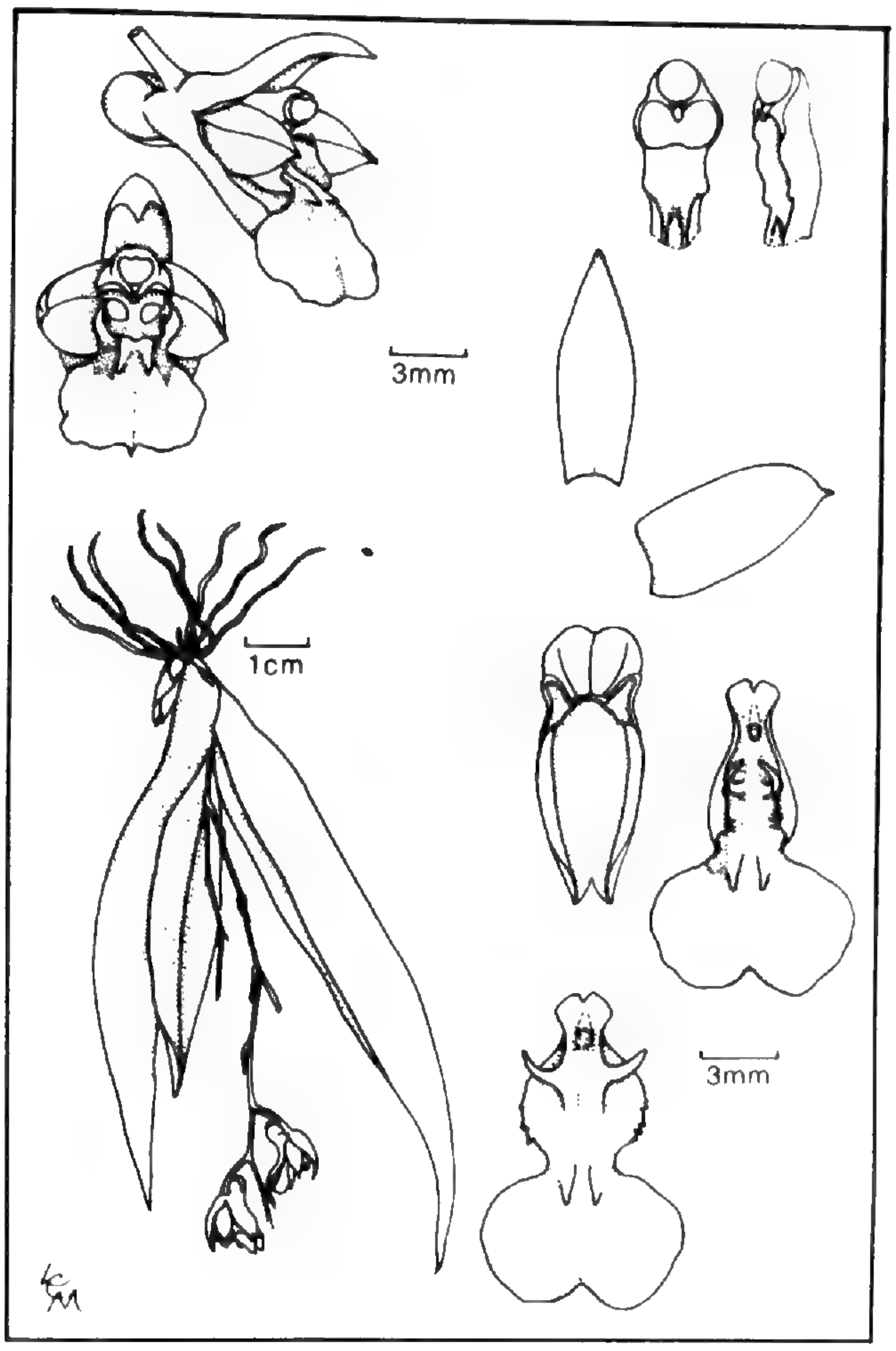
SCELOCHILUS EMBREEI Dodson



SCELOCHILUS FRYMIREI Dodson



SCELOCHILUS GENTRYI Dodson



SCELOCHILUS ROMANSII Dodson & Garay

tible to the rapid, even explosive, speciation that seems to have characterized a large element of the neotropical flora? At least in the case of orchids, unusually specific pollination systems have clearly played a major role in making possible very active speciation. Like the orchids, the nonorchid epiphyte families that have speciated the most profusely in the northern Andes and southern Central America—Gesneriaceae, Bromeliaceae, Ericaceae, and Araceae—all share, to a greater or lesser extent, relatively specialized pollinators and specific pollination systems as compared with the "average" tree, shrub, or free-climbing liana (e.g., prevalent hummingbird or euglossine pollination). On the other hand the epiphytic taxa that have speciated most profusely are characterized, as a group, by more generalized, higher risk dispersal strategies than typical of other mature forest habit groups. If speciation along the lower slopes of the Andes and in southern Central America typically derives from suboptimal genetic transilience related to multiply replicated founder events in a dynamic and kaleidoscopically changing habitat as Gentry (1982b) suggested, then epiphytes, characterized by their unique combination of r- and k-selected reproductive traits, might be uniquely equipped to react to this adaptive milieu. Like weeds, they have diaspores intrinsically adapted for quick colonization of newly available habitats. In epiphytes, like weeds, the primary need for such adaptation is presumably a response to the short-lived and unstable nature of their normal substrate, a reproductive strategy ideally preadapting epiphytes for rapid speciation in an environment in which the need to recolonize dynamically changing microhabits is unusually frequent. However, unlike weeds whose diversification is generally constrained by overly generalized pollination syndromes (frequently even with loss of sexual recombination), the rich array of specialized pollination systems that characterizes the successful epiphytic taxa would seem to preadapt them for rapid, pollinator-related evolutionary diversification. In this context, it is not likely to be an accident that the preeminently successful epiphytic family, Orchidaceae, is precisely that family that has both the most specific pollination systems and the tiniest, most r-selected diaspores of any angiosperm. Moreover, from the viewpoint of "accidental" speciation via founder effect phenomena, the unusual genetic similarity among the potential-colonizer orchid propagules that arrive together at a specific site—due to orchid seeds' unique sharing of fathers as well as mothers, thanks to their pollinia—might be expected to accentuate the potential for genetic drift in colonizing populations. Interestingly, the closest parallel to the postulated rapid speciation among Andean cloud forest epiphytes is found in herbaceous and palmetto taxa that most closely approximate the unique epiphyte combination of specific pollination systems and an r-selected high-risk dispersal mode.

CONCLUSION

Although many unrelated kinds of plants have evolved epiphytic habits, most of these represent isolated species or genera in otherwise terrestrial families. Only three nonfern families—Orchidaceae, Cyclanthaceae, Marcgraviaceae (and possibly also Bromeliaceae)—are predominantly epiphytic. Eighty percent of all vascular epiphytes are concentrated in only four families—Orchidaceae, Bromeliaceae, Polypodiaceae, and Araceae—and 89% in eight families. Very few families have been successful at undergoing extensive radiation as epiphytes. Indeed over two-thirds of all epiphyte species belong to the single family Orchidaceae, and to a large degree understanding epiphytic diversity is synonymous with understanding orchids.

Although notably few families have been very successful as epiphytes, these few taxa have made a tremendous contribution to the diversity of the world's flora. At least 10% of all vascular plant species are epiphytes and in some places epiphytes may constitute a third of all plant species in a local flora or 63% of the individual plants in a given sample area.

Epiphytes have speciated most profusely in the Neotropics, especially in northwest South Amer-

←

FIGURE 7. Postulated rapid speciation in *Scelochilus.* Top two species were described as new from 1957 collections from guava grove at km. 94 of Guayaquil-Cuenca road. In 1982 they had been replaced by bottom two species, both new and both closely related to *S. frymirei.* (Illustrations from Orchids of Ecuador, Icones Plantarum Tropicarum.)

TABLE 11. Major epiphyte genera (in part after Madison, 1977; Dressler, 1981; Kress, 1986).

Genus	No. Epiphytic Spp.	Total No. Spp.	Distribution
Pleurothallis	1,520	1,600	Neotropical
Bulbophyllum	1,000	1,000	Pantropical
Dendrobium	900	900	Australasian
Epidendrum	720	800+	Neotropical
Peperomia	700	1,000	Pantropical
Anthurium[1]	600	850	Neotropical
Lepanthes	600	600	Neotropical
Stelis	540	600	Neotropical
Ficus	500	800	Pantropical
Maxillaria	570	600	Neotropical
Eria	500	550	Australasian
Oncidium	475	500	Neotropical
Asplenium	400	650	Pantropical
Tillandsia	400	450	Neotropical
Grammitis	400	400	Pantropical
Philodendron[1]	350	475	Neotropical
Masdevallia	400	400	Neotropical
Medinilla	300+	400+	Paleotropical
Liparis	300	350	Cosmopolitan
Oberonia	300	300	Paleotropical
Odontoglossum	285	300	Neotropical
Columnea (sensu lato)	262	265	Neotropical
Elaphoglossum	250	500	Pantropical
Hymenophyllum	250	300	Pantropical
Angraecum	206	206	Trop. Africa
Lycopodium	200	400	Cosmopolitan
Polystachya	200	210	Pantropical
Ctenopteris	200	200	Pantropical
Vriesia	200	260	Neotropical
Phreatia	190	190	Australasian
Trichomanes	150	300	Pantropical
Polypodium	140	150	Pantropical
Encyclia	130	130	Neotropical
Octomeria	130	130	Neotropical
Taeniophyllum	120	120	Paleotropical, esp. Afr.
Guzmania	120	140	Neotropical
Dendrochilum	120	120	Australasia
Aechmea	120	150	Neotropical
Rhododendron	112	850	Mostly Asian
Coelogyne	100	100	Trop. Asia
Drymonia	100	110	Neotropical
Pyrrosia	100	100	Paleotropical
Rhaphidophora	100	100	Paleotropical
Appendicula	100	100	Australasia
Blakea[2]	98	100	Neotropical
Thrixspermum	90	100	Australasia
Cavendishia[3]	90	100	Neotropical

[1] Croat, pers. comm.

[2] Renner, 1986 and pers. comm.

[3] Luteyn, pers. comm.

ica and southern Central America. The explosive speciation of relatively few epiphyte genera in this region has been responsible to a large extent for the excess floristic diversity of the Neotropics as compared with the Paleotropics.

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APPENDIX I. Changes in data base from epiphyte list in Madison (1977).

Additions

- Lycopodiaceae
  - *Lycopodium* (200/450)
- Araceae (1,200 species, not 850)
  - *Anthurium* (600/850)
  - *Philodendron* (350/475)
- Cyclanthaceae (125 species, not 31)
  - *Dicranopygium* (few/44)
  - *Evodianthus* (1/1)
  - *Stelestylis* (4/4)
- Dioscoreaceae
  - *Dioscorea* (1/600) (Ecuador, pers. obs.)
- Liliaceae
  - *Rhodocodon* (1/8) (Madagascar, pers. obs.)
- Philesiaceae
  - *Philesia* (1/1) (Chile, pers. obs.)
  - *Luzuriaga* (3/3) (Chile, pers. obs.)
- Alzateaceae
  - *Alzatea* (1/2)
- Anacardiaceae
  - *Spondias* (1/10) (SE Asia, fide Kress)
- Apocynaceae
  - *Mandevilla* (1/114) (*M. pittieri*, Costa Rica)
- Begoniaceae
  - *Begonia* (40/1,000)
- Bignoniaceae
  - *Gibsoniothamnus* (11/11)
  - *Schlegelia* (18/18)
- Bombacaceae
  - *Spirotheca* (4/4)
- Burseraceae
  - *Bursera* (1/80) (*B. standleyana*, Costa Rica)
- Compositae (ca. 30 epiphytic species, not 3)
  - *Liabum* (*Sinclairia*) (2/90)
  - *Mikania* (1/300)
  - *Neomirandea* (20/24)
  - *Nelsoniothamnus* (1/1)
  - *Pseudogynoxys* (1/21)
  - *Senecio* (*Pentacalia*) (5/1,500) (epiphytic in Neotropics, Madagascar, N.Z.)
  - *Tuberostylis* (2/2)
- Crassulaceae
  - *Kalanchoë* epiphytic in Madagascar, pers. obs.
- Marcgraviaceae (89 epiphytic species, not 94)
  - *Marcgraviastrum* (10/15)
  - *Marcgravia* (ca. 50–55/55)
  - *Norantea* (1/2)
  - *Ruyschia* (7/7)
  - *Sarcopera* (4/10)
  - *Schwartzia* (8/14)
  - *Souroubea* (9/19)
- Melastomataceae (567 epiphytic species, not 483)
  - The paleotropical genera *Baekeria, Dalenia, Diccochaeta, Neodissochaeta, Omphalopus,* and *Plechiandra* each has at least one hemiepiphytic species fide Renner, 1986.
- Myricaceae
  - *Myrica* (1/35) (SE Asia, fide Kress, pers. comm.)
- Sapotaceae
  - *Bumelia* (1/60) (Costa Rica, fide Kress, pers. comm.)
- Saxifragaceae
  - *Hydrangea* (2/80) (epiphytic in Neotropics)
- Solanaceae
  - *Lycianthes* (also epiphytic in Neotropics)

Deletions

- Apostasiaceae = Orchidaceae
- Dulongiaceae = Saxifragaceae
- Bromeliaceae—*Ananas*
- *Cyclanthaceae—Carludovica*
- Balsaminaceae—*Impatiens* not epiphytic in Neotropics
- Bignoniaceae—*Radermachera*
- Guttiferae—*Clusia* only occurs in Neotropics
- Marcgraviaceae—*Caracasia*
- Araliaceae—*Sciadophyllum* = *Schefflera*

Note: Additional occasional or sporadic epiphytes included by Kress (e.g., *Myrrhidendron donnellsmithii, Cyperus, Pseudoeverardia* (= *Everardia*), *Arenaria, Stellaria, Maranta, Pourouma*) are also excluded.

NITROGEN FIXATION BY EPIPHYLLS IN A TROPICAL RAINFOREST[1]

BARBARA L. BENTLEY[2]

ABSTRACT

Bluegreen algae (Cyanobacteria) growing on the leaf surfaces of understory plants in a tropical rainforest can fix atmospheric nitrogen. Rates of fixation are strongly influenced by the presence of glucose and mineral nutrients leached from the host leaf, by light intensity as it relates to the photosynthetic rates of the algae, and by desiccation especially as it is influenced by the co-occurrence of epiphyllous bryophytes. A significant portion of this newly fixed nitrogen is transferred to the host leaf and may account for 10–25% of the total nitrogen in a leaf.

Although the major source of nitrogen for plant growth and reproduction is from decomposition of organic matter, most ecosystems can gain significant quantities from precipitation and biological fixation of atmospheric nitrogen. In fact, Burns & Hardy (1975) estimated that biological fixation alone may account for 43% of the nitrogen transferred worldwide. Subba Rao (1977) suggested that the rates in tropical areas may be even higher and thus fixation could have a major role in the tropics where available nitrogen can be limited.

In this paper, I will discuss one aspect of nitrogen fixation in a tropical ecosystem—that of fixation by epiphylls in a rainforest understory. Although epiphyll fixation can account for up to 25% of the nitrogen in a host leaf (Bentley & Carpenter, 1980), rates of fixation are quite variable in both time and space. Here I document some of the environmental factors that influence fixation rates.

What are epiphylls? Epiphylls are epiphytes that are restricted to the surfaces of leaves. In tropical rainforests, most visible epiphylls are leafy liverworts of the family Lejeuneaceae but may also include mosses, lichens and, on some occasions, seedlings of other epiphytes such as bromeliads and orchids. In this study, we focused on the microorganisms, especially the bluegreen algae (Cyanobacteria) growing in association with the visible forms (Fig. 1).

The epiphyll community is best developed in regions of high rainfall and low evaporation and is most diverse in tropical rainforests (Richards, 1964). Because they grow on photosynthetic surfaces, epiphylls are often considered to be detrimental to the host plant by interfering with light penetration to the leaf (Richards, 1964). Indeed, some epiphylls may actually be semiparasitic. For example, the rhizoids of *Radula flaccida,* an epiphyllous liverwort, penetrate the cuticle and absorb nutrients from their host leaf (Berrie & Eze, 1975).

Other workers feel that the presence of epiphylls increases the time that leaves remain wet and thus contributes to the growth of potentially pathogenic bacteria and fungi (Gregory, 1971; Stahl, 1891). Long-term wetting may also reduce the rates of transpiration and subsequent mineral uptake by the roots (Stahl, 1893; McLean, 1919). As early as 1891, Jungner suggested that rainforest plants may have adaptations such as leaf "drip tips" to increase the rates of drainage off the leaf and reduce the rate of colonization by epiphylls. Subsequent work has failed to either deny or confirm the adaptive role of these characters (Stahl, 1893; Shreve, 1914; Seybold, 1957; and pers. obs.).

Nitrogen fixation by epiphylls. Some species of epiphyllous microorganisms are known to fix nitrogen (Bentley & Carpenter, 1980, 1984; Ruinen, 1975). During our study at the La Selva Biological Station in Costa Rica, we found that fixation rates are extremely variable, both within and among species (Fig. 2). Interestingly, in contrast to Ruinen's data where fixation was by free-living bacteria (primarily *Beijerinckia*), fixation in the La Selva understory was most commonly

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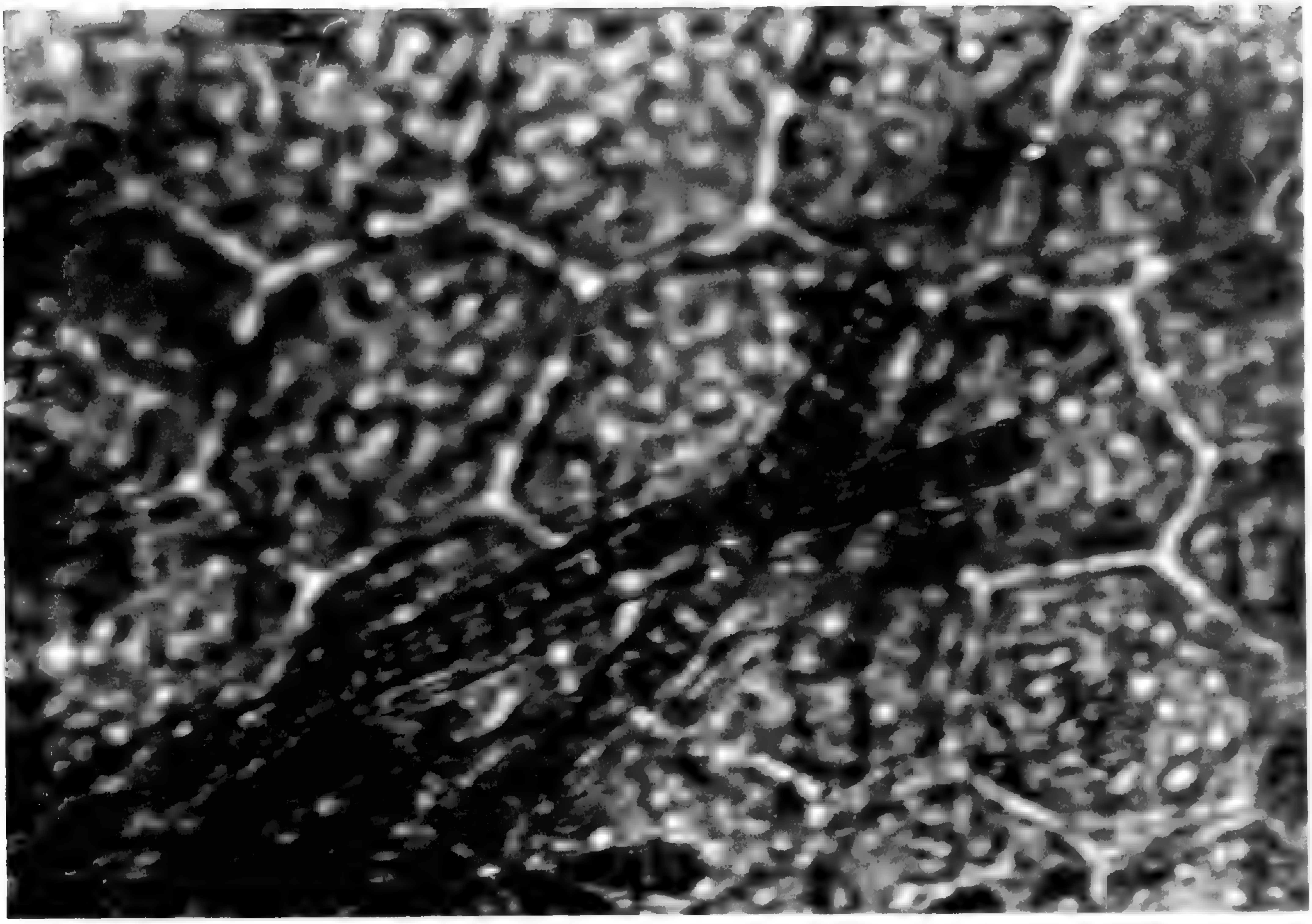

FIGURE 1. Photomicrograph of epiphylls. The strand of the nitrogen-fixing bluegreen alga is across the lower third of the photograph.

associated with the presence of bluegreen algae in the genera *Scytonema, Stigonema,* and *Hapalosiphon.* High fixation rates were invariably associated with a dense cover of bryophytes, suggesting that the bryophytes provide a good substrate for the nitrogen-fixing microorganisms.

Most of our work on fixation was done using the acetylene reduction method for determining nitrogenase activity (Bentley & Carpenter, 1980; Prestwich & Bentley, 1981; Burris, 1972). While this is an extremely easy field assay for estimating fixation, it is not a direct measure of *nitrogen* fixation, and cannot be used to answer the most critical question in our study: does the newly fixed nitrogen get into the host leaf? By using ^{15}N as a tracer, we were able to document that indeed this is the case (Bentley & Carpenter, 1984). There we showed that nitrogen fixation by epiphylls could account for up to 25% of the nitrogen in a host leaf.

In other studies with bluegreen algae, Stewart (1963) and Jones & Stewart (1969) found that the extracellular nitrogenous products are primarily amino acids or peptides, but less complex compounds, including ammonium nitrite and nitrate, can be present. The pathway for movement of the new nitrogen is not through the stomata, as might be assumed, but rather to the epidermal cells via threadlike ectodesmata penetrating through the cell wall to the cuticle (Franke, 1970). Because of the specific morphology of the ectodesmata, Franke felt that the movement of soluble materials into and out of the leaf is a normal process, closely correlated with foliar absorption of "foreign" substances such as fertilizers and pesticides.

Environmental factors affecting fixation. The rates of fixation and transfer that we measured were made under ideal conditions for the activities of microorganisms. Although the high temperatures and almost constant moisture in a tropical rainforest can permit high fixation rates and concomitant release of nitrogenous products, we have also observed extremely high variance both among and within species at the La Selva Station (Fig. 2). Thus, it becomes important to ask what environmental factors influence fixation rates by epiphylls. Basically, the answer lies in three factors: time, moisture, and nutrients.

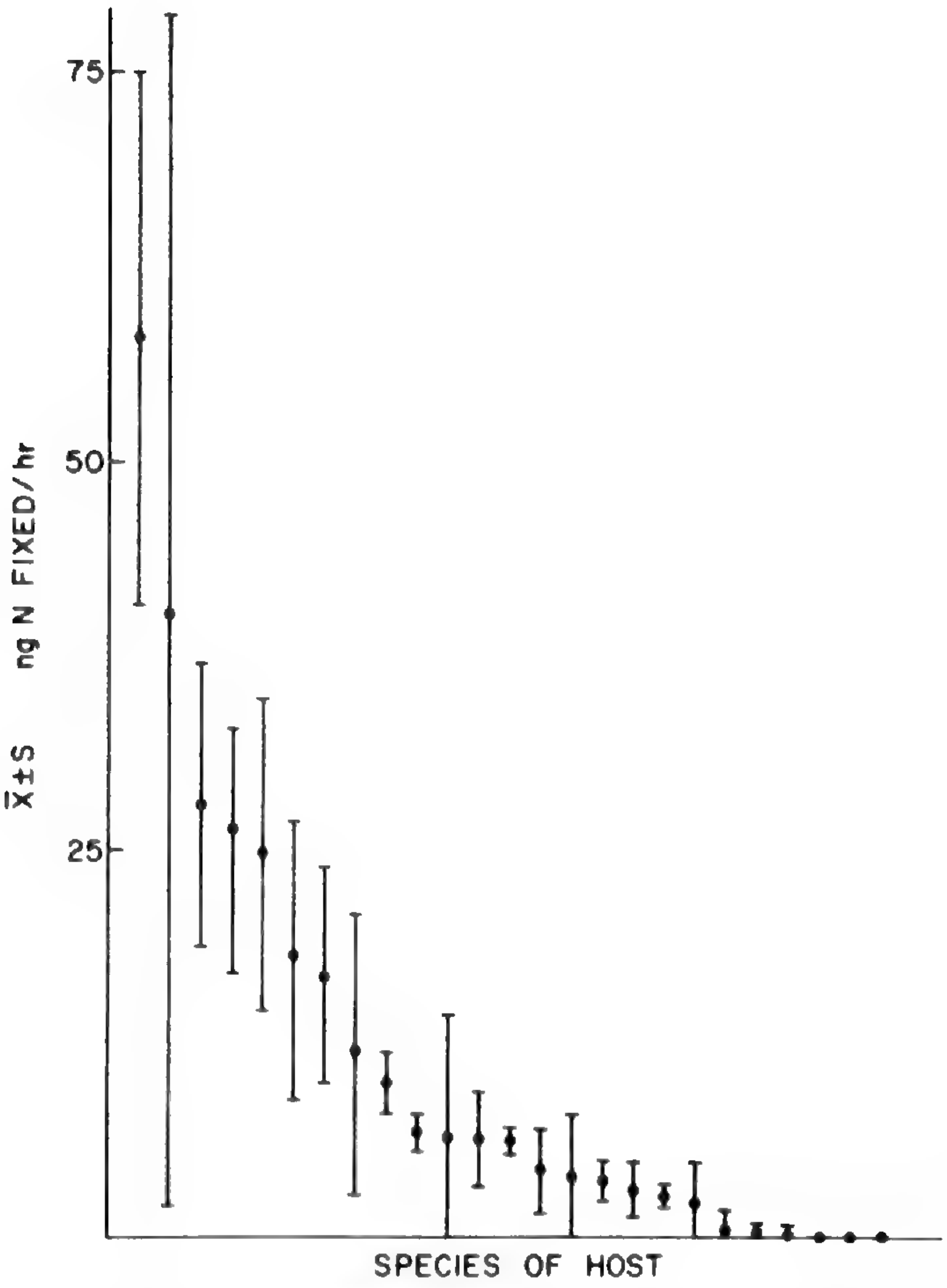

FIGURE 2. Nitrogen fixation rates by epiphylls on the surfaces of various host leaves. Means (O) and variance (error bars) are for five samples from each host. The host species, from highest to lowest fixation rates, are: *Ocotea atirrhensis, Proteum pittieri, Chamaedorea* sp., *Ficus* sp., *Swartzea* sp., *Miconia* sp., *Piper* sp. 1, *Piper* sp. 2, *Polypodium* sp., *Theobroma cacao, Inga* sp., *Costus* sp., *Syngonium* sp., *Asterogyne* sp., and *Geonoma* sp.

Time. Colonization by epiphylls is a time phenomenon. Young leaves are epiphyll-free simply because the epiphylls have not become established. Long-lived leaves have a much greater probability of having a well-established epiphyll community. To document the role of leaf longevity on fixation, we measured fixation on leaves which had been previously marked for up to 24 months (Bentley, 1979). Since we knew the average survivorship of leaves on a plant, we could then test for the correlation between the age of a leaf and the rate of fixation. As can be seen in Figure 3, fixation rates are significantly correlated with leaf longevity. At the same time, we measured fixation by leaves with differing levels of epiphyll biomass. Again, there is a significant correlation (Fig. 4).

Moisture. Interestingly, in the experiments described above, the rates of fixation were correlated with the biomass of the bryophytes, even though bryophytes per se do not fix nitrogen. On the other hand, bryophytes are correlated with and can influence the levels of moisture on the leaf surface (Richards, 1964). Since moisture can affect fixation rates in other systems (Balandreau et al., 1974; Horne, 1972; Fogg et al., 1973), we set up an experiment to test the effects of desiccation on fixation by epiphylls. In this case, individual pinnae of *Welfia georgii* were moistened with water 12, 4, 2, or 0 hours before incubation. As can be seen in Figure 5, desiccation has a very dramatic effect on fixation, yet the recovery is quite rapid and is almost that of the continuously moist control within four hours.

Although moisture conditions in a tropical rainforest are relatively constant compared with most other ecosystems, moisture conditions in the understory do vary, both seasonally and diurnally (Longman & Jenik, 1974; Ruinen, 1961). For example, water may continue to drip down through the forest canopy long after a rain has ceased, but the leaves of the upper canopy will dry within minutes. Seasonal variation can range from an increased frequency of dry periods in a day to days or weeks without any appreciable rainfall (Schnell, 1971). Thus, under field conditions, moisture can have significant effects. We documented this in another experiment, shown in Figure 6. In this case we found that fixation rates on rainy days were considerably higher than on dry days.

Although it is tempting to suggest that the bluegreens and the bryophytes have some close symbiotic relationship, the role of bryophytes is probably no more than to maintain appropriate moisture conditions on the surface of the leaf. Epiphyll-laden leaves dry more slowly, not only because capillary action holds water but also because bryophytes can draw water directly from the interior of the leaf (Berrie & Eze, 1975). In addition, the epiphyll-laden portion of a leaf surface will become wetter faster, again because of capillary action drawing water from surrounding areas. High fixation rates by algae are correlated with the presence of bryophytes simply because the moisture conditions surrounding epiphyllous bryophytes are appropriate for the growth and activity of microorganisms.

Energy sources. Nitrogen fixation consumes energy—free-living microorganisms may require 200 g of glucose for every gram of nitrogen fixed (Mulder, 1975). Unlike other microorganisms, bluegreen can use carbohydrates from photosyn-

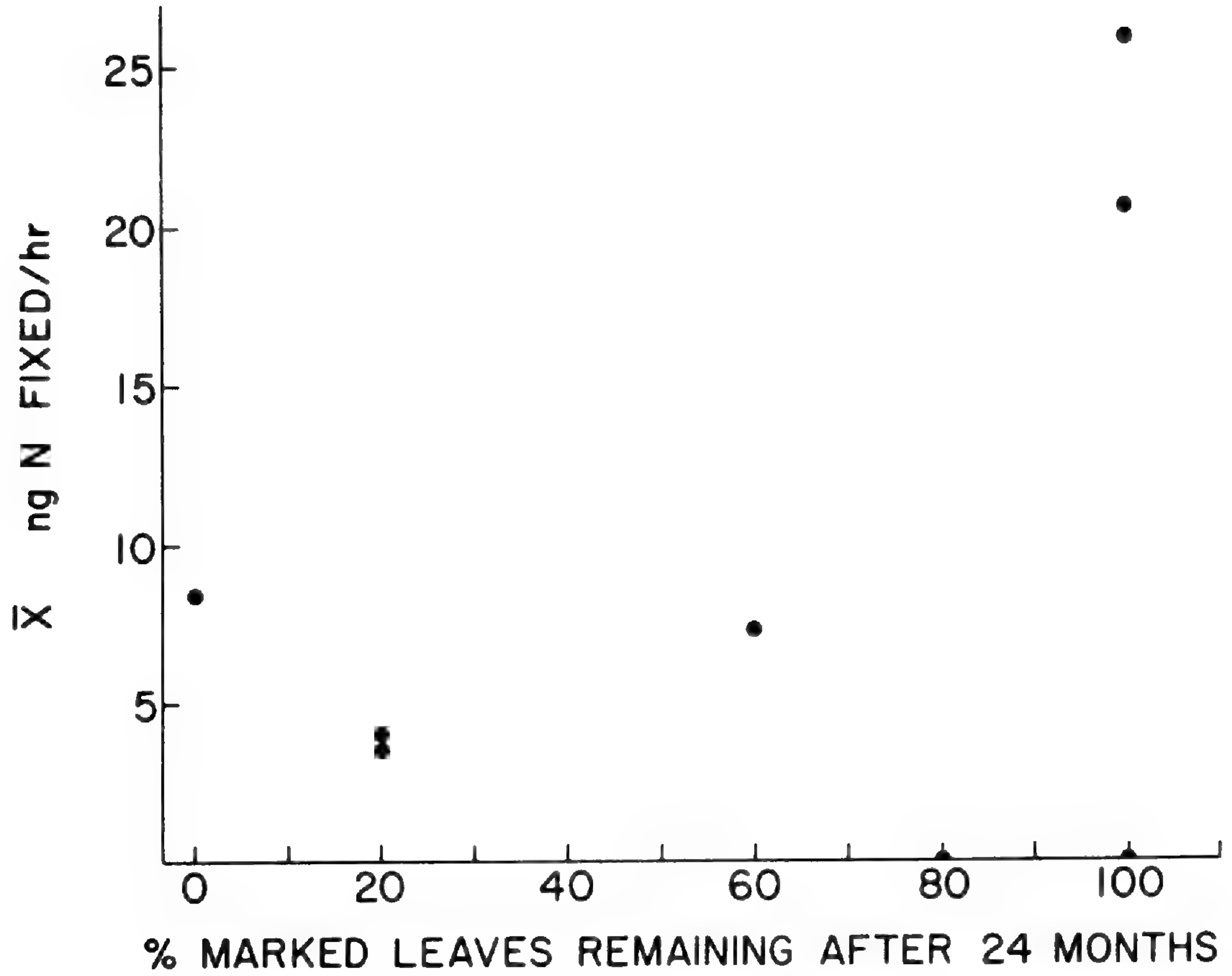

FIGURE 3. Nitrogen fixation rates by epiphylls on plants with different leaf longevities. Highest rates are on *Ocotea atirrhensis* in which all leaves live longer than 24 months. Lowest rates were on leaves of *Piper* (80% last less than two years). The rank correlation of fixation with longevity is significant ($r = 0.95$, $P < 0.01$).

thesis as well as exogenous carbon to supply the nitrogen fixation process. In addition, bluegreens may be able to use intermediate products of photosynthesis to provide electrons for nitrogen fixation (Mulder, 1975).

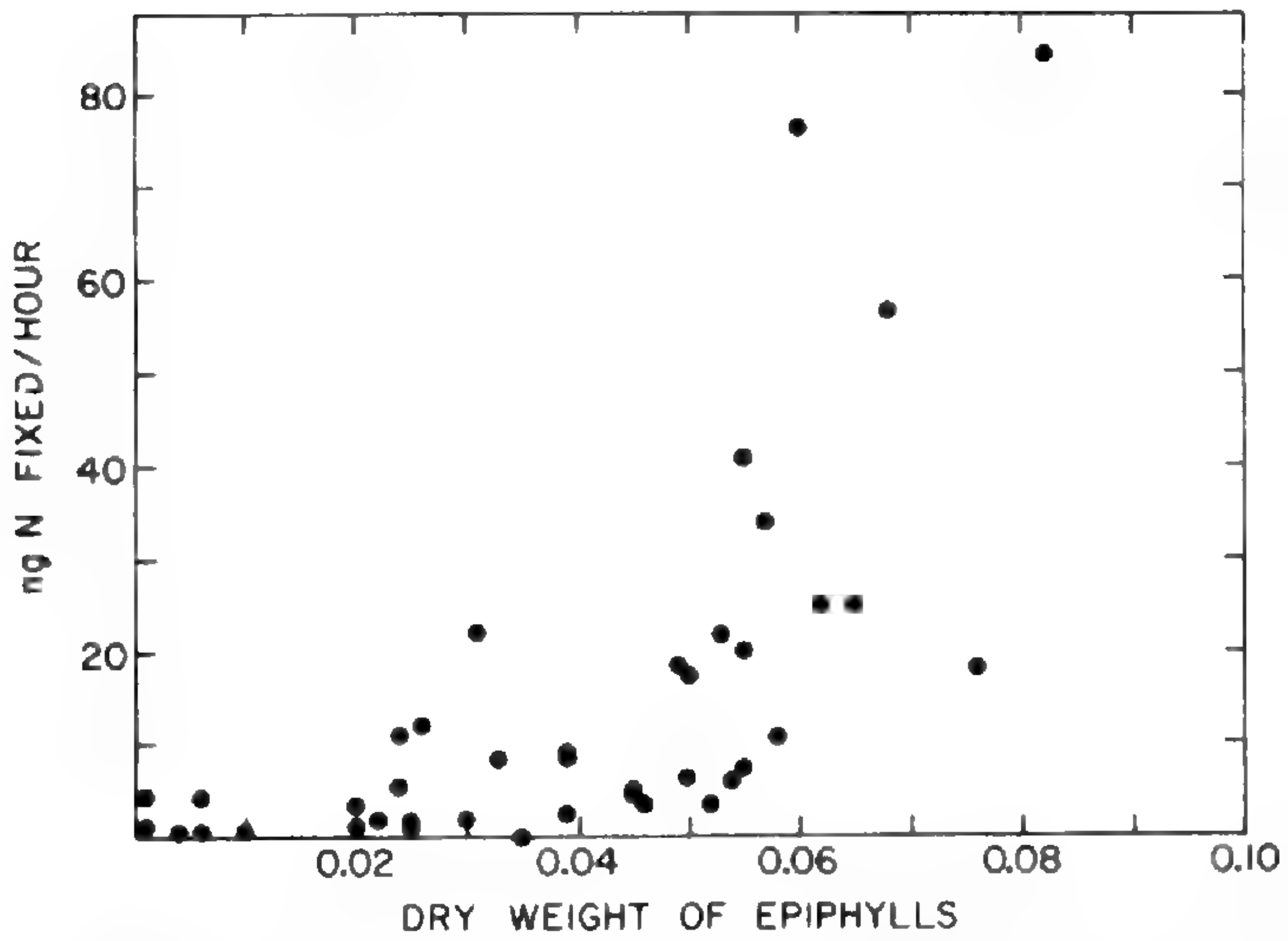

FIGURE 4. The relationship of epiphyll biomass and fixation rates. Fixation rates were measured on intact 2 cm × 5 cm leaf samples. After incubation, the epiphylls were removed by scraping and dried at 80°C for 24 hours. The epiphyll biomass includes both bryophytes and bluegreens. The correlation between fixation and biomass is significant at the $P < 0.05$ level ($r = 0.39$).

In the field, nitrogen fixation by bluegreen algae is usually light dependent (Henricksson & Simu, 1971; Horne & Viner, 1971; Stewart, 1973; and see Fig. 6) and has the same relationship to light as photosynthesis—decreasing with decreasing light intensity. However, low rates of fixation can occur in the dark (Forman, 1975; Dugdale & Dugdale, 1962), especially if the organisms are grown on substrates containing glucose, fructose, or sucrose (Fay, 1965). Thus, many workers feel that high rates of fixation under natural conditions are a function of both photomediated internal processes as well as various forms of exogenous carbohydrates.

Exogenous carbohydrates may come from a wide variety of sources. The major source for epiphylls is in leachate from the host leaf (Tukey & Morgan, 1962; Tukey, 1971). Since the amount of carbohydrate present in leachate is also a function of the photosynthetic rate of the host leaf (Tukey et al., 1957), the amount of exogenous carbohydrate available to the epiphylls will also be correlated with light intensity in the field.

To document the effects of light on the epiphyll system, we set up two series of experiments: the first to establish that levels of light commonly found in the rainforest understory could influ-

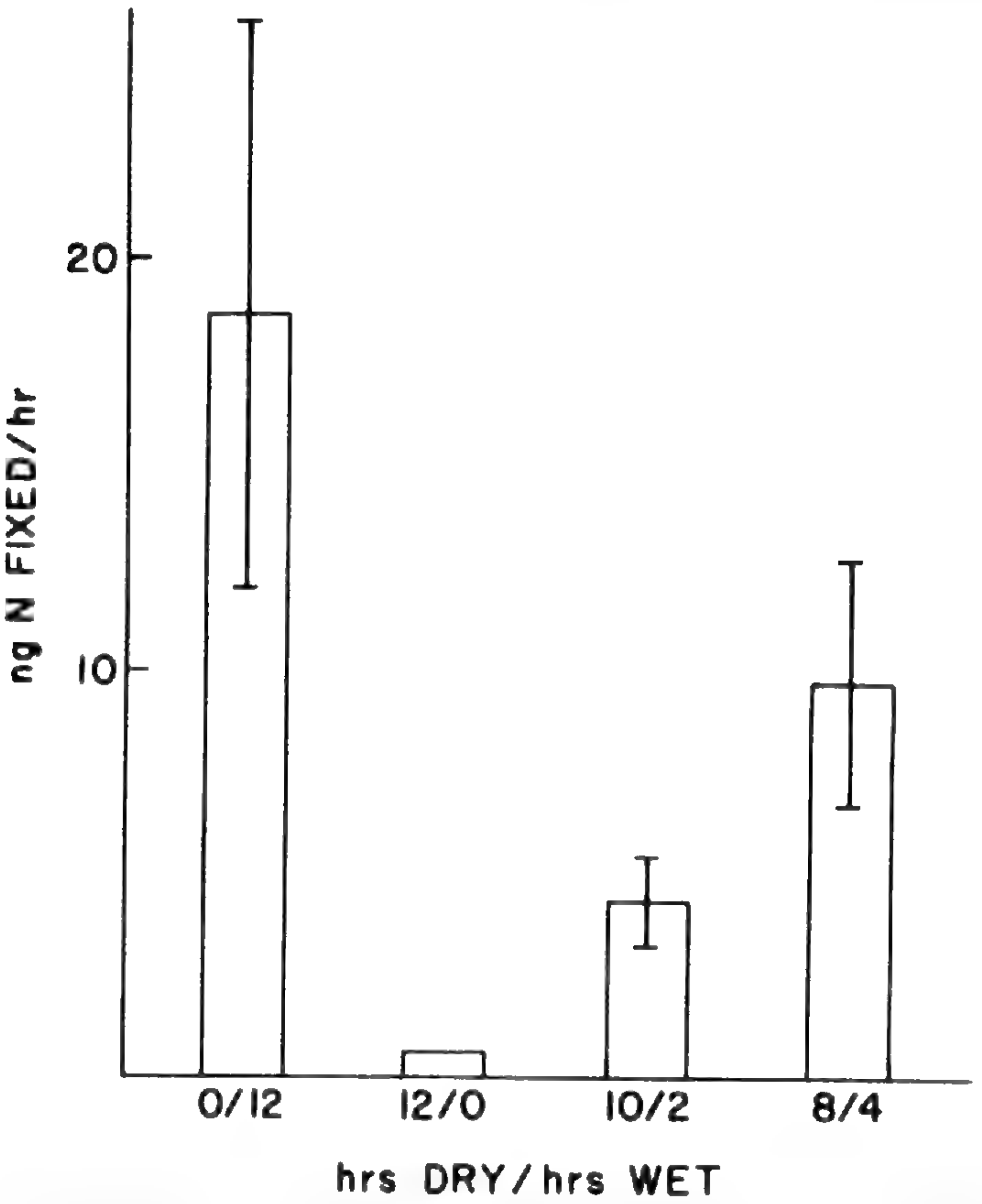

FIGURE 5. The effects of desiccation on nitrogen fixation by epiphylls. Leaflets from the same pinna of *Welfia georgii* were either kept constantly wet (0 hr. dry; 12 hr. wet), or were subjected to varying lengths of drying (12 hr. dry, 0 hr. wet; 10 hr. dry, 2 hr. wet; or 8 hr. dry, 4 hr. wet).

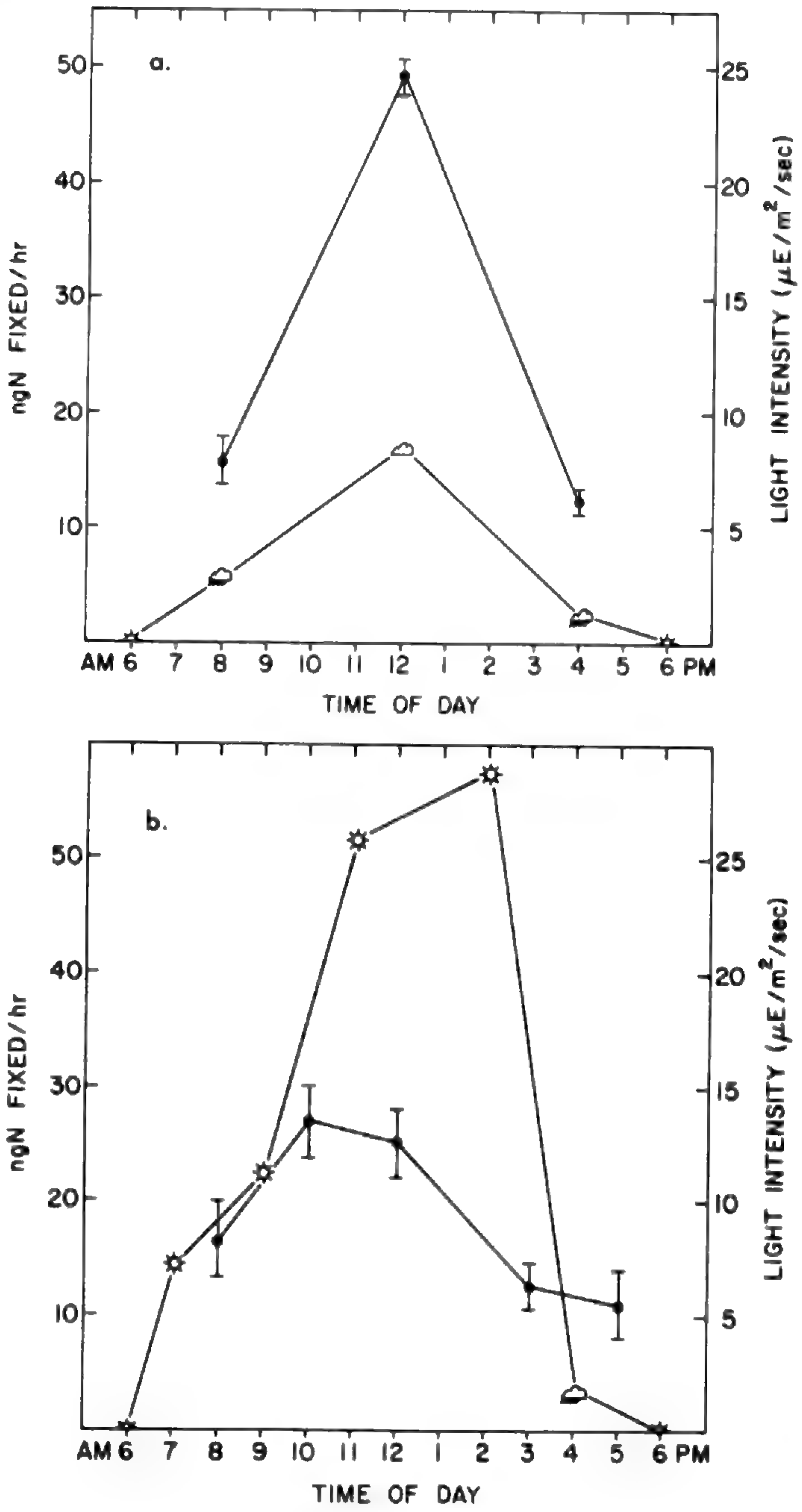

FIGURE 6. The effects of light intensity on nitrogen fixation rates by epiphylls.—a. Fixation rates measured at three times during day 1. Natural light intensities changed with time of day and degree of cloudiness.—b. Fixation rates measured at five times during day 2. Natural light intensities were abnormally high because of the lack of cloud cover.

ence fixation rates, and the second to differentiate between direct effects of light and effects of exogenous glucose on fixation rates by the blue-greens. In the first set of experiments, samples were incubated at three levels of light set to mimic those found in the forest: over epiphyll-laden leaves (12 μEinsteins m^{-2}), in a light gap (68 μEinsteins m^{-2}), and in the dark. As can be seen in Figure 7, fixation was highest at the highest light intensity and was still significant even at the usual light intensity for most epiphylls.

In the second set of experiments, we measured nitrogen fixation by leaf samples that had been dipped in a 0.1% glucose solution, a concentration chosen to mimic concentrations we measured in leaf leachate (Tukey et al., 1957). Again, we incubated the samples at two light intensities. In this case, we were able to separate out the effects of light from the effects of exogenous glucose. Note in Figure 8 that fixation is highest in those samples which were both dipped in the glucose solution and incubated in the light. The lowest rates were for the control samples dipped in water and incubated in the dark. Note, however, that fixation by the samples dipped in the sugar solution but incubated in the dark continued to fix nitrogen at a reasonable rate for at least eight hours. These results document that fixation by epiphylls is influenced by both light directly and by the presence of exogenous glucose. And perhaps as important, they document that fixation can continue at night if exogenous glucose is present on the leaf surface.

Mineral nutrients. Growth of nitrogen-fixing microorganisms may also be limited by availability of mineral nutrients—most commonly potassium, phosphorus, calcium, molybdenum, and iron (Mulder, 1975; Fogg, 1973; Mague, 1977). Deficiencies in any of these can have an

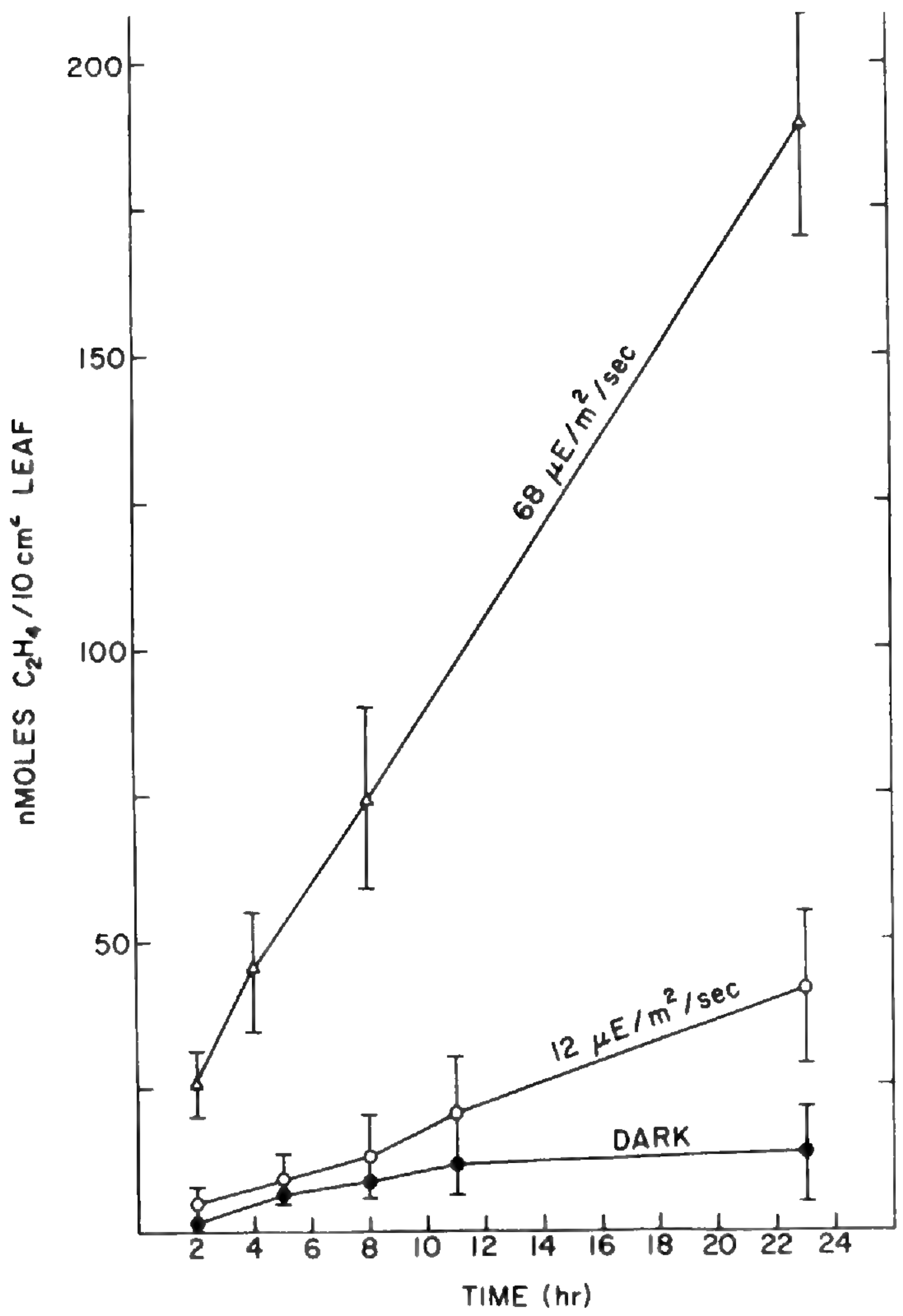

FIGURE 7. Experimental variation of light intensities. Fixation rates are given in terms of nM ethylene to illustrate continuing fixation throughout the 24 hours of the experiment. Ethylene concentrations of samples incubated in the dark do not change after 12 hours.

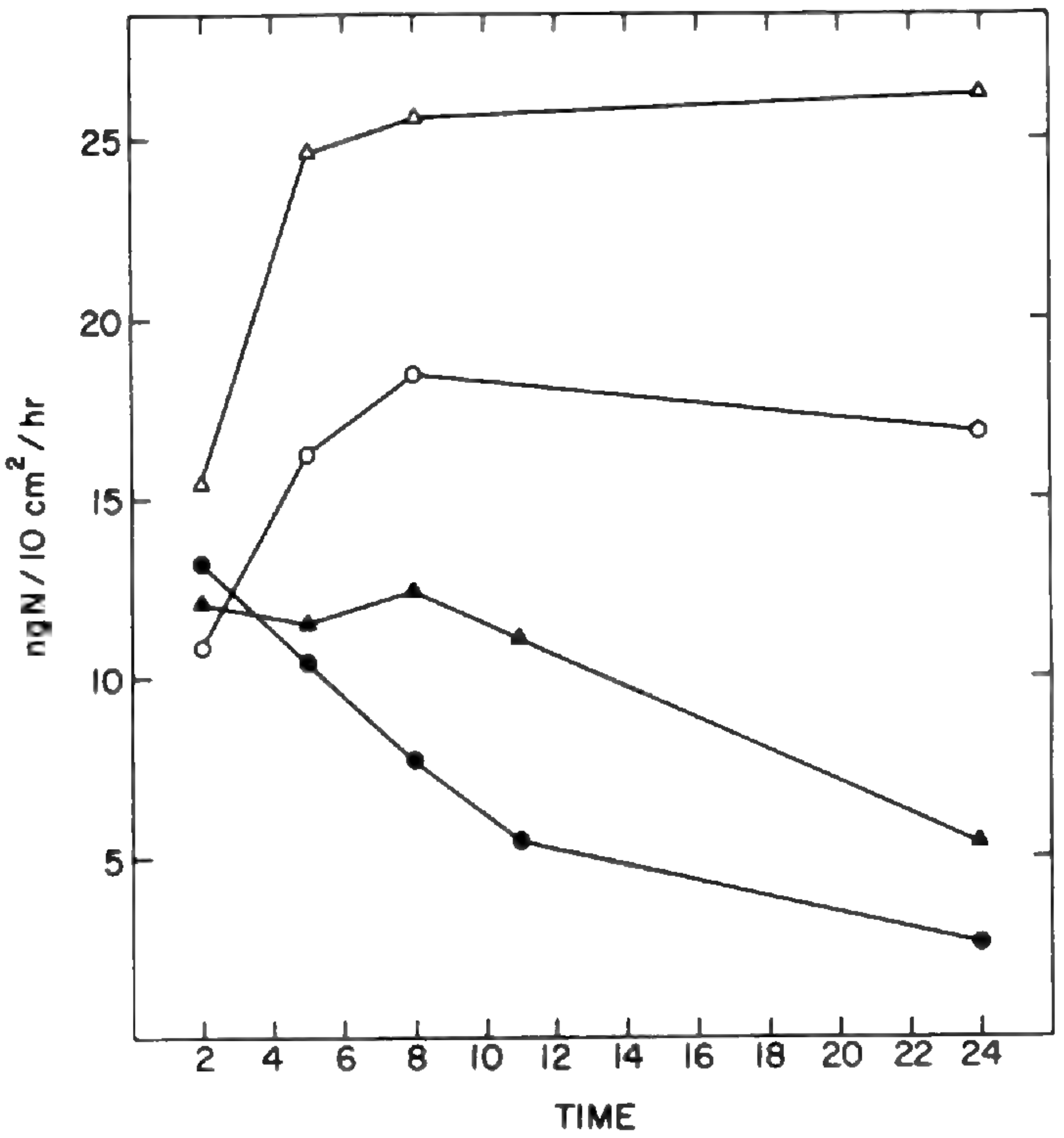

FIGURE 8. The influence of light and exogenous glucose on nitrogen fixation by epiphylls. Samples were incubated in the dark (solid symbols) or light (open symbols) and were either dipped in a 0.1% glucose solution (triangles) or deionized water (circles). The light treatments are significantly different after 4 hours ($P < 0.05$) and all treatments are significantly different after 8 hours ($P < 0.01$).

indirect effect on nitrogen fixation because each is involved in general metabolic activities. In addition, Mo and Fe are components in the nitrogenase molecule. Deficiencies in either of these reduces rates of enzyme synthesis and thus directly affect fixation (Burns & Hardy, 1975).

Exogenous combined nitrogen, most notably NH_4^+, will also inhibit nitrogen fixation (Stewart, 1973; Burns & Hardy, 1975; Fogg, 1973). Again, the effect is the result of reduced nitrogenase synthesis. Interestingly, the effects of combined nitrogen may explain why fixation rates are low in nongrowing cells: as growth slows down, nitrogenous products accumulate in the cell, which in turn impacts on enzyme synthesis. Thus, deficiencies in *any* substance required for growth may reduce nitrogenase activity.

As with exogenous carbohydrates, the main source of mineral nutrients is through decomposition of organic litter on the forest floor, although some may be available in leachate, stemflow, or throughfall water (Long et al., 1956). The latter, in fact, might be quite important in rainforest systems: often a large proportion of decomposition occurs before the dead materials reach the forest floor (Duvigneaud & Denaeyer-de Smet, 1970; UNESCO, 1978). Thus, stemflow and throughfall water can contain significant quantities of nutrient ions derived from "prefall" decomposition as well as that leached from living tissue.

To document the effects of mineral nutrients under field conditions, we performed two types of experiments. The first was to simply measure the nutrients present in rainfall, throughfall, and water flowing off the surfaces of epiphyll-laden leaves, and the second was to determine if nutrients in surface waters could affect fixation rates. We chose to measure phosphate and ammonium simply because these two ions have the most direct effects on fixation. As can be seen in Figure 9, both phosphate and ammonium are present in the environment. Interestingly, the water flowing off epiphyll-laden leaves actually has less nitrogen than the rainfall collected in the open. This suggests that the uptake mechanisms on the leaf surface are extremely efficient. As expected, the concentrations of these two nutrients were

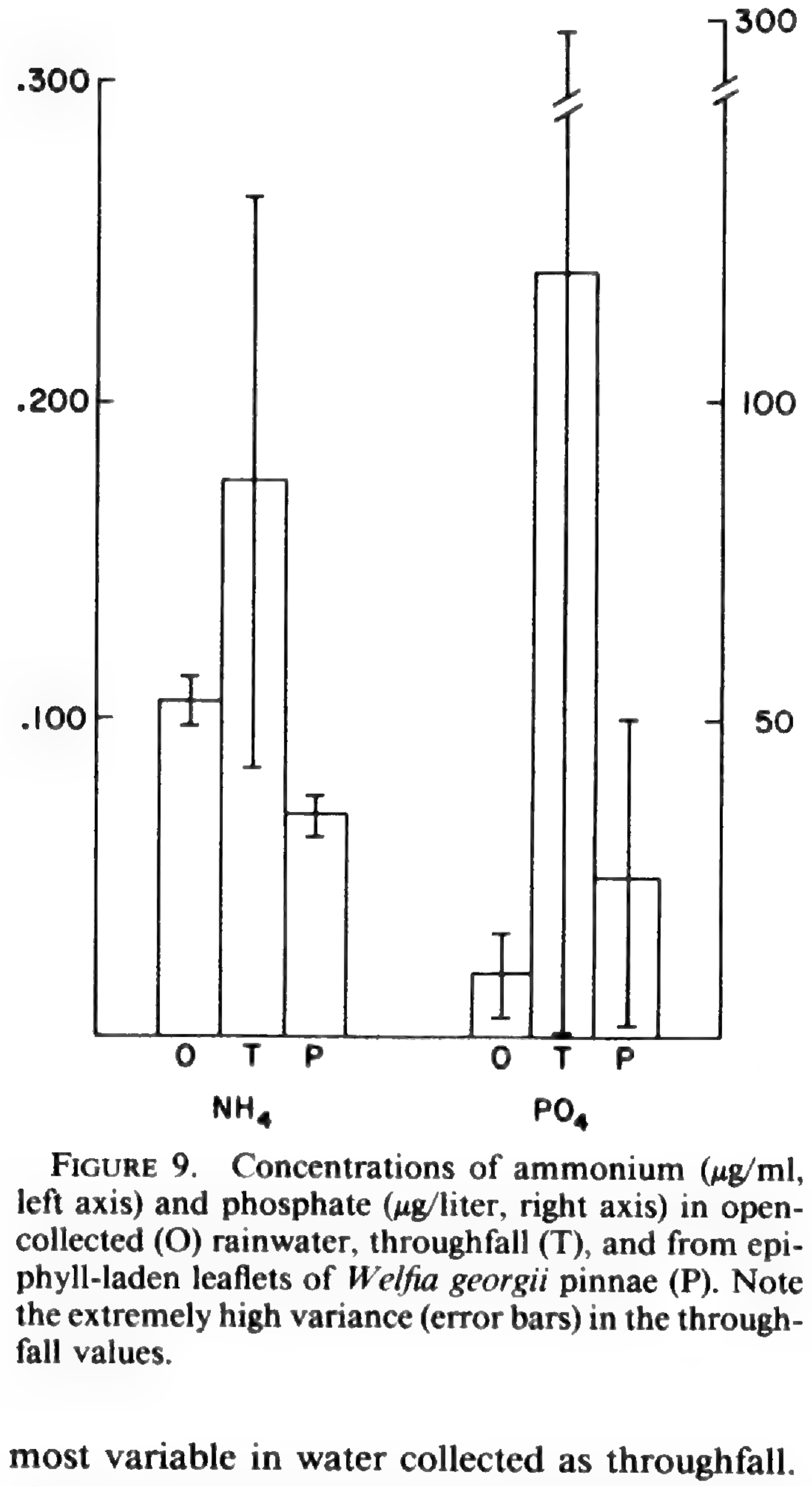

FIGURE 9. Concentrations of ammonium (μg/ml, left axis) and phosphate (μg/liter, right axis) in open-collected (O) rainwater, throughfall (T), and from epiphyll-laden leaflets of *Welfia georgii* pinnae (P). Note the extremely high variance (error bars) in the throughfall values.

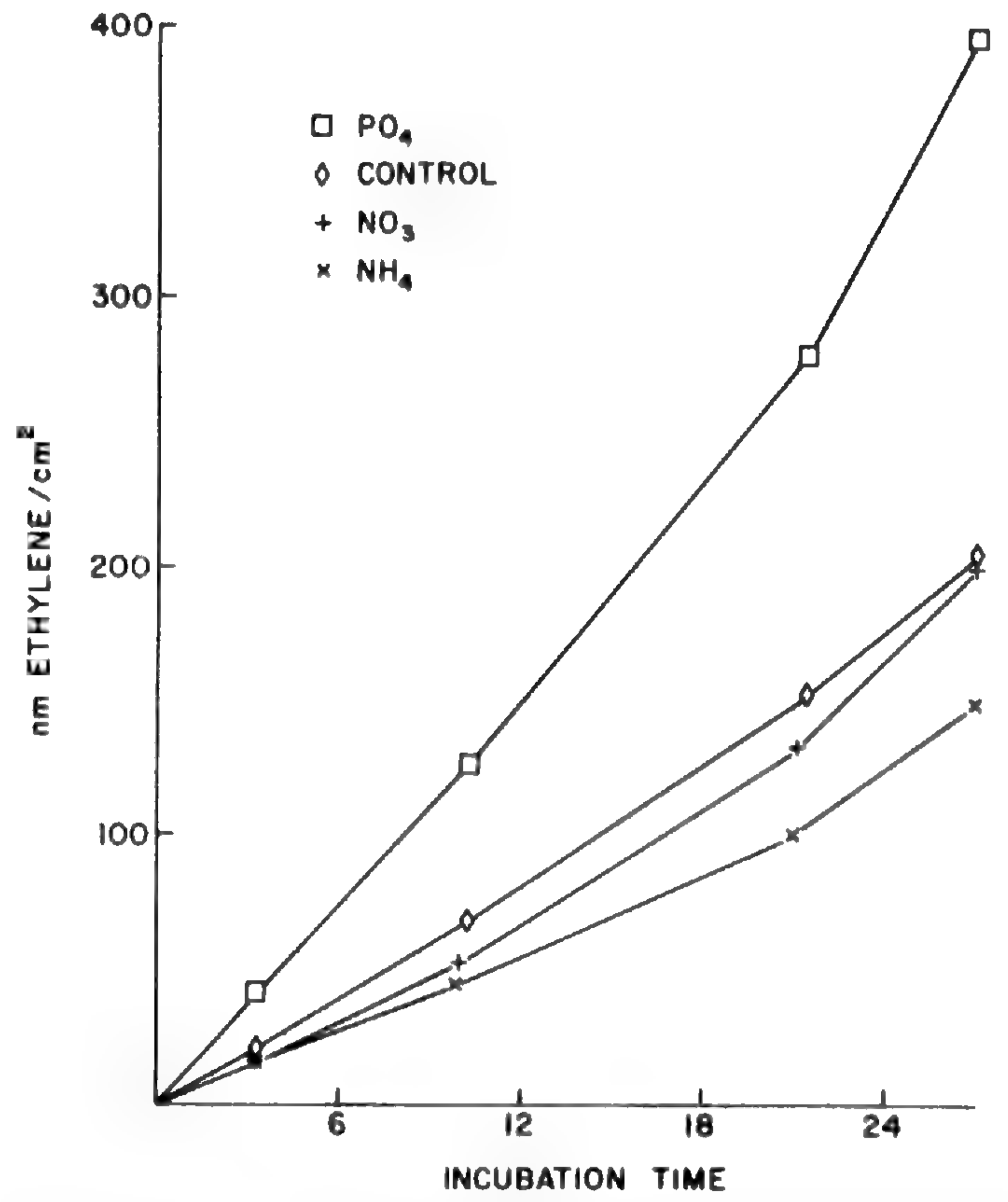

FIGURE 10. Effects of nutrient ions on nitrogen fixation by epiphylls. Leaf samples were dipped into solutions containing 176 μg/liter phosphate as NaH_2PO_4 (□), 429 μg/liter nitrate as $NaNO_3$ (+), 125 μg/liter ammonium as NH_4Cl (×), or deionized water (◊). Fixation rates are plotted as nM ethylene to document that fixation continued at a constant rate throughout the 24-hour incubation.

most variable in water collected as throughfall. Since these nutrients can affect fixation rates (Fig. 10), the concentrations of nutrients in the water washing over the leaf surface can be yet another component adding to the variances of fixation observed in the field.

Summary and conclusion. During the course of this study, we have documented that epiphyllous microorganisms can fix significant quantities of atmospheric nitrogen. This nitrogen can be absorbed by the host leaf and thereby contributes to the nitrogen economy of the host. However, fixation rates are extremely variable and are strongly influenced by environmental factors including substrate (leaf) longevity, light and concomitant desiccation, both organic and inorganic nutrients, and by the co-occurrence of bryophytes. Thus, while fixation by epiphylls can account for up to 25% of the nitrogen present in a host leaf, the contribution of new nitrogen by epiphylls to an ecosystem is probably fairly small. Nevertheless, the very patchiness of the process can free an individual plant from competition with its neighbors, which in turn could allow changes in community interactions. In other words, it is the variance in the system which has made this study so interesting.

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ADAPTIVE RADIATION OF SALAMANDERS IN MIDDLE AMERICAN CLOUD FORESTS[1]

DAVID B. WAKE[2]

ABSTRACT

Tailed amphibians, or salamanders, occur in the tropics only in the New World, where they are concentrated primarily in Middle America and northwestern South America. All are members of the family Plethodontidae, the lungless salamanders. As recently as 1926 only 30 species of tropical salamanders were known, and all were placed in a single genus. Today 11 genera are recognized. All occur in Middle America, and over 140 species have been described. Many local tropical regions are very rich in numbers of species, and as many as 21 species may be present along a single altitudinal gradient. Community organization of species of salamanders in the tropics differs from that in temperate regions in that species of tropical salamanders tend to be segregated into discrete elevational zones, with any given species restricted to a narrow elevational band. Within elevational zones, species are segregated by major habitat type, then by microhabitat, body size, and finally trophic and behavioral features. Cloud forests at middle elevations, from about 750 m to 2,500 m, are especially rich in salamanders, in both diversity and density. In Nuclear Central America nearly 50% of arboreal bromeliads in a local sample (N = 903) contained salamanders. Some species are found almost exclusively in bromeliads, and over 30 salamanders have been encountered in a single bromeliad. Farther south, in Costa Rica, cloud forests harbor salamanders in bromeliads as well as in arboreal and terrestrial moss mats. Extreme microhabitat specialization enriches the Costa Rican fauna to the maximum number of species present locally anywhere in the tropics. In the relatively lower latitudes (e.g., Costa Rica and Panama) the proportion of species occurring at lower elevations increases compared with Mexican and Guatemalan transects.

Bromeliads and moss mats in the mid-elevational wet and rain forests are ideal microhabitats for these insectivorous, direct developing amphibians. Bromeliads offer abundant food resources, egg deposition sites, protection from predation, and microenvironments buffered against temperature extremes and low humidity. Salamanders are top carnivores in the bromeliad microhabitat.

The extensive adaptive radiation of plethodontid salamanders in Middle America has featured both convergent and parallel evolution. The mid-elevational cloud forests, with their rich epiphytic assemblages and highly dissected topography, have been of great significance in speciation, morphological and behavioral diversification, geographical ecology, and historical biogeography of tropical plethodontid salamanders.

The cloud forests of Middle America are home to a unique group of vertebrates—lungless, climbing salamanders that belong to the family Plethodontidae. By "cloud forest" I refer rather loosely to those forest assemblages which form in the presence of fog. Clouds condense at varying elevational levels in Middle America, depending on many local and regional factors such as temperature of the water of the nearest ocean, topography, rainfall patterns, and wind direction (Grubb & Whitmore, 1966; Myers, 1969). In general, cloud forests form between elevations of about 800 and 2,700 m. Both upper and lower boundaries shift with climatic changes, with the lowest occurring along humid slopes in the low latitudes and the highest being found in the northern tropics along the Pacific slopes.

Cloud forests offer ideal conditions for tropical salamanders, all of which are nonaquatic, direct developing species. Although they do not breed in water, these organisms nevertheless require moist conditions for activity, and the cloud forest

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[1] Research reported in this paper has been a collaborative effort involving many individuals, especially James F. Lynch and Theodore J. Papenfuss, both of whom have given helpful criticisms of the manuscript. Marvalee H. Wake carefully reviewed the manuscript and David Darda and Nancy Staub also provided useful comments. My research has been supported by the National Science Foundation and the Museum of Vertebrate Zoology. I gratefully acknowledge the cooperation of governmental agencies in Mexico, Guatemala, and Costa Rica in obtaining permission to conduct research in their countries, and Douglas Robinson and Pedro Leon for their help and cooperation in Costa Rica.

I dedicate this paper to the memory of L. C. Stuart, who generously offered his unparalleled knowledge of the Guatemalan herpetofauna to me, and whose published work remains as an inspiration to future students of Guatemalan and other tropical environments.

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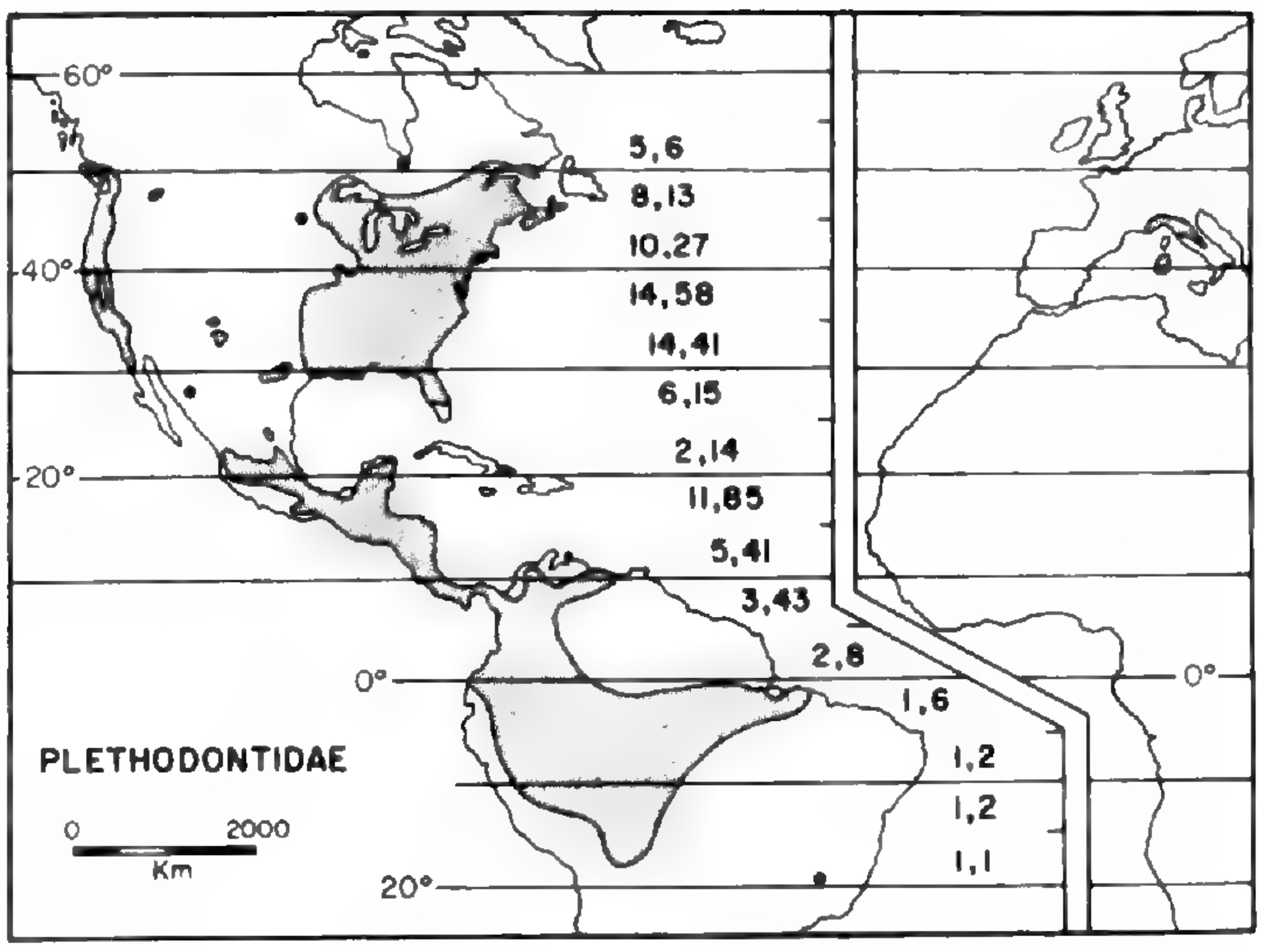

FIGURE 1. Latitudinal gradient of generic and species diversity in the salamander family Plethodontidae. The numbers of genera (first figure) and species (second figure) that occur in zones of five degrees latitude are indicated. Data are available from the author. Undescribed species for which descriptions are being prepared have been included.

environments are effectively buffered from desiccating conditions as well as from extremes of temperature. In addition, these forests typically support abundant epiphytes that are used extensively by salamanders.

There are more than 140 species of plethodontid salamanders in the New World tropics; about 80% occur in Middle America (Wake & Lynch, 1976; Frost, 1985). What makes them unusual is their great diversity in the New World tropics and their total absence from the Old World tropics. Middle America has been the setting for an extensive, unique adaptive radiation that has remained very localized.

The success of these species can be measured against that of salamanders generally. Worldwide, there are about 350 species of salamanders divided among nine families (Frost, 1985). Eight families are restricted to North Temperate regions. Over 200 of the species are members of the family Plethodontidae, the only group of salamanders to radiate in tropical regions. All tropical species of salamanders are members of the supergenus *Bolitoglossa* (Wake, 1966), which contains 11 genera and about 40% of the species of salamanders in the world. The supergenus is exclusively New World in distribution and does not occur north of Mexico.

The plethodontids have a curious distribution, with two primary areas of evolutionary diversification: North America with concentration in the Appalachian region, and Middle America (Fig. 1). In eastern North America are found three major groups of plethodontids, two of which have life histories involving an aquatic larval stage. The Middle American region contains members of a fourth major group, the tribe Bolitoglossini, members of which have a uniphasic life history featuring direct development without a larval stage (Wake, 1966). The other two supergenera in the Bolitoglossini occur in California and Oregon (and possibly in Alaska and Mexico), and on Sardinia, the Italian mainland, and a tiny portion of southeastern France.

I have argued elsewhere that the absence of an aquatic larval stage facilitated occupancy of the relatively densely crowded, predator-rich tropics (Wake, 1966; Hanken et al., 1980). A unique feeding mechanism and an associated behavioral repertoire (Lombard & Wake, 1977, 1986; Roth & Wake, 1985a, 1985b), which could evolve its particular characteristics only in a group lacking aquatic larvae, may have aided in the successful radiation of the tropical species. Those animals use a highly specialized, extremely fast tongue projection mechanism to capture moving prey at a considerable distance, and thus they are able to feed on a wide array of invertebrate animals.

We still know relatively little about the tropical plethodontids. The authoritative work of Dunn (1926) listed but 30 species and placed them all in a single genus. Taylor (1944) recognized the generic diversity of the group (seven genera), but four additional genera were described as recently as 1983 (Elias & Wake, 1983; Wake & Elias, 1983), and about one-half of the 140 species have been described since 1950. Not surprisingly, most published work has dealt with taxonomy and systematics, although there has been some research on life history (Vial, 1968; Houck, 1977a, 1977b) and geographical ecology (Schmidt, 1936a; Martin, 1958; Wake & Lynch, 1976; Wake et al., 1987).

The present paper attempts to evaluate the role of epiphytic communities in the evolution of the neotropical salamanders. I summarize information that my research collaborators and I have gathered over the past 15 years. In particular, I examine the results of transect studies from Mexico to Costa Rica and concentrate on an area that appears to have been of critical importance for salamanders, the mid-elevation cloud forests.

ECOLOGICAL GEOGRAPHY AND SYSTEMATICS

Salamanders in the tropics have diversified in three major regions, each characterized by a rel-

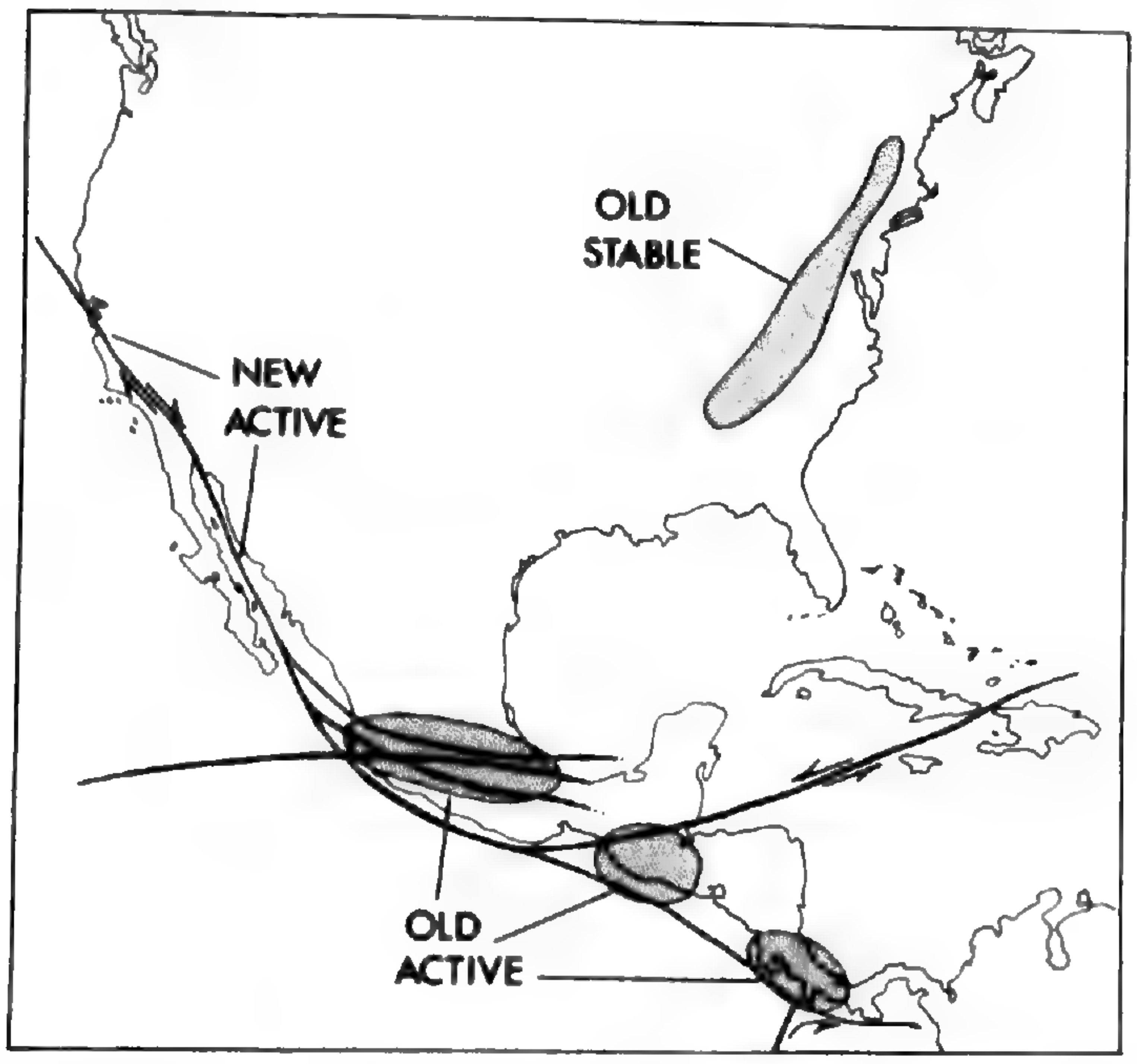

FIGURE 2. Generalized map illustrating regions of major evolutionary diversification within the family Plethodontidae during Cenozoic times. Some major fault systems are indicated. The family is thought to have originated in the old and tectonically relatively stable Appalachian region. For much of the Cenozoic, representatives of the family have been undergoing an adaptive radiation in what is today Middle America, with diversification concentrated especially in the three core regions indicated: the southeastern margin of the Mexican Plateau, Nuclear Central America, and Talamancan Central America. Two supergenera with affinities to the tropical supergenus *Bolitoglossa* may have been involved in a reinvasion of temperate North America through association with land movements and tectonic activity in the extended San Andreas fault system. For more detailed analysis of geological history in relation to salamander distribution see Hendrickson (1986).

atively ancient tectonic core, high topographic diversity, and high tectonic activity along some borders. From north to south, these regions are: 1) the southeastern margins of the Mexican Plateau and the highlands of northern Oaxaca, 2) Nuclear Central America, and 3) Talamancan Central America (Wake & Lynch, 1976; Fig. 2). Each region is characterized by species richness and a high degree of endemism (Savage, 1982). For example, *Chiropterotriton, Lineatriton, Thorius,* and *Parvimolge* are endemic to region 1, and *Pseudoeurycea* occurs mainly in region 1 with only a few species in region 2. *Dendrotriton, Bradytriton,* and *Nyctanolis* are endemic to region 2, and the great majority of the species of the beta assemblage of the large genus *Bolitoglossa* occur there. The few species of *Bolitoglossa* beta which occur in regions 1 and 3 are members of distinct subgroups (see Papenfuss et al., 1983). The genus *Oedipina* is centered in region 3, and only one species extends as far north as Chiapas. The alpha assemblage of *Bolitoglossa* is centered in region 3 and areas to the south, but a distinct species group extends northwestward to the other two regions. The genus *Nototriton* is something of a puzzle (see below). It has species in all three regions.

FIGURE 3. *Chiropterotriton arboreus,* a bromeliad-dwelling salamander from near Zacualtipán, Hidalgo, Mexico. This species has the typical features of a bromeliad specialist: a long prehensile tail, relatively long legs, large hands and feet with widely spread digits, and frontally directed eyes. The fine divisions on the scale are mm.

Early zoogeographic biases combined with inadequate collecting led to the perception of tropical salamanders as northern invaders that had "trickled" down into the tropics. Dunn (1926) placed all 30 species then recognized in a single genus, and several of his species groups later proved to be polyphyletic. For example, he united all elongate animals into one group, and all small, bromeliad dwellers into another, thereby obscuring the extensive parallelism and convergence that have occurred. Even after Taylor's (1944) generally progressive division of the genus *Oedipus* into several genera, the bias of recent

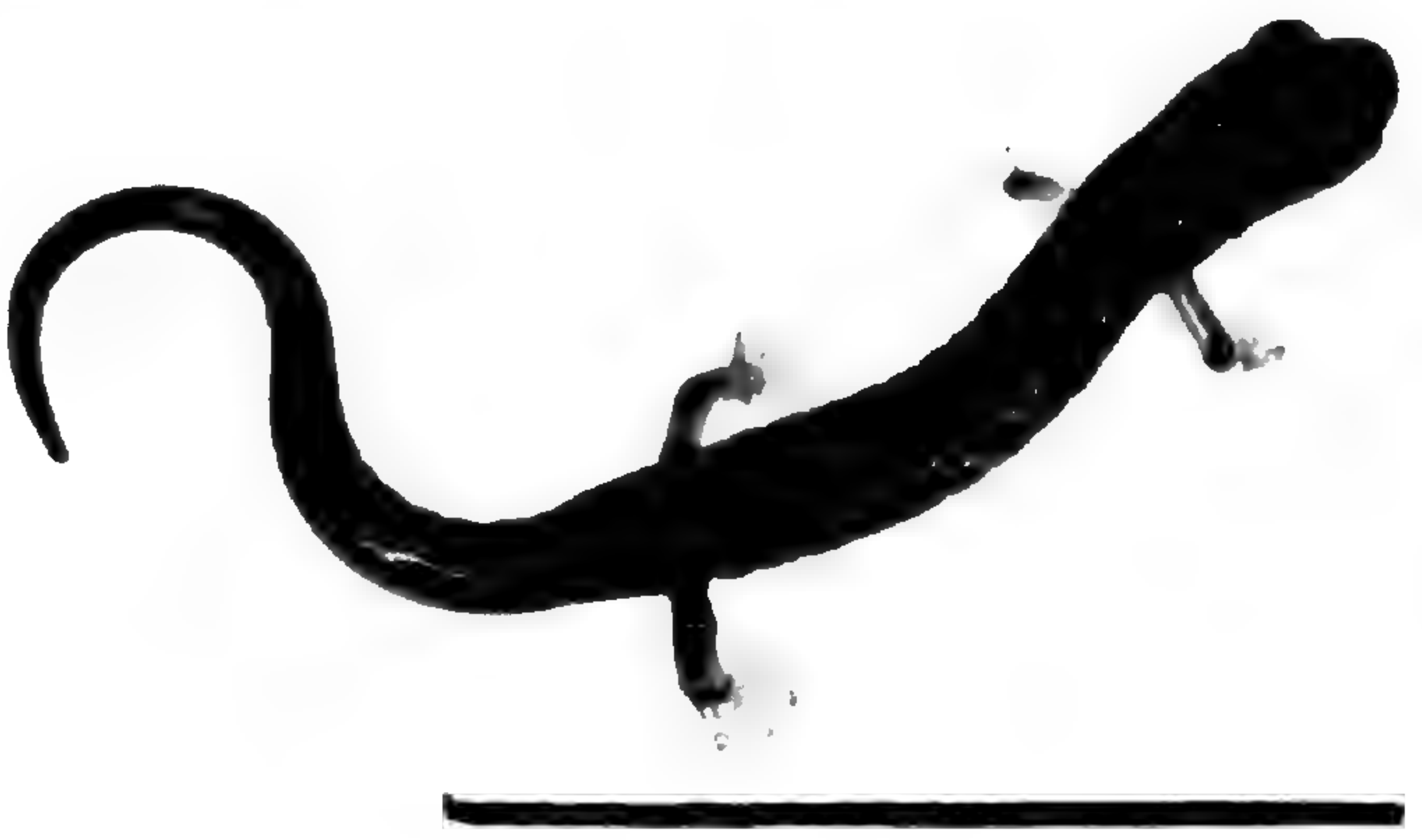

FIGURE 4. *Dendrotriton xolocalcae,* a bromeliad-dwelling salamander from the upper slopes of Cerro Ovando, Chiapas, Mexico. This bromeliad specialist shares many gross structural similarities with species that occupy similar microhabitats (Figs. 3, 5). The scale bar is 25 mm.

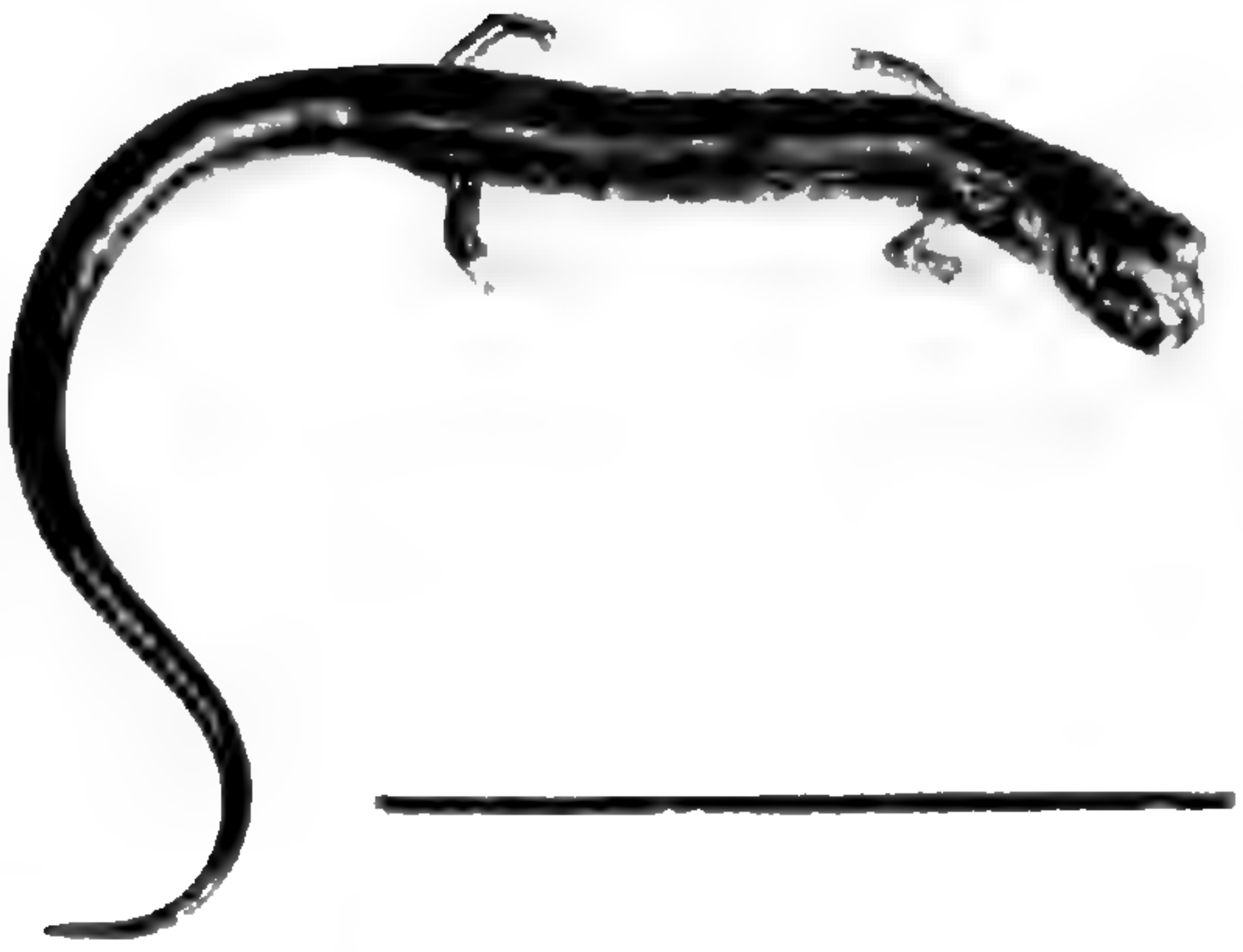

FIGURE 5. *Nototriton veraepacis,* a bromeliad-dwelling salamander from 10.5 km N Santa Cruz, Zacapa, Guatemala, in the Sierra de las Minas. Compare this species with unrelated bromeliad specialists in Figures 3 and 4. The scale bar is 25 mm.

penetration from the north persisted. The genus *Chiropterotriton* as recognized prior to 1983 provides an example. Its species mainly are bromeliad specialists living in cloud forests, and they are superficially similar in external morphology (Figs. 3–5). Both Rabb (1960) and Wake (1966) recognized that members of the genus differed substantially in osteology, but they chose to interpret this as increasing divergence and specialization toward the south. This especially instructive case is relevant to the main theme of this paper and is developed further below.

Species once assigned to *Chiropterotriton* are typically small, slender, long tailed, acrobatic forms, that are common inhabitants of cloud forests in Mexico, Nuclear Central America, and Costa Rica (Figs. 3–5). Based on their study of comparative osteology, Lynch & Wake (1975, 1978) recognized that the species below the Isthmus of Tehuantepec formed a cladistically distinct group, which they termed *Chiropterotriton* beta. The latter group was found to include at

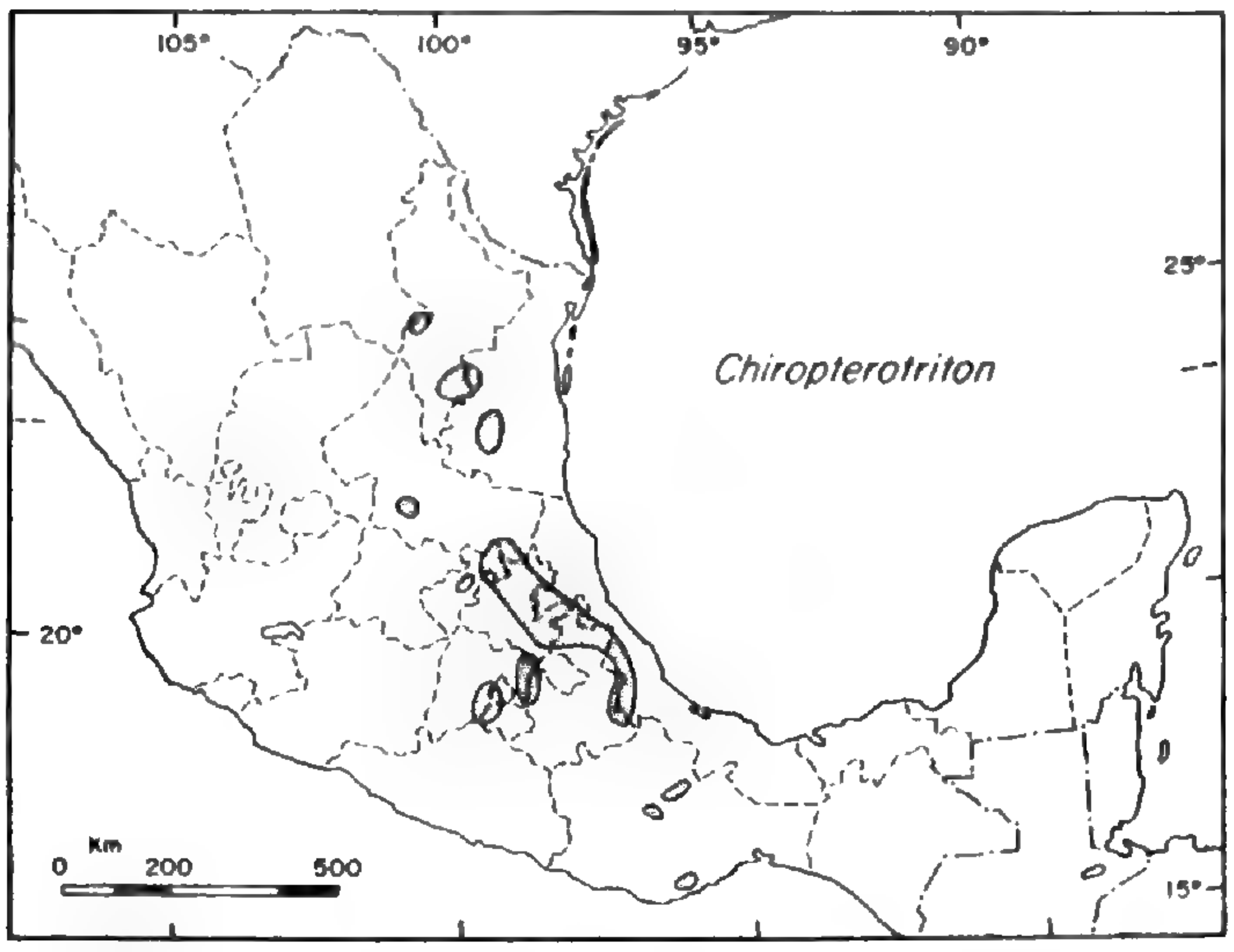

FIGURE 6. Probable distribution of the genus *Chiropterotriton.* Most species occur in cloud forests, and a number utilize bromeliads as microhabitats. The generalized ranges were derived by grouping known localities into potentially contiguous units, based on forest distribution. Information gathered by David M. Darda and the author.

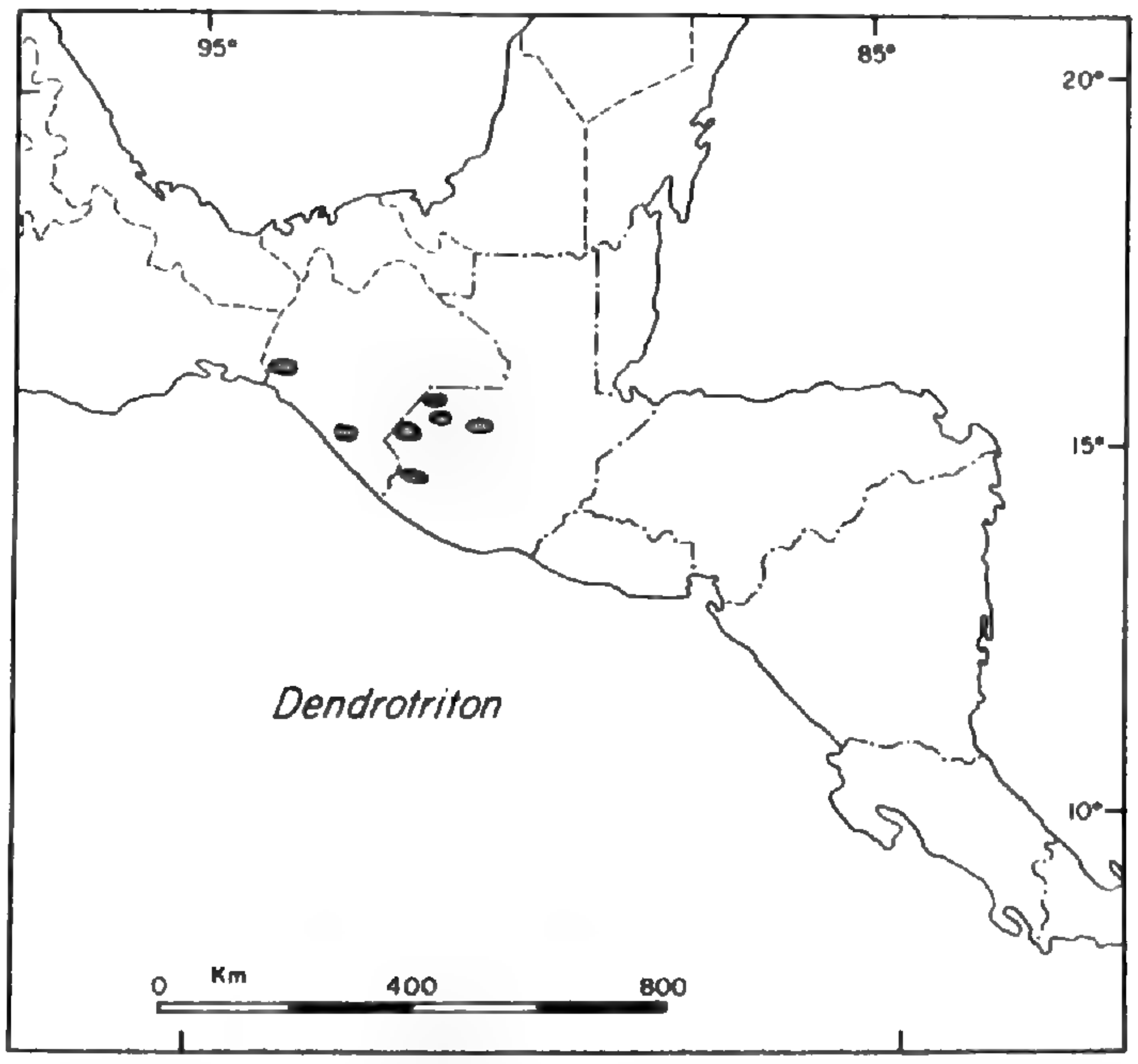

FIGURE 7. Distribution of the genus *Dendrotriton.* Species of this genus are bromeliad specialists restricted to cloud forests. All occupy small geographic ranges, and only *D. rabbi* occurs in more than one of the isolates indicated here (Elias, 1984).

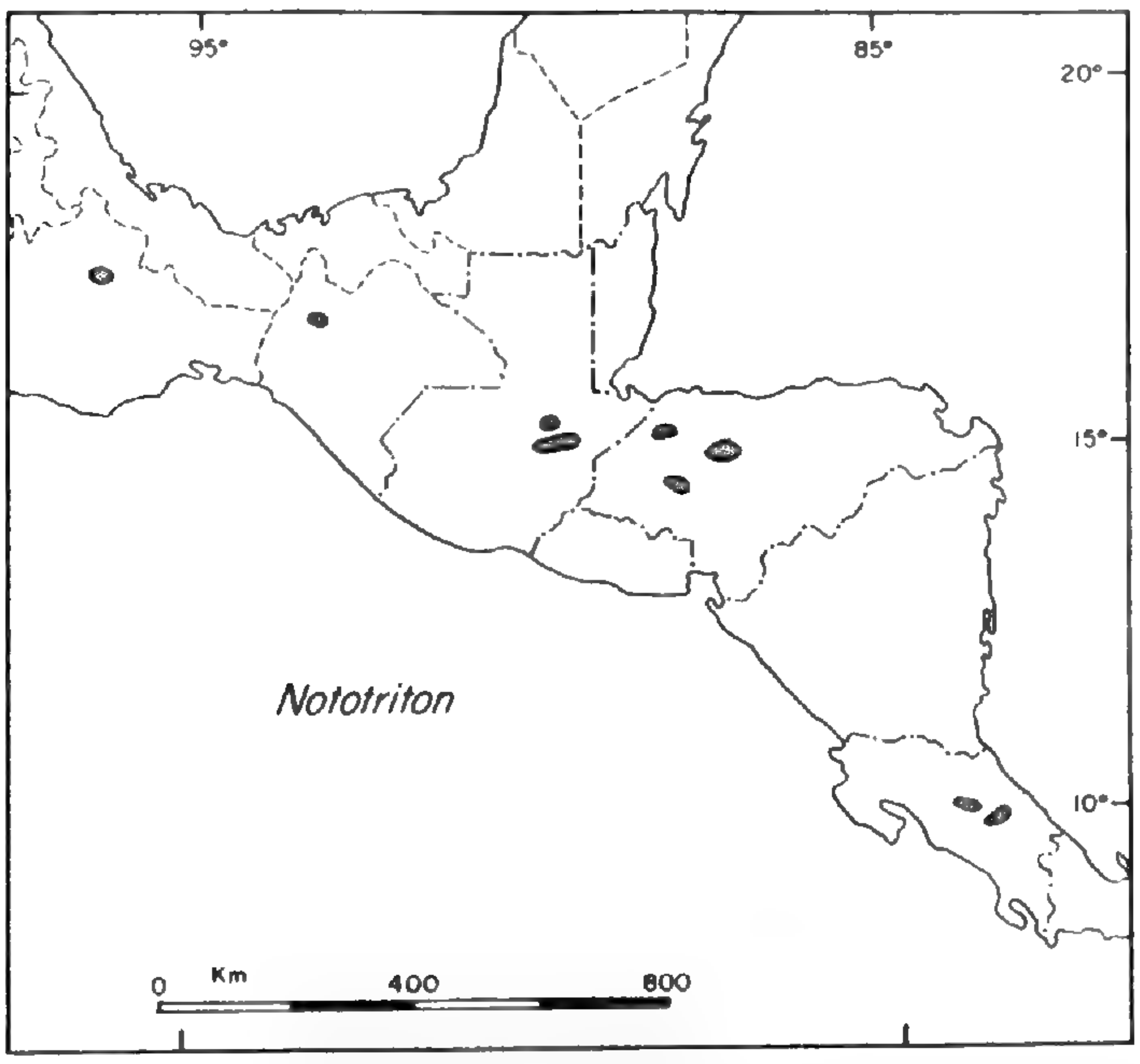

FIGURE 8. Distribution of the genus *Nototriton.* This genus may not be a monophyletic group. The species are all small and resemble one another in many external morphological and ecological features. All of the species inhabit cloud forests, but the Costa Rican species use moss mats as a primary microhabitat, while the Guatemalan and Honduran species are bromeliad specialists. The Chiapan and Oaxacan records are based on recently discovered and as yet undescribed species.

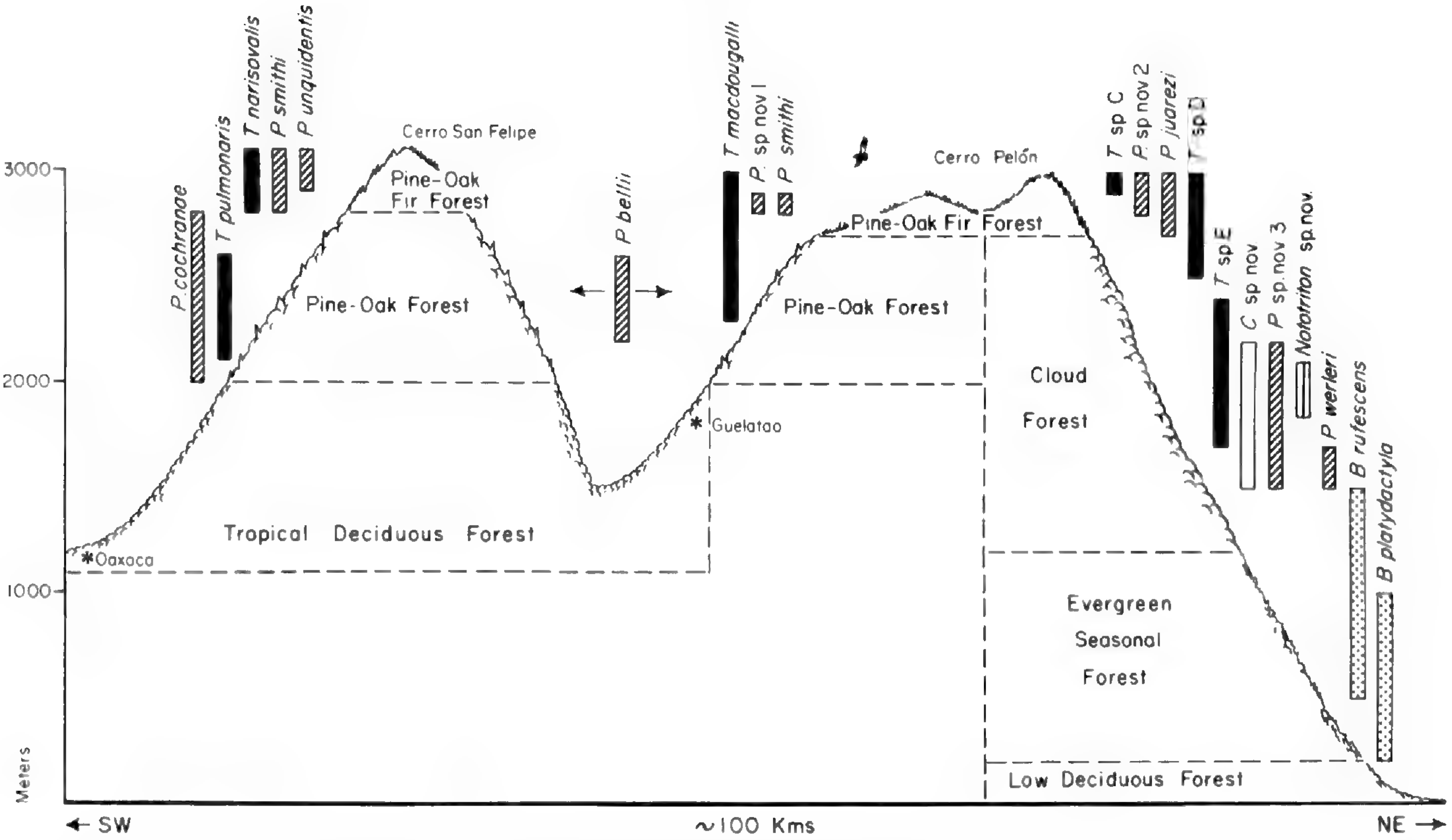

FIGURE 9. Distribution of plethodontid salamanders along the Northern Oaxacan transect, about 100 km in length, extending north-northeastward from Ciudad de Oaxaca, over Cerro San Felipe and the Sierra de Juarez to the vicinity of Tuxtepec, Oaxaca, Mexico. The northern slopes of the Sierra de Juarez are occupied by an extensive cloud forest which offers habitat to numerous species of salamanders. Updated version of diagram presented by Wake et al. (1987).

least two distinct subgroups, an interpretation subsequently supported by molecular biological data (Maxson & Wake, 1981). The two southern groups finally were given generic status as *Dendrotriton* and *Nototriton* by Wake & Elias (1983), who noted that *Nototriton* might prove to be paraphyletic. Some species of each of the three genera resulting from the subdivision of *Chiropterotriton* include members that are very similar in external morphology. Because the species are very small (frequently <40 mm in head plus body length), the critical differences in morphology can be difficult to detect. The species of the three genera typically have small ranges, and the widely disjunct ranges offer little opportunity for sympatry. These salamanders are found mainly in isolated cloud forests, and several of them remain rare and poorly known.

Until recently we thought that *Chiropterotriton, Dendrotriton,* and *Nototriton* were exclusively allopatric (Figs. 6–8). *Chiropterotriton* occurs as 11 or more discrete geographic isolates in eastern Mexico, north of the Isthmus of Tehuantepec. *Dendrotriton* is found only in Nuclear Central America, mainly on Pacific slopes, but also in some internal regions of Caribbean drainage. *Nototriton* is the southernmost of this group, and it occurs in regions of Caribbean drainage. An undescribed Oaxacan species of *Nototriton* occurs in sympatry with an undescribed species of *Chiropterotriton,* an association that was unexpected. Both were discovered as a result of detailed studies of vertical zonation along a transect (Fig. 9). Our knowledge of the groups probably remains far from complete, even at the alpha taxonomic level, but they clearly offer fascinating opportunities for the study of convergent evolution.

Lynch & Wake (1978) showed that bromeliad-inhabiting species currently placed in the genera *Dendrotriton* and *Nototriton* resemble each other very closely in external morphology. The bromeliad-dwelling species of *Nototriton* are more similar to bromeliad-dwelling species of *Dendrotriton* in external morphology (evaluated by methods of multivariate morphometrics) than to semi-fossorial congeners that live in moss mats on soil banks. These distantly related species have converged so that they share body forms that are especially well suited for life in bromeliads. Indeed, if *Nototriton* is, as I believe, paraphyletic it is possible that we actually have underestimated the true amount of evolutionary convergence.

The three genera discussed above are commonly encountered inhabitants of cloud forests and epiphytes. Other tropical salamander genera also contain cloud forest inhabitants, and many use epiphytes as their main microhabitats. Some of these, such as the Nuclear Central American *Nyctanolis* and *Bradytriton,* are recently discovered and their habits are very poorly known (Elias, 1984). The monotypic Mexican genera *Parvimolge* and *Lineatriton* (the latter an elongate fossorial form that utilizes moss mats to some degree; Fig. 11) are relatively rare within their restricted ranges, which lie at the lower margins of cloud forests. Some species of the Mexican genus *Thorius* occasionally occur in bromeliads; an undescribed species from the northern slopes of the Sierra de Juarez in Oaxaca seems to occur primarily in bromeliads (undescribed species E, fig. 9 in Hanken, 1983). The remaining genera (*Pseudoeurycea, Bolitoglossa,* and *Oedipina*) have numerous species that are inhabitants of cloud forests.

Pseudoeurycea is widespread in Mexican and southwestern Guatemalan cloud forests, but most species are terrestrial and are not often found in epiphytes. The only described species that are bromeliad specialists are *P. firscheini* (Werler & Smith, 1952; Shannon & Werler, 1955b) and *P. nigromaculata* of Veracruzian cloud forests (unpubl. data, contra Taylor, 1941). An undescribed species from our Northern Oaxacan transect (Fig. 9) uses arboreal microhabitats, and an additional undescribed species from our San Marcos transect (Wake & Lynch, 1976: 30) uses bromeliads consistently.

Bolitoglossa, with 68 currently recognized species, has by far the greatest geographic range of the tropical salamander genera (from Veracruz, Mexico, to Brazil, Bolivia, and Peru). Many of the species in Nuclear Central America are cloud forest specialists, and they frequently occur in bromeliads. Over one-half of the *B. engelhardti* encountered during an intensive investigation of an elevational transect on the lower slopes of Volcán Tajumulco, western Guatemala, were found in bromeliads, and *B. franklini* is also a frequent inhabitant of bromeliads (Wake & Lynch, 1976). Most records for *Bolitoglossa* in bromeliads refer to members of the beta assemblage (e.g., Stuart, 1943). Some of these occur north of the Isthmus of Tehuantepec (the northern limits of Nuclear Central America), including *B. hermosa* (Papenfuss et al., 1983), from the Pacific slopes of Guerrero, Mexico, and the widespread Gulf-Caribbean slope species *B. rufescens* (Taylor & Smith, 1945), which ranges from San Luis Potosí, Mexico, to Honduras. The only two species of the beta assemblage that reach Costa Rica (*B. alvaradoi, B. arborescandens*) have been taken in bromeliads (Taylor, 1954; unpubl. data).

Occurrence of members of the large alpha assemblage of *Bolitoglossa* in bromeliads is less well documented. The distribution of this group is centered in the Talamancan region and in northern Colombia; only the *mexicana* group (Wake & Lynch, 1976) occurs as far north as the eastern margins of the Mexican Plateau and Nuclear Central America. The *mexicana* group is found mainly in the lowlands, and there are no records of the species being found in bromeliads in cloud forests. Two members of the group, *B. platydactyla* and *B. mexicana,* have been recorded from bromeliads, mainly at elevations of <500 m (Taylor & Smith, 1945). There are scattered reports of *Bolitoglossa* alpha in cloud forest bromeliads in Talamancan Central America and regions to the south (e.g., *B. borburata* near Rancho Grande, Venezuela, Trapido, 1942; *B. lignicolor,* Dunn, 1937; *B. subpalmata,* Robinson, 1977; *B. taylori,* Wake et al., 1970). But in Costa Rica, where the assemblage is well represented, there are surprisingly few records of its occurrence in bromeliads (Robinson, 1977), although we now know that some species are common in such microhabitats (see below).

Several species of the alpha assemblage of *Bolitoglossa* are associated with arboreal microhabitats in cloud forests. The only known adult of *Bolitoglossa diminuta* was collected with an egg mass in a mat of liverworts (Robinson, 1976; recent examination of the tiny holotype, which lacks a sublingual fold, suggests that this species should remain in *Bolitoglossa,* contra Wake & Elias, 1983). Other species associated with moss mats covering tree trunks and branches include *B. marmorea* of Panama (Wake et al., 1973) and an undescribed species sympatric with *B. diminuta.*

The final genus, *Oedipina,* is widespread in cloud forest habitats in Costa Rica, the center of its diversity (Brame, 1968). These salamanders are elongate, mainly fossorial species that include some relatively specialized arboreal climbers in lowland forests (e.g., *O. parvipes*). The species that occur at intermediate elevations in cloud forests typically are found in moss mats covering downed vegetation and soil banks.

Information in the above paragraphs makes clear that there has been an extensive adaptive radiation of salamanders in the New World tropics, but the age of this radiation remains unknown. Since the initial effort of Dunn (1926), subsequent studies have for the most part suggested progressively earlier dates for the entry of salamanders into the region (Martin & Harrell, 1957, is a striking exception), and until recently an Early or Middle Tertiary origin of the group was accepted (Wake & Lynch, 1976). But biochemical and immunological studies in the last decade have shown that even within genera there has been very great genic differentiation, which implies relatively great age for the separation of the lineages studied (Hanken, 1983; Hanken & Wake, 1982; Larson, 1983, 1984; Lynch et al., 1983; Maxson & Wake, 1981; Papenfuss et al., 1983; Wake & Lynch, 1982). Progress has been made in defining monophyletic groups, but I believe that we have not yet achieved a robust cladistic hypothesis for the group (Wake & Elias, 1983), mainly because of the extensive parallelism and convergence that have obscured patterns. Nevertheless, Hendrickson (1986) has attempted to interpret the history of the group by combining what is known about likely cladistic patterns with knowledge of the geological history of the region in a vicariance biogeography study. He suggested that salamanders which gave rise to the tropical radiation first separated from those in the Appalachia area by rifting of an ancient Maya terrane from Appalachia or by a post-Middle Jurassic to Mid-Cretaceous marine transgression. In general he argues for much older times of separation than previous authors, based both on arguments from earth history and from his belief (although he has not studied these salamanders directly) that the extensive radiation of the tropical salamanders must have taken a long time. I cannot discuss this provocative study in detail here, but it is important to understand that available evidence suggests that salamanders and habitats have coevolved in areas that became present-day Middle America for a very long time.

SALAMANDERS AND EPIPHYTES

The epiphytic component of cloud forests offers two major classes of microhabitats for salamanders—arboreal bromeliads and moss mats (which are complex and contain diverse ferns, club mosses, and roots, stems, and entire small angiosperms). These microhabitats, particularly bromeliads, are used on occasion by other vertebrates: frogs (especially *Hyla* and *Eleutherodactylus*), lizards (especially *Abronia*), and snakes (e.g., *Bothrops schlegeli*). However, with the exception of a few species of frogs whose tadpoles are clearly adapted for life in the water of tank bromeliads, only salamanders rely on epiphytic plants as their main microhabitats, and salamanders are far more common in bromeliads than are any other vertebrates.

The density of salamanders in bromeliads is difficult to document. As many as 34 *Dendrotriton xolocalcae* have been found in a single bromeliad in Chiapas, Mexico (Taylor & Smith, 1945), but until recently we have had few quantitative data to indicate the frequency of occurrence of salamanders in bromeliads. Although one of the first reports of salamanders living in bromeliads was from Costa Rica (Picado, 1913), the general impression has been that salamanders are not common in bromeliads (Robinson, 1977). Bromeliads have been thought to be more important for salamanders in Mexico, Guatemala, and Honduras. In an early account, Gadow (1908) reported that a Mexican species of *Pseudoeurycea* leads a "partly arboreal life, their favorite hunting and hiding-places being in the clusters of epiphytic plants, such as tillandsias, orchids and the climbing phyllodendrons." Schmidt (1936a, 1942) described bromeliad-dwelling salamanders as relatively abundant in Guatemala and Honduras, apparently more so than in Costa Rica and Panama (Dunn, 1937).

In contrast to the above generalization, salamanders in Costa Rica use moss mats more commonly than do salamanders farther to the north and west. The genera *Nototriton* and *Oedipina* use moss mats extensively in Costa Rica, but apparently rarely do so in northern Middle America. To the north and west *Oedipina* is mainly fossorial, and *Nototriton* is associated mainly with bromeliads (an exception may be a poorly known, undescribed species from Chiapas that has been taken in a moss-covered bank).

There is a general morphology that characterizes most bromeliad-dwelling salamanders (Figs. 3–5). They typically are small animals (usually <50 mm body length) with long, prehensile tails, long limbs with widely spread digits, and frontally directed eyes. They are acrobatic climbers and are very adept in a three dimensional environment. Some larger salamanders use bromeliads on occasion, but the true specialists usually approximate the above description.

Occupants of moss mats are less characteristic in morphology. In general they are slender and have relatively short legs. The Appendix contains a list of species which have been reported to occur in bromeliads and moss mats. It also contains a few species known by me to have such habits, but which as yet are not reported in the literature. This list does not differentiate between species that specialize on these microhabitats and those that are but casual occupants.

COMMUNITY ORGANIZATION

For nearly 15 years my colleagues (James F. Lynch and Theodore J. Papenfuss) and I have been engaged in a broadly based survey of geographical ecology and community organization of the salamanders of Mesoamerica (Wake & Lynch, 1976; Wake et al., 1987). We established a series of line transects in Mexico, Guatemala, and Costa Rica and conducted intensive sampling over a multi-year period along each of them.

By far the most intensively studied of these transects is located in extreme southwestern Guatemala and adjacent Mexico, between San Marcos, Guatemala, and Tapachula, Chiapas, Mexico. Our San Marcos transect extends from the continental divide, down the Pacific slopes of Volcán Tajumulco, to the Pacific coastal plain. Here we have documented the presence of a rich salamander fauna comprised of 15 species, ranging from near sea level to nearly 4,000 m. This transect has provided an opportunity to study the ecological organization of this group of species, relative to each other and to various physical and biotic factors. An earlier study (Wake & Lynch, 1976) presented a general overview of our results, and a recent report (Wake et al., 1987) updates the main patterns of distribution. A summary of our primary results and data relevant to the use of epiphytes by salamanders is presented here.

Schmidt (1936a) collected seven species of salamanders on the slopes of Volcán Tajumulco and inferred the presence of two additional species. He outlined their main patterns of vertical distribution and presented comparisons with the nine species then known from Veracruz, Mexico. His basic conclusion was that zonation was sharper in Guatemala than in Mexico.

We (Wake & Lynch, 1976; Wake et al., 1987) found eight additional species on the Guatemalan transect and confirmed the main elements of Schmidt's preliminary analysis. We recognized four elevational assemblages of salamanders, including a lower cloud forest (1,600–2,400 m) group of four and an upper cloud forest (2,400–2,800 m) group of seven species. These ten species (one is present in both elevational belts) are restricted not only in elevational zonation, but also in geographic distribution; none of the species occurs beyond the limits of the southwestern Guatemalan volcanoes and the adjacent Sierra Madre of Chiapas, Mexico. The region between 1,600 m and 2,800 m is occupied by Evergreen Cloud Forest (above about 1,900 m) and Montane Rain Forest, using the terminology of Breedlove (1981), who also has characterized these formations floristically.

Within elevational zones we examined differential use of major habitat types. For example, some species are more common in edge situations, and some favor small clearings and open spaces, while others are found throughout the dense forest. Within a major habitat we examined the use of specific microhabitats. We recognized four categories: ground-dwelling (beneath logs, rocks, and other surface objects), log-dwelling (within and under the bark of logs and stumps), arboreal (within a leaf-axil microhabitat, including bromeliads), and fossorial (within subterranean passageways). We found no moss mat specialists and therefore did not recognize this microhabitat category. Within microhabitats we paid special attention to differences in body size and in trophic specializations (morphology of the jaws and teeth). The primary modes of ecological segregation of the 15 species are indicated in Table 1. Here a one-sided matrix of potential co-occurrence of the species records our assessment of primary segregation ordered according to decreasing spatial proximity of the segregated species: elevation, habitat, microhabitat, size, and trophic specialization. Nearly three-fourths of the potential sympatric associations of the 15 species are precluded by differences in elevational distribution, and habitat or microhabitat differences separate all but nine of the remaining paired associations. Of the nine pairs of species which show elevational, habitat, and microhabitat sympatry, eight differ importantly by size. The ninth case involves congeneric species similar in size and morphology, except that one species has about half as many substantially larger maxillary teeth and enlarged jaw muscles.

Six species on the transect commonly occur in arboreal microhabitats (in order of frequency in such microhabitats, from most frequent to least): *Bolitoglossa occidentalis, Dendrotriton bromelia-*

TABLE 1. Primary modes of ecological segregation among species that occur along the San Marcos transect. Species arranged in approximate order of appearance from high to low elevations. In order of decreasing spatial proximity: E = elevation; H = habitat; M = microhabitat; S = size; T = trophic specializations. From Wake & Lynch (1976).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1. *P. rex*															
2. *P.* sp.	(E) M														
3. *P. brunnata*	E	M													
4. *P. goebeli*	E	M	T?												
5. *B. rostrata*	H, S	(H) M	(E) H	(E) H											
6. *B. resplendens*	E	(H) M	(H) M	(H) M	(E) H										
7. *D. bromeliacia*	E	E	M	M	E	M									
8. *B. morio*	E	(H) M	H	H	(E) H	(M) S	(E) H								
9. *B. franklini*	E	E	E	E	E	E	(M) S	E							
10. *B. flavimembris*	E	E	E	E	E	E	M	E	M						
11. *B. engelhardti*	E	E	E	E	E	E	S, T?	E	S	M					
12. *B. occidentalis*	E	E	E	E	E	E	E	E	E	E	E				
13. *B. salvinii*	E	E	E	E	E	E	E	E	E	E	E	M, S			
14. *O. ignea*	E	E	E	E	E	E	E	E	E	E	E?, M	M	M, S		
15. *B. flaviventris*	E	E	E	E	E	E	E	E	E	E	E	S	E	E	

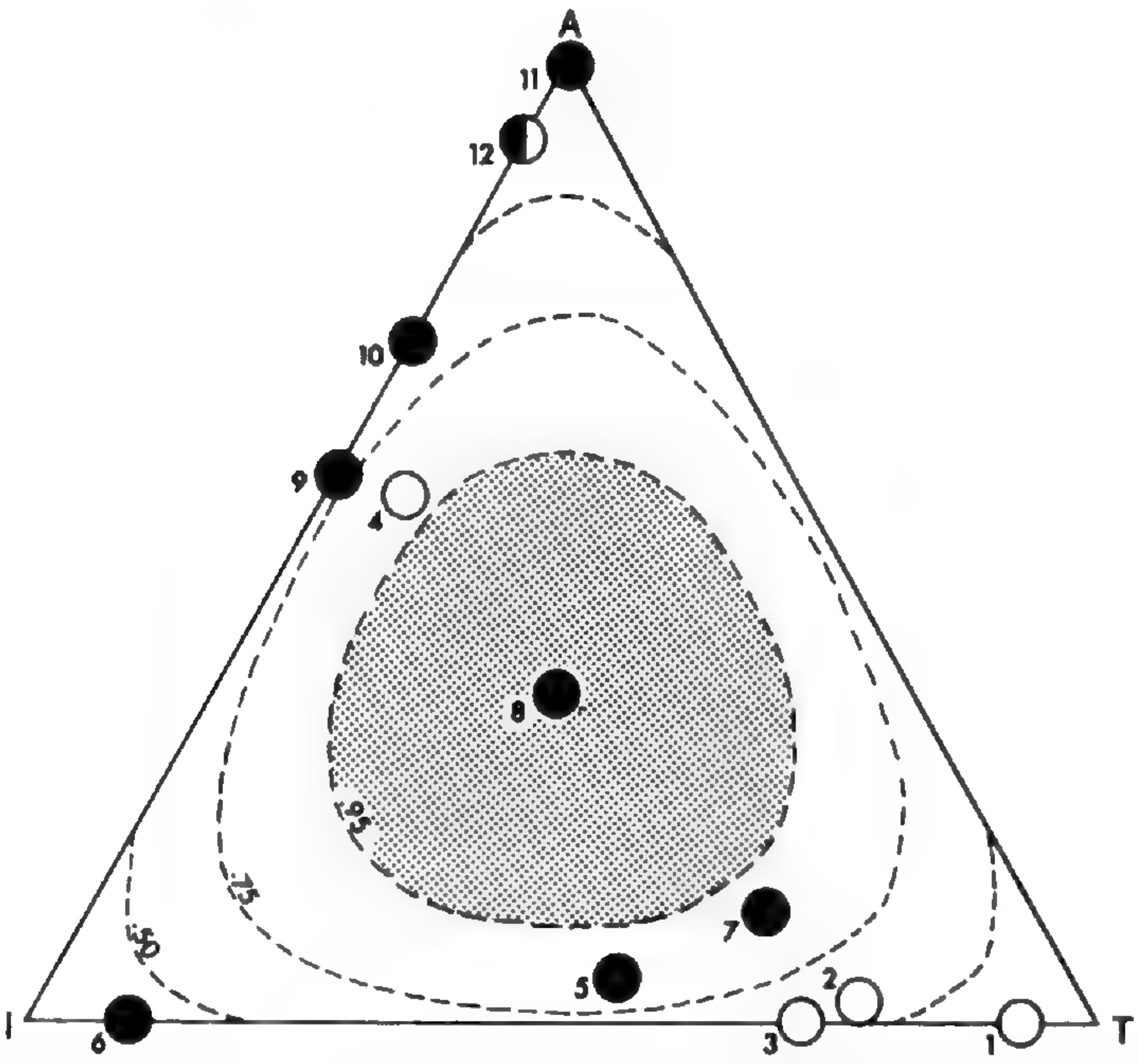

FIGURE 10. Proportional diagram indicating use of microhabitats by 12 species on the San Marcos transect. The dashed lines are isodiversity contours based on occurrences of approximately 1,100 salamanders. Microhabitats were scored as follows: A = arboreal bromeliads; T = under rocks, logs and debris, on the surface of the soil; I = under bark of stumps and standing trees, and inside fallen logs. Open symbol = *Pseudoeurycea*; half-closed symbol = *Dendrotriton*; closed symbol = *Bolitoglossa*. 1, *P. rex*; 2, *P. brunnata*; 3, *P. goebeli*; 4, *P.* sp.; 5, *B. morio*; 6, *B. flavimembris*; 7, *B. rostrata*; 8, *B. resplendens*; 9, *B. franklini*; 10, *B. engelhardti*; 11, *B. occidentalis*; 12, *D. bromeliacia*. Numbers 2 through 10, and 12, are cloud forest inhabitants. Figure from Wake & Lynch (1976).

cia, B. engelhardti, B. franklini, Pseudoeurycea sp., and *B. resplendens* (Fig. 10). All but the first, which occurs at relatively low elevations, are present in the cloud forest and make extensive use of bromeliads. *Bolitoglossa occidentalis* is a small, mainly lowland species that occurs in bromeliads, but it is most commonly found now within the so-called "coffee zone," where it occurs in agricultural plantings of bananas.

James F. Lynch and I are preparing a detailed ecological account of our work in this transect, and with his permission I present here some of our data concerning use of bromeliads in cloud forests by the above listed species. When we first visited this area in 1969 primary forest extended to roadside and bromeliads were abundant. When we last visited the cloud forest region in 1980 the forest had been removed and pasture occupied nearly the entire area between 1,500 m and 2,700 m. Below 1,500 m traditional coffee plantations, which feature large shade trees and extensive plantings of bananas, had given way to a near monoculture of coffee grown in hedgerows without any suitable cover for arboreal salamanders.

TABLE 2. Relative abundance of salamanders in bromeliads, San Marcos transect.

Elevation	Wet Season[1]	Dry Season[2]	Combined
Below 1,750 m	—	3/25 = 0.12[3]	3/25 = 0.12
1,750–2,000 m	6/39 = 0.15	41/75 = 0.55	47/114 = 0.41
2,000–2,250 m	48/239 = 0.20	29/64 = 0.45	77/303 = 0.25
2,250–2,500 m	89/121 = 0.74	140/191 = 0.73	229/312 = 0.73
2,500–2,750 m	81/25 = 0.72	27/30 = 0.90	45/55 = 0.82
Above 2,750 m	14/73 = 0.19	13/21 = 0.62	27/94 = 0.29

[1] May–September.

[2] November–February.

[3] Number of salamanders/number of bromeliads.

Salamanders are common inhabitants of bromeliads along the San Marcos transect (Table 2). We found salamanders in approximately every second bromeliad we opened. These bromeliads, primarily members of the genera *Tillandsia* and *Vriesia,* were located relatively low in the trees.

Salamanders in southwestern Guatemala are most abundant in bromeliads at elevations between 2,250 and 2,750 m. From these elevations down to approximately 1,700 m, bromeliads remain relatively common, and there are bromeliads present at elevations up to approximately 3,000 m. All of the bromeliad specialists occur in the cloud forest (roughly 1,500–2,750 m), even though bromeliads are found both above and below that formation. Above the cloud forest those species that use bromeliads at lower elevations (e.g., *Bolitoglossa rostrata, Pseudoeurycea rex*) shift almost entirely to terrestrial microhabitats. Salamanders are consistently more abundant in bromeliads during the dry season than during the wet season, except in the heart of the cloud forest (2,250–2,500 m), where there is less seasonality than elsewhere.

TABLE 3. Distribution of salamanders in bromeliads, San Marcos transect, 16 January 1972, 2,400 m elevation.[1]

Number of Salamanders per Bromeliad	Frequency
0	15
1	10
2	8
3	3
4	1
5	1
6	1
8	1

[1] These data are for 55 *Dendrotriton bromeliacia* and three *Bolitoglossa franklini* taken from a sample of 40 bromeliads ($\bar{x}$ = 1.45 salamanders per bromeliad).

Martin Feder accompanied us on one trip to our transect and studied the thermal ecology of some of the cloud forest salamanders (Feder, 1982). He found that bromeliads, even in the cloud forest, afford cooler and more stable temperatures than microhabitats in immediately surrounding areas. Bromeliad-dwelling salamanders appear not to thermoregulate behaviorally or physiologically, because thermal diversity in their microhabitats is so low as to offer little opportunity for such behavior. As is usual for salamanders, there is a high correlation between body temperatures of salamanders and prevailing microenvironmental conditions (Feder & Lynch, 1982), so the more stable the microenvironment, the less variable will be the temperature of the salamander. The tropical salamanders contrast sharply with more northern plethodontids in having very limited ability to undergo thermal acclimation (Feder, 1978, 1982). This may be either the cause or the effect of the high fidelity to elevational zone and microhabitat displayed by many of these species (Feder, 1983).

The data and analyses in Tables 3–5 indicate that the distribution of salamanders per bro-

TABLE 4. Distribution of salamanders in bromeliads, San Marcos transect, 18 January 1972, 2,300–2,350 m.[1]

Number of Salamanders per Bromeliad	Frequency
0	12
1	8
2	10
3	7
4	1
5	2

[1] These data are for 59 *Dendrotriton bromeliacia* and four *Bolitoglossa franklini* collected in a sample of 40 bromeliads ($\bar{x}$ = 1.58 salamanders per bromeliad).

TABLE 5. Test for randomness, combined data from Tables 3 and 4.[1]

Number of Salamanders per Bromeliad	Observed Frequency		Expected Frequency (Poisson)	
0	27		17.5	
1	18		26.6	
2	18		20.2	
3	10		10.3	
4	2	7	3.9	5.5
5	3		1.2	
6	1		0.3	
7	—		0.1	
8	1		0.0	

Chi-square (goodness of fit) = 8.50 with 4 df
$0.05 > P > 0.1$

[1] Data for 121 salamanders collected from 80 bromeliads ($\bar{x} = 1.52$ salamanders per bromeliad).

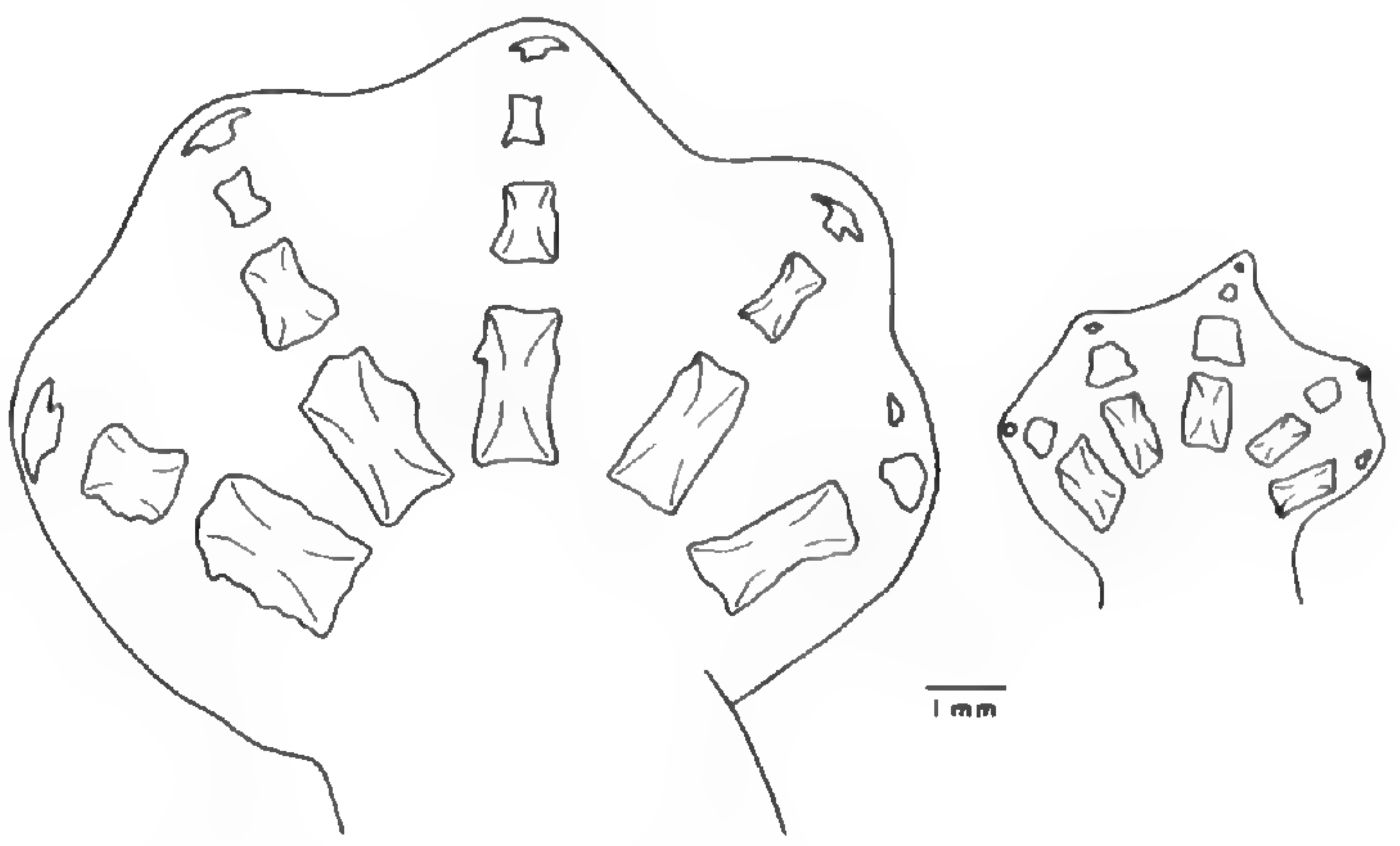

FIGURE 11. Outlines of the left hind foot of two lowland species of *Bolitoglossa* from Pacific coastal Guatemala. The digits and bony phalanges are indicated in each. *Bolitoglossa salvinii* is a large species (this specimen is 67.5 mm, snout-vent length) with extensive webbing and is capable of generating suction in arboreal situations. *Bolitoglossa occidentalis* is a diminutive species (this specimen is 38.7 mm, snout-vent length) with feet that superficially appear to be webbed, but in reality are just incompletely developed (paedomorphic) as suggested by the strong gradient in phalangeal structure within each digit.

meliad is not significantly different from random. However, there is at least a suggestion that there might be an excess of bromeliads that lack salamanders, as well as a deficiency of bromeliads containing single salamanders. Thus, there might be a tendency toward clumping under conditions of high salamander abundance.

Bromeliads might seem to be a near perfect microhabitat for salamanders, in terms of food availability, thermal stability, and constancy of humidity. But concentration of salamanders in bromeliads might attract predators. Spiders and salamanders are the top resident carnivores within bromeliads, and they do not prey on each other very extensively. Some arboreal snakes forage widely and may be important, although infrequent, predatory visitors to bromeliads; birds might also be important predators. All tropical salamanders have a specialized autotomy zone at the base of the tail, and Shaffer (1978) examined tail loss frequency as a rough index of relative predation pressure on 10 species of salamanders from the San Marcos transect (parts of tails may be lost in intraspecific aggressive encounters, but these species are not known to be very aggressive). He found an inverse correlation between rates of tail loss and elevation, and we know that snake densities also decrease with elevation. Two of the three cloud forest species commonly found in bromeliads (*Dendrotriton bromeliacia, Bolitoglossa franklini*) had the second and third highest tail loss percentages of the species studied (the highest was the arboreal lowland species *B. occidentalis*). Although exposure to predation may be a relative cost for living in bromeliads, the cost is apparently outweighed by other advantages, such as those mentioned above.

Although bromeliad dwellers in cloud forest habitats differ greatly in morphology, ecology, and behavior from even the most arboreal North American plethodontids (e.g., *Aneides*), they are not the most extremely specialized species on the San Marcos transect. At elevations below about 1,400 m the cloud forests, and the lower cloud forest salamander fauna, are absent. A new salamander community appears at about 1,000 m, composed of three extreme morphological and ecological specialists. This community includes a relatively large and a relatively small arboreal species of the genus *Bolitoglossa* and an elongate fossorial species of the genus *Oedipina.*

Bolitoglossa salvinii, a large species, is an active, climbing animal with a long prehensile tail and large hands and feet with extensive interdigital webbing (Fig. 11). These animals, which frequent surfaces of *Heliconia* and other large-leafed plants on moist evenings, are capable of producing suction with their large hands and feet (Alberch, 1981).

Bolitoglossa occidentalis, the small species, has small hands and feet that appear to be fully webbed. In reality the hands and feet manifest incomplete development, a phenomenon known as paedomorphosis that affects a number of features of the organism (Wake, 1966; Wake & Brame, 1969; Alberch et al., 1979; Alberch & Alberch, 1981). Such similarly affected features include a relatively short and strongly tapered tail, as well as a reduction in skull ossification. The hands and feet are essentially "embryonic," with digits that show a strong gradient of development (Fig. 11). Although these animals do not generate suction with their hands and feet (Alberch, 1981), they are very agile, partly as a result of their small size. They have an extensive ventral surface area (body, limb, and tail) relative to their mass, so they "stick" to moist plant surfaces by surface tension. Apparently these salamanders are virtually restricted to leaf axil retreats. They especially favor *Heliconia* and both cultivated and feral banana plants (*Musa* spp.). Smith (1945) reported finding *Bolitoglossa rufescens* (very similar in morphology and ecology to its close relative *B. occidentalis*) to be abundant in red bananas (he found about 250 per hour) at a Veracruzian site. These animals are adept at climbing small tendrils, stems, and strands of moss.

Members of the small species of *Bolitoglossa* are encountered only rarely in terrestrial sites, and the large species, while occasionally found on the ground (e.g., crossing roads on rainy nights), also are basically arboreal. (An exception may be the very large species *B. dofleini,* which can be very common in terrestrial situations.) But another group of lowland species, the very elongate, short-legged genus *Oedipina,* is found only at and beneath the surface of the ground. Species of *Oedipina* are elongated as a result of the addition of trunk and especially tail vertebrae, and they have bizarre long tails (Fig. 12). In addition to their extremely short legs and tiny hands and feet, they have heads and bodies of very small diameters; all of these features facilitate use of root channels and underground burrows.

The San Marcos transect is special because more species of salamanders occur there than in any other area of the Pacific Versant in Middle America. Volcán Tajumulco (4,200 m) is attached to the Guatemalan Plateau at about the 3,000 m level, so on both sides of the volcano there are substantial areas of moderate elevation which trap moisture and thereby create favorable salamander habitat. To the south and east the Plateau gradually lowers and rainfall declines. In the vicinity of Guatemala City, Volcán Agua (over 3,700 m) towers over the Plateau, to which it is attached along only its northern flank at a low elevation (about 1,000 m). The contrast in salamander faunas between Volcán Tajumulco and Volcán Agua is great. Only three species have been collected on the slopes of Agua. There is a single high elevation member of the genus *Pseudoeurycea* (*P. goebeli*), one low elevation species of the genus *Bolitoglossa* (*B. salvinii,* a large, fully webbed species), and a middle elevation generalized species of the genus *Bolitoglossa* (*B. morio*). All three of these species also are present on the San Marcos transect. There is a well-developed cloud forest with abundant bromeliads on Volcán Agua, but the forest is localized and it is isolated from similar habitats to the north and west by low elevations covered by drier vegetation types. In 1969 we opened about 600 bromeliads on Volcán Agua, but found only two salamanders! This contrasts sharply with the data presented earlier for the San Marcos transect. *Bolitoglossa morio,* the species we encountered, is a widespread and relatively common inhabitant of ground and log microhabitats in forested areas of the Guatemalan Plateau. On the San Marcos transect it is found only at the top of the cloud forest and in drier broadleaf forest above, where the edge of the Plateau contacts Volcán Tajumulco. Here the species occurs occasionally in bromeliads (Fig. 10). On Volcán Agua, although *B. morio* remains uncommon in bromeliads and apparently has not modified its microhabitat utilization patterns in any dramatic way, its elevational range is 1,300–2,500 m. At this site, where *B. morio* is the only salamander

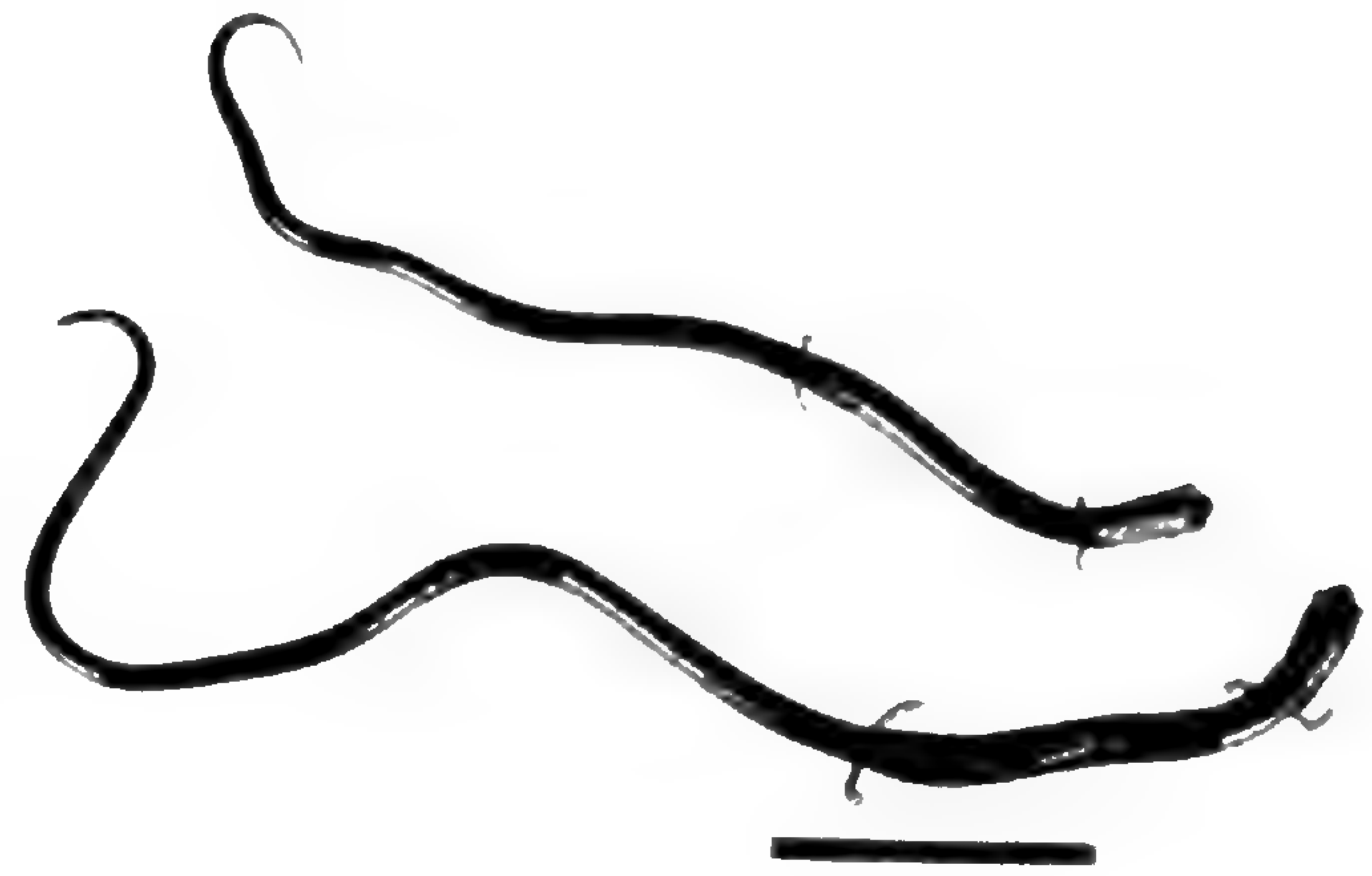

FIGURE 12. *Lineatriton lineola* (top), from near Fortín de las Flores, Veracruz, Mexico, and *Oedipina ignea* (bottom), from Finca Santa Julia, near San Rafael Pie de la Cuesta, San Marcos, Guatemala. The scale bar is 25 mm. These extremely elongated species are semi-fossorial to fossorial in habit, and have evolved convergently.

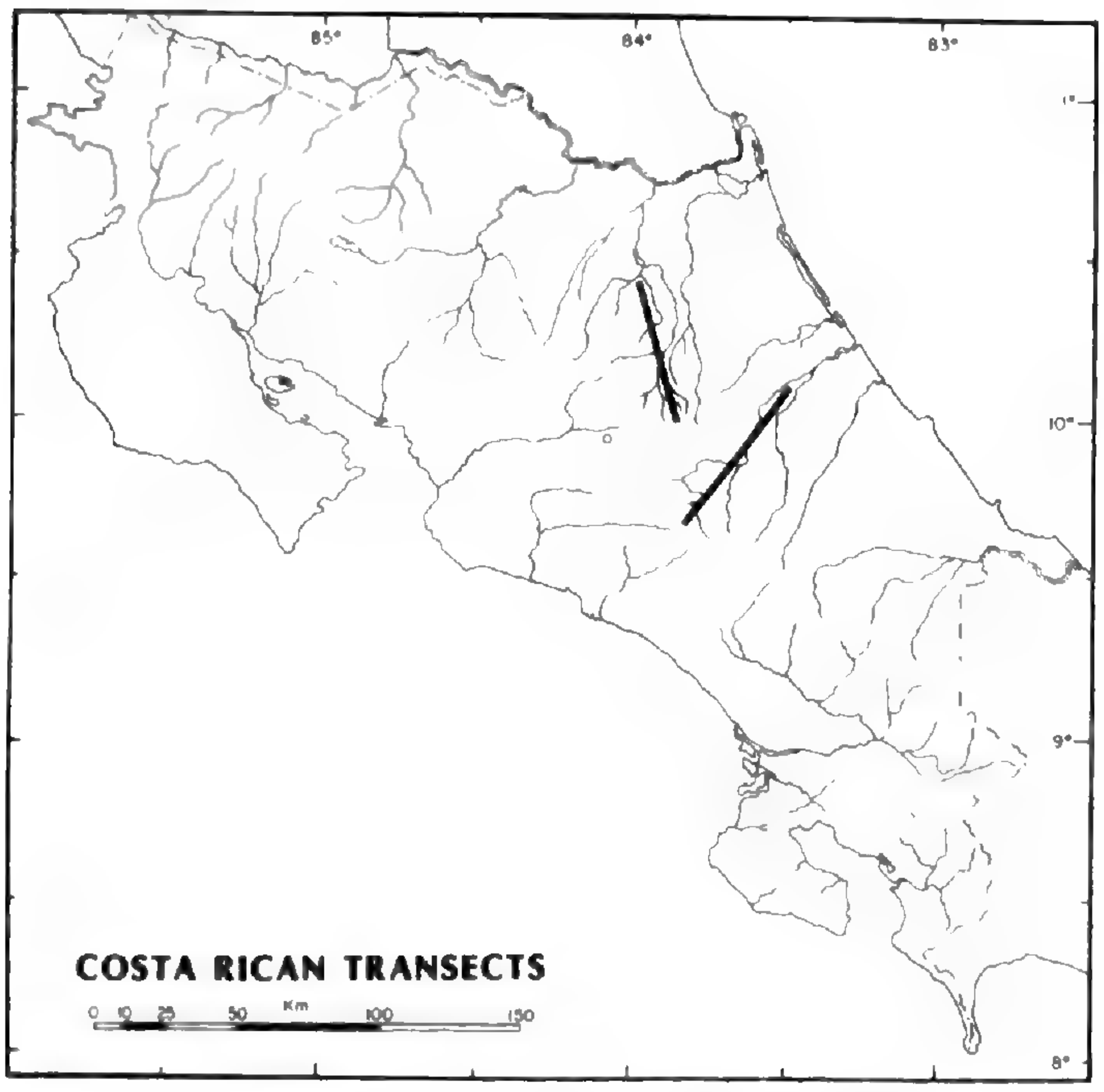

FIGURE 13. Map of Costa Rica indicating the location of the Irazú and Tapantí transects illustrated in Figures 14 and 15.

present, it occupies an elevational range that accommodates ten species on the San Marcos transect. The patterns of species distribution in the tropics (this example, but see below also) are probably determined by combinations of physiological constraints (in relation to physical factors in the environment) as well as such interspecific interactions as predation and competition.

COMPARATIVE ASPECTS OF COMMUNITY ORGANIZATION

Until recently most fieldwork by my group has been in Mexico and Guatemala (for general summaries see Wake & Lynch, 1976; Wake et al., 1987). In general, the results of our detailed studies of the San Marcos transect have been mirrored in other areas (cf. Fig. 9). Typically only one or two species occur at elevations above 3,500 m; as one moves lower the number of species present in a given habitat increases dramatically at about 3,000 m and continues to be relatively high until the lower limit of the cloud forest is reached. At elevations below 1,000 m the number of species present typically declines, and at sea level the largest number of species definitely known to be present is four on the Osa Peninsula of Costa Rica, where there are two species of *Bolitoglossa* and two species of *Oedipina*. Possibly five species occur together at sea level in the region of Bocas del Toro, Panama (Wake et al., 1973 and unpubl. data), and in northeastern Costa Rica seven species are known from elevations below 1,000 m, but not in local sympatry (see below). The proportion of the total salamander fauna present in the lowlands increases at lower latitudes within Middle America (see Table 5 in Wake & Lynch, 1976). There is evidence of increased "tropicality" (that is, of closer packing of species in communities and increased numbers of species present locally) as one moves into the deep tropics. Finally, however, in northwestern South America this trend stops, perhaps because plethodontids are not thought to have dispersed into South America until late Pliocene times (Wake & Lynch, 1976; Hanken & Wake, 1982). Except in the Chocó and the flanks of the northern Cordilleran regions of Colombia, the number of salamander species present in lowland sites in South America is not known to exceed two, even in such biotically rich forests as those of the Río Palenque area of Ecuador.

Throughout Middle America, salamanders are found in cloud forests. In Mexico and in Nuclear Central America, cloud forest salamanders make extensive use of bromeliads as microhabitats, even at the extreme northeastern limits of the range of the supergenus *Bolitoglossa* in the Gómez Farias region of Tamaulipas (where cloud forests also reach their northern limit; Martin, 1958). But the manner in which cloud forest microhabitats are utilized changes in Costa Rica. The Costa Rican salamander fauna justifiably has been considered one of the best known in the tropics, thanks primarily to the work of Taylor (1952, 1954). However, very little has been reported concerning microhabitat utilization and patterns of co-occurrence of Costa Rican species. Only four species are reported to occur in bromeliads (Robinson, 1977), although many more species are known to inhabit cloud forests.

Recently I have been investigating the systematics and distribution of Costa Rican salamanders in some detail. I have focused attention on two general transects (Figs. 13–15). Results for Costa Rica are preliminary, because major sections of these generalized transects have yet to be searched thoroughly. Nevertheless, certain marked contrasts with more northerly transects are apparent.

A dominant theme in the history of studies of tropical salamanders has been that the species which are the most conservative ecologically and the most primitive phylogenetically occur in Mexico, and that there is both increased specialization and a decline in the number of species

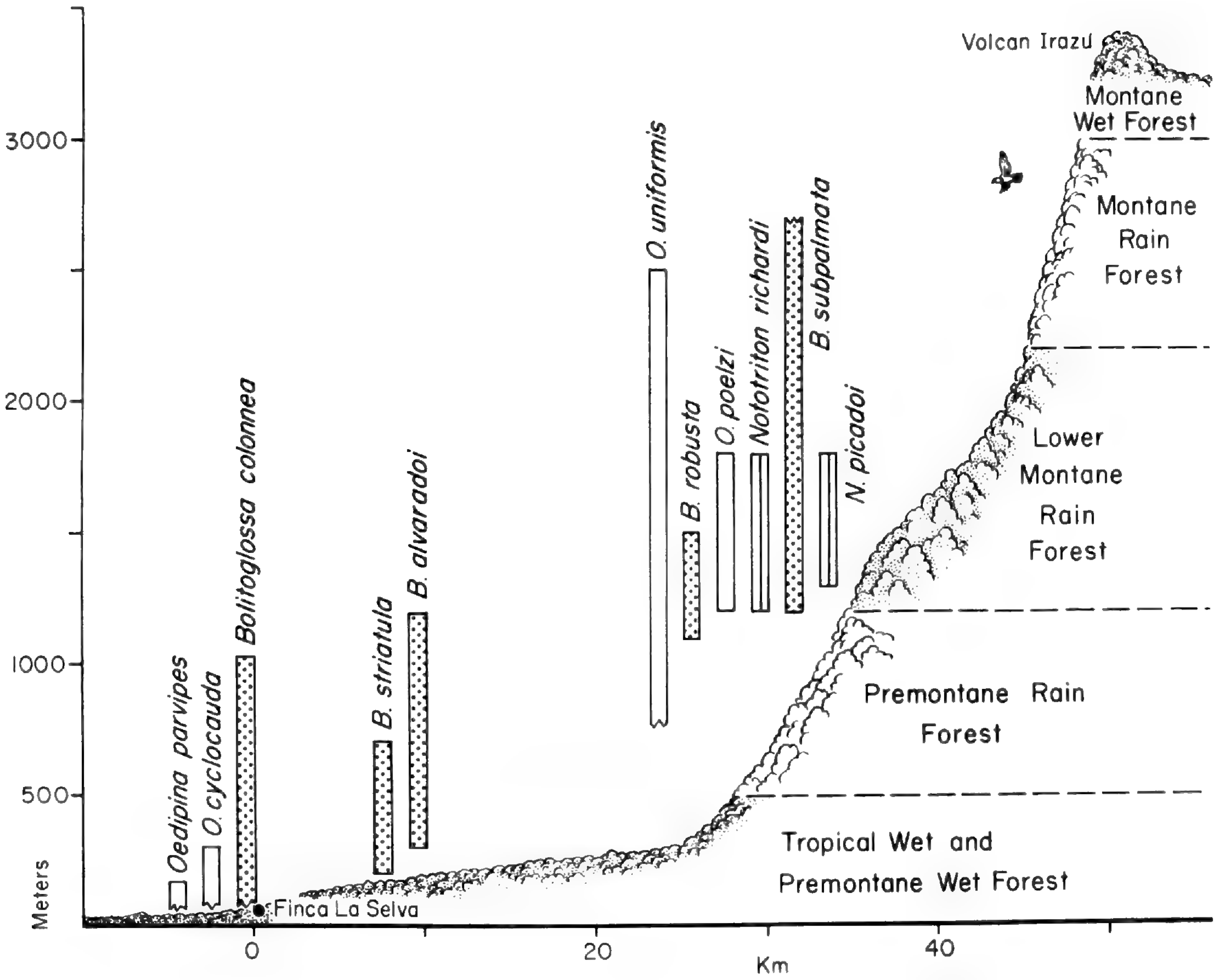

FIGURE 14. Vertical distribution of plethodontid salamanders along the Irazú transect, extending about 55 km from Finca La Selva to Volcán Irazú, Costa Rica.

to the south (Dunn, 1926; Taylor, 1944, 1952; Brame & Wake, 1963; Wake, 1966; Wake & Lynch, 1976). Even though Wake & Lynch (1976) documented the presence of a large number of species below 10° latitude, we continued to espouse the traditional view of relics in the north (e.g., *Chiropterotriton priscus* of Coahuila and Nuevo León, Mexico) and increasingly derived forms to the south. The recent discovery of the most primitive known genus of tropical plethodontid in Guatemala (Elias & Wake, 1983) and a fresh analysis of relationships of new and existing groups (Wake & Elias, 1983) have forced me to re-evaluate my earlier views. It now seems likely that salamanders have been in the tropics of present-day Middle America for a very long time, possibly throughout the Tertiary (see above section on Ecological Geography and Systematics). Middle elevations doubtless have been important areas of both survival and radiation in the group, and we have discovered that patterns of microhabitat utilization differ dramatically between Mexico and Nuclear Central America on one hand, and Talamancan Central America on the other.

Perhaps the most striking difference between the above regions is the presence of a rich fauna associated with moss mats in the cloud forests of Talamancan Central America. As noted earlier (Table 2), salamanders are sometimes very abundant in cloud forests of northern Middle America, where many species utilize bromeliads (Wake & Lynch, 1976). In Veracruz, Mexico, and in Nuclear Central America, elongate, fossorial species of *Lineatriton* and *Oedipina* occur only at elevations below the lower limit of cloud forest. In contrast, elongate members of the genus *Oedipina* are well represented in Costa Rican and Panamanian cloud forests, extending upwards to elevations in excess of 2,000 m (Figs. 14, 15). Here they utilize moss mats covering soil banks, downed logs, and stumps. Furthermore, living

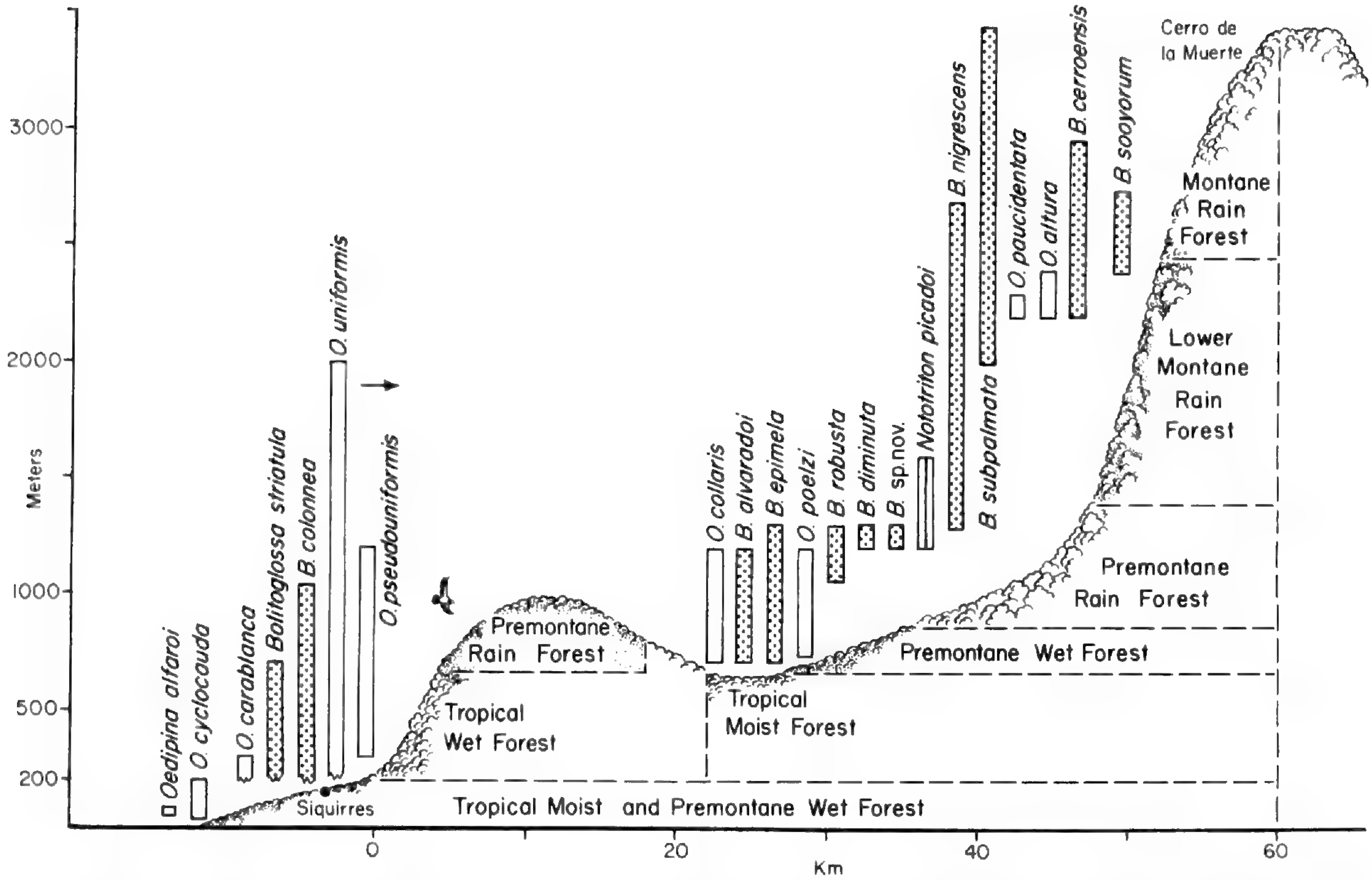

FIGURE 15. Vertical distribution of plethodontid salamanders along a generalized Tapantí transect, which extends between Siquirres and Cerro de la Muerte, Costa Rica. This region, about 60 km long, contains more species of plethodontid salamanders than any known area in tropical America.

in moss mats in these cloud forests are species of *Nototriton*, a genus that is mainly confined to bromeliads in Nuclear Central America. There is even an undescribed Costa Rican species of *Bolitoglossa* that has been taken only in moss surrounding twigs on trees and shrubs in cloud forests. This substantial fauna represents an ecological component that is rare (e.g., *Dendrotriton cuchumatanus* occurs in moss mats in Guatemala, Lynch & Wake, 1975) or is missing in cloud forests of Nuclear Central America.

The two Costa Rican transects offer some interesting contrasts. Both extend up the Caribbean slopes from near sea level to elevations well above 3,000 m. The first (Fig. 14), the Irazú transect, extends from the vicinity of Finca La Selva for about 55 km to the peak of Volcán Irazú. Salamander distributions along this transect are poorly known except for the region between 1,000 and 2,500 m. For example, Scott et al. (1983) listed two species of *Oedipina* from Finca La Selva, but study of specimens from the area suggests that three occur there. The taxonomy of the group is difficult, but it may be that none of the three are the species listed. (Note that only two species are indicated on Fig. 14.) There are presently 11 species of salamanders (in three genera) known from this transect. As with the more northerly transects, only one species (*Bolitoglossa subpalmata*) is likely to occur at elevations of >3,000 m (and I cannot document its presence at that elevation as yet, although I expect it may be found). However, in contrast with more northerly transects (cf. Wake et al., 1987), there are at least five species present at elevations of <500 m. Eight species occur in cloud forest between 750 and 2,000 m, including two species that specialize on moss mat microhabitats (the two species of *Nototriton*; see also comments in Taylor, 1954), two others that utilize moss mats extensively but also use burrows in soil (the two species of *Oedipina*), and two *Bolitoglossa* (*B. subpalmata, B. robusta*) that I have found in moss mats, although other microhabitats are used more frequently. Both *B. subpalmata* (at this elevation) and *B. alvaradoi* use bromeliads.

I expect that more species will be found on the Irazú transect, in part because of the unusually high numbers of species present on the Tapantí transect (Fig. 15). The latter transect is far more generalized in its boundaries than the first, and is essentially a broad (ca. 20 km) swath of territory extending about 60 km from the vicinity of Siquirres to the summit of Cerro de la Muerte. The Tapantí transect is not a straight line, but twists somewhat to encompass sites where some of the rarer species are known to occur. There is extensive habitat disturbance along this transect (for example, in the vicinity of Turrialba), and I justify weaving together an indirect transect as an attempt to demonstrate the potential number of species one might reasonably expect to find on a continuous altitudinal transect under pristine conditions. The Tapantí transect thus offers a greater diversity of habitats than does the Irazú transect and one might expect more species to be present. To my surprise, the Tapantí transect is the richest that I have found in the tropics, with 21 species. There are only 26 species of plethodontids known from Costa Rica (Scott et al., 1983; their list and mine differ slightly but we obtain the same total number of species), and that about 80% of them occur along this transect attests to its richness.

The Tapantí transect has a higher number of species (seven) occurring below 500 m than does the Irazú transect, and in both Panama and Nicaragua another species (*Oedipina collaris*) occurs at elevations of <500 m (Brame, 1968), so there is the likelihood that an eighth species eventually will be found. *Bolitoglossa alvaradoi* apparently occurs at elevations of <500 m elsewhere in Costa Rica. Thus, as many as nine species might be expected in the lowlands in the area crossed by this transect.

Thirteen species occur in the cloud forest of the Tapantí transect, if we accept 750–2,000 m as its elevational bounds. In fact, cloud forest conditions exist almost to 3,000 m, although in general cloud forests are less well defined in Costa Rica and Panama than farther to the north (Myers, 1969). This transect contains the richest cloud forest salamander fauna found anywhere in the tropics. Here, too, I have probably underestimated the number of species present. At least one more species of *Bolitoglossa* may be present, and the two poorly known highland species of *Oedipina* may well extend to lower elevations, since the genus as a whole is strongly concentrated at lower elevations. Two species of *Bolitoglossa* (an undescribed species and *B. diminuta,* Robinson, 1976) use mats of vegetation including mosses and liverworts that surround twigs and branches of trees. Several other species use bromeliads and moss mats, but no quantitative data are available. In the forests of Refugio Tapantí there is an especially rich epiphyte fauna, and this is the locality where the largest number of species are found. However, in marked contrast to the situation in the cloud forest on our San Marcos transect, the density of individual species is uniformly low on this transect. This situation of high species diversity and low density of individual species is one more indication of the increased "tropicality" of the Costa Rican salamander fauna.

The contrast between the cloud forest that occurs at around 1,000 m and the forest around 3,000 m on this transect is sharp. At high elevations the density of *Bolitoglossa subpalmata* is extraordinarily great, on the order of 9,000/ha (Vial, 1968). Four species occur in sympatry at around 2,500 m; in my experience *B. subpalmata* is about 100 times more common than *B. cerroensis,* about 1,000 times more common than *B. sooyorum,* and about 10,000 times more common than *B. nigrescens*! Doubtless there is a collecting artifact involved, but the first species is remarkably abundant and the last has been, at the very least, elusive. The high density of a single species at high elevation is a common theme in tropical salamander biology.

Bolitoglossa subpalmata, which can be exceedingly abundant at high elevations in Costa Rica, displays a marked shift in microhabitat utilization and a reduction in abundance at lower elevations. The species is primarily ground-dwelling at high elevation, although it also uses bromeliads. I have collected *B. subpalmata* from bromeliads 30 m above ground level in an oak tree at 3,000 m elevation. At elevations of <2,000 m the species becomes increasingly common in bromeliads and is encountered only infrequently in terrestrial situations. This species can be extraordinarily persistent in the face of even drastic habitat change, so long as bromeliads remain. An anecdote illustrates this point. An old collecting locality in the Montes de Aguacate, west of San José, was visited recently. Only tiny fragments of forest remain at this site, at about 1,500 m. Salamanders were common residents of bromeliads in one forest fragment where trees were being felled. We opened 130 bromeliads and found 55 salamanders, including 14 adults and a subadult in a single bromeliad. As many as three adults were found in the axil of a single leaf. This is a graphic demonstration of the suitability of bromeliads as microhabitat for salamanders, especially under conditions of great habitat modification. I have had similar experiences with *Chiropterotriton lavae* in fragments of cloud forest above Jalapa, Veracruz, Mexico, and with *Bolitoglossa morio* in an area devastated by volcanic activity on Volcán Pacaya, Guatemala.

It is still too early to generalize very extensively from our comparative transect studies. We have come to be suspicious of species with broad elevational ranges (such as *O. uniformis*, Figs. 14, 15), and these deserve careful taxonomic re-evaluation, for most species occur within rather narrow elevational limits. We also have come to expect few extreme highland or lowland species, but there are more lowland species at low latitudes. Cloud forests and salamanders are most abundant at mid-elevations.

FACTORS INFLUENCING SALAMANDER SPECIATION AND RADIATION

Species of plethodontid salamanders characteristically display a high degree of genetic fragmentation (Larson et al., 1984; Larson, 1984). Larson (1984) has argued that a general pattern for the history of population structure in plethodontids is that following origination they expand gradually and contiguously into regions to which they have ecological access. Later, as a result of climatic change which may result from many proximal causes, their populations become fragmented into islands among which there is little or no genetic exchange. Subsequent climatic changes may lead to re-establishment of ecological access to areas separating isolated populations. This may lead either to renewed genetic exchange or, depending on the level of genetic divergence and its effect on isolating mechanisms or mate recognition systems, to a variety of interactions. There may be a hybrid swarm, a narrow hybrid zone, a narrow zone of overlap with occasional hybridization, partial sympatry with boundaries set by competitive interactions, or coexistence with different ecological requirements. All of these interactions have been documented among plethodontids. The many studies of population structure based on electrophoretic analysis of proteins, together with studies of distribution, phylogenetic history, and biogeography (reviewed by Larson, 1984), suggest that geographic or allopatric speciation by subdivision is the common mode in plethodontids. There are similarities with the concept of "taxon cycles" (Wilson, 1961; Ricklefs & Cox, 1972), which usually have involved examples from island chains. These postulated cycles of expansion and contraction of geographic ranges and population densities would establish the setting for the kind of speciational processes I envision having taken place among the tropical salamanders.

The two primary factors in the history of the tropical salamander fauna probably have been the combination of adaptation of species to cloud forest environments and the long, complex history of tectonic activity in Middle America. There are some relatively stable areas, such as the ancient core of Nuclear Central America, where the upper and lower boundaries of the cloud forest have shifted, but where cloud forest in a broad sense probably has been present for much of the Tertiary and Quaternary periods (see discussion in Wake & Lynch, 1976). However, there are many other areas where tectonic movements and associated volcanic activity have been so great and so persistent that cloud forests have been only an ephemeral presence, shifting almost constantly.

The three foci for salamander radiation in the tropics (Fig. 2) all have stable, ancient tectonic core areas surrounded by regions of great tectonic activity. (For summary of tectonic history, see Hendrickson, 1986.) These areas have been cited by other workers as having phylogenetically distinctive faunal components. For example, Savage (1982) stated:

> I now believe that the distinctive montane herpetofaunas of the southern Sierras of Mexico, Nuclear Central America, and the Talamanca area developed more or less *in situ* from ancestors that "rode" the uplifted areas and evolved with them. Each endemic montane area then represents an uplifted island biota vicariated from a more or less similar sea of widely distributed ancestors.

Nuclear Central America (Fig. 16) illustrates the ideas outlined above. That region has as its core the ancient Sierra de los Cuchumatanes, located on the southern part of the North American plate. The area has been characterized as the Middle American Megathrust by Plafker (1976), because it is the conjunction of three major plates. The Cocos plate, to the southwest, is being subducted near the intersection of the North American and Caribbean plates (for evidence of the widespread influence of this phenomenon see Singh et al., 1985). The latter is being forced eastward by the combined plate movements, and a small western tip of the plate is effectively "caught" between the North American and the Cocos plates. The zone between the Caribbean

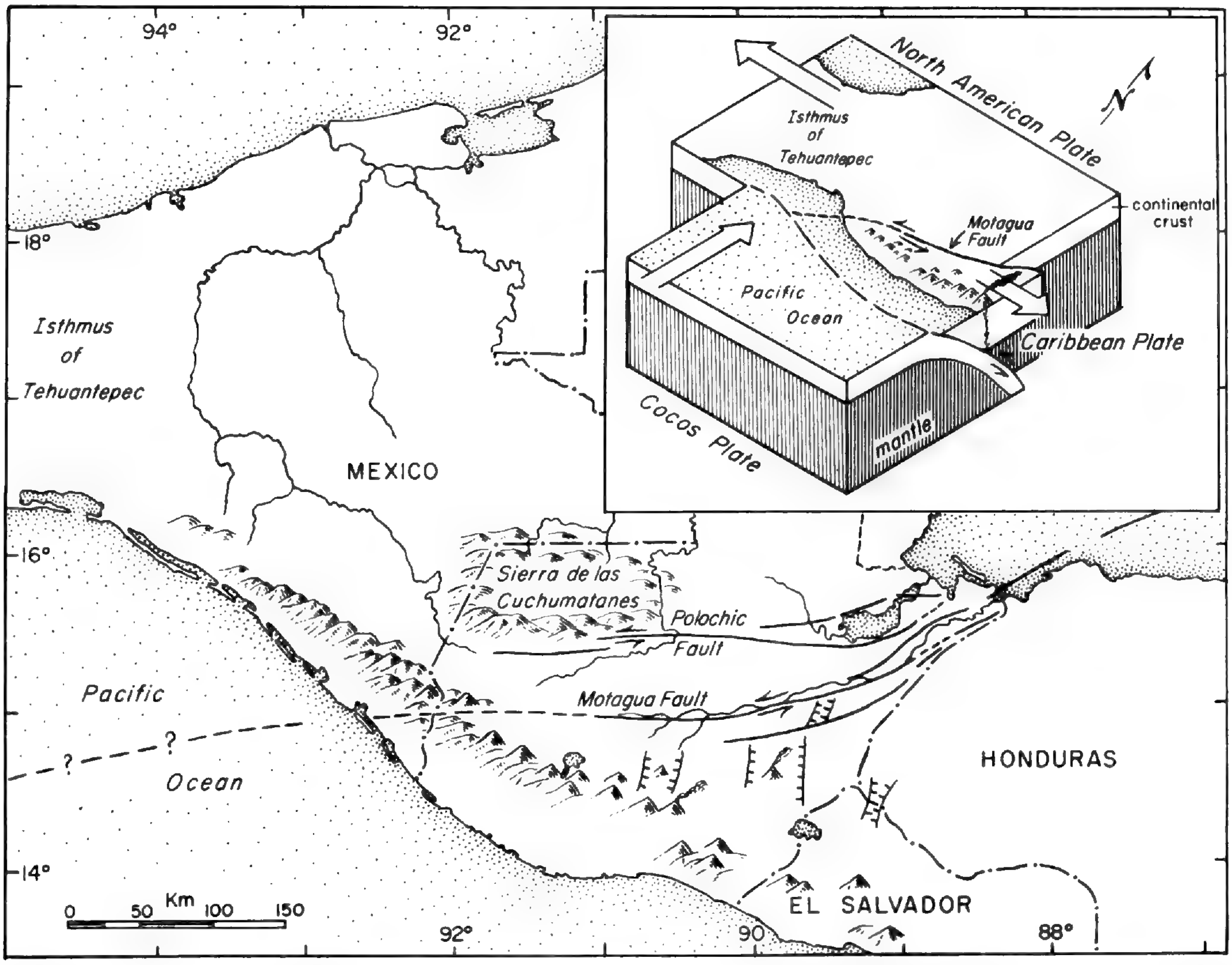

FIGURE 16. Nuclear Central America. A generalized diagram illustrating relationship of the core region, north of the Polochic Fault, to the intersection of three crustal plates. The margins of the core region are areas of intense tectonic activity because of the complex geology of the region. Nuclear Central America has been an area both of preservation of apparently ancient lineages, because of the continued stability of the core, and of speciation of cloud forest forms, due in large part to the fragmentation and reassembly of areas of cloud forest. Inspired by and based largely on Plafker (1976).

and North American plates is outlined by the Motagua and Polochic fault zone. This has been an area of intense tectonic activity for millions of years and Plafker (1976) has estimated that at least 200 km of lateral movement of plates along this fault zone has occurred since the Miocene. The western tip of the Caribbean plate, trapped between the other plates, is being ripped, or decoupled (Plafker, 1976). Grabens have formed, with small volcanic cones rising within them. Parallel to the Pacific versant, above the zone where the earth's mantle is being pierced by the subducted Cocos plate, the famous Guatemalan volcanoes are lined up. Volcán Tajumulco and Volcán Tacaná lie at the northwestern corner of the Caribbean plate, where the three plates meet. In this topographically complex zone of maximal geological turbulence, the largest number of co-occurring species of salamanders in Middle America is found, along our San Marcos transect.

The relatively stable upland of the Sierra de los Cuchumatanes is in many ways an even more interesting area than the Pacific volcanic belt. We began fieldwork in this area in 1974, at a time when only two species of salamanders were known from the Caribbean slopes of the Cuchumatanes, despite a number of brief collecting trips by different herpetologists. Results of our investigations have been summarized by Elias (1984), who found 13 species of salamanders in this region (see also Wake et al., 1987). As elsewhere in Middle America, the cloud forest is of special interest, for six species with narrow elevational ranges occur just above the cloud line, here located at about 1,300 m. Two new genera of salamanders were discovered in this cloud forest

(Elias & Wake, 1983; Wake & Elias, 1983), including the exceptional *Nyctanolis,* a morphologically primitive genus which appears to be the sister group of all other tropical salamanders. Thus, on the one hand, the ephemeral cloud forests of the tectonically active and topographically complex margins of the Cuchumatan uplands have contributed to speciation and led to the highly disjunct distributional patterns illustrated previously for *Dendrotriton* and *Nototriton* (Figs. 7, 8). On the other hand, the more stable cloud forests on the northeastern slopes of the core of the Cuchumatan region have served as refugia for what must be extremely ancient lineages.

CONCLUSIONS

We still have much to learn about the salamanders of the New World tropics, and even the best known areas of Middle America have yielded many recent surprises. Earlier misconceptions concerning the probable history and ecology of tropical salamanders have led to underestimates of the age and diversity of the group and have contributed to our relative ignorance of the ecology of the cloud forest and lowland species, especially the arboreal and fossorial forms. New species are being discovered more rapidly than they can be described, for many species are known from small series. Our knowledge of the comparative osteology and of molecular evolution of this group, while still fragmentary, is sufficient to demonstrate that parallelism and convergence are rampant.

This, in turn, implies both that there may be only a limited number of ecological roles available to tropical salamanders, and that there may be functional and developmental-historical constraints which impose limits on the evolutionary potential of the group. An especially clear case of convergence is the elongation associated with fossorial life in the genera *Oedipina* (from south and east of the Isthmus of Tehuantepec) and *Lineatriton* (from north of the Isthmus) (Fig. 12). The former has become elongate by increasing the numbers of vertebrae; the latter by increasing the length of the individual vertebrae, which are identical in number (in the trunk) to all tropical genera except *Oedipina* (Tanner, 1950; Wake & Lynch, 1976). Earlier in this paper I highlighted the convergence in the *Chiropterotriton-Dendrotriton-Nototriton* assemblage. Within *Bolitoglossa* webbing of hands and feet has evolved both convergently (Alberch & Alberch, 1981) and in parallel (Wake, 1966; Wake & Brame, 1969; Larson, 1983; Elias, 1984). These phenomena have made phylogenetic analysis very difficult, for any phylogenetic hypothesis requires extensive convergence, parallelism, or evolutionary reversal (Wake & Elias, 1983).

Epiphytes appear to have been significant factors in the evolution of tropical salamanders. The convergence in morphology and behavior of bromeliad-dwelling salamanders is one indication of this importance, and the extent to which bromeliads and moss mats are utilized as microhabitats is another. It is also significant that salamanders persist in the face of great environmental change so long as fragments of forest with the preferred microhabitats remain.

The tropical salamanders, which originated from a Laurasian ancestral group (Savage, 1973), are a marked exception to a common pattern of tropical origin and subsequent temperate invasion. Late in the history of salamanders as a group, but nevertheless a very long time ago (perhaps at the beginning of Tertiary), they invaded the area that has become modern Middle America. Compared with salamanders generally, the tropical salamanders have been phenomenally successful. But now their survival and, indeed, the survival of much of the diversity of tropical ecosystems is at risk, for the lowland forests and the middle elevation cloud forests that harbor most tropical salamanders are being cleared at rates that almost defy belief. Not a tree is standing over extensive parts of our San Marcos transect, which was in an almost pristine state as recently as 1969. In a single human lifetime the results of perhaps a hundred million years of evolution will have been dramatically changed, if not extinguished.

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APPENDIX I

Use of bromeliads and moss mats by neotropical salamanders. All species known to occur in either of these microhabitats are listed below. Literature references do not include all observations for a given species, but either the first or the best documented example. Where no publication exists field notes or notes from museum collections made by the author are cited.

Bromeliad Occurrence:

Bolitoglossa alvaradoi	DBW notes
B. arborescandens	Taylor (1954)
B. borburata	Trapido (1942)
B. cuchumatana	Stuart (1943), Elias (1984)
B. dunni	Schmidt (1942)
B. engelhardti	Schmidt (1936a), Wake & Lynch (1976)
B. flavimembris	DBW notes
B. franklini	Taylor (1941), Wake & Lynch (1976)
B. hartwegi	Wake & Brame (1969), Elias (1984)
B. helmrichi	Schmidt (1936a)
B. hermosa	Papenfuss et al. (1983)
B. jacksoni	Elias (1984)
B. lignicolor	Dunn (1926)
B. lincolni	Wake & Lynch (1976), Elias (1984)
B. meliana	Wake & Lynch (1982)
B. mexicana	Taylor & Smith (1945)
B. minutula	Wake et al. (1973)
B. morio	Wake & Lynch (1976), Elias (1984)
B. mulleri	Stuart (1943)
B. nicefori	Brame & Wake (1963)
B. occidentalis	Shannon & Werler (1955a)
B. odonnelli	Stuart ("probably," 1948)
B. platydactyla	Taylor & Smith (1945)
B. ramosi	Brame & Wake (1972)
B. resplendens	Wake & Lynch (1976)
B. rostrata	Wake & Lynch (1976)
B. rufescens	Schmidt (1936a), Taylor & Smith (1945)
B. savagei	Ruthven (1922)
B. subpalmata	Dunn (1937)
B. taylori	Wake et al. (1970)
B. vallecula	Brame & Wake (1963)
B. walkeri	Brame & Wake (1972)
B. yucatana	DBW notes
Chiropterotriton arboreus	Rabb (1955)
C. chiropterus	DBW notes
C. chondrostega	Martin (1958)
C. lavae	Taylor (1942)
C. multidentatus	Martin (1958)
Dendrotriton bromeliacia	Schmidt (1936a), Wake & Lynch (1976)
D. megarhinus	Rabb (1960)
D. rabbi	Lynch & Wake (1975), Elias (1984)
D. xolocalcae	Taylor (1941)
Nototriton barbouri	Schmidt (1936b)

APPENDIX I. Continued

N. nasalis	Dunn (1926), Schmidt (1942)
N. picadoi	Picado (1913)
N. veraepacis	Lynch & Wake (1978)
Pseudoeurycea bellii	DBW notes from T. J. Papenfuss
P. brunnata	Wake & Lynch (1976), and DBW notes
P. exspectata	Stuart (1954)
P. firscheini	Werler & Smith (1952), Shannon & Werler (1955b)
P. goebeli	Schmidt (1936a), and DBW notes
P. leprosa	DBW notes
P. nigromaculata	DBW notes
P. scandens	Walker (1955), Martin (1958)
P. smithi	DBW notes from T. J. Papenfuss
Thorius dubitus	DBW notes
Moss Mat Occurrence:	
Bolitoglossa diminuta	Robinson (1976—in a liverwort mat)
B. marmorea	Wake et al. (1973)
B. subpalmata	Taylor (1952)
Dendrotriton cuchumatanus	Lynch & Wake (1975)
Nototriton picadoi	Taylor (1954)
N. richardi	DBW notes
Nyctanolis pernix	Elias & Wake (1983)
Oedipina poelzi	Brame (1963)
O. pseudouniformis	Brame (1968)
O. uniformis	Brame (1968)
Pseudoeurycea rex	Elias (1984)
P. scandens	Martin (1958)
P. werleri	Shannon & Werler (1955a)
Thorius dubitus	Taylor (1941)

REVISION OF *EREMANTHUS* (COMPOSITAE: VERNONIEAE)[1]

NANDA F. F. MACLEISH[2]

ABSTRACT

Historically, *Eremanthus* s. lat. has comprised an amalgam of seven genera that exhibit the combined traits of syncephaly (secondary aggregation of heads into a glomerule), pluriseriate involucres, and achenes with a persistent pappus. Syncephaly is characteristic of the Lychnophorinae, which is considered by modern authors to be an artificial assemblage. In the present treatment *Eremanthus* includes *Vanillosmopsis,* but excludes *Albertinia, Chresta, Glaziovianthus, Prestelia, Pycnocephalum, Paralychnophora* (formerly *Sphaerophora*), and *Stachyanthus* (now *Argyrovernonia*). *Eremanthus* thus comprises 18 species of syncephalous trees and shrubs that are largely restricted to cerrado of the arid Central Plateau of Brazil. Additionally, six new combinations (required by the transfer of *Vanillosmopsis* taxa) are presented.

Recent studies have shown that *Eremanthus* Less. (Compositae: Vernonieae) includes both *Eremanthus* Less. (sensu Schultz-Bip.) and *Vanillosmopsis* Schultz-Bip., but excludes *Albertinia* Sprengel, *Chresta* Vell. Conc., *Glaziovianthus* G. Barroso, *Prestelia* Schultz-Bip., *Pycnocephalum* (Less.) DC., *Sphaerophora* Schultz-Bip., and *Stachyanthus* DC. (MacLeish, 1984a, 1984b, 1984c, 1985a, 1985b, and MacLeish & Schumacher, 1984). Thus, *Eremanthus* comprises 18 species of syncephalous trees and shrubs largely restricted to cerrado (sensu Eiten, 1978, 1983) of the arid Central Plateau of Brazil. This is a region dominated by woody Compositae; geographic dominance is relatively rare in the family (Heywood et al., 1977).

The name *Eremanthus* is derived from the Greek *eremos* (solitary) and *anthos* (flower bearing) in reference to the heads, which bear single flowers. *Vanillosmopsis* refers to the vanillalike odor characteristic of this group of plants. *Vanillosmopsis* is locally called *candeia,* candle, which refers to its ability to burn luminously. The close relationship between *Vanillosmopsis* and members of *Eremanthus* sensu Schultz-Bip. is frequently noted by the Brazilians who often refer to the latter as "não candeia," not a candle.

De Candolle (1836) is the only other author to combine *Eremanthus* and *Vanillosmopsis,* although he mistakenly placed them in *Albertinia.* He correctly noted that *E. incanus* and *E. elaeagnus* approach *Vanillosmopsis* in degree of syncephaly, number of florets per head, and achene and pappus characters; and that *V. erythropappa* and *V. polycephala* resemble *Eremanthus* in their high degree of syncephaly and, in the latter, reduced number of florets per head. In the course of the present study, numerous specimens of natural hybrids between these two genera were identified. It soon became apparent that the taxonomic distinction between *Eremanthus* and *Vanillosmopsis* was largely artificial.

Host/parasite relationships and terpenoid chemistry support the close relationship of these two groups. Dr. J. F. Hennen (pers. comm.) has noted that a rust pathogen, *Puccinia vanillosmopsidia* H. S. Jackson & Holway, has been found on *E. mattogrossensis* and on *V. erythropappa.* Because rusts (Uredinales) have evolved with their vascular plant hosts, their taxonomy may suggest relationships among vascular plant taxa (Thorne, 1979; McCain & Hennen, 1982). Urban (1973) demonstrated the systematic utility of *Puccinia* and *Vernonia* coevolution in determining subgeneric categories. Hence, a close relationship between *Eremanthus* and *Vanillosmopsis* is supported by the presence of a single rust species on members of both genera. In addition, terpenoid profiles appear to be very similar in members of *Eremanthus* and *Vanillosmopsis* (H. Schumacher, pers. comm.). Also, many authors have noted the presence of identical terpenoid

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compounds in the two groups, which further supports a close relationship (Baker et al., 1972; Garcia et al., 1976; Vichnewski et al., 1977; Harborne & Williams, 1977; Robinson et al., 1980). The systematic utility of terpenoids in members of Vernonieae has been discussed by Abdel-Baset et al. (1971), Mabry et al. (1975), Harborne & Williams (1977), and Robinson et al. (1980).

Eremanthus can be distinguished from other syncephalous genera by a combination of characteristics (MacLeish, 1984a, 1984c). These include woody habit; indument composed primarily of stellate hairs; terminal compound cymes (rarely reduced to a cyme) of glomerules; 1–4 florets per head; 10-ribbed (rarely 20-ribbed) achenes with 3–5-seriate pappus and prominent nectary; and advanced pollen of type A (sensu Keeley & Jones, 1977). Members of *Eremanthus* have complex glomerules derived from reduction of internodes between subglomerules arranged in a compound cyme. A complete discussion of glomerulescence arrangement and derivation for *Eremanthus* and related genera can be found in chapter 1 of MacLeish (1984c). The only other syncephalous Vernonieae that approach the combination of characteristics evident in *Eremanthus* are *Paralychnophora* MacLeish and *Lychnophora* Martius (MacLeish, 1984c). However, both of these have a biseriate pappus and glomerules derived from the internode reduction of corymbose subglomerules. In addition, *Paralychnophora* is characterized by axillary, solitary glomerules and angled achenes; and *Lychnophora* by ericoid leaves and prominently twisted inner pappus series.

Among nonsyncephalous Vernonieae, *Eremanthus* appears to be related to *Vernonia* subsect. *Eremosis* (DC.) S. B. Jones (MacLeish, 1984c). This subsection also has a woody habit, congested terminal capitulescences, reduced numbers of florets per head, ribbed achenes, and pollen of type A. However, this group is distributed primarily in Central America and northern South America and has a biseriate pappus. If *Eremanthus* is derived from *Eremosis* stock, there are two Brazilian refugia that may have served as centers of diversification and dispersal: Veadeiros and Rondônia (also called "Araguaia" and "Airpuana" by Prance, 1982). Veadeiros is the current site of several locally endemic members of sect. *Nectaridium* (subg. *Vanillosmopsis*) that are virtually indistinguishable from many members of *Vernonia* subsect. *Eremosis*. Rondônia contains a single *Eremanthus* species, *E. rondoniensis*, which is restricted to that area and is the most unspecialized member of subg. *Eremanthus*.

TAXONOMIC HISTORY

Historically, *Albertinia* Sprengel, *Chresta* Vell. Conc., *Glaziovianthus* G. Barroso, *Pithecoseris* DC., *Prestelia* Schultz-Bip., *Pycnocephalum* (Less.) DC., *Sphaerophora* Schultz-Bip., *Stachyanthus* DC., and *Vanillosmopsis* Schultz-Bip. have been placed adjacent to or in synonymy with *Eremanthus*. These genera are restricted to the arid Central Plateau of Brazil and have not been evaluated comprehensively since Baker's (1873) treatment of Compositae in Martius's *Flora Brasiliensis*.

In 1829, Lessing established *Eremanthus* to include syncephalous trees or shrubs with one floret per head and a paleaceous pappus. At the same time he placed syncephalous trees and shrubs with (presumably) numerous florets per head, filiform pappus, and alveolate receptacles in *Albertinia* and syncephalous herbs in *Vernonia* sect. *Pycnocephalum*. Also in 1829, two species referable to *Eremanthus* s. lat. were described by Velloso as *Chresta*: *C. cordata* and *C. lanceolata*. However, the portion of *Flora Fluminensis* containing *Chresta* was not effectively published until 1881 (Carauta, 1973). Thus, de Candolle accomplished valid publication of *Chresta* in 1836 when he cited Velloso's figures, which had been published in *Florae Fluminensis Icones* (Velloso, 1831). Of the two species described by Velloso, only *C. cordata* was included by de Candolle in *Chresta* (as *C. spherocephala*). This distinctive taxon is widespread throughout Brazil. In contrast, the figure and description of *C. lanceolata* could represent any one of several species. If one takes into account the itineraries of Velloso and contemporary collectors (Urban, 1906), *C. lanceolata* is either *Vanillosmopsis erythropappus*, *Eremanthus incanus*, *E. glomerulatus*, or *E. mattogrossensis*. Kuntze (1898) believed this taxon to be synonymous with *V. erythropappus* but provided no account of his reasoning. In the present treatment, *C. lanceolata* is excluded because of doubtful identity, and *C. cordata* is retained in *Chresta*.

Two years later, Lessing (1831) dissolved *Albertinia* when he transferred the type species into *Vernonia*, and a second taxon, correctly considered to have one floret per head, into *Eremanthus*. In 1836, de Candolle treated syncephalous taxa as five different genera. Syncephalous trees and shrubs were included in *Albertinia* (he incorrectly assumed that the type species had a single floret per head), and syncephalous herbs were placed variously in *Chresta, Pycnocephalum, Stachyanthus,* and *Pithecoseris.* Schultz-Bipontinus (1861, 1863) recognized the error implicit in de Candolle's interpretation of the deeply pitted receptacle *Albertinia* as fused heads homologous with those found in many *Eremanthus* species. In contrast, Schultz-Bipontinus considered the heads of *Albertinia* to contain many florets, each of which is partially enclosed in a receptacle cavity, and the genus to be monotypic and closely related to *Vernonia.* However, Schultz-Bipontinus placed taxa with one (rarely three) floret(s) per head, high degrees of syncephaly, and achenes with a persistent pappus in *Eremanthus* or the newly-described *Sphaerophora* (further delimited by achene surface features), and those with three (to one) florets per head, various degrees of fusion, and achenes with a deciduous pappus in *Vanillosmopsis,* a second new genus (Schultz-Bipontinus, 1861, 1863). In 1873, Baker followed Schultz-Bipontinus in his delimitation of *Vanillosmopsis*; however, in his classification, *Eremanthus* comprised not only the species of Schultz-Bipontinus, but also those of *Sphaerophora, Chresta, Pycnocephalum, Prestelia,* and *Stachyanthus.* Except for Barroso's (1947) transfer of herbs with yellow and red corollas to *Glaziovianthus,* and Robinson's (1980) suggested recombination of all herbaceous taxa into *Chresta,* the boundaries of *Eremanthus* and related genera have remained largely as Baker delineated in 1873.

Following Baker, curators endeavoring to identify Brazilian specimens have placed most syncephalous Vernonieae with achenes bearing a persistent pappus in *Eremanthus.* However, syncephalous heads are characteristic of Lychnophorinae, which is currently considered to be an artificial assemblage (Jones, 1977; MacLeish, 1984c). Traditionally, the distinction between *Eremanthus* and *Vanillosmopsis* has been based on the presence or absence of syncephalous heads, one versus three florets per head, and paleaceous and persistent versus filiform and deciduous pappus. In fact, the characteristic of lacking syncephaly was used to exclude *Vanillosmopsis* from Lychnophorinae (where *Eremanthus* was placed) despite generic descriptions that clearly describe *Vanillosmopsis* as including several highly syncephalous taxa (Baker, 1873; Bentham, 1873). De Candolle is the only author until now to combine *Eremanthus* and *Vanillosmopsis,* although erroneously, in *Albertinia.* Currently, following de Candolle, *Eremanthus* is considered to include trees and shrubs with reddish-purple corollas, compound cymes (rarely reduced to a cyme) of glomerules, 1–4 florets per head, ribbed achenes with persistent or deciduous pappus of 3–5 intergrading series, and advanced pollen of type A (subechinolophate with elongated germinal furrows often barely separated at the poles, sensu Keeley & Jones, 1977).

De Candolle and Schultz-Bipontinus used the number of florets per head, degree of syncephaly, number of pappus series, and various achene surface features to delineate subdivisions of genera. These are good characters that readily indicate natural groups of related species. Thus, subg. *Eremanthus* includes sect. *Eremanthus* and sect. *Synglomerulus. Eremanthus* sect. *Eremanthus* is a group of closely related taxa (*E. glomerulatus, E. goyazensis, E. mattogrossensis,* and *E. rondoniensis*) that may have arisen along an east-west gradient across southern portions of the Central Plateau (Fig. 1). This section is characterized by coriaceous leaves, a compound cyme of 10–60 glomerules, 5–100 heads per glomerule, head fusion via the interwoven pubescence of phyllaries, one floret per head, and sericeous achenes with a stramineous, coroniform, persistent, paleaceous pappus. Section *Synglomerulus* comprises *Eremanthus argenteus, E. auriculatus,* and *E. cinctus.* They differ from sect. *Eremanthus* primarily in reduction of the glomerulescence to a cyme (not compound) of 2–10 glomerules.

Eremanthus subg. *Vanillosmopsis* comprises two sections and is characterized by membranaceous to subcoriaceous leaves, compound cymes of more than 100 glomerules, 1–12 heads per glomerule, 1–4 florets per head, and glabrous achenes with a purple or white (rarely stramineous), not coroniform, deciduous, filiform pappus. *Eremanthus pohlii, E. graciellae,* and *E. brasiliensis* form sect. *Nectaridium,* which is characterized by near absence of syncephaly (heads solitary or slightly appressed basally in pairs) and is restricted to the northwestern arm of the Central Plateau. *Eremanthus capitatus, E. arboreus,* and *E. uniflorus* are members of sect. *Vanillosmopsis* and have 2–9 heads per glomerule, with bases slightly appressed and fused by the interwoven pubescence of the phyllaries. The first two of these species range south to north along the northeastern arm of the Plateau, and

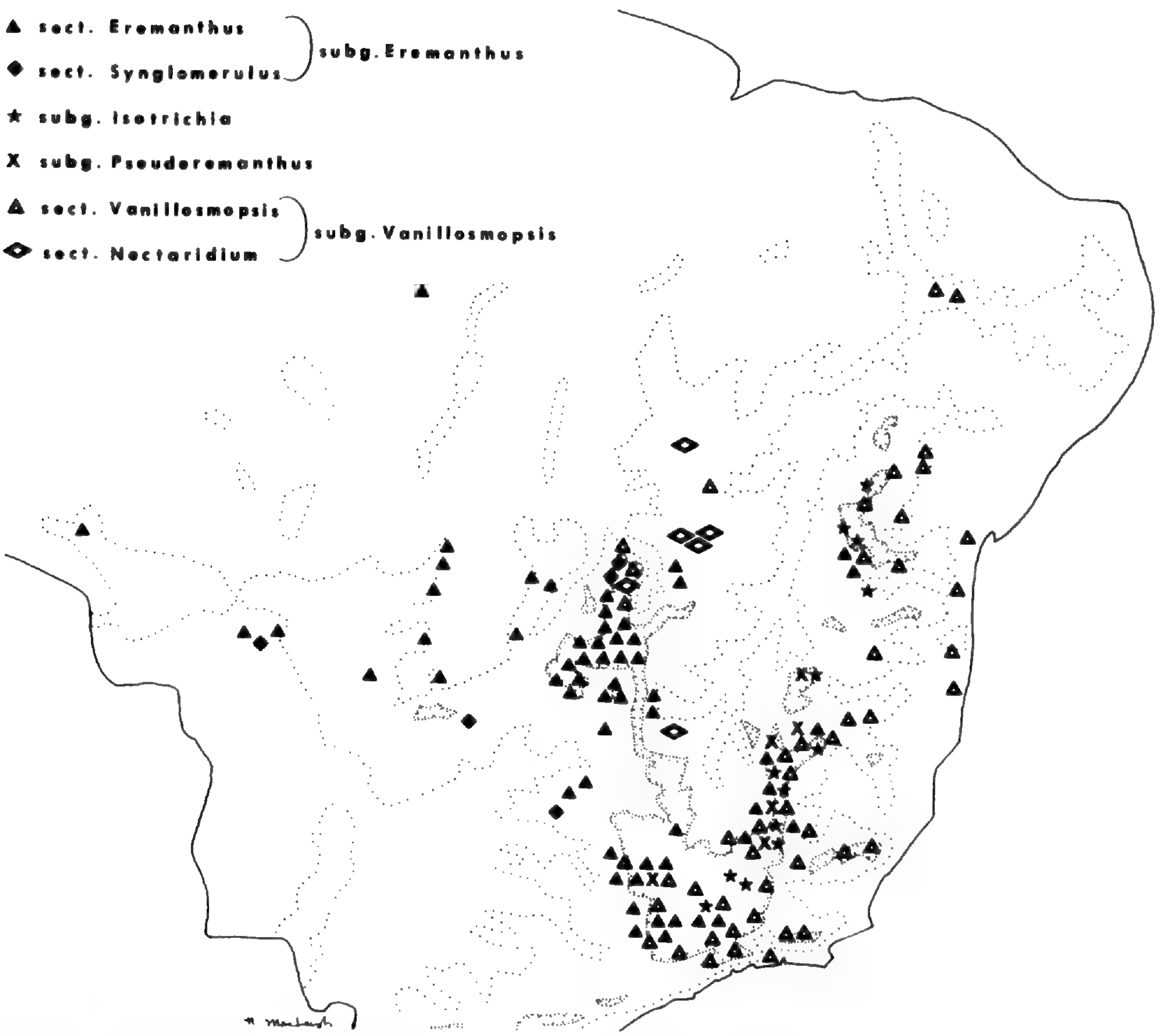

FIGURE 1. Distribution of *Eremanthus* in the Central Plateau of Brazil.

the last is restricted to the northwestern arm. *Eremanthus erythropappus* and *E. polycephalus* are also members of sect. *Vanillosmopsis* and have glomerules with 6–12 heads that are closely appressed and fused by the concrescence of phyllary and receptacle tissues. These two species are found only in the southern part of the Central Plateau.

In contrast, three species (*E. incanus, E. elaeagnus, E. seidelii*), historically assigned to *Eremanthus* s. str., exhibit characteristics intermediate to those of both subg. *Eremanthus* and subg. *Vanillosmopsis.* Not surprisingly, these species are largely restricted to the southern part of the Plateau, an area where the two major complexes are sympatric. This is also the region where a majority of hybrids are found, and it is possible that subg. *Pseuderemanthus* (*E. elaeagnus* and *E. seidelii*) and subg. *Isotrichia* (*E. incanus*) represent established hybrids between members of the major complexes.

TAXONOMIC TREATMENT

Eremanthus Less., Linnaea 4: 317. 1829. TYPE: *Eremanthus glomerulatus* Less.

Vanillosmopsis Schultz-Bip., Jahresber. Pollichia 18–19: 166. 1861. TYPE: *Vanillosmopsis glomerata* Schultz-Bip. = *Eremanthus erythropappus* (DC.) MacLeish.

Trees or shrubs to 10 m tall; stems reddish-brown lanate-tomentose or gray lepidote-tomentulose, often darkened basally by fire; branches few to many, often tortuous. Leaves cauline, alternate, strongly coriaceous to membranaceous, largely restricted to ends of branches, subsessile to petiolate; blades 2–20 cm long, 0.5–10 cm wide, narrowly elliptic to obovate, the bases acuminate to obtuse (occasionally auriculate, panduriform, or retuse), the apices acuminate to obtuse, the margins entire, adaxially glabrate to lepidote, abaxially silvery-canescent to gray-brown, lanate-tomentulose to lepidote-tomentulose; trichomes stellate, the stalk with 1–2 cells; primary venation pinnate and abaxially prominent, the midrib furrowed; petioles 1–20 mm long, lanate or lepidote, base slightly expanded. Peduncles slender, to 35 cm tall, terete, reddish-brown to gray, lanate-tomentose to lepidote-tomentulose, expanded at apex; bracts foliaceous, both intra- and extraglomerular. Glomerulescence a terminal cyme of 2–20 glomerules or a compound cyme of 8–60(–100) glomerules; maturation of glomerules centrifugal. Glomerules 5–15 mm tall, 4–12 mm diam., hemispherical to spherical; head maturation concurrent to centrifugal within a glomerule. Heads homogamous, 1–100 per glomerule, closely to slightly appressed and free, or coherent by pubescence of phyllaries, or connate by concrescence of receptacle and phyllary tissues. Involucres obconic or cylindrical, 2–12 mm tall, 0.3–4 mm diam.; phyllaries in 4–7 imbricate, graduated (rarely subequal) series; innermost phyllaries deciduous at maturity; margins subscarious, entire to subfimbriate; abaxial surfaces stramineous, often with purple apex, glabrate to lanate-tomentulose or lepidote-tomentulose, the inner surfaces stramineous and vernicose; single vein (when present) often with mucronate extension. Florets 1–3(4) per head; corollas purple to white, 5–9 mm tall, the tube and lobes subequal; tube 2–4.5 mm tall; throat 0.5–1 mm tall; lobes 2.5–3.5 mm tall. Anthers 2–4 mm long. Pollen tricolporate with a continuous micropunctate tectum, short echinate (*Vernonia* type A). Style 4–6 mm long, 0.15–0.3 mm wide, noticeably flattened, the branches short to medium bifid, 1–2.5 mm long. Achenes cylindric to cylindric-turbinate (rarely turbinate), 1–4 mm tall, glandular, glabrous or sericeous, 10-ribbed (often obscurely or rarely to 20), apex constricted and dark; carpopodium absent or minute; nectary 0.2–0.45 mm tall, persistent or tardily deciduous, occasionally pubescent. Pappus 3–5-seriate, of stramineous, white, or purple, strongly coroniform to not coroniform, often basally fused, persistent to promptly deciduous, paleaceous to filiform, strigose bristles; outermost series 0.4–3 mm long, innermost series 3–8 mm long. Chromosome number: $n = 15$.

KEY TO SPECIES OF *EREMANTHUS*

1a. Glomerulescence a compound cyme of 3–60 glomerules or a cyme of 2–20 glomerules; heads (1–)20–100 per glomerule, with phyllaries in 3–6 series; florets 1(2–4) per head; achenes cylindric-turbinate or cylindric, sericeous with stramineous (rarely white or purple), strongly to subcoroniform, persistent (rarely tardily deciduous), paleaceous pappus; leaves strongly coriaceous to subcoriaceous.

2a. Florets 1 per head; heads closely appressed, coherent either by interwoven pubescence or connate by tissue concrescence; achenes cylindric-turbinate or cylindric; glomerule subspherical to hemispherical.

3a. Achenes cylindric-turbinate (rarely turbinate), 10-ribbed; pappus stramineous (rarely purple), coroniform, persistent, paleaceous; heads obconic (rarely cylindric), coherent by interwoven pubescence of phyllaries (subg. *Eremanthus*).

4a. Glomerulescence a compound cyme of (3–)10–60 glomerules (sect. *Eremanthus*).

5a. Stem pubescence reddish-brown lanate-tomentose; heads 20–100 per glomerule.

6a. Heads coherent ¼–½ length; leaves subcoriaceous, abaxially rarely lepidote-tomentose ..... 1. *E. glomerulatus*

6b. Heads coherent entire length; leaves strongly coriaceous, abaxially lepidote-tomentose ..... 2. *E. goyazensis*

5b. Stem pubescence gray lepidote-tomentulose; heads 5–45 per glomerule.

7a. Heads coherent ½ length; leaf blades 6–16 cm long, 2–10 cm wide ..... 3. *E. mattogrossensis*

7b. Heads coherent ¼ length; leaf blade 2–7 cm long, 0.5–1.5 cm wide ..... 4. *E. rondoniensis*

4b. Glomerulescence a cyme (not compound) of 5–20(–30) glomerules (sect. *Synglomerulus*).

8a. Stem pubescence gray lepidote-tomentulose; leaf base acute to attenuate ..... 5. *E. argenteus*

8b. Stem pubescence reddish-brown lanate-tomentose; leaf base variously lobed (rarely acute).

9a. Leaf bases auriculate, the blades 5–8 cm long, appressed-ascending; heads 30–80 per glomerule, coherent ½ length ..... 6. *E. auriculatus*

9b. Leaf bases retuse to acute, the blades 6–19 long, not appressed-ascending; heads 20–50 per glomerule, coherent entire length ..... 7. *E. cinctus*

3b. Achenes cylindric, 15–20-ribbed; pappus off-white to purple, subcoroniform, tardily deciduous, subpaleaceous; heads cylindric, connate by concrescence of tissues (subg. *Isotrichia*) ..... 8. *E. incanus*

2b. Florets 3–4 per head; heads slightly appressed, free; achenes cylindric; glomerule hemispherical (subg. *Pseuderemanthus*).
10a. Heads per glomerule 1–7 .... 9. *E. seidelii*
10b. Heads per glomerule 9–20 .... 10. *E. elaeagnus*
1b. Glomerulescence a compound cyme of more than 100 glomerules; heads 1–12 per glomerule, with phyllaries in 5–7 series; florets 1–4 per head; achenes cylindric (rarely cylindric-turbinate), glabrate with a purple or white (rarely stramineous), not coroniform, promptly (rarely tardily) deciduous, filiform pappus; leaves membranaceous to subcoriaceous (subg. *Vanillosmopsis*).
11a. Heads solitary or in pairs slightly appressed basally, cylindric; pappus never twisted (sect. *Nectaridium*).
12a. Florets 2–3 per head; involucre with prominent truncate base, phyllaries purple.
13a. Florets 3 per head .... 11. *E. pohlii*
13b. Florets 2 per head .... 12. *E. graciellae*
12b. Florets 1 per head; involucre without truncate base, phyllaries brown .... 13. *E. brasiliensis*
11b. Heads (2–)5–12 per glomerule, cylindric or obconic; pappus often twisted (sect. *Vanillosmopsis*).
14a. Heads closely appressed and connate by tissue concrescence, 6–12 per glomerule.
15a. Floret 1 per head; heads coherent ½ length .... 14. *E. polycephalus*
15b. Florets 3–4 per head; heads coherent nearly entire length .... 15. *E. erythropappus*
14b. Bases of heads slightly appressed and coherent by pubescence of phyllaries, 2–9 per glomerule.
16a. Florets 1 per head .... 16. *E. uniflorus*
16b. Florets 3–4 per head.
17a. Heads 2–5 per glomerule .... 17. *E. capitatus*
17b. Heads 6–9 per glomerule .... 18. *E. arboreus*

Eremanthus Less. subg. **Eremanthus**. *Eremanthus* subg. *Eueremanthus* Schultz-Bip., Jahresber. Pollichia 20–21: 393. 1863.

Leaves strongly coriaceous to subcoriaceous. Glomerulescence a compound cyme of 3–60 glomerules or a cyme of 2–20 glomerules. Glomerules subspherical to hemispherical. Heads (1–) 20–100 per glomerule, obconic; with phyllaries in 3–6 series, closely appressed, coherent by interwoven pubescence of phyllaries. Florets 1 per head. Achenes cylindric-turbinate, 10-ribbed, sericeous. Pappus stramineous (rarely purple), coroniform, persistent, paleaceous, strigose bristles.

Eremanthus Less. sect. **Eremanthus**

Glomerulescence a compound cyme of (3–)10–60 glomerules. Glomerules 5–10(–15) mm tall, 5–15 mm diam.

1. **Eremanthus glomerulatus** Less., Linnaea 4: 317. 1829. *Albertinia glomerulata* (Less.) DC., Prodr. 5: 82. 1836. TYPE: Brazil: no other data, *Sellow s.n.* (holotype, P; isotype, TEX).

Albertinia rufiseta DC., Prodr. 5: 81. 1836. TYPE: Brazil. Minas Gerais: siccis apricis montosis Serro Frio, *Martius s.n.* (holotype, M).

Albertinia pallidiseta DC., Prodr. 5: 81. 1836. *Eremanthus pallidisetus* (DC.) Schultz-Bip., Jahresber. Pollichia 18–19: 165. 1861. TYPE: Brazil. Minas Gerais: campis editis ad Calumbi Praed. Serro Frio, *Martius s.n.* (holotype, M).

Albertinia stellata Gardner, London J. Bot. 5: 235. 1846. *Eremanthus stellatus* (Gardner) Schultz-Bip., Jahresber. Pollichia 18–19: 164. 1861. *Eremanthus stellatus* (Gardner) Schultz-Bip. var. *gardneriana* Schultz-Bip., Jahresber. Pollichia 20–21: 394. 1863, nom. superfl. TYPE: Brazil. "Pernambuco" (now Bahia): Santa Rosa, district of the Rio Preto, Sept. 1839, *Gardner 2896* (holotype, BM; isotypes, 2 in F (fragment and photo of W), G, GH, K, 2 in NY).

Eremanthus stellatus (Gardner) Schultz-Bip. var. *pohliana* Schultz-Bip., Jahresber. Pollichia 20–21: 394. 1863. TYPE: Brazil, in summitate montium S. Felis prope Engenb. S. Anna, *Pohl 174* (holotype, W; isotypes, F (fragment), 2 in NY).

Slender to robust tree, 2–10 m tall, to 20 cm diam.; stems reddish-brown lanate-tomentose; branches few to many. Leaves subcoriaceous, sessile to petiolate; petioles to 10 mm long, lanate-tomentulose; blades 4–14(–20) cm long, 1–5.5(–7.5) cm wide, elliptic to ovate, the bases acute to obtuse, the apices obtuse (rarely rounded or retuse), margins entire; adaxially tomentulose to glabrate, abaxially gray-brown lanate-tomentulose (rarely lepidote-tomentulose). Peduncle slender, to 20 cm tall, ribbed, reddish-brown lanate-tomentose to gray lepidote-tomentulose. Glomerulescence a compound cyme of 20–60 glomerules. Glomerules 5–15 mm tall, 9–15 mm diam., hemispherical. Heads 20–90 per glomerule, closely appressed basally, fused ¼ to ½ length by pubescence of phyllaries. Involucres obconic, 3.5–5.5 mm tall, 1.3–2.5 mm diam.; phyllaries in 4–6 series; outermost phyllaries narrowly obtrullate, 1.2–3 mm long, 0.4–1.6 mm wide, the apices acute; innermost phyllaries oblanceolate, 3.1–5.2 mm long, 0.6–1.4 mm wide,

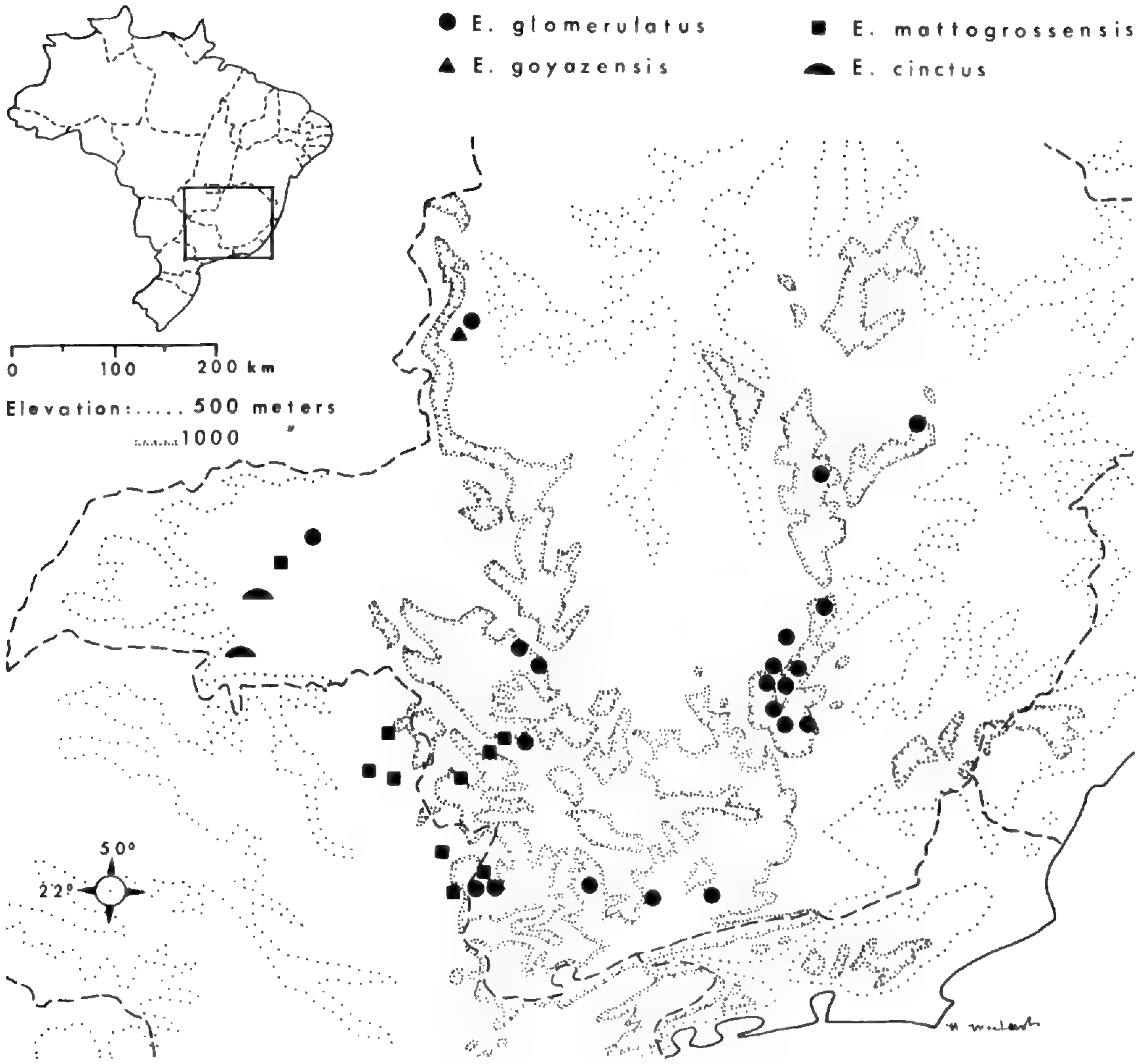

Figure 2. Distribution of *Eremanthus* subg. *Eremanthus* in Minas Gerais.

the apices acute; margins entire; abaxial surfaces stramineous with purple apex, glabrate to lanate-tomentulose. Corollas purple to white, 4–7.8 mm tall, the lobes acuminate. Anthers 2–3.4 mm long, the apical appendage acuminate to rounded, the bases obtuse to rounded. Achenes 2.5–4.1 mm tall, glandular, sericeous between the 10 ribs, the apex slightly constricted; nectary 0.15–0.25 mm tall, tardily deciduous. Pappus 4–5-seriate, of strongly coroniform (at maturity) strigose bristles; outermost series 1–2.2 mm long; innermost series 4–6.2 mm long.

Flowering and fruiting occur from March to October.

Eremanthus glomerulatus is distributed throughout Minas Gerais, Goiás, and adjacent regions in Bahia and São Paulo (Figs. 2, 3, 6), at altitudes of 700 to 1,500 meters. It is found commonly in large colonies and may dominate cerrado and campo rupestre habitats. In Minas Gerais, this species often is used for fence posts because of its abundance.

Eremanthus glomerulatus is the eastern member of a group of closely related taxa (sect. *Eremanthus*) found throughout the Central Plateau. *Eremanthus goyazensis* is slightly more robust with a greater fusion of heads and is found in the northcentral branch of the Plateau. In contrast, *E. mattogrossensis* is less robust and has lepidote-tomentose (rather than lanate-tomentose) stems and leaves; it extends throughout the western arm and into the southwestern side. *Eremanthus rondoniensis* is closely related to *E. mattogrossensis* and is restricted to the far western portions of the western arm. *Eremanthus glomerulatus* appears to be the member of this complex most closely related to the taxa historically considered to compose *Vanillosmopsis.* The subcoriaceous leaves, strongly ribbed achenes, and occasionally purple pappus of *E. glomerulatus* are reminiscent of characteristics found in the transitional taxa, *E. incanus, E. elaeagnus,* and *E. seidelii.* In addition, it is the only member of this complex that is sympatric with both the transitional taxa and the majority of the *Vanillosmopsis* complex.

The many epithets ascribed to *E. glomerulatus* represent variations in pappus color (purple or white) and number of series, branch position (angular or not), and leaf shape. *Eremanthus glomerulatus* can be found throughout most of the Central Plateau, and the observed variation can be attributed to maturity and habitat differences. These epithets were applied by earlier authors who were attempting to identify Brazilian collections in the absence of adequate documentation. Baker (1873) was the first author to recognize *E. glomerulatus* as a widespread and slightly variable species.

The Paris specimen of *E. glomerulatus* is clearly the holotype. It is annotated appropriately by both Lessing and Schultz-Bipontinus and matches the description given by Lessing in 1829. Originally both the Paris specimen and the Texas specimen were housed in Berlin because both are stamped "hb. berol."

Additional specimens examined. BRAZIL. BAHIA: Rio das Contas, 22 Jul. 1979, *King et al. 8099* (US). DISTRITO FEDERAL: Gama, 28 Aug. 1965, *Irwin et al. 7926* (MO, NY, US). GOIÁS: Cristalina, 3 Apr. 1973, *Anderson 8004* (F, MO, NY, UB, US). MINAS GERAIS: Nova Lima, 15 Apr. 1945, *Williams & Assis 6626* (F, GH, MO, NY, S).

Possible hybrids. × *E. elaeagnus* (C. Martius ex DC.) Schultz-Bip. MINAS GERAIS: Serra do Cipó, 7 Oct. 1980, *MacLeish et al. 715* (BR, F, GA, GH, K, M, MO, NY, RB, S, US), 7 Oct. 1980, *MacLeish et al. 716* (GA, RB), 30 Jan. 1980, *King & Almeda 8354* (US). × *E. mattogrossensis* Kuntze. MINAS GERAIS: Sacramento, 22 Jul. 1980, *Schumacher B10* (GA). × *E. seidelii* MacLeish & Schumacher. MINAS GERAIS: between Furnas and Piuí, 25 Aug. 1981, *Schumacher 1008* (GA).

2. **Eremanthus goyazensis** (Gardner) Schultz-Bip., Jahresber. Pollichia 18–19: 165. 1861. *Albertinia goyazensis* Gardner, London J. Bot. 6: 425. 1847. TYPE: Brazil. Goiás: hilly campos near Villa de Arrayas, Apr. 1840, *Gardner 3804* (holotype, BM; isotypes, 2 in F (fragment and photo of B), 3 in G, GH (photo of B), 3 in NY, TEX (photo of B), W).

Eremanthus weddellii Schultz-Bip., Jahresber. Pollichia 18–19: 165. 1861. TYPE: Brazil, Goiás, env. in Salinas, May 1844, *Weddell 2032* (holotype, P).

Small tree, 1–3 m tall, the trunk often gnarled; stems reddish-brown to gray-black lanate-tomentose, to 8 cm diam.; branches few. Leaves strongly coriaceous, sessile to petiolate; petioles to 10 mm long, lanate-tomentulose; blades 7.5–18 cm long, 3.5–10 cm wide, elliptic to ovate, the bases obtuse, the apices obtuse to rounded (rarely retuse), the margins entire; adaxially sparsely lepidote to glabrate; abaxially gray-brown lepidote-tomentulose. Peduncle slender, to 20 cm tall, ribbed, gray-brown lepidote-tomentulose. Glomerulescence a compound cyme of 10–40 glomerules. Glomerules 5–15 mm tall, 7–15 mm diam., hemispherical. Heads 25–100 per glomerule, closely appressed, coherent entire length by lanose pubescence of phyllaries. Involucres obconic, 2–4.6 mm tall, 0.5–1.5 mm diam.; phyllaries in 3–4 series; outermost phyllaries narrowly obtrullate, 1.8–3.2 mm long, 0.2–0.8 mm wide, the apices acute to acuminate; innermost phyllaries oblanceolate, 2.9–4.8 mm long, 0.3–0.8 mm wide, the apices acute; margins entire; abaxial surfaces stramineous, glandular, glabrate to lanose-tomentose. Corollas pale purple to white basally, 5.2–8.2 mm tall, the lobes acuminate. Anthers 2.4–4.4 mm long, the apical appendage acuminate; bases obtuse to rounded. Achenes 2–2.8(–3.8) mm tall, glandular, sericeous between 10 ribs, often obscurely ribbed; apex slightly constricted; nectary 0.25–0.35 mm tall, tomentose, tardily deciduous. Pappus 4–5-seriate, of strongly coroniform (at maturity) strigose bristles; outermost series 0.8–2.3 mm long, the innermost series 4.6–6 mm long. Chromosome number: $n = 15$.

Flowering and fruiting occur from January to September.

Eremanthus goyazensis is distributed throughout southern Goiás and nearby Minas Gerais (Figs. 2, 3). It is infrequent in cerrado and campo rupestre at altitudes of 700 to 1,600 meters.

Eremanthus goyazensis is the northcentral extension of the *glomerulatus* complex. It is distinguished from *E. glomerulatus* by its strongly coriaceous leaves with abaxial lepidote-tomentose surfaces and heads entirely coherent by interwoven pubescence. In addition, it can be easily distinguished from the *mattogrossensis-rondoniensis* complex by its lanate stem pubescence, 25–100 heads per glomerule, and high degree of cohesion.

Additional specimens examined. BRAZIL. DISTRITO FEDERAL: Chapada da Contagem, 18 Aug. 1964, *Irwin & Soderstrom 5287* (NY, TEX, UB). GOIÁS: Terezina, 18 Mar. 1973, *Anderson 7354* (F, MO, NY, UB, US).

3. **Eremanthus mattogrossensis** Kuntze, Revis. Gen. Pl. 3(2): 145. 1898. TYPE: Brazil: "Mat-

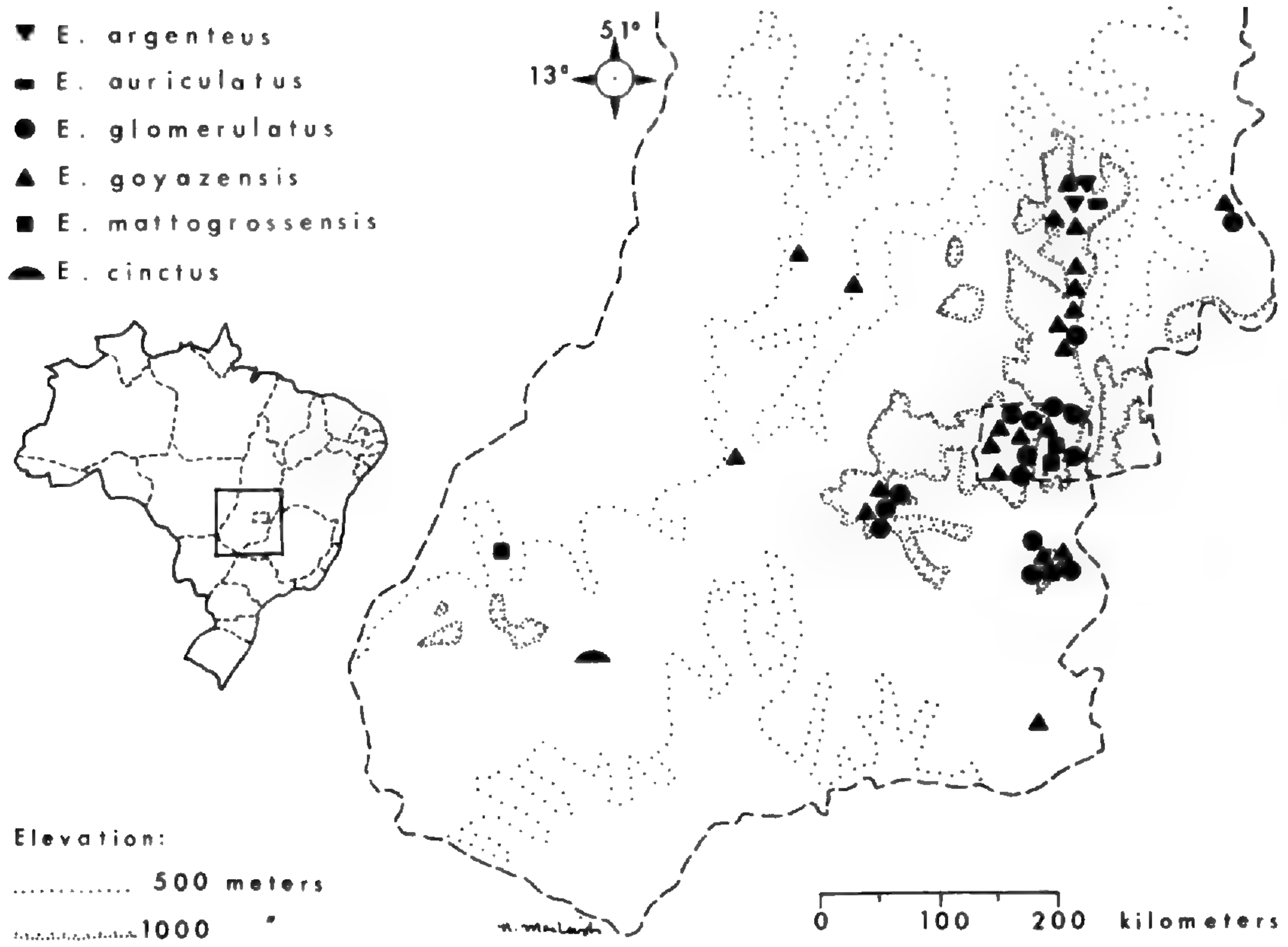

FIGURE 3. Distribution of *Eremanthus* subg. *Eremanthus* in Goiás.

togrosso" (now Mato Grosso): Jul. 1892, *Kuntze s.n.* (holotype, NY; isotypes, photos of B, F, GH, TEX).

Shrub or slender tree, 1–4 m tall; stems gray-brown lepidote-tomentulose; branches few. Leaves coriaceous, sessile to petiolate; petioles to 15 mm long, lepidote; blades 6–16 cm long, 2–10 cm wide, elliptic to narrowly elliptic, the bases acute to acuminate, the apices acute to rounded, the margins entire; adaxially sparsely lepidote to glabrate, abaxially gray lepidote-tomentulose. Peduncle slender, to 32 cm tall, ribbed, gray-brown lepidote-tomentulose. Glomerulescence a compound cyme of 6–35 (–80) glomerules. Glomerules 4.5–10 mm tall, 5.5–12 mm diam., subspherical. Heads 10–45 per glomerule, closely appressed basally, coherent ½ length by pubescence of phyllaries. Involucres cylindric, 2.3–4 mm tall, 1.1–2.4 mm diam.; phyllaries in 5–6 series; outermost phyllaries narrowly obtrullate, 1.3–2.3 mm long, 0.2–0.6 mm wide, the apices acute; innermost phyllaries oblanceolate, 1.8–3.4 mm long, 0.5–0.9 mm wide, the apices acute; margins entire; abaxial surfaces stramineous, glabrate to lepidote-tomentulose. Corollas pale purple to white, 4.4–7.6 mm tall, the lobes acuminate. Anthers 2.1–3.4 mm long, the apical appendage acuminate to acute, the bases obtuse to rounded. Achenes 2–3 mm tall, glandular, sericeous between ribs, 10-ribbed (often obscurely), the apex slightly constricted; nectary 0.15–0.25 mm tall, tomentose, tardily deciduous. Pappus 3–5-seriate, of strongly coroniform (at maturity) strigose bristles; outermost series 0.8–3.1 mm long; innermost series 3.3–6 mm long.

Flowering and fruiting occur from April to August.

Eremanthus mattogrossensis is widely distributed throughout the western section of the Central Plateau of Brazil (Figs. 2–4) at elevations of 500 to 1,000 meters in cerrado. It is particularly common in Mato Grosso, where it is called "veludo do cerrado," velvet of the cerrado, or "casca freta," cleft bark.

Eremanthus mattogrossensis is transitional between *E. goyazensis* and *E. rondoniensis* and is intermediate in geographical location. All three are found within the western arm of the Central Plateau. *Eremanthus rondoniensis* is restricted to the far western portion of the Serra dos Parecis near the border of Mato Grosso and Rondônia, and *E. goyazensis* is restricted to eastern portions of the western arm (principally southern Goiás).

The type specimen, bearing only the citation "Mattogrosso," must have been collected in western Mato Grosso, near Rondônia. Zanoni (1980), in his excellent survey of Kuntze's collecting trips, pointed out that Kuntze entered Brazil through Bolivia and explored only a small

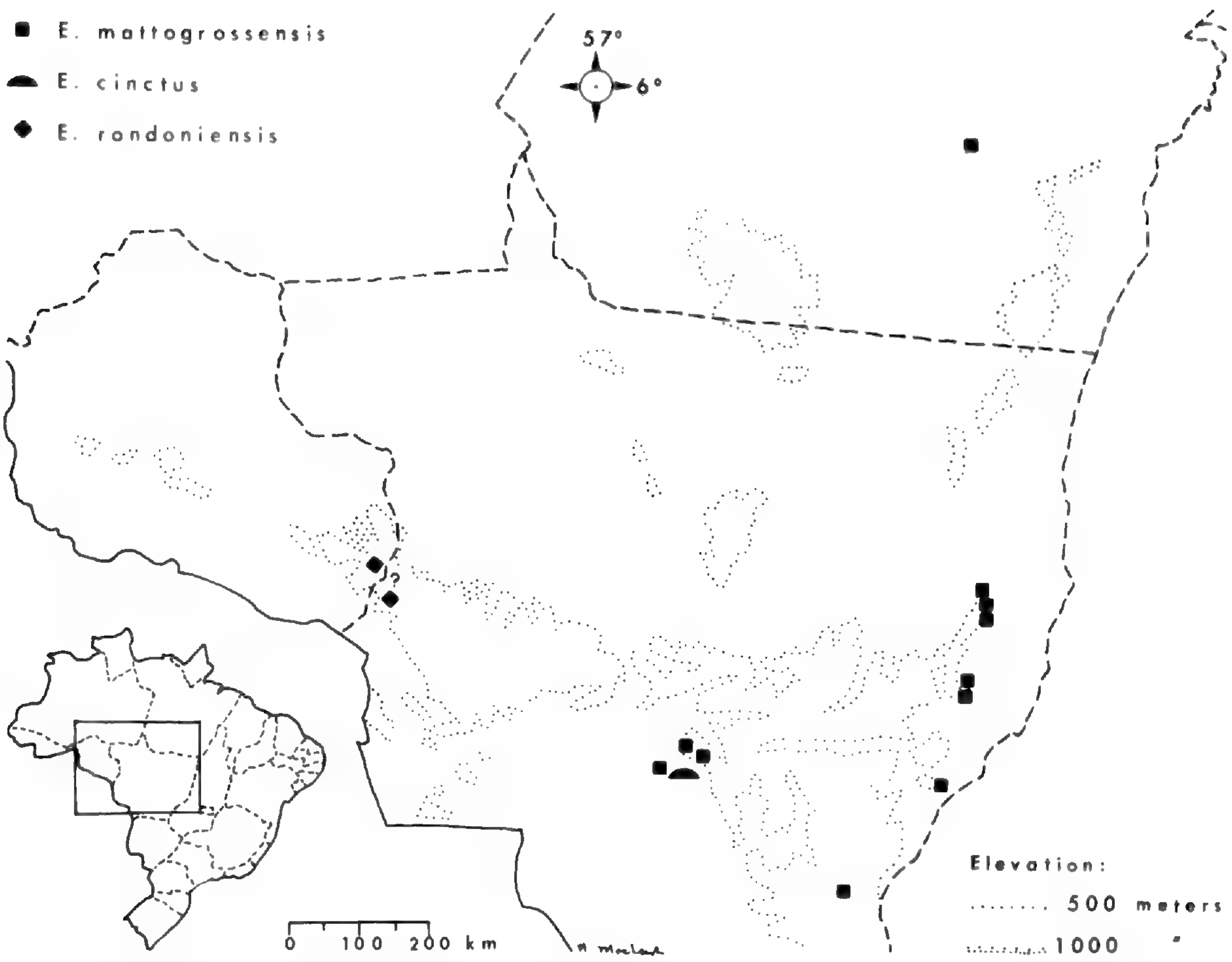

FIGURE 4. Distribution of *Eremanthus* subg. *Eremanthus* in western Central Plateau.

area of Mato Grosso near the border. Zanoni also noted that the bulk of Kuntze's personal herbarium, including many type specimens, is at the New York Botanical Garden. Thus, their specimen of *E. mattogrossensis,* which bears the appropriate collecting information in Kuntze's handwriting and which matches his type description, is likely the holotype.

Additional specimens examined. BRAZIL. DISTRITO FEDERAL: Brasília, 15 Jun. 1981, *Heringer et al. 7057* (MO). GOIÁS: 75 km from Aragarças, near Piranhas, 23 Jun. 1966, *Hunt & Ramos 6160* (MO, NY, UB). MATO GROSSO: Barra do Garças, 6 May 1973, *Anderson 9801* (G, MO, NY, UB). MINAS GERAIS: Furnas, 5 Jul. 1982, *Schumacher 2008, 2009, 2010, 2012, 2014* (GA, MB). PARÁ: São Felix do Xingu, 12 Jul. 1978, *Rosario 68* (RB, NY). SÃO PAULO: inter Canna Verde et S. José, *Regnell III.670* (BR, S).

Possible hybrids. × *E. glomerulatus* Less. MINAS GERAIS: Sacramento, 22 Jul. 1980, *Schumacher B10* (GA). × *E. seidelii* MacLeish & Schumacher. MINAS GERAIS: between Furnas and Piuí, 25 Aug. 1981, *Schumacher 1003, 1004* (GA).

4. **Eremanthus rondoniensis** MacLeish & Schumacher, Syst. Bot. 9: 89. 1984. TYPE: Brazil. Rondônia: Vilhena, 13°16′S, 58°52′W, 18 Apr. 1977, *Bantel & Silva s.n.* (holotype, RB).

Small tree, ca. 1 m tall; stems gray-brown lepidote-tomentulose, often basally darkened by fire. Leaves coriaceous, sessile to petiolate; petioles to 5 mm long, lepidote; blades 2–7 cm long, 0.5–1.4 cm wide, narrowly elliptic, the bases obtuse, the apices obtuse; margins entire; adaxially sparsely lepidote to glabrate, abaxially gray-brown lepidote-tomentulose. Peduncle slender, height unknown, terete, gray-brown lepidote-tomentulose. Glomerulescence a compound cyme of 3–20 glomerules. Glomerules 5–7 mm tall, 7–10 mm diam., hemispherical. Heads 5–15 per glomerule, closely appressed, coherent ¼ length by pubescence of phyllaries. Involucres obconic, 3.5–5 mm tall, 1–2.2 mm diam.; phyllaries in 4–6 imbricate graduated series; outermost phyllaries widely trullate, 1.4–2.1 mm long, 0.5–0.7 mm wide, the apices obtuse; innermost phyllaries oblanceolate, 2.4–4 mm long, 0.8–1 mm wide, the apices acute; margins entire; abaxial surfaces stramineous with purple apex, glabrate to lepidote-tomentulose. Corollas white, 5.1–6 mm tall, the lobes acuminate. Anthers 2.6–3 mm long, the apical appendage acuminate, the bases rounded. Achenes turbinate, 1.9–2.2 mm tall, glandular, obscurely-ribbed, the base sericeous, the apex constricted with prominent dark collar;

nectary 0.2–0.5 mm tall. Pappus 3–5-seriate, of strongly coroniform (at maturity) strigose bristles; outermost series 0.6–1.8 mm long; innermost series 5–6.8 mm long.

Flowering and fruiting occur from April to July.

Eremanthus rondoniensis is distributed along the Rondônia-Mato Grosso border in the western portion of the Serra dos Parecis (Fig. 4). It is found in periodically burned cerrado. *Eremanthus rondoniensis* is closely related to *E. mattogrossensis* and represents a western extension of the *glomerulatus-goyazensis-mattogrossensis* complex.

Additional specimens examined. BRAZIL. MATO GROSSO (latitude and longitude indicate Rondônia): 12°38'S, 60°8'W, 5 Jul. 1977, *Olivieira s.n.* (RB). RONDÔNIA (latitude and longitude indicate Mato Grosso): Vilhena, 13°46'S, 59°50'W, 17 Apr. 1977, *Bantel & Silva s.n.* (RB).

Eremanthus sect. **Synglomerulus** MacLeish, sect. nov. TYPE: *Eremanthus argenteus* MacLeish & Schumacher.

Glomerulescentiae cymosae. Glomerulis 5–10(–30); (5–)10–25 mm longis, 10–25 mm diam.

5. **Eremanthus argenteus** MacLeish & Schumacher, Syst. Bot. 9: 84. 1984. TYPE: Brazil. Goiás: 33 km N of Alto Paráiso towards Cavalcante, 1,370 m, 14 Oct. 1980, *MacLeish, Martinelli, Smith & Stutts 734* (holotype, RB; isotypes, F, G, GA, GH, MO, NY, UB, US).

Slender tree, 2–3 m tall; stems ash gray lepidote-tomentulose; branches few. Leaves coriaceous, sessile to petiolate; petioles to 5 mm long, lepidote-tomentulose; blades 7.5–14(–18) cm long, 2.5–6 cm wide, elliptic, the bases acute to attenuate, the apices rounded to obtuse, the margins entire; adaxially silvery lepidote; abaxially silvery lepidote-tomentulose. Peduncle slender, to 30 cm tall, terete, ash gray lepidote-tomentulose. Glomerulescence a cyme of 6–20 glomerules. Glomerules 5–20 mm tall, 10–25 mm diam., subspherical. Heads 10–80 per glomerule, closely appressed, coherent for ⅔ their lengths by pubescence of phyllaries. Involucres obconic, 3.5–5 mm tall, 1–2.5 mm diam.; phyllaries in 4–5 series; outermost phyllaries narrowly obtrullate, 1.7–2.9 mm long, 0.4–0.8 mm wide, the apices acute; innermost phyllaries narrowly obtrullate, 3.6–5.1 mm long, 0.5–1.1 mm wide, the apices acuminate; margins entire to subfimbriate; abaxial surfaces stramineous with purple apex, glandular, glabrate to tomentose. Corollas purple, 5.2–7.4 mm tall, the lobes acuminate. Anthers 3–3.6 mm long, the apical appendage acuminate to acute, the bases acute to obtuse. Achenes 2.5–4 mm tall, glandular, sericeous, obscurely ribbed, the apex slightly constricted; nectary 0.2–0.5 mm tall. Pappus 3–5-seriate, of coroniform (at maturity; strigose bristles; outermost series 1–2.5 mm long; innermost series 5–7 mm long.

Flowering and fruiting occur from July to October.

Eremanthus argenteus is found only in the Chapada dos Veadeiros of southcentral Goiás (Fig. 3). Although common, it is restricted to the granite outcrops of campo rupestre at high altitudes.

This species resembles *E. cinctus* and *E. auriculatus* which also show glomerulescence reduction to a cyme of glomerules from the compound cyme, which is more typical of sect. *Eremanthus*. *Eremanthus argenteus* is easily separated from both species by its silvery lepidote surfaces and absence of auriculate or retuse leaf bases and apiculate phyllaries. At present, it does not appear to be related to any particular species of *Eremanthus*.

Additional specimens examined. BRAZIL. GOIÁS: Brasília Richtung Campos Belos, 22 km nach Alto Paráiso, 1,500 m, 28 Aug. 1981, *Schumacher 1035* (GA, K, M, MB, RB, W).

Possible hybrids. × *E. uniflorus* MacLeish & Schumacher. GOIÁS: Alto Paráiso, 28 Aug. 1981, *Schumacher 1038, 1039, 1041* (GA).

6. **Eremanthus auriculatus** MacLeish & Schumacher, Syst. Bot. 9: 86. 1984. TYPE: Brazil. Goiás: Brasília Richtung Campos Belos, 22 km nach Alto Paráiso, 1,500 m, 28 Aug. 1981, *Schumacher 1037* (holotype, RB; isotypes, GA, MB).

Shrub to small tree, 0.8–1.5 m tall; stems reddish-brown lanate-tomentose; branches few. Leaves coriaceous, sessile, conspicuously ascending-appressed; blades 5–8 cm long, 2–3 cm wide, trullate to ovate, the bases auriculate, the apices acute, the margins entire; adaxially tomentulose, abaxially gray-brown lanate-tomentose. Peduncle slender, to 20 cm tall, ribbed, reddish-brown lanate-tomentose. Glomerulescence a cyme (rarely compound) of 9–20 glomerules. Glomerules 5–15 mm tall, 15–20 mm diam., subspherical. Heads 30–80 per glomerule, closely appressed basally, coherent ½ length by lanate pubescence of phyllaries. Involucres obconic, 4–5.5 mm tall, 1.5–2.5 mm diam.; phyllaries in 4–5 series; outermost phyllaries narrowly obtrullate, 2.3–4 mm long, 0.4–0.7 mm wide, the apices acute; innermost phyllaries narrowly obtrullate, 4.2–4.6 mm long, 0.5–0.8 mm wide, the apices apiculate; margins entire to subfimbriate; abaxial surfaces stramineous with purple apex, often axially green, tomentulose to lanate. Corollas purple, 5.5–7 mm tall, the lobes acuminate to acute, sparsely glandular. Anthers 3.3–3.6 mm long, the apical appendage acute, the bases acuminate. Achenes 3–3.6 mm tall, glandular, sericeous, obscurely-ribbed, apex slightly constricted; nectary 0.2–0.5 mm tall. Pappus 3–5-seriate, of coroniform (at maturity) strigose bristles; outermost series 1.2–2.2 mm long; innermost series 5.5–7 mm long.

Flowering and fruiting occur from July to September.

Eremanthus auriculatus is known only from the Chapada dos Veadeiros in southcentral Goiás (Fig. 3). It occurs on campo rupestre adjacent to the cerrado characteristic of this region.

This species superficially resembles *E. cinctus*; however, *E. auriculatus* is distinguished by ascending coriaceous leaves with auriculate bases, apiculate phyllaries, and partial coherence of heads. *Eremanthus auriculatus* appears to be related to *E. glomerulatus* and *E. goyazensis* and represents a further reduction in glomerulescence internodes from a compound cyme to form a cyme of glomerules. It is easily separated from the *glomerulatus*-complex by the cyme of glomerules (vs. compound cyme), by auriculate leaf bases (vs. acute to obtuse), and by apiculate phyllaries (vs. acute to acuminate).

Additional specimen examined. BRAZIL. GOIÁS: Alto Paráiso, 4 Jul. 1983, *Schumacher 3045* (GA, MB).

7. **Eremanthus cinctus** Baker in C. Martius, Fl. Bras. 6(2): 162. 1873. TYPE: Brazil. Mato Grosso: "Cuyaba" (now Cuiabá), 1834, *Silva Manso 55* (holotype, BR).

Eremanthus pandurifolius Baker in C. Martius, Fl. Bras. 6(2): 162. 1873. TYPE: Brazil, no other data, *Tamberlik s.n.* (holotype, W; photos of W, F, TEX).

Shrub or small tree, 0.5–4 m tall; stems reddish-brown lanate-tomentose; branches few. Leaves subcoriaceous, sessile; blades 6–19 cm long, 2–6 cm wide, elliptic, narrowly elliptic, or obovate, the bases retuse to acute, the apices acute to obtuse, the margins entire; adaxially glabrate, abaxially tomentulose. Peduncle robust, to 15 cm tall, ribbed, reddish-brown lanate-tomentose; 3–9 bracts with prominently enlarged bases surrounding each glomerule. Glomerulescence a cyme (rarely compound) of 5–30 glomerules. Glomerules 10–25 mm tall, 10–25 mm diam., hemispherical. Heads 20–50 per glomerule, closely appressed, coherent entire length by lanate pubescence of phyllaries. Involucres obconic, 3.5–5 mm tall, 0.7–2 mm diam.; phyllaries in 4–5 subequal series; outermost phyllaries oblanceolate, 3.3–4.3 mm long, 0.5–0.7 mm wide, apices obtuse; innermost phyllaries oblanceolate, 3–4.8 mm long, 0.7–1 mm wide, apices acute; margins entire; abaxial surfaces stramineous with purple apex, glabrate to lanate-tomentose. Corollas white to purple, 6.2–7.2 mm tall, lobes acuminate and glandular. Anthers 4–4.4 mm long, apical appendage acuminate, bases acute. Achenes 2.5–3.5 mm tall, glandular, sericeous between 10 ribs, apex slightly constricted and dark; nectary 0.1–0.2 mm tall. Pappus 3–4-seriate, of stramineous (occasionally rusty on dried specimens), coroniform (at maturity) strigose bristles; outermost series 1.5–2.5 mm long; innermost series 5.5–7.5 mm long.

Flowering and fruiting occur from April to September.

Eremanthus cinctus is known only from three locations: western Minas Gerais, western Goiás, and near Cuiabá in central Mato Grosso (Figs. 2–4). Schumacher was able to locate this species in southwestern Goiás, but reported (pers. comm.) that the Minas Gerais locations cited by Goodland on his 1967 collections have been completely logged for charcoal.

Baker (1873) separated *E. pandurifolius* from *E. cinctus* on the basis of a solitary glomerule versus a cyme of glomerules. This distinction is artifactual—the type specimen of *E. pandurifolius* is fragmented, making the glomerules appear solitary. *Eremanthus pandurifolius* appears to have been collected in western Minas Gerais, because that is the region Tamberlik is known to have explored (Urban, 1906). Likewise, Silva Manso was known to have been practicing medicine in Cuiaba during the year recorded on the label of the type specimen of *E. cinctus*. Although

E. cinctus and *E. pandurifolius* were published simultaneously, *E. cinctus* has been chosen because the type specimen is intact, whereas that of *E. pandurifolius* is badly fragmented. Until recently *E. cinctus* appeared to have a disjunct distribution since there were no collections from intervening mountainous regions, particularly Serra do Verdinho, Serra das Araras, and Serra da São Jeronimo.

Eremanthus cinctus superficially resembles *E. auriculatus* but is distinguished by subcoriaceous leaves with acute to retuse bases, several prominent extraglomerular bracts, and total fusion of heads. By contrast, *E. auriculatus* has coriaceous leaves with prominent auriculate bases, and heads appressed only at the bases. *Eremanthus cinctus,* like *E. auriculatus,* is clearly related to *E. glomerulatus,* and represents a further reduction in glomerulescence internodes from a compound cyme to form a cyme of glomerules.

Additional specimens examined. BRAZIL. MATO GROSSO: known only from the type specimen. MINAS GERAIS: 36 km N of Frutal on BR-14, 9 Aug. 1967, *Goodland 3766* (UB). Prata, 29 Sep. 1967, *Goodland 4001* (MO). GOIÁS: Montividiu towards Amorinopolis, 21 km after Montividiu, 800 m, 28 Apr. 1984, *Schumacher 4004* (GA, MB, UNICAMP).

Eremanthus Less. subg. **Isotrichia** (DC.) MacLeish, comb. nov. *Albertinia* Sprengel sect. *Isotrichia* DC., Prodr. 5: 82. 1836. *Vanillosmopsis* Schultz-Bip. subg. *Isotrichia* (DC.) Schultz-Bip., Jahresber. Pollichia 18–19: 168. 1861. LECTOTYPE, here designated: *E. incanus* (Less.) Less.

Leaves coriaceous. Glomerulescence a compound cyme of 8–50 glomerules. Glomerules subspherical. Heads per glomerule 30–100, cylindric, connate by concrescence of tissues, with phyllaries in 4–6 series. Florets 1 per head. Achenes cylindric, 15–20-ribbed, sericeous. Pappus off-white to purple, subcoroniform, tardily deciduous, subpaleaceous.

8. **Eremanthus incanus** (Less.) Less., Linnaea 6: 682. 1831. *Albertinia incanus* Less., Linnaea 4: 342. 1829. *Cacalia incana* (Less.) Kuntze, Revis. Gen. Pl. 2: 970. 1891. LECTOTYPE, here designated; Brazil, no other data, *Sellow s.n.* (B; isolectotypes, BR, F (fragment from P)).

Slender to robust tree, 2–10 m tall, to 15 cm diam.; stems gray-brown lepidote; branches few. Leaves coriaceous, petiolate; petioles 4–17 mm long, lepidote; blades 5.5–14 cm long, 2–6 cm wide, elliptic to ovate, the bases acute, the apices rounded to obtuse, the margins entire; adaxially glabrate, abaxially gray lepidote. Peduncle slender, to 27 cm tall, terete, gray lepidote. Glomerulescence a compound cyme of 8–50 glomerules. Glomerules 5–15 mm tall, 7–15 mm diam., spherical. Heads 30–100 per glomerule, closely appressed, connate nearly entire length by concrescence of phyllary tissues. Involucres cylindric, 2.4–5 mm tall, 0.3–1.5 mm diam.; phyllaries in 4–5 series; outermost phyllaries triangular, 1.7–3 mm long, 0.1–0.5 mm wide, the apices acute to obtuse; innermost phyllaries narrowly obtrullate, 2.6–4 mm long, 0.3–0.6 mm wide, the apices acuminate, the margins entire; abaxial surfaces stramineous with purple apex, glabrate to lepidote-tomentulose. Corollas pale purple to white, 4.2–6.6 mm tall, the lobes acuminate. Anthers 2.2–2.7 mm long, the apical appendage acuminate, the bases acute. Achenes cylindric, 2.2–2.6 mm tall, glandular, sparsely sericeous, 15–20-ribbed, the apex slightly constricted; nectary 0.15–0.25 mm tall. Pappus 3–4-seriate, off-white to purple, subcoroniform (at maturity), tardily deciduous, subpaleaceous, strigose bristles; outermost series 1–1.5 mm long; innermost series 5–5.8 mm long.

Flowering and fruiting occur from July to October.

Eremanthus incanus is distributed throughout the southern section and northeastern arm (Figs. 5, 6) of the Central Plateau of Brazil at elevations of 800 to 1,850 meters in cerrado, secondary forest, or caatinga. It is particularly common in Minas Gerais where it is called "pão candeia" (candlestick) or "candeia da serra" (mountain candle), names normally attributed to subg. *Vanillosmopsis.*

Eremanthus incanus is transitional between subg. *Eremanthus* and subg. *Vanillosmopsis.* It approaches *E. glomerulatus* in its coriaceous leaves, fewer than 100 heads per glomerule, single floret per head, large sericeous achenes, and subpaleaceous pappus. In contrast, in its lepidote tomentum, relatively small glomerules, phyllary tissue fusion, cylindrical achenes, and off-white to purple, tardily deciduous pappus it approaches *E. erythropappus* of the *Vanillosmopsis* complex.

Lessing's specimens were deposited at Charkow. Because Lessing's original material was unavailable, a Sellow collection from B herbarium that bears appropriate annotations by Lessing

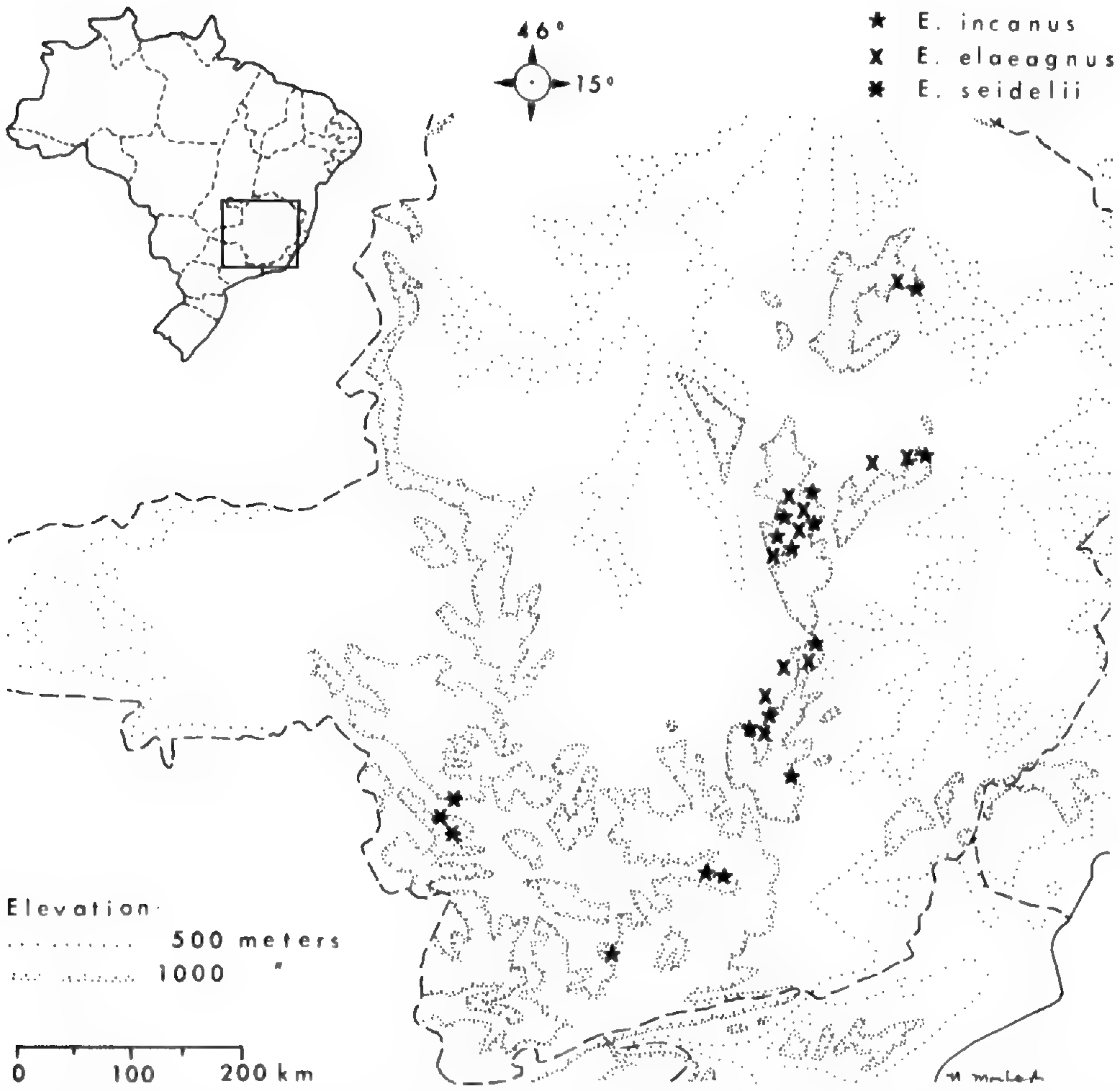

FIGURE 5. Distribution of *Eremanthus* subg. *Isotrichia* and subg. *Pseuderemanthus* in Minas Gerais.

was chosen as the lectotype. Historically, the name *Albertinia bicolor* (now *Paralychnophora bicolor*) has been confused often with *E. incanus* due to the prominent spherical glomerules in both taxa. *Paralychnophora bicolor* is characterized by solitary, relatively large, axillary glomerules, 2–4 or 8–12 florets per head, and angled, glabrous achenes with a biseriate pappus.

Additional specimens examined. BRAZIL. BAHIA: Mun. de Rio das Contas, Pico das Almas at 18 km NW de Rio das Contas, 1,600–1,850 m, 24 Jul. 1979, *King et al. 8136* (CEPEC, MO, US). MINAS GERAIS: between Parãopeba and Diamantina, 3 Oct. 1980, *MacLeish et al. 687* (C, G, GA, GH, NY, RB, UB, UC, US), between Mendanha and Diamantina, 4 Oct. 1980, *MacLeish et al. 703* (BR, CEPEC, F, GA, M, MO, RB, TEX).

Possible hybrids. × *E. elaeagnus* (C. Martius ex DC.) Schultz-Bip. MINAS GERAIS: between Parãopeba and Diamantina, 3 Oct. 1980, *MacLeish et al. 688* (F, G, GA, GH, MO, NY, RB, US). × *E. erythropappus* (DC.) MacLeish. MINAS GERAIS: Tiradente, 10 Sep. 1936, *Barreto 4792* (F). × *E. polycephalus* (DC.) MacLeish. MINAS GERAIS: Itamarandiba, 6 Sep. 1981, *Schumacher 1116a* (GA, MB).

Eremanthus Less. subg. **Pseuderemanthus** Schultz-Bip., Jahresber. Pollichia 20–21: 395. 1863. *Eremanthus* Less. subg. *Pseuderemanthus* Schultz-Bip. "A. *Elaeagnus*" Schultz-Bip., Jahresber. Pollichia 20–21: 395. 1863. LECTOTYPE: here designated; *Eremanthus elaeagnus* (C. Martius ex DC.) Schultz-Bip.

Leaves coriaceous. Glomerulescence a compound cyme of 10–60 hemispheric glomerules. Heads 1–20 per glomerule, cylindric, slightly appressed, free, with phyllaries in 4–6 series. Florets 3–4 per head. Achenes cylindric, 10-ribbed, sericeous. Pappus stramineous or purple, coroniform, persistent, subpaleaceous.

9. **Eremanthus seidelii** MacLeish & Schumacher, Syst. Bot. 9: 89. 1984. TYPE: Brazil. Minas Gerais: Furnas in Richtung Piuí, kurz von Staumauer, 800 m, 25 Aug. 1981, *Schumacher 1006* (holotype, RB; isotypes, 2 in GA, K, M, MB).

Tree, to 4 m tall; stems gray lepidote-tomentulose; branches many. Leaves coriaceous, sessile to petiolate; petioles to 10 mm long, densely lepidote-tomentose; blades 4–9 cm long, 1.2–3 cm wide, elliptic, the bases acute, the apices acu-

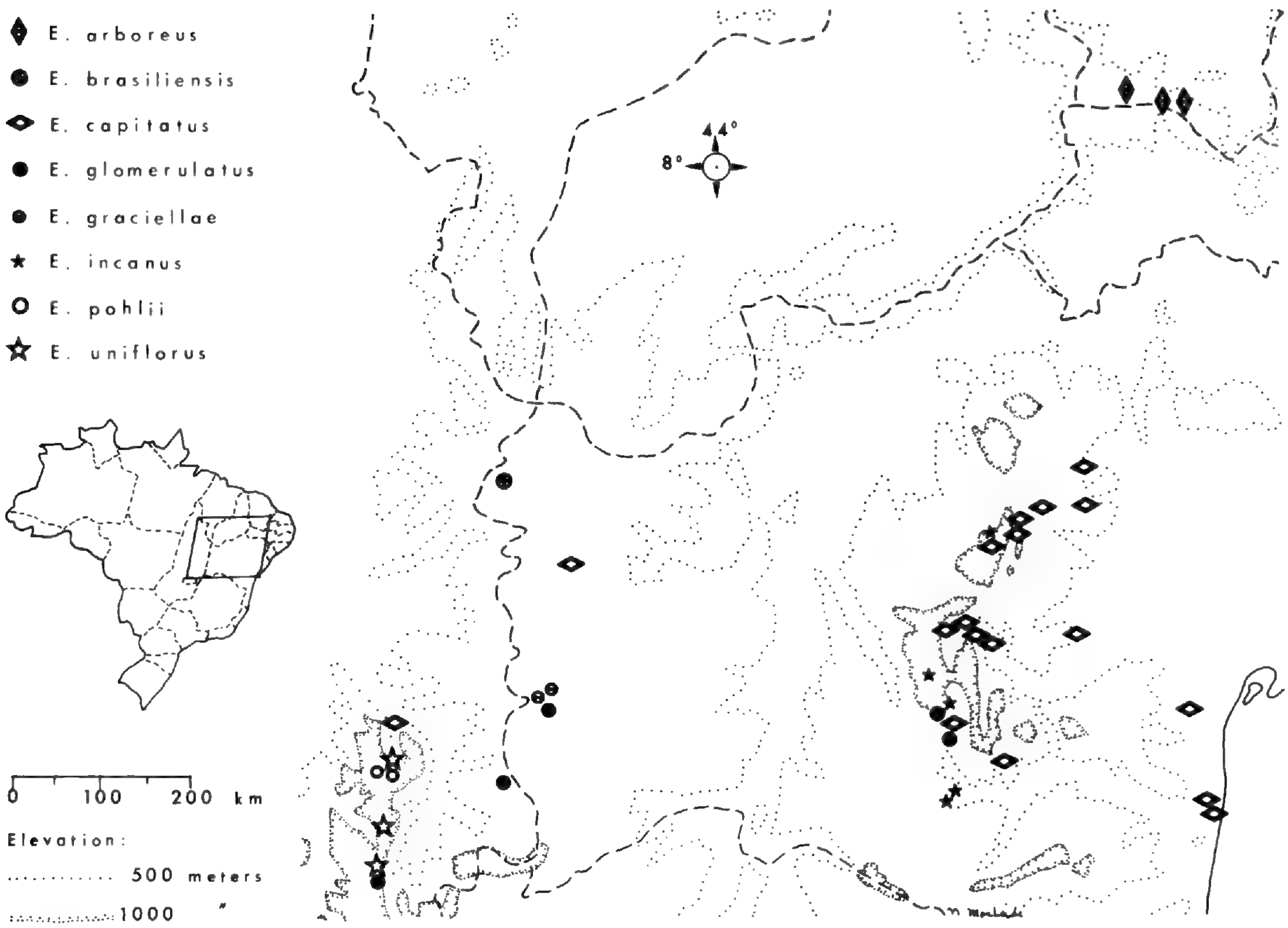

FIGURE 6. Distribution of *Eremanthus* subg. *Vanillosmopsis, E. glomerulatus,* and *E. incanus* in Bahia and Goiás.

minate to acute, the margins entire; adaxially sparsely lepidote, abaxially densely gray lepidote-tomentose. Peduncle slender, to 15 cm tall, terete, gray lepidote-tomentulose. Glomerulescence a compound cyme of 10–60 glomerules. Glomerules 5–10 mm tall, 6–15 mm diam., hemispherical. Heads 1–7 per glomerule, closely appressed basally, free. Involucres cylindric, 5.5–7.2 mm tall, 2.5–4 mm diam.; phyllaries in 4–6 series; outermost phyllaries trullate, 1.3–4 mm long, 1–1.5 mm wide, the apices acute; innermost phyllaries narrowly rhombic to obtrullate, 4.7–7 mm long, 0.5–1.2 mm wide, the apices acute; margins entire to subfimbriate; abaxial surfaces stramineous with purple apex, lepidote-tomentulose. Florets 3 per head; corollas purple to white, 5.4–6.5 mm tall, the lobes acuminate. Anthers 2.5–3 mm long, the apical appendage acuminate, the bases acuminate. Achenes 2.2–3.1 mm tall, glandular, sparsely sericeous between 10 ribs, apex slightly constricted; nectary 0.1–0.2 mm tall. Pappus 3–4-seriate, of stramineous, subcoroniform (at maturity) strigose bristles; outermost series 0.8–1.2 mm long; innermost series 4.5–6.2 mm long.

Flowering and fruiting occur from June to August.

Eremanthus seidelii is restricted to the cerrado surrounding the Furnas reservoir in southwestern Minas Gerais (Fig. 5). This species is closely related to *E. elaeagnus,* which is restricted to the Serra da Espinhaço of northeastern Minas Gerais. However, *E. seidelii* is distinguished from *E. elaeagnus* by having fewer heads per glomerule (1–7 vs. 9–20), straw vs. mostly purple pappus color, elliptic vs. narrowly elliptic leaves, and flowering June–July vs. August–September.

Eremanthus seidelii and *E. elaeagnus* are transitional between subg. *Eremanthus* and subg. *Vanillosmopsis.* They approach *E. glomerulatus* in their coriaceous leaves, only 10–60 glomerules per glomerulescence, large sericeous achenes, and persistent subpaleaceous pappus. In contrast, in their lepidote tomentum, 1–20 heads per glomerule, relative lack of head fusion, 3–4 florets per head, and occasionally purple pappus they approach many members of subg. *Vanillosmopsis.*

Additional specimens examined. BRAZIL. MINAS GERAIS: vor Alpinopolis, 12 Jun. 1977, *Seidel s.n.* (RB); bei Capitolio, 800 m, 25 Aug. 1981, *Schumacher 1009* (GA, MB); Furnas in Richtung Capitolio, 18 Oct. 1980, *Schumacher s.n.* (GA, MB).

Possible hybrids. × *E. erythropappus* (DC.) MacLeish. MINAS GERAIS: Furnas towards Piuí, 25 Aug. 1981, *Schumacher 1005* (GA); Alpinopolis, 12 Sep. 1077, *Seidel s.n.* (RB). × *E. glomerulatus* Less. MINAS GERAIS: between Furnas and Piuí, 25 Aug. 1981, *Schumacher 1008* (GA). × *E. mattogrossensis* Kuntze. MINAS GERAIS: Furnas towards Piuí, 25 Aug. 1981, *Schumacher 1003, 1004* (GA).

10. **Eremanthus elaeagnus** (C. Martius ex DC.) Schultz-Bip., Jahresber. Pollichia 20–21: 395. 1863. *Albertinia elaeagnus* C. Martius ex DC., Prodr. 5: 81. 1836. *Vernonia elaeagnus* (C. Martius ex DC.) Schultz-Bip., Jahresber. Pollichia 18–19: 166. 1861. TYPE: Brazil, Minas Gerais, altis lapidosis Serro Frio prope Tejuco (now Diamantina), *Martius s.n.* (holotype, M).

Small tree or shrub, 2–5 m tall; stems gray lepidote-tomentulose; branches many. Leaves coriaceous, sessile to petiolate; petioles to 10 mm long, densely lepidote-tomentose; blades 5–12 cm long, 1.5–3 cm wide, narrowly elliptic, the bases acute to acuminate, the apices acute to rounded, the margins entire; adaxially sparsely lepidote, abaxially densely gray lepidote-tomentose. Peduncle slender, to 14 cm tall, terete, gray lepidote-tomentulose. Glomerulescence a compound cyme of 10–60 glomerules, these 5–10 mm tall, 10–15 mm diam., hemispherical. Heads 9–20 per glomerule, closely appressed basally, free. Involucres cylindric, 5–10 mm tall, 2.5–4 mm diam.; phyllaries in 4–5 series; outermost phyllaries trullate, 1.5–3 mm long, 0.6–1.2 mm wide, the apices acute; innermost phyllaries narrowly rhombic to obtrullate, 3.5–6.5 mm long, 0.7–1.5 mm wide, the apices acute; margins entire to subfimbriate; abaxial surfaces stramineous with purple apex, lepidote-tomentulose. Florets 3–4 per head; corollas purple to white, 5.5–7 mm tall, the lobes acuminate. Anthers 2.5–3 mm long, the apical appendage acute to acuminate, the bases acuminate. Achenes 2.5–3.5 mm tall, glandular, sparsely sericeous between 10 ribs, the apex slightly constricted; nectary 0.1–0.15 mm tall. Pappus 3–4-seriate, of purple (rarely stramineous), subcoroniform (at maturity), strigose bristles; outermost series 1–1.5 mm long; innermost series 6–6.5 mm long.

Flowering and fruiting occur from August to September.

Eremanthus elaeagnus is restricted to the Serra do Espinhaço in northeastern Minas Gerais at elevations of 900 to 1,370 meters (Fig. 5). It is locally common and dominant along with members of *Lychnophora* in campo rupestre. Because of the gray tomentum covering most of this plant's surface and its general resemblance to members of the *Vanillosmopsis* complex, it is locally known as "candeia branca," or white candle. This taxon is closely related to *E. seidelii* and, as noted under that species, both represent intermediates between subgenera *Eremanthus* and *Vanillosmopsis.*

Additional specimens examined. BRAZIL. MINAS GERAIS: between Parãopeba and Diamantina, 3 Oct. 1980, *MacLeish et al. 689* (F, GA, GH, MO, NY, RB); Diamantina, Barão, about 1 km along railroad, 1,170 m, 20 May 1931, *Mexia 5887* (BM, F, G, GH, MO, NY, S, TEX).

Possible hybrids. × *E. glomerulatus* Less. MINAS GERAIS: Serra do Cipó, 7 Oct. 1980, *MacLeish et al. 715* (BR, F, GA, GH, K, M, MO, NY, RB, S, US), *MacLeish et al. 716* (GA, RB), 30 Jan. 1980, *King & Almeda 8354* (US). × *E. incanus* (Less.) Less. MINAS GERAIS: between Parãopeba and Diamantina, 3 Oct. 1980, *MacLeish et al. 688* (F, G, GA, GH, MO, NY, RB, US). × *E. polycephalus* (DC.) MacLeish. MINAS GERAIS: Serra do Cipó. 7 Oct. 1980, *MacLeish et al. 718* (GA).

Eremanthus Less. subg. **Vanillosmopsis** (Schultz-Bip.) MacLeish, comb. nov. *Vanillosmopsis* Schultz-Bip., Jahresber. Pollichia 18–19: 166. 1861. *Vanillosmopsis* subg. *Euvanillosmopsis* Schultz-Bip., Jahresber. Pollichia 20–21: 398. 1863. TYPE: *Vanillosmopsis glomerata* Schultz-Bip. = *Eremanthus erythropappus* (DC.) MacLeish.

Leaves membranaceous to subcoriaceous. Glomerulescence a compound cyme of 100 or more hemispheric glomerules. Heads per glomerule 1–12, cylindric or obconic, solitary or slightly to closely coherent by interwoven pubescence of phyllaries or connate by tissue concrescence, phyllaries in 5–7 series. Florets per head 1–4. Achenes cylindric (rarely cylindric-turbinate), 10-ribbed, glabrate. Pappus purple or white (rarely stramineous), not coroniform, promptly (rarely tardily) deciduous, filiform.

Eremanthus Less. sect. **Nectaridium** (Schultz-Bip.) MacLeish, comb. nov. *Vanillosmopsis* Schultz-Bip. subg. *Nectaridium* Schultz-Bip., Jahresber. Pollichia 20–21: 400. 1863. TYPE: *Vanillosmopsis brasiliensis* (Gardner) Schultz-Bip. = *Eremanthus brasiliensis* (Gardner) MacLeish.

Heads cylindric, solitary or in pairs slightly appressed basally. Pappus never twisted.

11. **Eremanthus pohlii** (Baker in C. Martius) MacLeish, comb. nov. *Vanillosmopsis pohlii* Baker in C. Martius, Fl. Bras. 6(2): 18. 1873. TYPE: Brazil: foz do Viera, *Pohl 556* (holotype, K, not seen; isotypes, 2 in F (one a photo of B), 2 in GH (one a photo of B), NY).

Small tree, to 3 m tall; stems gray-brown lepidote; branches many. Leaves subcoriaceous, petiolate; petioles 7–10 mm long, lepidote; blades 6.4–7.6 cm long, 1.8–2.4 cm wide, lanceolate, the bases attenuate, the apices obtuse, the margins entire; adaxially glabrate, abaxially gray lepidote. Peduncle slender, to 25 cm tall, terete, gray lepidote. Glomerulescence a compound cyme of numerous (>100) glomerules. Glomerules 6–9 mm tall, 5–12 mm diam., hemispherical. Heads 1–2 per glomerule, slightly appressed, free. Involucres cylindric, 5–7.5 mm tall, 2–3.5 mm diam. with prominent truncate base; phyllaries in 6–7 series; outermost phyllaries widely deltate, 0.5–1.2 mm long, 0.5–1.0 mm wide, the apices obtuse; innermost phyllaries lanceolate, 4–6.2 mm long, 0.6–2 mm wide, the apices acute to acuminate; margins entire to subfimbriate; abaxial surfaces stramineous with purple apex, glabrate to lepidote-tomentulose. Florets 3 per head; corollas purple, 5–6 mm tall, the lobes acuminate. Anthers 2–3 mm long, the apical appendage acuminate, the bases acute to rounded. Achenes 2.5–4 mm tall, sparsely glandular, rarely pilose, 10-ribbed, the apex slightly constricted and dark; nectary 0.2–0.5 mm tall. Pappus 3–4-seriate, of stramineous (rarely purple), tardily deciduous, strigose bristles; outermost series 1–2 mm long; innermost series 5.5–7.5 mm long.

Flowering and fruiting occur from July to September.

Eremanthus pohlii is restricted to the Chapada dos Veadeiros, which runs north to south in south central Goiás, and nearby parts of Minas Gerais (Figs. 6, 7). It occurs in colonies on the cerrado at high elevations (ca. 1,400 m).

Eremanthus pohlii is one of the more primitive (i.e., approaching *Vernonia*) members of the subg. *Vanillosmopsis*. It is closely related to *E. graciellae* and *E. brasiliensis*, both of which are restricted to the northwestern arm of the Central Plateau. *Eremanthus pohlii* can be separated from *E. graciellae* and *E. brasiliensis* by its three florets per head and relatively long leaves (6.5–7.5 vs. 2.5–6.5 cm long). The only other member of the *Vanillosmopsis* complex that occurs sympatrically with these taxa is *E. uniflorus*. *Eremanthus uniflorus* is most closely related to *E. capitatus* and is distinguished (among other less discriminating characters) by a single floret per head and 3–9 heads per glomerule.

Additional specimens examined. BRAZIL. GOIÁS: Brasília towards Campos Belos, 15 km from Alto Paráiso, 1,400 m, 28 Aug. 1981, *Schumacher 1032, 1033* (GA, MB), *Schumacher 1034* (MB, NY). MINAS GERAIS: João Pinheiro, 15 Aug. 1967, *Heringer 11531* (NY, RB).

12. **Eremanthus graciellae** MacLeish & Schumacher, Syst. Bot. 9: 87. 1984. TYPE: Brazil. Bahia: BR 020 Brasília Richtung Barreiras, 15 km weiter in Richtung Barreiras von Fazenda Prainha, km 374, 800 m, 28 Aug. 1981, *Schumacher 1048* (holotype, RB; isotypes, GA, K, M, MB).

Small tree, to 2.5 m tall; stems gray-brown lepidote; branches many. Leaves subcoriaceous, petiolate; petioles 8–15 mm long, lepidote; blades 4.5–6.5 cm long, 1.5–3 cm wide, elliptic to narrowly elliptic, the bases acute, the apices acute to obtuse, the margins entire; adaxially glabrate, abaxially gray lepidote. Peduncle slender, to 25 cm tall, terete, gray lepidote. Glomerulescence a compound cyme of numerous (more than a hundred) glomerules. Glomerules 6–9 mm tall, 4–9 mm diam., obconic. Heads 1–2 per glomerule, slightly appressed, free. Involucres cylindric, 5.2–7.5 mm tall, 2.1–2.8 mm diam., with prominent truncate base; phyllaries in 6–7 series; outermost phyllaries widely deltate, 0.6–1.2 mm long, 0.7–1.2 mm wide, the apices acute; innermost phyllaries lanceolate, 3.8–6.1 mm long, 0.6–1.4 mm wide, the apices acute to acuminate; margins entire to subfimbriate; abaxial surfaces stramineous with purple apex, glabrate to lepidote-tomentulose. Florets 2 per head; corollas purple to white, 4.2–7 mm tall, the lobes acu-

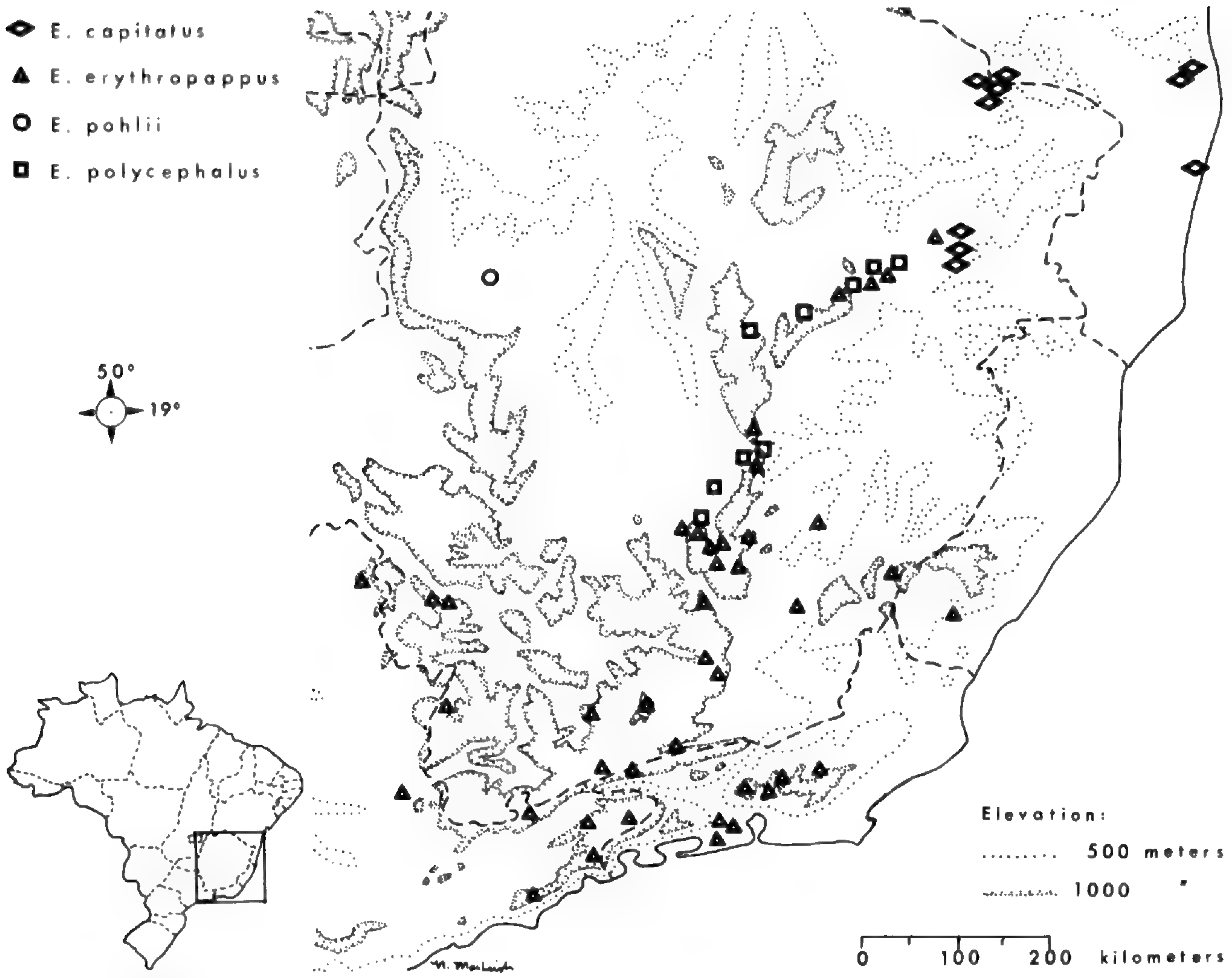

FIGURE 7. Distribution of *Eremanthus* subg. *Vanillosmopsis* in Minas Gerais.

minate. Anthers 2.1–2.8 mm long, the apical appendage acuminate, the bases acuminate. Achenes 2.2–3.5 mm tall, sparsely glandular, 10-ribbed, the apex slightly constricted and dark; nectary 0.2–0.5 mm tall. Pappus 3–5-seriate, of stramineous to white, deciduous, strigose bristles; outermost series 1–2 mm long; innermost series 5–7.2 mm long.

Flowering and fruiting occur from July to August.

Eremanthus graciellae is distributed along the Serra Geral de Goiás, which runs north to south along the border of Goiás and Bahia (Fig. 6). It occurs in colonies on the quartzite grasslands characteristic of this plateau.

Eremanthus graciellae is also one of the primitive (approaching *Vernonia*) members of *Eremanthus*. It can be separated from close relatives, *E. graciellae* and *E. brasiliensis*, by its two florets per head and intermediate length leaves.

Additional specimens examined. BRAZIL. BAHIA: BR 020 Brasília Richtung Barreiras, 15 km weiter in Richtung Barreiras von Fazenda Prainha, 800 m, 28 Aug. 1981, *Schumacher 1046* (GH, MB), *Schumacher 1047* (GA, MB).

13. **Eremanthus brasiliensis** (Gardner) MacLeish, comb. nov. *Monosis brasiliensis* Gardner, London J. Bot. 5: 230. 1846. *Vernonia brasiliensis* (Gardner) Schultz-Bip., Jahresber. Pollichia 18–19: 161. 1861, nom. illeg. (nom. rej. pro *Vernonia brasiliensis* (Sprengel) Less., Linnaea 6: 681–682. 1831. = *Albertinia brasiliensis*). *Vanillosmopsis brasiliensis* (Gardner) Schultz-Bip., Jahresber. Pollichia 20–21: 400. 1863. TYPE: Brazil, "Pernambuco" (now Bahia): woods in the district of the Rio Preto, Sep. 1834, *Gardner 2897* (holotype, BM; isotypes, 5 in F (fragments from G and P, photos of G and W), G, GH).

Small tree, to 4 m tall; stems gray-brown lepidote; branches many. Leaves subcoriaceous, petiolate; petioles 5–10 mm long, lepidote; blades 2.4–4.2 cm long, 0.8–2.6 cm wide, elliptic to narrowly elliptic, the bases acute to attenuate, the apices obtuse, the margins entire; adaxially glabrate and glandular, abaxially gray lepidote. Peduncle slender, terete, gray lepidote. Glomerulescence a compound cyme of 100 or more glomerules. Glomerules 6–8 mm tall, 4–8 mm diam., obconic. Heads 1–2 per glomerule, slightly appressed, free. Involucres cylindric, 5–6.5 mm tall, 2–2.5 mm diam.; phyllaries in 6–7 series; outermost phyllaries widely deltate, 0.6–1 mm long, 0.5–1 mm wide, the apices acute; innermost phyllaries lanceolate, 3.5–6 mm long, 0.5–1 mm wide, the apices acute to acuminate; margins entire to subfimbriate; abaxial surfaces stramineous, glabrate to lepidote-tomentulose. Florets 1 per head; corollas not seen. Achenes 2–3.5 mm tall, sparsely glandular, obscurely-ribbed, the apex slightly constricted and dark; nectary 0.3–0.4 mm tall. Pappus 3–4-seriate, of stramineous, tardily deciduous, strigose bristles; outermost series 1–2 mm long; innermost series 5–7 mm long.

Flowering and fruiting probably occur from August to September.

Eremanthus brasiliensis is distributed in the northern part of the Serra Geral de Goiás (Fig. 6), which runs north to south along the border of Goiás and Bahia. This species is known only from the type specimens. Schumacher (1982) unsuccessfully attempted to locate it at the same time that he rediscovered *E. arboreus* in southern Ceará.

Like *E. graciellae* and *E. pohlii, E. brasiliensis* is one of the more primitive members of the *Vanillosmopsis* complex. It is distinguished by one floret per head, small leaves (2.5–4.5 vs. 4.5–7.5 cm long), and heads which lack the prominent truncate bases of its closest relatives.

Eremanthus Less. sect. *Vanillosmopsis* (Schultz-Bip.) MacLeish, comb. nov. *Vanillosmopsis* subg. *Euvanillosmopsis* Schultz-Bip., Jahresber. Pollichia 20–21: 398. 1863. LECTOTYPE: *Eremanthus erythropappus* (DC.) MacLeish.

Heads cylindric or obconic. Heads per glomerule (2–)5–12. Pappus often twisted.

14. **Eremanthus polycephalus** (DC.) MacLeish, comb. nov. *Albertinia polycephala* DC., Prodr. 5: 82. 1836. *Vanillosmopsis polycephala* (DC.) Schultz-Bip., Jahresber. Pollichia 18–19: 168. 1861. TYPE: Brazil. Minas Gerais: planitie alta ad Piedade Villam, *Martius s.n.* (holotype, M; isotype, M).

Albertinia saligna C. Martius ex DC., Prodr. 5: 82. 1836. *Vanillosmopsis saligna* (DC.) Schultz-Bip., Jahresber. Pollichia 18–19: 168. 1861. TYPE: Brazil. Minas Gerais: in editis siccis rupestribus montium Serro Frio, *Martius s.n.* (holotype, M).

Shrub or small tree, to 3.5 m tall; stems gray-brown lepidote; branches many. Leaves membranaceous to subcoriaceous, sessile to petiolate; petioles to 8 mm long, lepidote; blades 4.5–7 cm long, 1–1.8 cm wide, lanceolate, the bases acuminate to attenuate, the apices acute to obtuse, the margins entire; adaxially glabrate, abaxially gray lepidote. Peduncle slender, to 23 cm tall, terete, gray lepidote. Glomerulescence a compound cyme of 100 or more glomerules, these 5–7 mm tall, 4–8 mm diam., hemispherical. Heads 6–12 per glomerule, closely appressed, connate ½ length by concrescence of phyllary tissues. Involucres cylindric, 4–5.5 mm tall, 0.5–2 mm diam.; phyllaries in 6–7 series; outermost phyllaries widely deltate, 0.6–1.2 mm long, 0.7–1.2 mm wide, the apices obtuse; innermost phyllaries lanceolate, 3–5 mm long, 0.5–1.2 mm wide, the apices acute to acuminate, the margins entire to subfimbriate; abaxial surfaces stramineous with purple apex, lepidote-tomentose. Florets 1 per head; corollas purple, 4–6.5 mm tall, the lobes acuminate to acute. Anthers 2–2.5 mm long, the apical appendage acuminate, the bases acute. Achenes 1.5–2.8 mm tall, glandular, 10-ribbed, the apex slightly constricted and dark; nectary 0.2–0.4 mm tall. Pappus 3–4-seriate, of stramineous, white or purple, tardily deciduous, strigose bristles; outermost series 0.2–1 mm long, the innermost series 3–5.5 mm long.

Flowering and fruiting occur from June to November.

Eremanthus polycephalus is distributed along the Serra do Espinhaço, which runs north to south through the center of Minas Gerais (Fig. 7). It occurs in colonies on the campo rupestre habitats characteristic of high elevations (700–1,370 meters). The common name of "candeia," or candle, is applied locally.

Eremanthus polycephalus is most closely related to *E. erythropappus* and is sympatric with it in the northernmost portion of its range. Uniquely, in subg. *Vanillosmopsis,* both of these taxa exhibit concrescence of phyllary and receptacle tissues. However, *E. polycephalus* is easily distinguished by its single floret per head (vs. 3–4) and partial fusion of heads (vs. nearly total fusion). This species, because of its single floret per head and various characteristics associated with the *Vanillosmopsis* complex, superficially resembles *E. uniflorus* and *E. brasiliensis,* taxa that are restricted to Goiás and nearby Bahia and which are distinguished by their lack of tissue fusion within glomerules.

Additional specimens examined. BRAZIL. MINAS GERAIS: 14 km NE of Diamantina towards Mendanha on Estrada 367, 1,370 m, 4 Oct. 1980, *MacLeish et al. 702* (GA, GH, K, LE, NY, RB, UB, US).

Possible hybrids. × *E. elaeagnus* (C. Martius ex DC.) Schultz-Bip. MINAS GERAIS: Serra do Cipó, 7 Oct. 1980, *MacLeish et al. 718* (GA). × *E. incanus* (Less.) Less. MINAS GERAIS: Itamarandiba, 6 Sep. 1981, *Schumacher 1116a* (GA).

15. **Eremanthus erythropappus** (DC.) MacLeish, comb. nov. *Albertinia erythropappa* DC., Prodr. 5: 82. 1836. *Vanillosmopsis erythropappa* (DC.) Schultz-Bip., Jahresber. Pollichia 18–19: 167. 1861. TYPE: Brazil. Minas Gerais: Marianne, *Vauthier 334* (holotype, G-DC (as IDC microfiche); isotypes, G, 2 in GH).

Albertinia candolleana Gardner, London J. Bot. 5: 235. 1846. TYPE: Brazil. Minas Gerais: near Villa do Principe, Aug. 1840, *Gardner 4812* (holotype, BM; isotypes, F, 2 in G, 2 in GH, 3 in NY, S).

Vanillosmopsis glomerata Schultz-Bip., Jahresber. Pollichia 18–19: 167. 1861. *Vernonia glomerata* Schultz-Bip., Bot. Zeitung. (Berlin) 3: 155. 1845. nom. nud. LECTOTYPE: here designated from among syntypes; Brazil. Minas Gerais: Aug.–Apr. 1840, *Claussen 2063* (G; isolectotypes, G, 2 in GH, M, MO). Syntypes: Brazil. (Rio de Janeiro): in collibus siccis calidisque inter Mandioca et Serra Estrella, *Riedel s.n.* (*577*) (not found); no other data, *Claussen 863* (*853*) (not found); no other data, *Schucht 75* (W, not found).

Shrub or tree, to 10 m tall, to 10 cm diam.; stems gray-brown lepidote; branches many. Leaves membranaceous, petiolate; petioles 3–15 mm long, lepidote; blades 5–10.2 cm long, 1.6–3.6 cm wide, oblanceolate to elliptic, the bases acute to acuminate, the apices acute to attenuate, the margins entire; adaxially glabrate to lepidote, abaxially gray lepidote. Peduncle slender, to 23 cm tall, terete, gray lepidote. Glomerulescence a compound cyme of 100 or more glomerules. Glomerules 6–15 mm tall, 4–12 mm diam., hemispherical. Heads 6–12 per glomerule, closely appressed, connate nearly entire length by concrescence of phyllary tissues and pubescence. Involucres obconic, 5–7.2 mm tall, 2.1–4.2 mm diam.; phyllaries in 5–6 series; outermost phyllaries widely deltate, 0.6–1.5 mm long, 0.7–1.3 mm wide, the apices acute; innermost phyllaries lanceolate, 3.6–6.8 mm long, 0.5–1.2 mm wide, the apices acute to acuminate; margins entire to subfimbriate; abaxial surfaces stramineous with purple apex, lepidote-tomentulose (rarely glabrate). Florets 3(–4) per head; corollas purple to white with age, 4–6.5 mm tall, the lobes acuminate. Anthers 2.1–2.7 mm long, the apical appendage acuminate, the bases acute. Achenes cylindric-turbinate, 1.2–2.5 mm tall, glandular, 10-ribbed, the apex slightly constricted and dark; nectary 0.15–0.25 mm tall. Pappus 3–4-seriate, of stramineous, white or purple, often curling, promptly deciduous, strigose bristles; outermost series 1.2–3 mm long; innermost series 3–6.5 mm long.

Flowering and fruiting occur from June to November.

Eremanthus erythropappus is distributed throughout southeastern portions of the Central Plateau (Fig. 7) at 700 to 2,400 meters. It is extremely common in colonies amidst secondary forest of the coastal range and cerrado of the interior plateau. It is often used as a living fence around fields because the high terpenoid content of its leaves deters insects. Also, it is commonly known as "candeia," candle, or "pau de candeia," candlestick.

Because of its extensive range, *E. erythropappus* is one of the most commonly collected members of *Eremanthus.* Along with *E. polycephalus* and *E. incanus,* it exhibits a distinctive concrescence of phyllary and receptacle tissues. *Eremanthus erythropappus* is further distinguished by its 3–4 florets per head (vs. 1), 6–12 heads per glomerule (vs. 30–100 in *E. incanus*), and nearly total connation of heads (vs. partial connation in *E. polycephalus*). The epithets assigned by Gardner (1846) and Schultz-Bip. (1861) to this species are indicative of the variation ascribable to age and habitat differences.

Additional specimens examined. BRAZIL. ESPÍRITO SANTO: Mun. de Cachoeus do Itapemirim, Vargem Alta Morro do Sal, 700 m, 3 Aug. 1980, *Ferreira & Borges 1882* (GA), 21 Aug. 1948, *Brade 19340* (RB). MINAS GERAIS: Serra do Curral, Nova Lima, 1,300 m, 6 Aug. 1945, *Williams & Assis 8029* (BM, BR, C, F, G, GH, MO, NY, RB, S, TEX). RIO DE JANEIRO: Teresopolis, Serra das Orgãos, 24 Sep. 1980, *MacLeish et al. 670* (C, GA, GH, LE, MO, NY, RB, TEX, UB, W). SÃO PAULO: Serra da Bocaina, 25 km from São José do Barreiro towards Park of Bocaina, 1,640 m, 30 Sep. 1980, *MacLeish et al. 679* (B, BM, CEPEC, GA, RB, S, TEX, W).

Possible hybrids. × *E. capitatus* (Sprengel) MacLeish. MINAS GERAIS: Carai, 6 Sep. 1981, *Schumacher 1083, 1085, 1089* (GA). × *E. incanus* (Less.) Less. MINAS GERAIS: Tiradente, 10 Sep. 1936, *Barreto 4792* (F). × *E. seidelii* MacLeish & Schumacher. MINAS GERAIS: Furnas towards Piuí, 25 Aug. 1981, *Schumacher 1005* (GA), Alpinopolis, 12 Sep. 1977, *Seidel s.n.* (RB).

16. **Eremanthus uniflorus** MacLeish & Schumacher, Syst. Bot. 9: 93. 1984. TYPE: Brazil. Goiás: 33 km N of Alto Paráiso towards Cavalcante, 1,370 m, 14 Oct. 1980, *MacLeish, Martinelli, Smith & Stutts 736* (holotype, RB; isotypes, F, G, GA, K, M, NY, P, S, UB, US).

Shrubby tree, to 2.5 m tall; stems gray-brown lepidote; branches many. Leaves membranaceous to subcoriaceous, petiolate; petioles 5–20 mm long, lepidote; blades 3.8–8 cm long, 1.2–4 cm wide, elliptic, the bases acute, the apices acute, the margins entire; adaxially glabrate, abaxially gray lepidote. Peduncle slender, to 25 cm tall, terete, gray lepidote. Glomerulescence a compound cyme of 100 or more glomerules, these 3–7 mm tall, 3–10 mm diam., hemispherical. Heads 3–9 per glomerule, slightly appressed and adherent basally by pubescence of phyllaries. Involucres cylindric, 4–7 mm tall, 1–2 mm diam.; phyllaries in 5–7 series; outermost phyllaries trullate, 0.7–2 mm long, 0.4–1 mm wide, the apices acute; innermost phyllaries lanceolate, 3.5–5.5 mm long, 0.5–0.9 mm wide, the apices acuminate; margins entire to subfimbriate; abaxial surfaces stramineous with purple apex and midvein, glabrate to lepidote-tomentulose. Florets 1 per head; corollas purple (to white with age), 5–7 mm tall, the lobes acuminate. Anthers 2.7–3.8 mm long, the apical appendage acuminate, the bases acuminate. Achenes 2.4–3.2 mm tall, glandular, 10-ribbed, the apex slightly constricted and dark, occasionally pilose at base; nectary 0.05–0.1 mm tall. Pappus 3–5-seriate, of purple to stramineous, deciduous, strigose bristles; outermost series 0.8–1.8 mm long; innermost series 5.5–7 mm long.

Flowering and fruiting occur from August to October.

Eremanthus uniflorus is restricted to the Chapada dos Veadeiros in central Goiás (Fig. 6). Although locally abundant, it is found only on campo rupestre outcrops.

A single floret per head, the relatively weak coherence of heads, and 3–9 heads per glomerule distinguish *E. uniflorus* from other members of sect. *Vanillosmopsis.* This taxon is closely related to *E. capitatus,* which is primarily restricted to the northeast arm of the Central Plateau and differs in that *E. capitatus* has 3–4 florets per head and 2–5 heads per glomerule.

Additional specimens examined. BRAZIL. GOIÁS: Brasília Richtung Alto Paráiso de Goiás, 50 km nach São João de Aliança, 1,000 m, 27 Aug. 1981, *Schumacher 1030* (GA, K, M, MB, RB, W); Chapados Veadeiros, 33 km N of Alto Paráiso, 1,220 m, 24 Jan. 1980, *King & Almeda 8291* (US).

Possible hybrids. × *E. argenteus* MacLeish & Schumacher. GOIÁS: Alto Paráiso, 28 Aug. 1981, *Schumacher 1038, 1039, 1041* (GA).

17. **Eremanthus capitatus** (Sprengel) MacLeish, comb. nov. *Conyza capitata* Sprengel, Syst. Veg. 3: 507. 1826. *Vernonia capitata* (Sprengel) Less., Linnaea 4: 270. 1829. *Albertinia capitata* (Sprengel) DC., Prodr. 5: 82. 1836. *Vanillosmopsis capitata* (Sprengel) Schultz-Bip., Jahresber. Pollichia 18–19: 167. 1861. LECTOTYPE: here designated; Brazil. Bahia: inter Victoria et Bahia (now Salvador), *Sellow s.n.* (K; isolectotype, GH).

Polypappus discolor DC., Prodr. 7: 281. 1838. *Vanillosmopsis discolor* (DC.) Baker in C. Martius, Fl. Bras. 6(2): 17. 1873. TYPE: Brazil. Bahia: Jacobina, Jan. 1843, *Blanchet 2591* (holotype, G; isotypes, BM, 4 in BR, C, 3 in F (one photo of C), 2 in G, GH, MO, 2 in NY, P).

Vanillosmopsis albertinioides Schultz-Bip., Jahresber. Pollichia 18–19: 168. 1861. TYPE: Brazil: no other data, *Sellow s.n.* (holotype, B, not found).

Shrub or tree, to 6 m tall, to 8 cm diam.; stems gray-brown lepidote; branches many. Leaves membranaceous to subcoriaceous, sessile to petiolate; petioles 1–12 mm long, lepidote; blades 4.6–10.5 cm long, 2.4–4.2 cm wide, elliptic to obovate, the bases acute, the apices acute to acuminate, the margins entire; adaxially glabrate to lepidote, abaxially gray lepidote. Peduncle slender, to 30 cm tall, terete, gray lepidote. Glomerulescence a compound cyme of 100 or more glomerules. Glomerules 4–10 mm tall, 3–12 mm diam., hemispherical. Heads 2–5 per glomerule, slightly appressed and coherent basally by pubescence of phyllaries. Involucres cylindric to obconic with age, 5–8 mm tall, 2–4 mm diam.; phyllaries in 5–6 series; outermost phyllaries widely deltate, 0.5–1.1 mm long. 0.7–1.2 mm wide, the apices acute; innermost phyllaries lanceolate, 3.4–7.6 mm long, 0.6–1.4 mm wide, the apices acuminate; margins entire to subfimbriate; abaxial surfaces stramineous to green, glabrate to lepidote-tomentulose. Florets 3(–4) per head; corollas purple with white tube and becoming white with age, 4.2–7.2 mm tall, the lobes acuminate. Anthers 2.2–2.8 mm long, the apical appendage acuminate, the bases acute. Achenes 2–2.5 mm tall, glandular, 10-ribbed, the apex slightly constricted and dark; nectary 0.3–0.4 mm tall. Pappus 3–4-seriate, of purple, white or stramineous, often curling, promptly deciduous, strigose bristles; outermost series 2.5–3.5 mm long; innermost series 4–6.5 mm long.

Flowering and fruiting occur from July to November.

Eremanthus capitatus is distributed throughout the northeastern arm of the Central Plateau (Figs. 6, 7) at elevations of 100 to 1,000 meters. It occurs in large colonies in cerrado or on the border of secondary forest and is known as "candeia," or candle, in Bahia.

Eremanthus capitatus is closely related to *E. uniflorus, E. arboreus,* and *E. erythropappus.* It is distinguished by its 3–4 florets per head and 2–5 heads per glomerule. *Eremanthus uniflorus* is likely derived from an isolated population of *E. capitatus* in the northwestern arm of the Central Plateau whose number of florets per head has decreased from three to one. In contrast, *E. arboreus* represents a population found in the extreme northeastern part of the plateau whose number of heads per glomerule has increased from 2–5 to 6–9. *Eremanthus capitatus* and *E. erythropappus* have the same number of florets per head, but *E. capitatus* lacks the fusion of receptacle and phyllary tissues observed in *E. erythropappus.*

Flowering or immature specimens of this taxon are frequently misidentified as *E. pohlii.* When young, each head is noticeably cylindric like those of *E. pohlii*; however, as fruits mature, the innermost phyllaries drop off and the outermost spread out so that heads appear to be cylindric-turbinate.

Sprengel's types are generally considered to have been deposited at B, BM, BR, or P. Unfortunately, a holotype was not located in any of these herbaria. However, a specimen was located at K bearing the citation "ex herb. B" and the correct citation in Sprengel's handwriting. Therefore, the Kew specimen has been chosen as lectotype.

Additional specimens examined. BRAZIL. BAHIA: 33 km from BR 101 on road S to Canavieiras, 23 Oct. 1980, *MacLeish & Soares Nunes 758* (BR, C, CEPEC, F, GA, GH, MO, NY, RB, UC, US). GOIÁS: 5–10 km N of Veadeiros, Valley of the Rio Paraná, 19 Jul. 1964, *Prance & Silva 58251* (F, NY, RB, S, UB). MINAS GERAIS: BR 116 Téofilo Otôni towards Bahia, 2 km from Padre Paráiso, 8 Sep. 1981, 600 m, *Schumacher 1082* (GA, MB).

Possible hybrids. × *E. erythropappus* (DC.) MacLeish. MINAS GERAIS: Carai, 6 Sep. 1981, *Schumacher 1083, 1085, 1089* (GA).

18. **Eremanthus arboreus** (Gardner) MacLeish, comb. nov. *Albertinia arborea* Gardner, London J. Bot. 5: 236. 1846. *Vanillosmopsis arborea* (Gardner) Baker *in* C. Martius, Fl. Bras. 6(2): 16. 1873. TYPE: Brazil. Ceará: Serra de Araripe, Nov. 1838, *Gardner 1713* (holotype, BM; isotypes, BR, 4 in F (including fragment from P and photo of B), 2 in G, 3 in GH (one is photo of B), 2 in NY).

Tree, to 6 m tall; stems gray-brown lepidote; branches many. Leaves membranaceous to subcoriaceous, petiolate; petioles 5–10 mm long, lepidote; blades 5–6.5 cm long, 1.6–2 cm wide, narrowly elliptic to obovate, the bases attenuate, the apices acute to acuminate, the margins entire; adaxially glabrate to lepidote, abaxially gray lepidote. Peduncle slender, to 30 cm tall, terete, gray lepidote. Glomerulescence a compound cyme of 100 or more glomerules. Glomerules 5–12 mm tall, 8–15 mm diam., hemispherical. Heads 6–9 per glomerule, slightly appressed and coherent basally by pubescence of phyllaries. Involucres obconic, 5–7.5 mm tall, 2–3.5 mm diam.; phyllaries in 5–6 series; outermost phyllaries widely deltate, 0.6–1 mm long, 0.5–1.2 mm wide, the apices acute; innermost phyllaries lanceolate, 4–6 mm long, 0.5–1.2 mm wide, the apices acute to acuminate; margins entire to subfimbriate; abaxial surfaces stramineous to green, glabrate to lepidote-tomentulose. Florets 3(–4) per head; corollas white or purple, 4–7 mm tall, the lobes acuminate. Anthers 2–3 mm long, the apical appendage acute, the bases acute. Achenes 1.5–2.5 mm tall, sparsely glandular, 10-ribbed, the apex slightly constricted and dark; nectary 0.25–0.35 mm tall. Pappus 3–5-seriate, of stramineous to off-white (occasionally purple basally), often curling, promptly deciduous, strigose bristles; outermost series 2.5–3 mm long; innermost series 4–6 mm long.

Flowering and fruiting occur from August to September.

Eremanthus arboreus is restricted to the northeastern slope of the Chapada do Araripe (Fig. 6), near Crato, which runs along the border of Ceará and Pernambuco at elevations of 700 meters. It occurs in colonies on wooded slopes near the top of the plateau which are less dry than the surrounding caatinga.

Eremanthus arboreus is closely related to *E. capitatus* and is distinguished by its 6–9 heads per glomerule. This species probably represents an extreme northeastern population of *E. capitatus* whose number of heads per glomerule has increased from 2–5 to 6–9. Until recently, this species was known only from the type collection. However, Schumacher (1982) was able to collect it again from what was probably Gardner's original site during several expeditions designed to rediscover members of *Eremanthus* that were known only from type specimens.

Additional specimens examined. BRAZIL. CEARÁ: Chapada do Araripe, hillside on street out of Crato, 25 Aug. 1980, *Schumacher s.n.* (GA, MB, RB), Crato towards Nova Olinda, at slope near top of plateau, 700 m, 31 Aug. 1981, *Schumacher 1049* (B, GA, K, MB, RB).

EXCLUDED TAXA

1. *Eremanthus* Less. sect. *Chresta* (Vell. Conc. ex DC.) Baker in C. Martius, Fl. Bras. 6(2): 166. 1873. *Chresta* Vell. Conc. ex DC., Prodr. 5: 85. 1836. TYPE: (Robinson, 1980): *Chresta sphaerocephala* DC. = *Chresta* Vell. Conc. ex DC.
2. *Eremanthus* Less. sect. *Pycnocephalum* (Less.) Baker in C. Martius, Fl. Bras. 6(2): 168. 1873. *Vernonia* Schreber sect. *Pycnocephalum* Less., Linnaea 6: 629. 1831. TYPE: (MacLeish, 1985a): *Pycnocephalum plantaginifolium* (Less.) DC. = *Pycnocephalum* (Less.) DC.
3. *Eremanthus* Less. sect. *Sphaerophora* (Schultz-Bip.) Baker in C. Martius, Fl. Bras. 6(2): 165. 1873. *Sphaerophora* Schultz-Bip., Jahresber. Pollichia 20–21: 402. 1863, nom. illeg. (non *Sphaerophora* Blume, 1850, Rubiaceae). *Paralychnophora* MacLeish, Taxon 33: 106. 1984. TYPE: *Paralychnophora bicolor* (DC.) MacLeish = *Paralychnophora* MacLeish.
4. *Eremanthus* Less. sect. *Stachyanthus* (DC.) Baker in C. Martius, Fl. Bras. 6(2): 167. 1873. *Stachyanthus* DC., Prodr. 5: 84. 1836, nom. rej. (vs. *Stachyanthus* Engler, 1897, Icacinaceae). *Argyrovernonia* MacLeish, Taxon 33: 106–107. 1984. TYPE: *Argyrovernonia martii* (DC.) MacLeish = *Argyrovernonia* MacLeish.
5. *Eremanthus* Less. subg. *Pseuderemanthus* Schultz-Bip. "B. Jodopappus" Schultz-Bip., Jahresber. Pollichia 20–21: 396. 1863. TYPE: *Vernonia crotonoides* (DC.) Schultz-Bip. = *Vernonia* Schreber subg. *Vernonia* sect. *Vernonia.*
6. *Eremanthus angustifolius* (Gardner) Baker in C. Martius, Fl. Bras. 6(2): 170. 1873. *Chresta angustifolia* Gardner, London J. Bot. 1: 240, tab. 8. 1842. TYPE: Brazil. Goiás: shady places at Arrayas, *Gardner 3802* (holotype, BM); isotypes, 3 in F (includes fragment from P and photo of B), 2 in G, GH (photo of B), NY, S, W) = *Pycnocephalum angustifolium* (Gardner) MacLeish (1985a).
7. *Eremanthus bicolor* (DC.) Baker in C. Martius, Fl. Bras. 6(2): 165. 1873. *Albertinia bicolor* DC., Prodr. 5: 81. 1836. TYPE: Brazil. Minas Gerais: altis, *Martius s.n.* (holotype, M; isotype, M) = *Paralychnophora bicolor* (DC.) MacLeish (1984a).
8. *Eremanthus crotonoides* (DC.) Schultz-Bip., Jahresber. Pollichia 20–21: 396. 1863. *Albertinia crotonoides* DC., Prodr. 5: 81. 1836. TYPE: Brazil. Minas Gerais: montium sepibus, *Martius s.n.* (holotype, M) = *Vernonia crotonoides* (DC.) Schultz-Bip.
9. *Eremanthus curumbensus* Philipson, Kew Bull. 1938: 298. 1938. TYPE: Brazil. Goiás: valley of the Rio Curumbo in the plains between the mountains, *Glaziou 21645* (holotype, K; isotypes, BR, C, 4 in G, NY) = *Glaziovianthus curumbensis* (Philipson) MacLeish (1985b).
10. *Eremanthus descampsii* Klatt ex De Wild. & T. Durand, Ann. Mus. Congo, Ser. 1, Bot. 1: 99. 1898, non *Vernonia descampsii* De Wild., Bull. Jard. Bot. État. 5: 97. 1915. TYPE: Rep. of the Congo, Katanga, Vallee de la Liula, 1891, *Descamps s.n.* (holotype, BR not seen; fragment and drawing of BR, GH) = *Vernonia klattii* MacLeish (1984b).
11. *Eremanthus eriopus* (Schultz-Bip.) Baker in C. Martius, Fl. Bras. 6(2): 169. 1873. *Prestelia eriopus* Schultz-Bip., Naturf. Ges. Emden 1864: 73. 1864. TYPE: Brazil. Minas Gerais: in glareosis S. da Lapa, *Riedel 1127* (holotype, LE; isotypes, 2 in F (fragment and photo of P), P, TEX (photo of P)) = *Prestelia eriopus* Schultz-Bip.
12. *Eremanthus exsuccus* (DC.) Baker in C.

Martius, Fl. Bras. 6(2): 166. 1873. *Chresta exsucca* DC., Prodr. 5: 85. 1836. TYPE: Brazil. Minas Gerais: montosis Minarum, *Martius s.n.* (holotype, M; photos of M, F, TEX) = *Chresta exsucca* DC.

13. *Eremanthus harmsianus* Taub., Bot. Jahrb. Syst. 21: 453. 1896. TYPE: Brazil. Goiás: Serra dos Pyreneos, *Ule 2984* (holotype, HBG, not seen; isotype, P) = *Glaziovianthus speciosus* (Gardner) MacLeish (1985b).
14. *Eremanthus imbricatus* G. Barroso, Rodriguésia 23–24: 6. 1962. TYPE: Brazil. Distrito Federal: Brasilândia, *Macedo 4* (holotype, RB; isotype RB) = *Chresta exsucca* DC.
15. *Eremanthus jelskii* Hieron., Bot. Jahrb. Syst. 36: 462. 1905, non *Vernonia jelskii* Hieron., Bot. Jahrb. Syst. 36: 459. 1905. TYPE: Peru, crescit prope Shanyn, *Jelskii 776* (lectotype, US (MacLeish, 1984b); isolectotypes, photos of B, F, GH, NY, TEX) = *Vernonia shanynensis* MacLeish (1984b).
16. *Eremanthus labordeii* Glaz., Mem. Soc. Bot. France 3: 380. 1909. TYPE: Brazil. Goiás: entre Paranaua et Rajadinho, 31 Jun. 1895, *Glaziou 21675* (lectotype, P (MacLeish, 1985a); isolectotypes, BR, C, 2 in F, 2 in G, GH) = *Chresta exsucca* DC.
17. *Eremanthus leucodendron* Mattf., Bot. Gart. Notizbl. 9: 378. 1925. TYPE: Brazil. Bahia: Rio de Contas, Serra das Almas, Carrasco, *Luetzelburg 242* (holotype, M; isotypes, F (photo of B), 2 in GH (includes photo of B), M, TEX (photo of B)) = *Vernonia leucodendron* (Mattf.) MacLeish (1984b).
18. *Eremanthus martii* (DC.) Baker in C. Martius, Fl. Bras. 6(2): 167. 1873. *Stachyanthus martii* DC., Prodr. 5: 84. 1836. TYPE: Brazil. Bahia: siccis sylvis aestu aphyllis, ad Juazeiro, *Martius s.n.* (holotype, M; isotypes, 3 in M) = *Argyrovernonia martii* (DC.) MacLeish (1984a).
19. *Eremanthus mollis* Schultz-Bip., Jahresber. Pollichia 18–19: 166. 1861, non *Vernonia mollis* Kunth, Nov. Gen. & Sp. 4: 36. 1820. TYPE: Brazil. Goiás: Montes Claros et Ponte Alto, ante Bomfim, *Pohl 171* (lectotype, W (MacLeish, 1984b); isolectotype, 2 in F (fragment and photo of B), GH (photo of B), 2 in NY, TEX (photo of B)) = *Vernonia pannosus* (Baker in C. Martius) MacLeish (1984b).
20. *Eremanthus pabstii* G. Barroso, Sellowia 16: 173. 1964. TYPE: Brazil. Goiás: Cristalina, *Heringer 9229/1442* (holotype, HB; isotypes, RB, UB) = *Vernonia pabstii* (G. Barroso) MacLeish (1984b).
21. *Eremanthus pannosus* Baker in C. Martius, Fl. Bras. 6(2): 164. 1873. TYPE: Brazil. Goiás: Curralinho, *Manso 1* (holotype, BR) = *Vernonia pannosus* (Baker in C. Martius) MacLeish (1984b).
22. *Eremanthus pinnatifidus* Philipson, Kew Bull. 1938: 299. 1938. TYPE: Brazil. Rio de Janeiro: env. de Rio de Janeiro, *Glaziou 14033* (lectotype, C (MacLeish, 1985a)) = *Pycnocephalum pinnatifidum* (Philipson) MacLeish (1985a).
23. *Eremanthus plantaginifolius* (Less.) Baker in C. Martius, Fl. Bras. 6(2): 168. 1873. *Vernonia plantaginifolius* Less., Linnaea 4: 251. 1829. TYPE: Brazil: no other data, *Sellow s.n.* (lectotype, P (MacLeish, 1985a)) = *Pycnocephalum plantaginifolium* (Less.) DC.
24. *Eremanthus purpurascens* Glaz. ex Oliver, Hooker's Icon. Pl. 4(3): plate 2282. 1894. TYPE: Brazil. Minas Gerais: Serra do Cipó, *Glaziou 19464* (holotype, P; isotypes, BR, C) = *Prestelia eriopus* Schultz-Bip.
25. *Eremanthus pycnocephalus* (DC.) Baker in C. Martius, Fl. Bras. 6(2): 166. 1873. *Chresta pycnocephala* DC., Prodr. 5: 85. 1836. TYPE: Brazil. Minas Gerais: campis deserti inter Min. Nov. et f. S. Francisci, *Martius s.n.* (holotype, M) = *Chresta pycnocephala* DC.
26. *Eremanthus reflexo-auriculatus* G. Barroso, Rodriguesia 23–24: 6. 1962. TYPE: Brazil. Pernambuco: Buique, Chapada de S. José, *Lima s.n.* (holotype, RB) = *Paralychnophora reflexoauriculata* (G. Barroso) MacLeish (1984a).
27. *Eremanthus rivularis* Taubert, Bot. Jahrb. Syst. 21: 453. 1896. TYPE: Brazil. Goiás: regiao de Maranhão superior, *Ule 26 (2962)* (holotype, HBG, not seen; isotypes, 2 in F (fragment and photo of P), GH (photo of P), P) = *Pycnocephalum angustifolium* (Gardner) MacLeish (1985a).
28. *Eremanthus scapigerus* (Less.) Baker in C. Martius, Fl. Bras. 6(2): 168. 1873. *Vernonia scapigera* Less., Linnaea 4: 250. 1829. TYPE: Brazil: no other data, *Sellow s.n.* (lectotype, B (MacLeish, 1985a); isolectotypes, K, P) = *Chresta scapigera* (Less.) Gardner.
29. *Eremanthus schwackei* Glaz., Bull. Soc. Bot. France 3: 380. 1909. TYPE: Brazil. Minas Gerias: Biribiry, *Glaziou 19562* (lectotype, here designated, P; isolectotypes, BR, C, G)

= *Paralychnophora schwackei* (Glaz.) MacLeish (1984a).

30. *Eremanthus speciosus* (Gardner) Baker in C. Martius, Fl. Bras. 6(2): 169. 1873. *Chresta speciosa* Gardner, London J. Bot. 1: 240. 1842. TYPE: Brazil. Goiás: dry campos near Villa de Arrayas, *Gardner 3801* (holotype, BM; isotype, BM) = *Glaziovianthus speciosus* (Gardner) MacLeish (1985b).
31. *Eremanthus sphaerocephalus* (DC.) Baker in C. Martius, Fl. Bras. 6(2): 167. 1873. *Chresta spherocephala* DC., Prodr. 5: 85. 1836. TYPE: Brazil. Minas Gerais: Tejuco (now Diamantina), *Vauthier 294* (lectotype, G-DC (as IDC microfiche, MacLeish, 1985a); isolectotypes, G, GH) = *Chresta sphaerocephala* DC.
32. *Eremanthus sphaerocephalus* (DC.) Baker in C. Martius var. *intermedia* (Gardner) Baker in C. Martius, Fl. Bras. 6(2): 167. 1873. *Chresta intermedia* Gardner, London J. Bot. 5: 235. 1846. TYPE: Brazil. Minas Gerais: near Formigas (now Montes Claros), *Gardner 4818* (holotype, BM) = *Chresta sphaerocephala* DC.
33. *Eremanthus veadeiroensis* H. Robinson, Phytologia 45: 94. 1980. TYPE: Brazil. Goiás: Chapada dos Veadeiros, ca. 20 km N of Alto Paráiso, *Irwin et al. 32752* (holotype, UB; isotype, US) = *Vernonia veadeiroensis* (H. Robinson) MacLeish (1984b).
34. *Eremanthus verbascifolius* (C. Martius ex DC.) Schultz-Bip., Jahresber. Pollichi 20–21: 397. 1863. TYPE: Brazil. Minas Gerais: ferruginosis Serra do Ant. Pereira, *Martius s.n.* (holotype, M) = *Vernonia crotonoides* (DC.) Schultz-Bip.
35. *Vanillosmopsis bicolor* (DC.) Schultz-Bip., Jahresber. Pollichia 18–19: 168. 1861. *Albertinia bicolor* DC., Prodr. 5: 81. 1836. TYPE: Brazil. Minas Gerais: altis, *Martius s.n.* (holotype, M; isotype, M) = *Paralychnophora bicolor* (DC.) MacLeish (1984a).
36. *Vanillosmopsis lanceolata* (Vell. Conc.) Kuntze, Rev. Gen. Pl. 3(2): 183. 1898. *Chresta lanceolata* Vell. Conc., Arq, Mus. Nac. Rio de Janeiro 8: 350. 1881. TYPE: Brazil: mediterraneis transalpinus prope pagum Cunha, *Velloso s.n.* (lectotype, as figure, Fl. Flum. Ic. 8: tab. 151. 1831 (MacLeish, 1985a)) = Identity doubtful.
37. *Vanillosmopsis syncephala* Schultz-Bip., Jahresber. Pollichia 18–19: 168. 1861, non *Vernonia syncephala* Schultz-Bip. ex Baker in C. Martius, Fl. Bras. 6(2): 64. 1873. TYPE: Brazil: no other data, *Sellow 948* (holotype, B (destroyed); photos of B, F, GH) = *Vernonia crispa* (Mattf.) MacLeish (1984b).
38. *Vanillosmopsis weberbaueri* Hieron., Bot. Jahrb. Syst. 40: 352. 1908, non *Vernonia weberbaueri* Hieron., Bot. Jahrb. Syst. 40: 354. 1908. TYPE: Peru: propre Ramospata in via a Sandia ad Chunchusmayo, *Weberbauer 1324* (lectotype, NY, photo of B (MacLeish, 1984b); isolectotypes, photos of B, GH, TEX) = *Vernonia ramospatana* MacLeish (1984b).

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BIOSYSTEMATICS OF TETRAPLOID *EUCHARIS* (AMARYLLIDACEAE)[1]

ALAN W. MEEROW[2]

ABSTRACT

Eucharis is a genus of 16 species of petiolate-leaved, neotropical Amaryllidaceae restricted to rainforest understory from Guatemala to Bolivia. The two northernmost species, *E. bonplandii* and *E. bouchei*, are the only two tetraploid ($2n = 92$) species so far known in the genus. *Eucharis bonplandii* is known from only a few localities in central Colombia. *Eucharis bouchei*, restricted to Central America, is particularly polymorphic and three varieties are recognized largely on the basis of staminal cup morphology. Data from phenetic, chromosomal, and preliminary electrophoretic analyses are presented for both tetraploid species. On the basis of 17 floral characters, the three varieties of *E. bouchei* do not resolve into discrete phenetic groups. The tetraploid representatives of *Eucharis* exhibit a wide degree of karyotypic heteromorphism. *Eucharis bouchei* var. *dressleri* is an unstable tetraploid. Electrophoretic banding patterns for aspartate-amino-transferase exhibit additive effects of polyploidy in some individuals. Isozyme phenotypes of *Eucharis bouchei* var. *bouchei* are quite variable and cladistic analysis of the isozyme data suggests that this variety may be polyphyletic. *Eucharis bonplandii* and *E. bouchei* may be monophyletic sister taxa and the remnants of a once more widespread tetraploid complex. The entry of *Eucharis* into Central America was probably a geologically recent event. It is hypothesized that *E. bouchei* has been steadily migrating away from the Colombian border. *Eucharis bouchei* is a semi-species complex of geographically isolated populations in the process of morphological diversification. The evolution of *E. bouchei* var. *dressleri* may be a sympatric speciation event. Founder effects, rapid chromosomal change, and geographical isolation are considered the most important factors in the evolution of the *E. bouchei* complex. Tetraploidy and attendant increased levels of heterozygosity may have been important in facilitating the migration of *Eucharis* across the Isthmus of Panama.

The genus *Eucharis* Planchon & Linden [Amaryllidaceae "infrafamily" Pancratioidinae sensu Traub (1957, 1963)] consists of 16 species of rare, petiolate-leaved, bulbous geophytes inhabiting the understory of primary rainforest from Guatemala to Bolivia (Meerow, 1986). Most of the species are found in the western Amazon basin and adjacent slopes of the eastern Andes. *Eucharis bouchei* Woodson & Allen is a highly polymorphic tetraploid ($2n = 92$) complex of Central America (Fig. 1). The species is concentrated in Panama (Fig. 2), but has also been recorded from Costa Rica and Guatemala. *Eucharis bouchei* is the northernmost species of *Eucharis* and the only one found north of the Darién Gap. It is also the most variable species in the genus, in characteristics that elsewhere justify specific delimitation. Patterns of variation in floral size and tube and limb habit form a complete mosaic throughout the range of *E. bouchei*, showing little or no geographic consistency.

In my recent monograph of *Eucharis* (Meerow, 1986), three varieties are recognized chiefly on the basis of staminal cup morphology (Fig. 3): *E. bouchei* var. *bouchei*, var. *darienensis* Meerow, and var. *dressleri* Meerow.

Variety *bouchei*, most common around El Valle de Antón in Coclé Province (Fig. 2), is recognized by its largely edentate staminal cup in which the trapezoidal free filament is not markedly constricted distally into a narrow subulate portion (Figs. 1C, 3A, B). It is the most variable of the three varieties, both in flower size and staminal cup morphology. The staminal cup of variety

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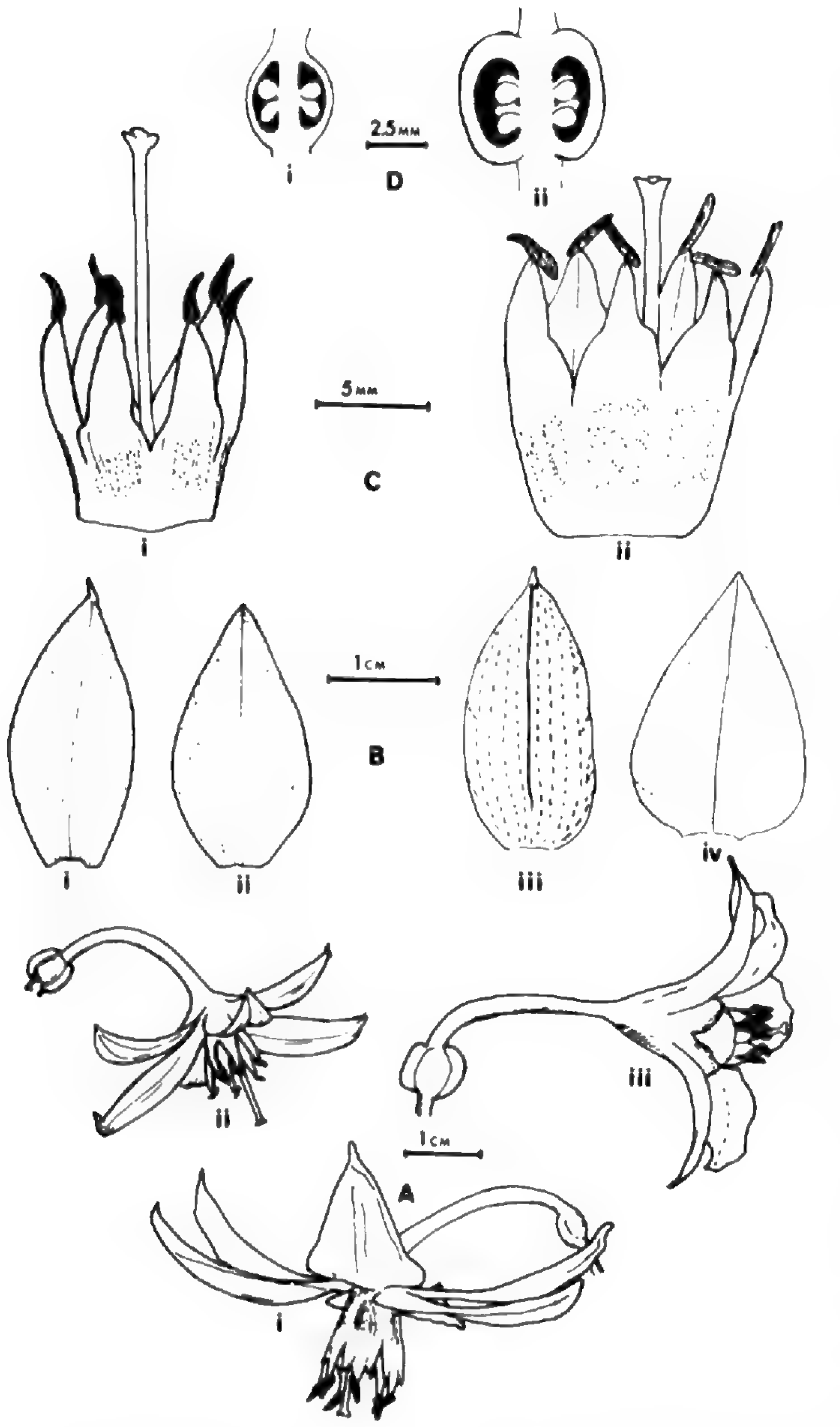


FIGURE 1. *Eucharis bouchei.*—A. Flowers.—i. Variety *dressleri* (holotype, *Meerow 1107,* FLAS). ii, iii. Variety *bouchei.*—ii. *Meerow 1125,* FLAS.—iii. *Meerow 1157,* FLAS.—B. Tepals, variety *bouchei.* i, ii. *Meerow 1125.*—i. Outer tepal.—ii. Inner tepal. iii, iv. *Meerow 1157.*—iii. Outer tepal.—iv. Inner tepal.—C. Staminal cups, variety *bouchei.*—i. *Meerow 1125.*—ii. *Meerow 1157.*—D. Ovaries, variety *bouchei,* longitudinal section.—i. *Meerow 1125.*—ii. *Meerow 1157.*

darienensis, found in Panamá and Darién provinces, is obtusely bidentate or lobed (Fig. 3D). The free filament constricts distally into a narrow (<2 mm wide) subulate portion. These two varieties occur in close proximity in one location near Cerro Campana in Panamá Province. The rare var. *dresslerii* (Fig. 1Ai), with its acutely toothed staminal cup (Fig. 3C) and non-trigonous ovary, occurs close to populations of var. *bouchei* near El Valle.

Northwesternmost populations in Panama representing var. *bouchei* have the most derived androecial morphology (Fig. 3A, B) relative to more southeastern populations (var. *darienensis,* Fig. 3D). The latter have staminal cups similar to the generalized morphology characteristic of Andean and Amazonian species of subg. *Eucharis.* This may indicate that general movement of *E. bouchei* in Central America has been away from the Colombian border.

The only other naturally occurring tetraploid *Eucharis* species known is the rare Colombian *E. bonplandii* (Kunth) Traub. It is separated from *E. bouchei* by its slightly glaucous leaves (all other *Eucharis* species have nonglaucous foliage), shorter petioles, and longer pedicels. *Eucharis bonplandii* is the northernmost species of *Eucharis* subg. *Eucharis* in South America.

Results of phenetic, karyotype, and preliminary electrophoretic analyses of *E. bouchei* and *E. bonplandii* are presented in this paper. These data offer insight into the evolutionary history of Central American *Eucharis* and the origins of tetraploidy in the genus, and provide a basis for understanding the enormous degree of phenotypic variation present within *E. bouchei.*

The use of electrophoretic analyses of isozyme variation in plant systematics has been extensive in recent years. The subject has been reviewed by Gottlieb (1971, 1977, 1981a, 1981b, 1982, 1984) and Crawford (1983, 1985). Unlike many morphological characters, which may be influenced by a great deal of environmental or developmental plasticity, the electrophoretic phenotype is more directly equitable with genotype (Crawford, 1983; Gottlieb, 1977).

Electrophoretic studies of tropical plants are few (Hamrick & Loveless, 1986; Heywood & Fleming, 1986; Sytsma & Schaal, 1985). Neither have plants of limited or rare distribution been widely investigated (Babbel & Selander, 1974).

Members of *Eucharis* are tropical monocots exclusive to rainforest understory. They are rare and widely dispersed in the wild. Studies of isozyme variation of any plant group fitting any one of these characteristics are very limited. Isozyme analyses of polyploid taxa are also not abundant (Crawford, 1985; Soltis & Rieseberg, 1986). Thus, an attempt to explore isozyme variation in natural polyploid *Eucharis* seemed a worthy avenue of investigation.

MATERIALS AND METHODS

PHENETIC ANALYSES

Principal component and hierarchical cluster analyses of 20 herbarium specimens of *Eucharis*

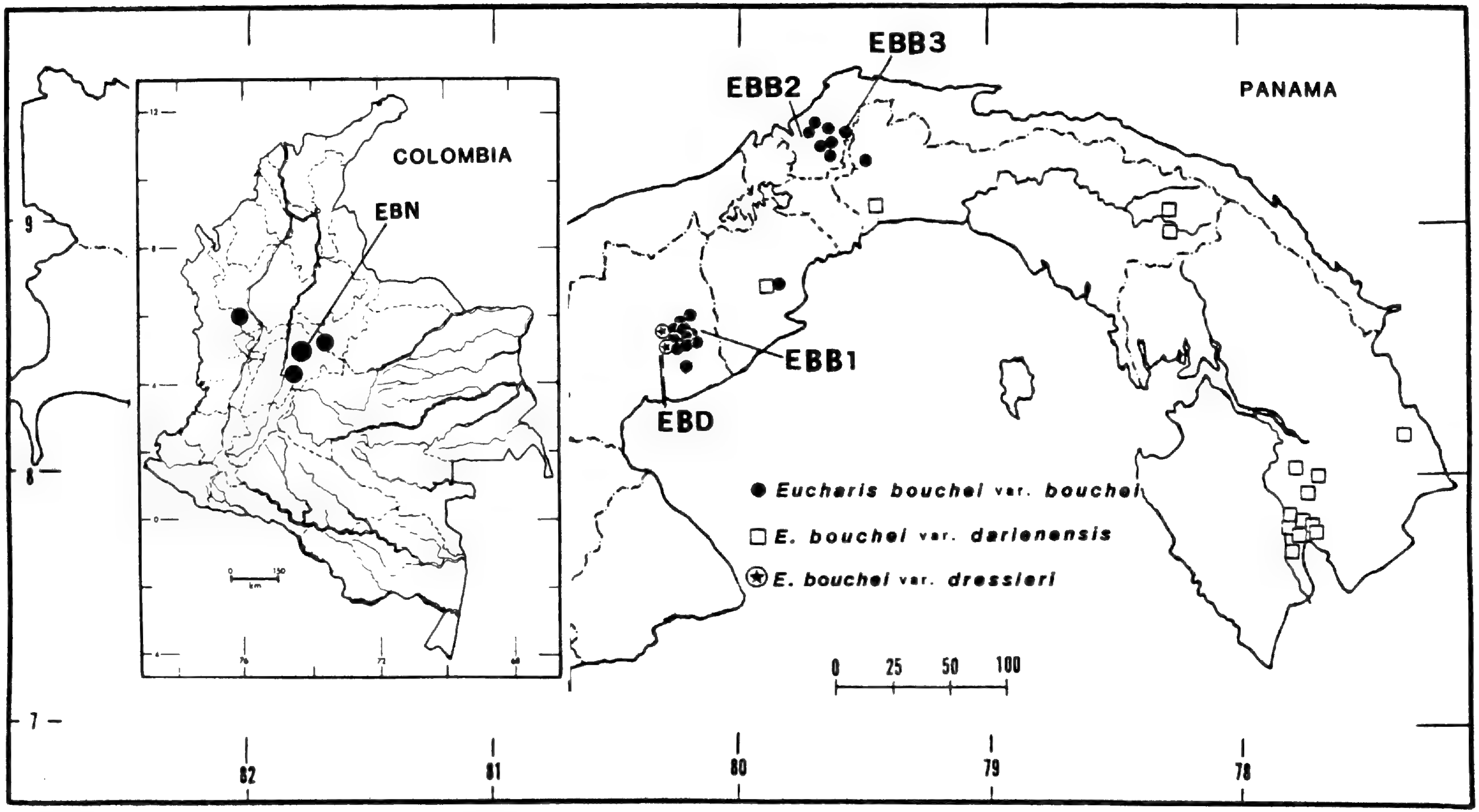


FIGURE 2. Distribution of *Eucharis bouchei* in Panama and *E. bonplandii* (Colombia, inset). Letter designations refer to populations analyzed electrophoretically (see Table 4).

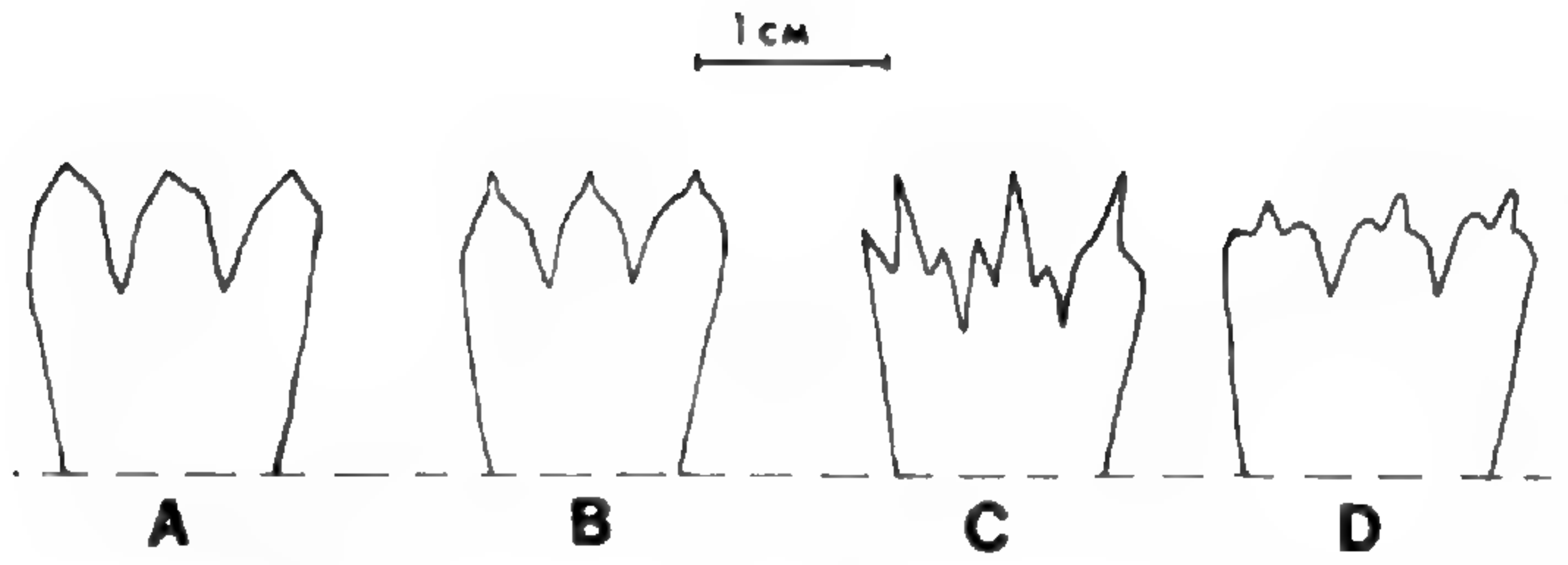


FIGURE 3. Staminal cup variation in *Eucharis bouchei*. A, B. Variety *bouchei*.—A. *Lewis et al. 2617* (MO).—B. *Allen 120* (US).—C. Variety *dressleri* (*Meerow 1107*, FLAS).—D. Variety *darienensis* (*Gentry & Mori 13945*, MO).

bouchei (Table 1) were conducted with CLUSTAN 2 vers. 2.1 (University of St. Andrews, Scotland) on the North Florida Regional Data Center (NERDC) system of the University of Florida. Three-dimensional scattergrams were constructed from PCA factor scores utilizing PCAPLOT, a program written by Bart Schutzman at the University of Florida. The small number of OTUs (operational taxonomic units) underscores the relative rarity with which *Eucharis* is encountered in the field. These 20 specimens represent the only specimens from which the full character set could be recorded. A number of additional specimens examined were collected in fruit and therefore were useless for these analyses.

Twenty-seven characters were used initially. The results suggested that some of these characters (e.g., all foliage characters, scape height, ovary length) were unreliable due to environmental plasticity, developmental variation, or specimen preparation. Although living material provides additional characters of potential utility (e.g., leaf surface texture, pigmentation pattern of the staminal cup), the inability to consistently determine these characters in dried specimens precluded their inclusion. Where any two characters were highly correlated (more than 80% correlation), which can result in data redundancy (Sneath & Sokal, 1973), one of the two was removed from the data matrix. In the final analyses, 17 floral characters (Tables 2, 3) were selected as the basic data set, of which 14 were continuous, quantitative characters. The remaining three qualitative characters were treated by assigning a numerical value for each character state. Since CLUSTAN would treat these values as continuous, the character states were numbered in a progressive transformation series, such that any two successive numbers would reflect putative character state relationship. These transformation series were constructed by study of morphological patterns and trends in the genus *Eucharis* and by comparative study with closely related genera of Amaryllidaceae.

Raw data were standardized using the "z-score" method (Sneath & Sokal, 1973) by which initial values for each character were replaced by stan-

TABLE 1. Operational taxonomic units (OTUs) for multivariate analysis of the *Eucharis bouchei* complex. CR = Costa Rica, G = Guatemala, P = Panama.

No.	Collection and Herbarium	Variety	Origin
1	*Alston 8727* (BM)	*dressleri*	P, Coclé
2	*Meerow 1107* (FLAS)	*dressleri*	P, Coclé
3	*Wendland 207* (GOET)	*darienensis*	G
4	*Sullivan 718* (MO)	*darienensis*	P, Darién
5	*Folsom 4402* (MO)	*darienensis*	P, Darién
6	*Folsom et al. 6582* (MO)	*bouchei*	P, Panamá
7	*Allen 5347* (US)	*bouchei*	CR
8	*Kirkbride & Hayden 305* (MO)	*bouchei*	P, Panamá
9	*Witherspoon & Witherspoon 8372* (MO)	*darienensis*	P, Panamá
10	*Duke & Elias 3661* (GH)	*darienensis*	P, Darién
11	*Gentry & Mori 13945* (MO)	*darienensis*	P, Darién
12	*Stern et al. 499* (GH)	*darienensis*	P, Darién
13	*Skutch 1585* (F)	*bouchei*	G
14	*Seibert 466* (MO)	*bouchei*	P, Coclé
15	*Lewis 2617* (MO)	*bouchei*	P, Coclé
16	*Witherspoon & Witherspoon 8736*	*bouchei*	P, Coclé
17	*Allen 1228* (GH)	*bouchei*	P, Coclé
18	*Mori & Kallunki 2014* (AAU)	*bouchei*	P, Colón
19	*Mori et al. 6586* (AAU)	*bouchei*	P, Colón
20	*Meerow 1158* (FLAS)	*bouchei*	P, Colón

dard deviations from the mean value for that character. A distance matrix was then calculated using squared euclidean distance (Cormack, 1971). In addition to PCA, cluster analysis using average linkage (unweighted pair group method (UPGMA) of Sneath & Sokal, 1973) was also applied to the 20 OTUs as a further test of phenetic relationship.

CHROMOSOME CYTOLOGY

Root tips were collected from living collections, pretreated for 2–3 hours at room temperature in 10 ppm solution of o-isopropyl-N-phenylcarbamate (Storey & Mann, 1967), rinsed in distilled water, fixed in 3 : 1 mixture of 95% EtOH and chloroform at 18°C for 24 hours, then stored after fixation in 70% EtOH at 18°C. Root tips were hydrolyzed in 1 N HCl at 50°C for 2–3 minutes, squashed, and stained with iron acetocarmine. Only temporary slides were made. Metaphase configurations were photographed on a Nikon Labophot photomicroscope with AFX-II camera attachment; haploid idiograms were constructed from photomicrographs.

As absolute chromosome length can vary appreciably from cell to cell due to differential effects of pretreatment (Tjio & Hagberg, 1951; Schlarbaum & Tsuchiya, 1984), relative length based on a value of 100 for the haploid complement was used to designate size class. Relative size classes are based on 80% or greater correlations between absolute size class (modified from Battaglia, 1955) and relative length (RL) of mitotic metaphase preparations of various species of *Eucharis, Eucrosia, Phaedranassa,* and other Amaryllidaceae with $2n = 46$, all of which have similar relative length ranges: large, RL $\geq$ 7.0 [absolute length (AL): $> 10\ \mu$m]; moderately large, RL = 5.0–7.0 (AL: 7–10 μm); medium, RL = 3.5–5.0 (AL: 5–7 μm); small, RL $\leq$ 3.5 (AL: 2–5 μm). For tetraploid karyotypes, diploid RL values were halved to assign size class. Chromosome morphology, modified from Battaglia (1955), is defined as follows: metacentric, Arm Ratio (AR; long arm/short arm) = 1.00–1.10; near-metacentric, AR = 1.10–1.50; submetacentric, AR = 1.50–3.00; subtelocentric, AR = >3.00.

ELECTROPHORETIC ANALYSES

Population selection and sample size. Five populations were included in these analyses (Fig. 2; Table 4), representing all living collections of *E. bouchei* and *E. bonplandii* in cultivation at the University of Florida. These included three populations of *E. bouchei* var. *bouchei,* one from El Valle de Antón in Coclé Province of Panama, and one each from Cerro Brujo and Río Iguanita, respectively, in Colón Province; and one population of var. *dressleri,* also from El Valle. The fifth population represented *E. bonplandii,* a rare species from Colombia, also tetraploid. Sample size was one or three for each population (Table 4).

TABLE 2. Characters used for multivariate analysis of *Eucharis* species.

1. Flower number
2. Limb spread (mm)
3. Length of free filament (mm)
4. Width of free filament (mm)
5. Width of stamen (mm)
6. Length of tube (mm)
7. Width of tube at throat (mm)
8. Length of outer tepal (mm)
9. Length of inner tepal (mm)
10. Width of outer tepal (mm)
11. Width of inner tepal (mm)
12. Staminal cup length (mm)
13. Staminal cup width (mm)
14. Toothing of staminal cup:
    - 1: Bidentate, teeth acute
    - 2: Bidentate, teeth obtuse
    - 3: Irregularly toothed
    - 4: Quadrate
    - 5: Lobed
    - 6: Edentate
15. Cleft of staminal cup:
    - 0: None
    - 1: < ⅙ length of cup
    - 2: ⅙–⅓ length of cup
    - 3: ⅓–½ length of cup
    - 4: > ½ length of cup
16. Relative length of teeth:
    - 0: Edentate
    - 1: < ½ length of filament
    - 2: ½ length of filament
    - 3: = length of filament
    - 4: > length of filament
17. No. ovules per locule

Unfortunately, the small sample size does not allow statistically significant exploration of genetic variation among these populations. Most electrophoretic studies in plant systematics have involved taxa of characteristically large population size in nature (see Crawford, 1983; Gottlieb, 1981a). Populations of *Eucharis,* however, are characteristically small. Many species of *Eu-*

TABLE 3. Data matrix for PCA and cluster analyses of the *Eucharis bouchei* complex.

	Character																
OTU	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1	05	43	3.5	1.8	2.5	33.0	06.5	26.2	25.8	05.5	08.0	09.4	09.5	4	2	1	3
2	06	53	4.2	1.8	5.0	41.0	10.5	32.0	28.0	10.0	13.5	16.0	11.5	3	2	2	3
3	06	42	3.5	1.8	3.7	36.0	06.5	25.0	23.0	09.5	12.7	11.0	12.0	3	2	1	2
4	04	46	3.1	2.0	4.6	25.5	09.5	20.8	20.0	08.0	11.1	06.0	13.2	6	2	1	2
5	05	43	2.5	2.2	4.3	36.3	07.1	21.8	21.0	10.5	15.5	07.0	14.5	6	3	0	2
6	06	55	3.6	2.8	5.2	46.0	12.2	31.4	30.0	13.8	15.2	10.6	17.4	6	3	0	3
7	06	69	3.5	2.8	5.2	44.0	12.0	35.0	31.5	15.5	17.5	11.0	18.2	6	3	0	2
8	04	45	2.8	2.5	4.9	31.0	10.5	27.7	25.5	11.4	14.5	10.0	16.0	5	4	0	2
9	04	38	3.0	2.0	4.3	33.0	10.0	20.0	19.0	09.5	12.5	09.2	14.0	3	3	1	2
10	05	42	2.1	1.7	4.2	27.1	06.0	23.8	22.0	10.0	12.0	09.0	12.8	2	2	2	2
11	06	55	2.0	2.0	4.5	43.4	12.0	27.0	25.0	10.2	16.5	14.0	18.2	3	2	2	4
12	05	38	1.8	1.8	5.0	30.0	09.8	22.0	21.0	11.5	15.0	09.0	12.3	2	3	2	2
13	04	41	5.0	5.1	5.1	35.0	10.5	24.2	21.1	09.8	14.5	12.0	15.4	4	3	0	2
14	05	45	5.3	4.3	5.3	36.0	08.7	28.0	26.0	12.0	14.0	11.0	14.0	4	3	0	2
15	07	50	6.9	5.0	6.9	43.7	10.8	26.8	25.0	14.0	14.6	16.7	16.0	4	3	0	2
16	05	49	4.5	3.5	4.5	43.0	10.6	21.0	20.0	09.0	11.0	08.0	12.5	4	3	0	2
17	03	50	6.5	4.7	6.5	45.0	12.0	23.5	22.0	11.5	15.5	12.8	14.5	4	3	0	2
18	05	34	5.9	3.7	3.7	34.0	08.3	18.0	16.0	09.0	11.5	11.6	11.5	4	3	0	2
19	05	35	3.7	4.0	4.0	33.0	07.0	21.6	19.5	08.0	10.0	10.0	12.4	4	2	0	2
20	05	40	5.3	3.8	3.8	40.0	08.0	26.0	24.0	11.2	13.7	11.8	09.7	4	3	0	2

charis frequently occur as single, widely dispersed clumps (Meerow, 1986). Herbarium specimens of *Eucharis* regularly include some notation indicating the rarity of the plants encountered. Yet, if most *Eucharis* are primarily visited by trap-lining insects (sensu Janzen, 1971) flying long distances, as may be the case (Meerow, 1986), population size from the perspective of potential gene exchange may in fact be greater than otherwise expected from known population densities. Few workers have addressed the problem of how to apply electrophoretic data to rare plants of characteristically small population size. Nei (1978) presented modified formulas for unbiased genetic identities and distances that could be used for sample sizes as low as one. Nei stressed, however, that with a limited population sample, a large number of loci must be analyzed. The number of enzyme systems assayed in the present study is not sufficient for this purpose. Instead, individuals were scored for the presence or absence of putatively identical bands (Table 5). These scores were used to generate distance coefficients by the unweighted pair group method (Sneath & Sokal, 1973). Bands showing the same mobility, as determined by their position in the gel, were considered to be identical. The resulting dendrogram could then be compared with the results of phenetic analysis of morphological variation, as well as with the data derived from

TABLE 4. *Eucharis bouchei* and *E. bonplandii* populations examined electrophoretically.

Taxon	Designation	N	Collection Information	Voucher[a]
Eucharis bouchei var. *dressleri*	EBD	3	Panama, Coclé, El Valle de Antón	*Meerow 1107*
E. bouchei var. *bouchei*	EBB1	3	Panama, Coclé, El Valle de Antón	*Meerow 1125*
E. bouchei var. *bouchei*	EBB2	1	Panama, Colón, Río Guanche, Cerro Brujo	*Meerow 1157*
E. bouchei var. *bouchei*	EBB3	1	Panama, Colón, Río Iguanita	*Meerow 1158*
E. bonplandii	EBN	1	Colombia, Cundinamarca, vicinity of Bogotá	*Bauml 686* (HUNT)

[a] All vouchers deposited at FLAS unless otherwise indicated.

TABLE 5. Presence-absence data matrix for electrophoretic analysis of tetraploid *Eucharis*. Refer to Table 4 for population designations, Figure 14 for bands. (*) = used only for cladistic analysis. Blank space indicates data unavailable.

	Band																		
Population	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	*18	*19
EBD	1	0	0	1	1	0	0	0	0	0	0	0	1	1	0	0	1	1	1
EBD	1	0	0	0	1	1	0	0	0	0	0	0	1	1	0	0	1	1	1
EBD	1	0	0	0	1	1	0	0	0	0	0	0	1	1	0	0	1		
EBB1	0	0	1	1	1	1	1	0	0	0	0	0	1	1	1	1	0	0	1
EBB1	1	1	1	0	1	1	1	1	0	0	0	0	0	0	1	0	1		
EBB1	1	1	1	0	0	0	1	1	0	0	0	0	0	0	1	0	1	1	1
EBB2	0	0	1	0	1	1	1	1	0	0	0	0	1	1	1	1	0	0	1
EBB3	1	0	0	0	1	1	1	1	0	0	0	0	0	0	1	0	1	0	1
EBN	1	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	0	1	0

comparative chromosome morphology. A similar method for analyzing isozyme data was used by Ashton et al. (1984) for *Shorea* (Dipterocarpaceae), and Chou et al. (1986) for several genera of bambusoid grasses. The data matrix was additionally subjected to cladistic analysis using PAUP by David Swofford (Illinois Natural History Survey). The "Wagner method" of simple parsimony (Farris, 1970; Kluge & Farris, 1969) was applied in constructing the cladogram, and *E. bonplandii* was designated as the outgroup for polarization of character states.

Of course, without the benefits of formal genetic analysis, there is no guarantee of genetic homology between any two bands of seemingly identical mobility. Future studies may allow more precise analysis of genetic variation within and among populations of tetraploid *Eucharis*.

Isozyme extraction and electrophoresis Crude extracts for isozyme electrophoresis were prepared by grinding ten 5 mm diameter leaf discs in 1 ml of extraction buffer [100 mM Tris-HCl, 10 mM DTT, 20% glycerol, and 1 mM PMSF adjusted to pH 6.8 (Hames & Rickwood, 1981)]. Extracts were centrifuged twice, for ten minutes and two minutes, and the supernatant was decanted by pipette after each centrifugation.

Electrophoresis was performed on a BIO-RAD Protean II polyacrylamide gel apparatus. Gel recipes were adopted from Hames & Rickwood (1981). Running gels were 0.75 mm thick and 7.5% acrylamide (10 ml 30% acrylamide-bis acrylamide, 10 ml 1.5 Tris-HCl at pH 8.8, 19.85 ml H_2O, 100 μl 10% ammonium persulfate, and 15 μl TEMED). A 2.5% acrylamide stacking gel (1 ml 30% acrylamide-bis acrylamide, 1.92 ml 0.5 M Tris-HCl at pH 6.8, 9 ml H_2O, 20 μl ammonium persulfate, and 7.5 μl TEMED) was employed. Running buffer was 25 mM Tris-glycine at pH 8.3 (Hames & Rickwood, 1981). A 20 μl sample of the supernatant was loaded into each stacking gel column. Gels were electrophoresed at a constant current of 50 mA until a blue indicator line (40 μl of bromophenol blue added to cathodal buffer) migrated off the anodal end of the gel, generally four to five hours.

Five enzyme systems were assayed: aspartate amino-transferase (AAT), glutathione reductase (GSSGR), malate dehydrogenase (MDH), phosphoglucoisomerase (PGI), and shikimate dehydrogenase (SKDH). Staining recipes of Vallejos (1983) were followed for AAT, PGI, and SKDH. The staining system for MDH was that of Shaw & Prasad (1970), and that of Kaplan (1968) was used for GSSGR.

Resolution of additional enzyme systems (galactose dehydrogenase, glutamate dehydrogenase, hexokinase, and isocitrate dehydrogenase) using the same buffer system were unsuccessful. Extracts of *Eucharis* leaf tissue are characteristically mucilaginous, which may impede electrophoretic separation or contribute to degradation of some enzymes after extraction. Also, cathodally migrating isozymes cannot be resolved in the same vertical acrylamide gel as anodally migrating isozymes.

RESULTS

PHENETIC ANALYSES

Principal Component Analysis (Figs. 4, 5; Table 6). Cumulative variance of 71.9% across 20 OTUs was resolved in the first three principal components (PCs). Characters 5 (stamen width),

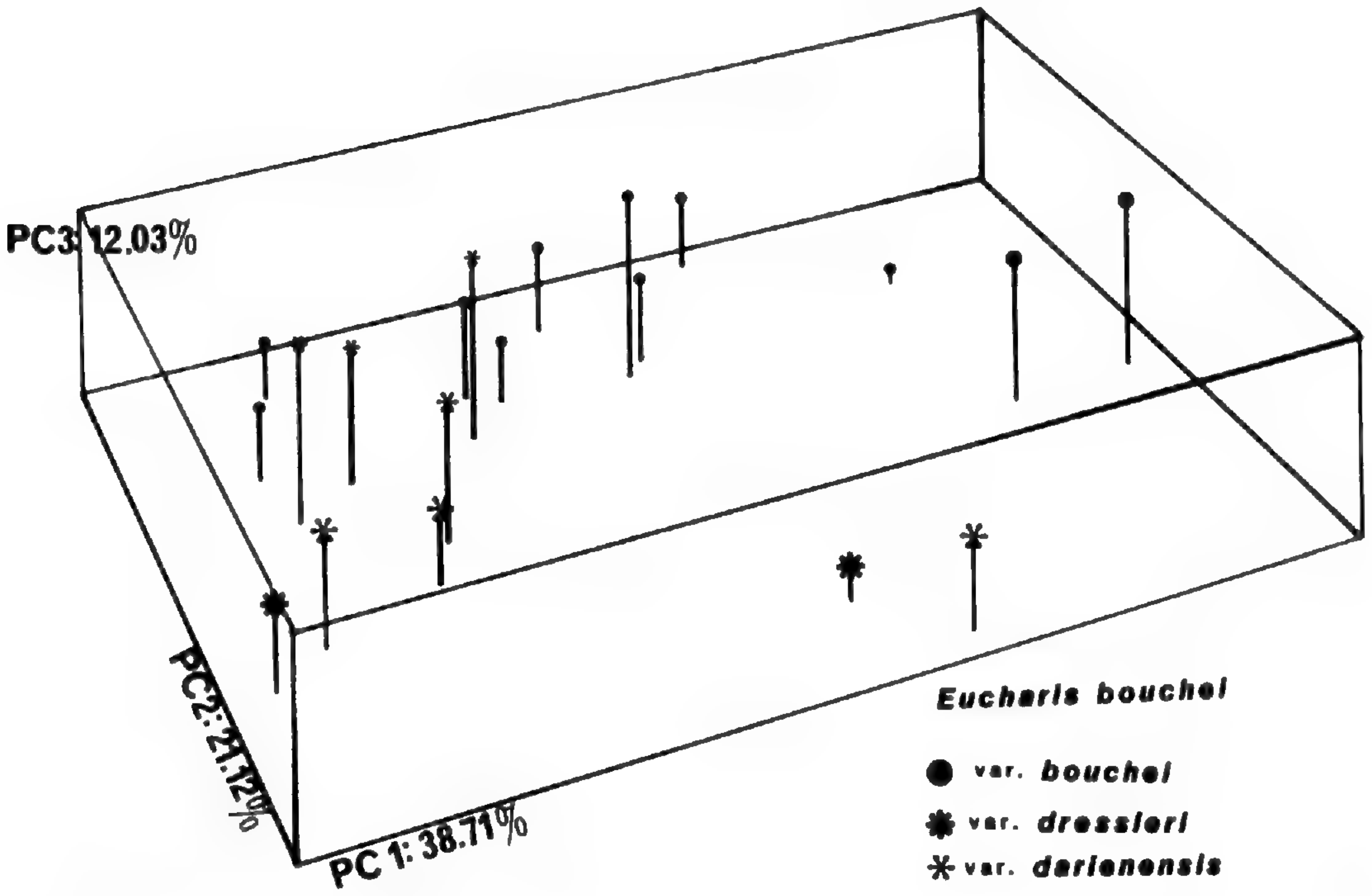


FIGURE 4. PCA scattergram based on variance across 17 floral characters in 20 OTUs representing *Eucharis bouchei*.

6 (tube length), 9 (inner tepal length), and 14 (toothing) contributed the greatest magnitude of variance to PC1, especially character 6. PC2 is largely a measure of outer tepal length (character 8), inner tepal width (11), staminal cup width (13), and toothing (14). Characters 1, 7, and 14 also substantially contributed to the variance reflected in PC2. Characters 2 (limb spread), 3 (length of free filament), 13 (staminal cup width), and 15 (toothing) were the most important sources of variance in PC3.

The three varieties of *E. bouchei* do not clearly resolve into three phenetic groups in Figure 4. Although var. *bouchei* shows a tendency to assemble along PC2 (21.1% total variance), this variety is still widely distributed along PC1 (38.7% total variance). One OTU each of var. *darienensis* (no. 11) and var. *dressleri* (no. 2) form an outlying group, as do OTUs 6, 7, and 15 of var. *bouchei*. Variety *darienensis* shows a measure of phenetic congruence, but intergrades with var. *bouchei*.

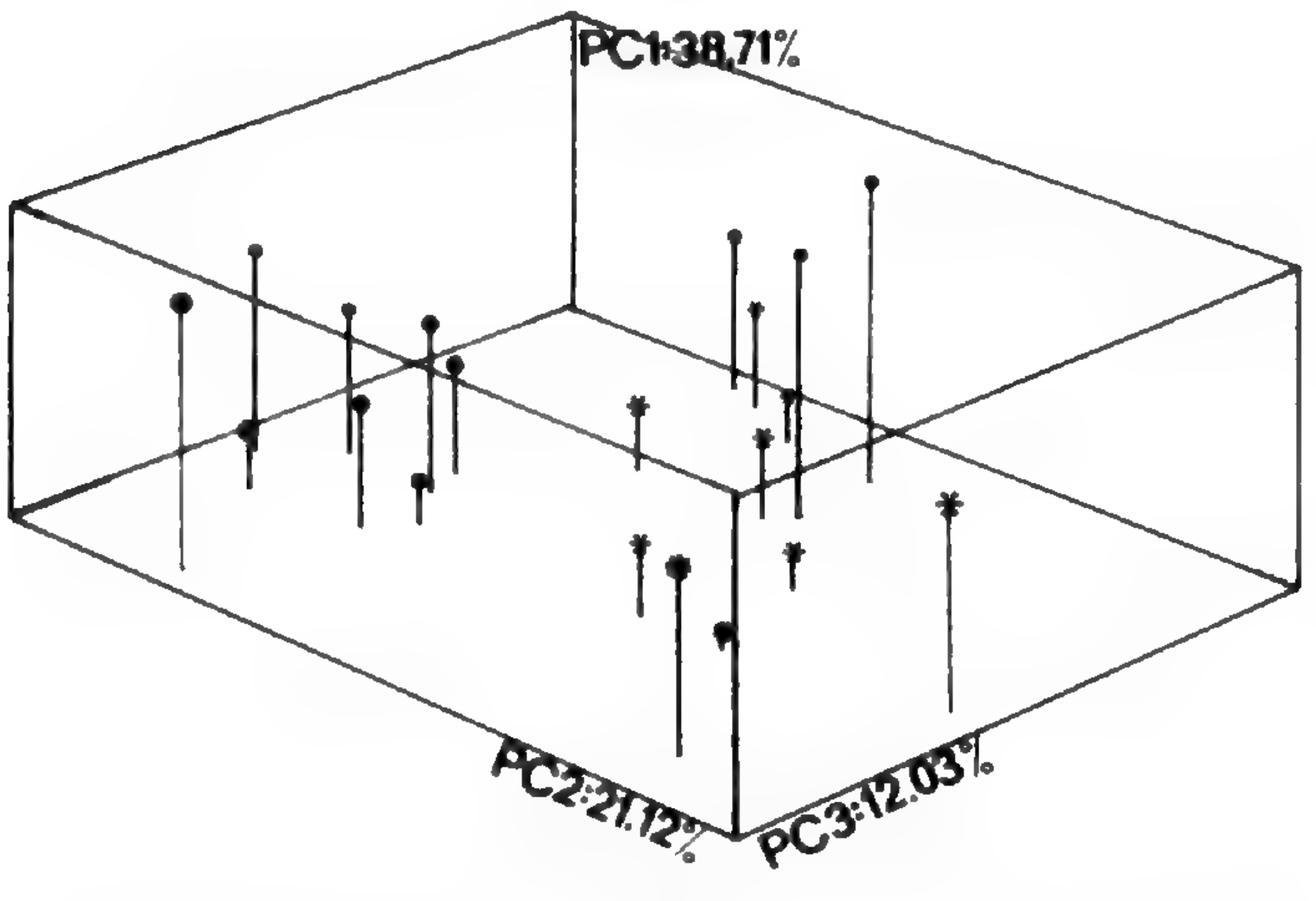


FIGURE 5. PCA scattergram based on variance across 17 floral characters in 20 OTUs representing *Eucharis bouchei*, with PC2&3 emphasized.

If the scattergram for the *E. bouchei* complex is rotated so that PC2 and PC3 are visually accentuated (Fig. 5), grouping of OTUs becomes largely a measure of androecial variance. In this scattergram, the three varieties are resolved more clearly, particularly var. *bouchei*. Variety *darienensis*, however, still intergrades with several OTUs of var. *bouchei*, but one of these OTUs (8) was collected from Cerro Campana in Panamá Province, an area of sympatry between these two varieties. The third (no. 7) is a Costa Rican collection.

Cluster analysis (Fig. 6). Two major clusters are resolved in the UPMGA dendrogram, each fairly heterogeneous. The first clusters at a distance coefficient (DC) of 1.356. An outlying OTU (one of two representing var. *dressleri*) fuses with this cluster at DC 1.921. Within this first cluster, two subgroups emerge at DCs 1.207 and 1.213, respectively. The former is made up entirely of OTUs representing var. *darienensis*. The second represents var. *bouchei*, with the single exception of OTU 5 (var. *darienensis*). OTU 5 forms together with OTU 8 (var. *bouchei*) an outlying cluster to this second subgroup.

The second major cluster is formed at a DC of 2.502, near where all clusters finally merge (DC 2.779). This smaller cluster is more hetero-

TABLE 6. First three principal components for multivariate analysis of the *Eucharis bouchei* complex.

Character Number	Component Number 1	2	3
1	0.151	0.317	0.120
2	−0.265	−0.189	0.340
3	−0.244	0.112	−0.440
4	−0.197	−0.141	−0.147
5	−0.375	0.129	0.059
6	−0.615	0.099	0.133
7	0.032	−0.302	−0.116
8	−0.100	−0.336	−0.106
9	−0.404	0.069	−0.061
10	0.017	0.168	−0.239
11	−0.030	0.386	0.137
12	0.156	−0.062	−0.045
13	0.013	−0.353	−0.524
14	−0.232	−0.381	0.216
15	−0.184	0.322	−0.436
16	−0.007	0.056	−0.121
17	−0.046	−0.195	0.020
Percent of Variance	38.71	21.12	12.03

geneous than the first, but four OTUs of var. *bouchei* cluster at a DC of 2.112. As in PCA, OTUs 2 and 11 (var. *dressleri* and *darienensis* respectively) form a phenetic group.

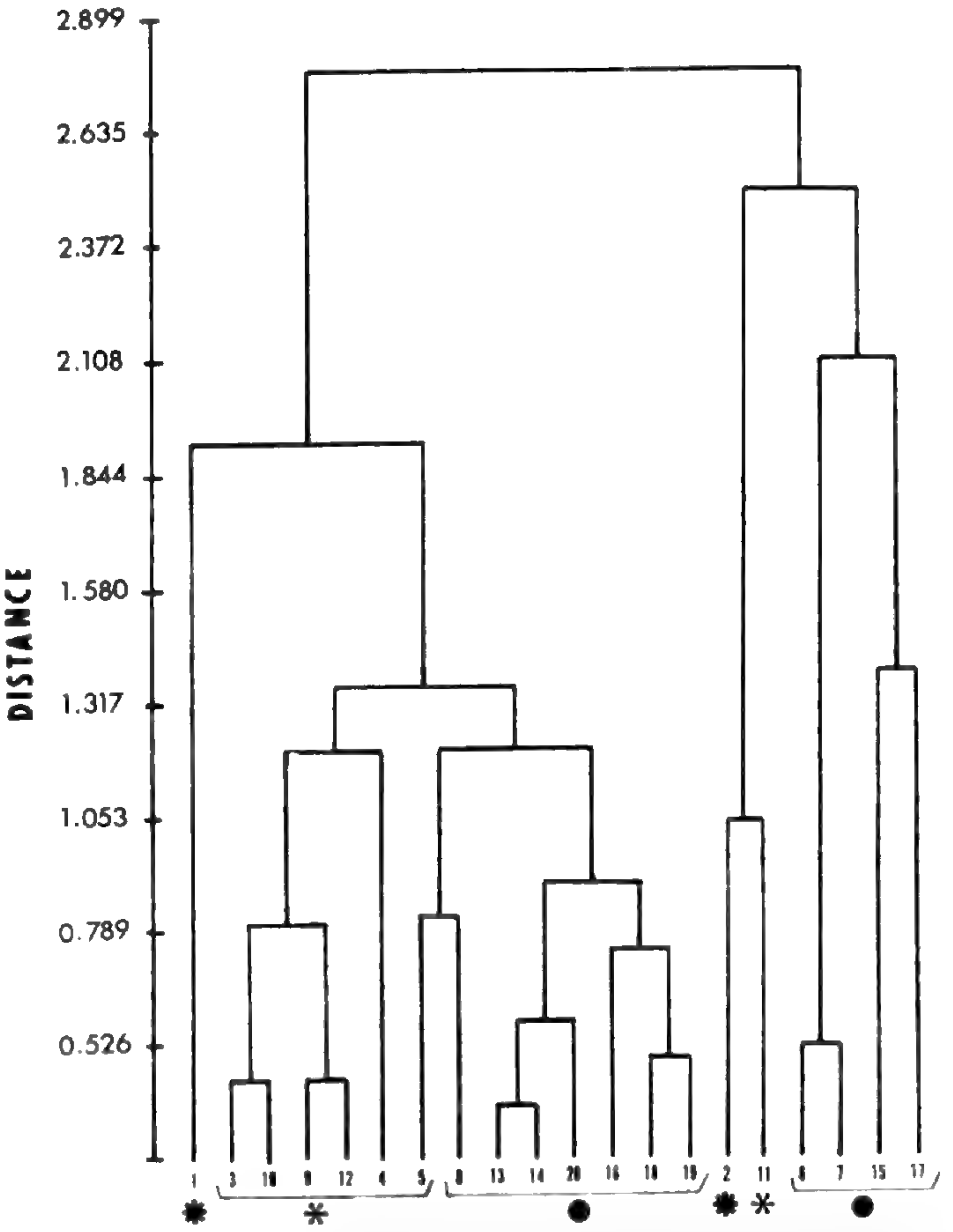


FIGURE 6. Cluster analysis dendrogram based on variance across 17 floral characters in 20 OTUs representing *Eucharis bouchei*. Refer to Table 1 for identification of OTUs.

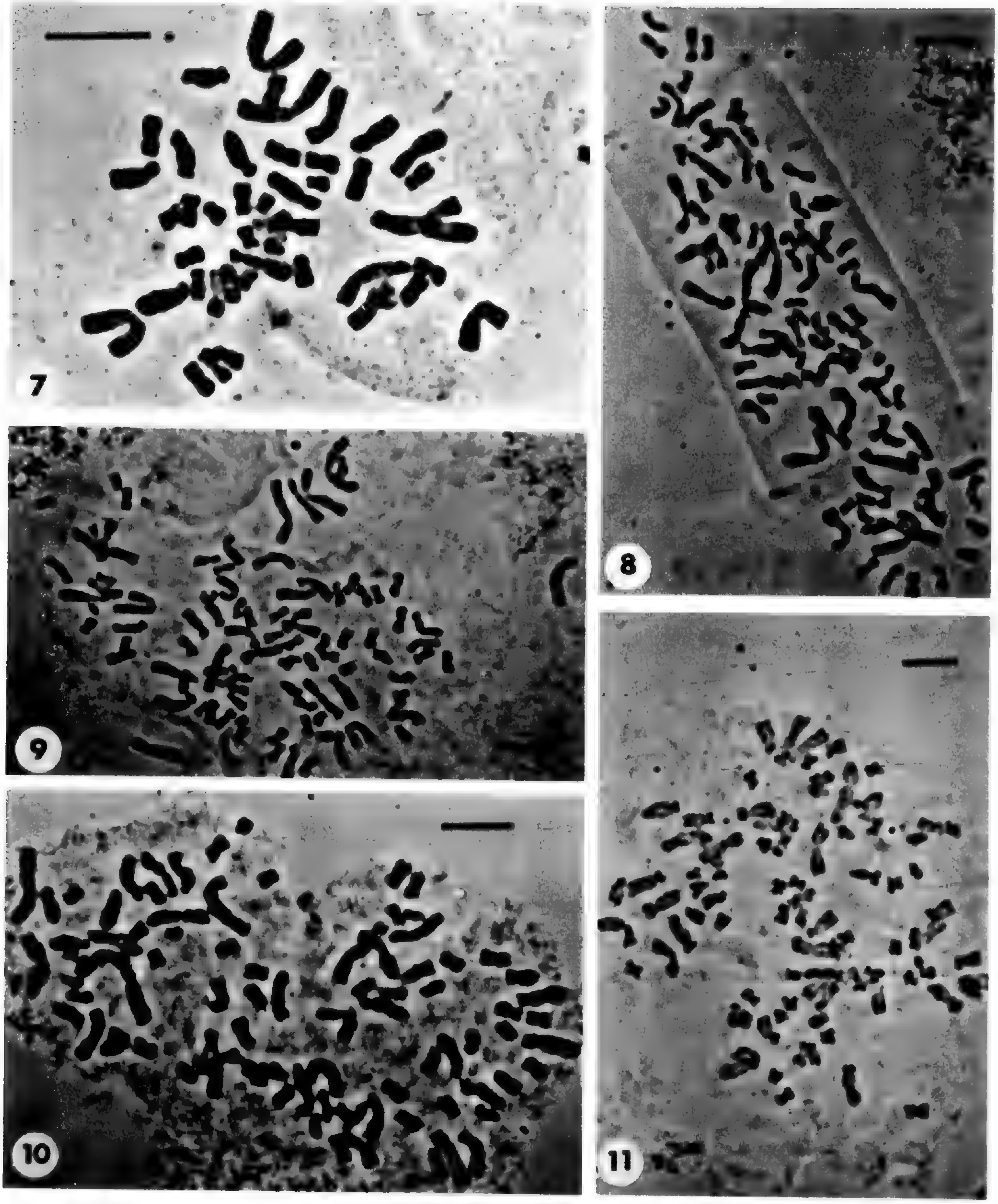
KARYOTYPE ANALYSIS

Tetraploidy in *Eucharis* is known so far to characterize only *E. bonplandii* and *E. bouchei*. Karyotypically, the tetraploid *Eucharis* species are strongly heteromorphic (Figs. 7–12; Table 7). Karyotypes of two geographically isolated and morphologically distinct populations of *E. bouchei* var. *bouchei*, from Coclé and Colón provinces of Panama (Figs. 9, 10, 12A, B; Table 7) are quite different. The second largest chromosome pair is submetacentric in the Cerro Brujo (Colón) population of *E. bouchei* (Figs. 10, 12B) and also in *E. bonplandii* (Figs. 11, 12C). *Eucharis bouchei* var. *dressleri* is an unstable tetraploid (Figs. 7, 8, 12D). Fifty percent of all root cells from which metaphase counts were obtained had 46 chromosomes.

ELECTROPHORETIC ANALYSES

Of the five enzyme systems assayed, only SKDH was monomorphic across all populations of *E. bouchei* and *E. bonplandii*. Only polymorphic loci are discussed below and diagrammed in Figure 14.

AAT (Figs. 13A, 14). Two well-separated regions of activity were resolved for AAT, one rapidly migrating anodally (AAT-1) and the other (AAT-2) considerably slower; these probably represent two different loci of this dimeric enzyme. Electromorphs at both loci were considerably more complex than in diploid species of *Eucharis* (Meerow, 1986). Two putative alleles are inferred from the phenotypes of AAT-1 in the *E. bouchei* complex. Each "allele" of AAT-1 in all *Eucharis* characteristically resolves as two very closely spaced bands. This may be the result of breakdown products forming after extraction (see Fig. 1 in Shields et al., 1983). Electromorphs of pollen of diploid ($2n = 46$) *Eucharis* (Meerow, unpubl.) also showed this banding pattern. Were each component band of the doublet a distinct allele, pollen would be expected to show only one of the two (Gottlieb, 1982, 1984). Alternatively, if the high diploid chromosome number ($2n = 46$) of *Eucharis* was originally tetraploid-derived (Meerow, 1987a), the doublet banding pattern may reflect duplication of the genome and would show up in pollen.



FIGURES 7–11. Root-tip cell mitotic metaphase configurations of tetraploid *Eucharis* species. 7, 8. *E. bouchei* var. *dressleri*.—7. Diploid cell.—8. Tetraploid cell.—9. *E. bouchei* var. *bouchei* from Colón Province in Panama.—10. *E. bouchei* var. *bouchei* from Coclé Province in Panama.—11. *E. bonplandii*. Two small chromosomes are outside the figure frame. All scales = 10 μm.

Band a was the most common "allele" of AAT-1, found in all individuals analyzed except for two putative homozygotes for "allele" c (the Cerro Brujo population and one individual of the El Valle population of var. *bouchei*). Variety *dressleri* and *E. bonplandii* are homozygous for "allele" a. The Río Iguanito individual of var. *bouchei* is homozygous for "allele" b, while two individuals of the El Valle population show a putatively heterozygous phenotype with apparent heterodimerization.

Four *E. bouchei* individuals resolved a four-banded electromorph at the putative AAT-2 locus. Bands f and g were found only in *E. bon-*

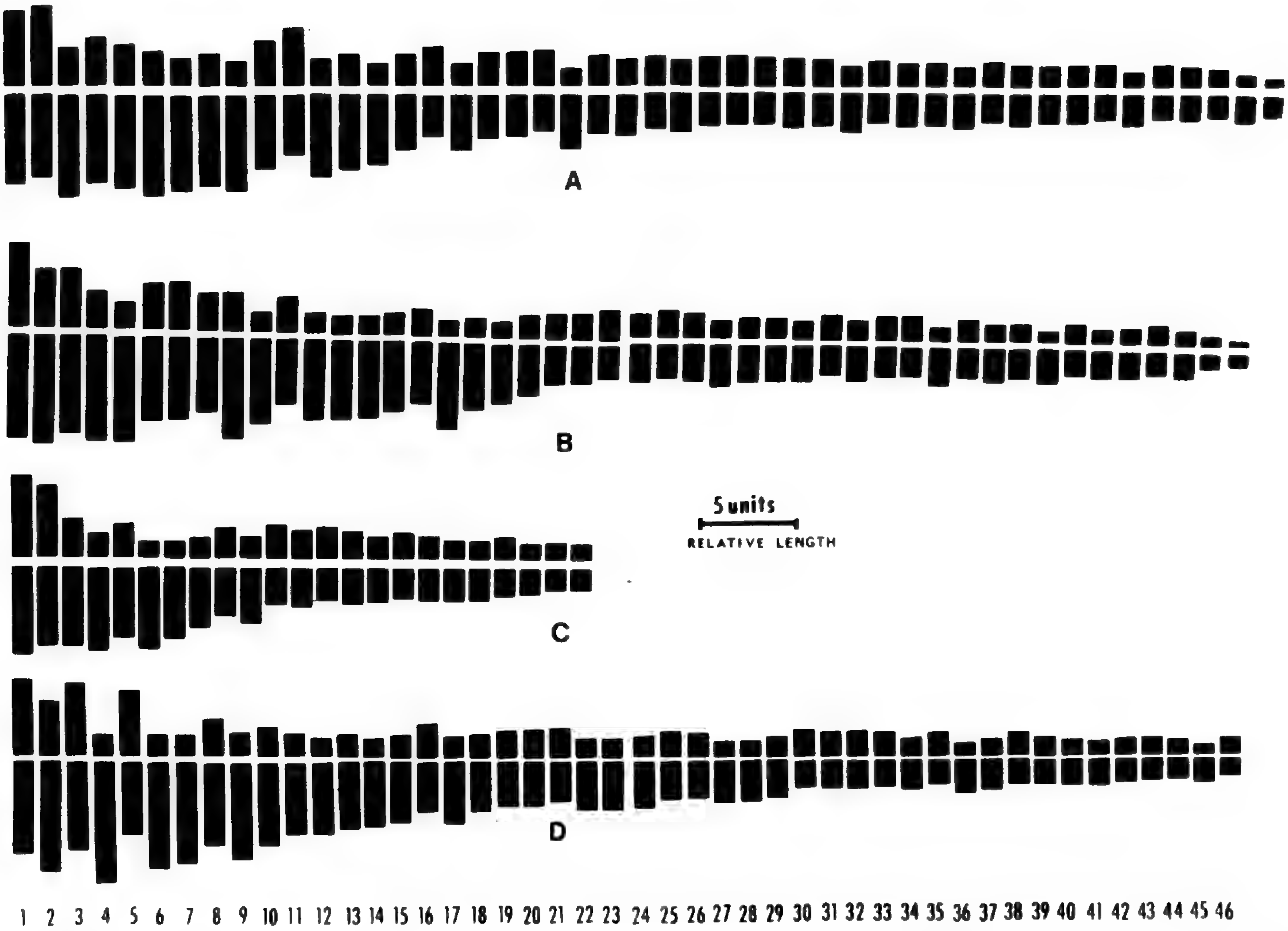


FIGURE 12. Haploid idiograms of tetraploid *Eucharis* karyotypes.—A. *E. bouchei* var. *bouchei* from Coclé Province in Panama.—B. *E. bouchei* var. *bouchei* from Colón Province in Panama.—C. *E. bouchei* var. *dressleri*, diploid cell.—D. *E. bonplandii.*

plandii. Only two bands were observed in var. *dressleri* (an unstable tetraploid), representing "alleles" a and b or b and c, and one individual of var. *bouchei* from El Valle ("alleles" c and d). All other individuals of *E. bouchei* resolved a four-banded electromorph for AAT-2. Band e was found in one of the three individuals of var. *bouchei* from El Valle. As all diploid species of *Eucharis* species resolve only a two-banded electromorph for this isozyme (Meerow, 1986), it was inferred that the proliferation of bands within *E. bouchei* represented the additive effects of tetraploidy (Crawford, 1983, 1985; Gottlieb, 1982).

MDH (Figs. 13B, 14). Malate dehydrogenase characteristically forms complex banding patterns that require genetic analysis to decipher (Kirkpatrick et al., 1985; Torres & Mau-Lastovicka, 1982). Consequently, no attempt is made to infer genotypes in any detail from the banding pattern. However, the phenotype of the most anodal bands in *E. bonplandii* suggests the presence of two alleles and their heterodimer [pollen of this species resolved only a single band at this locus in a repetitive run (Meerow, unpubl.), supporting this interpretation]. The intensity of the bands in the two most cathodal regions of several individuals suggests dosage effects in putative homozygotes (two individuals of EBB1, and EBB3 in Figs. 12B, 13).

GSSGR (Fig. 14). Two bands were observed in the single locus resolved for GSSGR, all individuals manifesting one or the other.

PGI (Fig. 14). Only a single region of activity was resolved for PGI. Two bands were observed, but the more anodal one was found only in the putative heterozygotes (two individuals of *E. bouchei* var. *dressleri,* and one of var. *bouchei* from El Valle), and in *E. bonplandii.*

Isozyme relationships. The nine individuals for which electrophoretic phenotypes were resolved were coded for presence or absence of the numbered bands in Figure 14, creating a data set of 19 characters. Phenotypes for PGI were not included in the cluster analysis, as data were not available for all nine individuals. The resulting

TABLE 7. Karyotype data, *Eucharis bouchei* and *E. bonplandii*. All vouchers deposited at FLAS unless otherwise stated.

Taxon, Voucher, & Fig. No.	Chromosome Number	Chromosome Size Range (μm)	Chromosome Size Range (relative length)[a]	Chromosome Size[b] Groups				Chromosome[c] Morphology				
				L	ML	M	S		L	ML	M	S
Eucharis bouchei var. *dressleri*[d] (*Meerow 1107*) Figs. 7, 8, 12C	46, 92	2.4–11.9	2.0–9.7	4	10	14	18	m:	4		2	
								nm:			6	10
								sm:		4	6	8
								st:		6		
E. bouchei var. *bouchei* (*Meerow 1157*) Figs. 9, 12B	92	1.6–15.5	0.5–5.3	14	16	14	48	m:				2
								nm:	2		2	18
								sm:	10	6	6	28
								st:	2	10	6	
E. bouchei var. *bouchei* (*Meerow 1125*) Figs. 10, 12A	92	2.0–10.4	0.8–4.5	10	18	16	48	m:	2	2	4	6
								nm:	2		6	28
								sm:	6	8	4	14
								st:		8	2	
E. bonplandii (*Bauml 686*, HUNT) Figs. 11, 12D	92	1.9–9.7	1.0–4.9	14	12	24	42	m:				6
								nm:	6		6	18
								sm:	2	4	16	18
								st:	6	8	2	

[a] Based on a value of 100 for the haploid complement.
[b] L = long, ML = moderately long, M = medium, S = small.
[c] m = metacentric, nm = near-metacentric, sm = submetacentric, st = subtelocentric.
[d] Diploid cell analyzed.

UPGMA dendrogram (Fig. 15) and cladogram (Fig. 16) illustrate the isozyme relationships among these individual plants. As might be expected, both trees are similar in topology. All three individuals of *E. bouchei* var. *dressleri* (EBD) cluster at a distance coefficient (DC) of only 0.118, indicating their close isozyme relationship. The El Valle (Coclé Province) population of var. *bouchei* (EBB1) is rather diverse in its patterns of isozyme variation. Two individuals are similar, clustering at a DC of 0.118. This cluster then fuses with the Río Iguanita (Colón Province) individual of var. *bouchei* (EBB3) at a DC of 0.176. The remaining individual of El Valle var. *bouchei* EBB1 shows greater isozyme relationship to Cerro Brujo (Colón Province) var. *bouchei* EBB2 than other convarietal individuals from El Valle. This heterogeneous cluster then fuses with var. *dressleri* (EBD) at a DC of 0.431, followed by the other El Valle individuals (EBB1) and the single Río Iquanita (EBB3) individual (DC 0.443). The single individual representing *E. bonplandii* (EBN) remains a distant outlyer from all plants of *E. bouchei*, joining the latter species at a DC of 0.625.

The cladogram based on isozyme data was 27 steps long with a consistency index (Kluge & Farris, 1969; CI = total length minus homoplasies, divided by total length) of 0.704. The cladogram supports a monophyletic origin of *E. bouchei* var. *dressleri* (EBD) from var. *bouchei* (EBB1) in Coclé Province, but suggests that var. *bouchei* may be polyphyletic. The Río Iguanita (Colón Province, EBB3) individual of var. *bouchei* forms a monophyletic group with two individuals of El Valle (Coclé province, EBB1) var. *bouchei*, while the other Colón individual (Cerro Brujo, EBB2) forms a monophyletic group with the third El Valle individual.

DISCUSSION

The Central American *E. bouchei* complex does not resolve into discrete phenetic groups. Staminal cup morphology, however, does separate varieties to a fair degree (Fig. 5). Floral size characters in this group (Figs. 4, 6) do not succeed as well in resolving phenetic groups.

Chromosome number is very stable in *Eucharis*, and polyploidy is infrequent. The origins of the polyploids (i.e., whether auto- or alloploid)

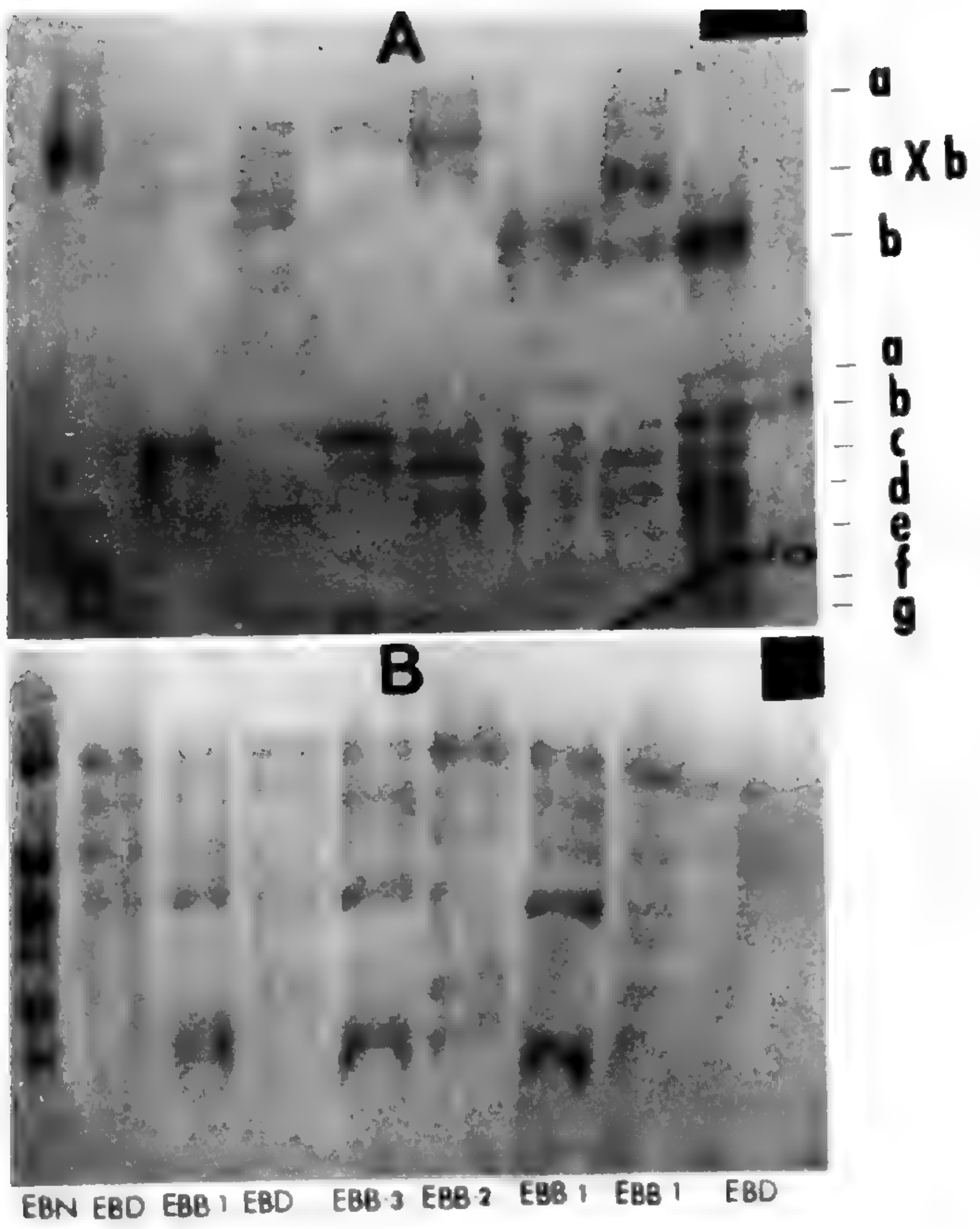


FIGURE 13. Representative gels for electrophoretic analysis of *Eucharis bouchei* complex.—A. Aspartate amino transferase (AAT).—B. Malate dehydrogenase (MDH). Anodal end of gel is at top of figure. Where no activity is apparent, it was subsequently resolved in repetitive runs. Lower case letters to right refer to putative alleles discussed in text. Refer to Table 4 for population designations.

are inconclusive (attempts to secure meiotic figures have been unsuccessful), but the high levels of morphological diversity in *E. bouchei* might suggest that they are alloploids. Differences in chromosome morphology among the populations of *E. bouchei* examined (Table 7) suggest that structural changes in the chromosomes may have been important in interpopulational divergence. *Eucharis bouchei* var. *dressleri* is an unstable tetraploid. Somatic cells of the root tips have both tetraploid (92) and diploid (46) counts. Snoad (1955) reported karyotype instability in *Hymenocallis narcissiflora* (Jacq.) Macbr. (Amaryllidaceae), but aneuploid numbers as well as polyploid counts were observed in the cells of the latter species.

Polyploid species of *Eucharis* do not show any marked effects of increased chromosome number beyond an increase in size of root cells and stomata, and slight thickening of the leaf blades. *Eucharis bonplandii,* in addition, develops a glaucous bloom on the leaves in strong light, a novel characteristic for the genus.

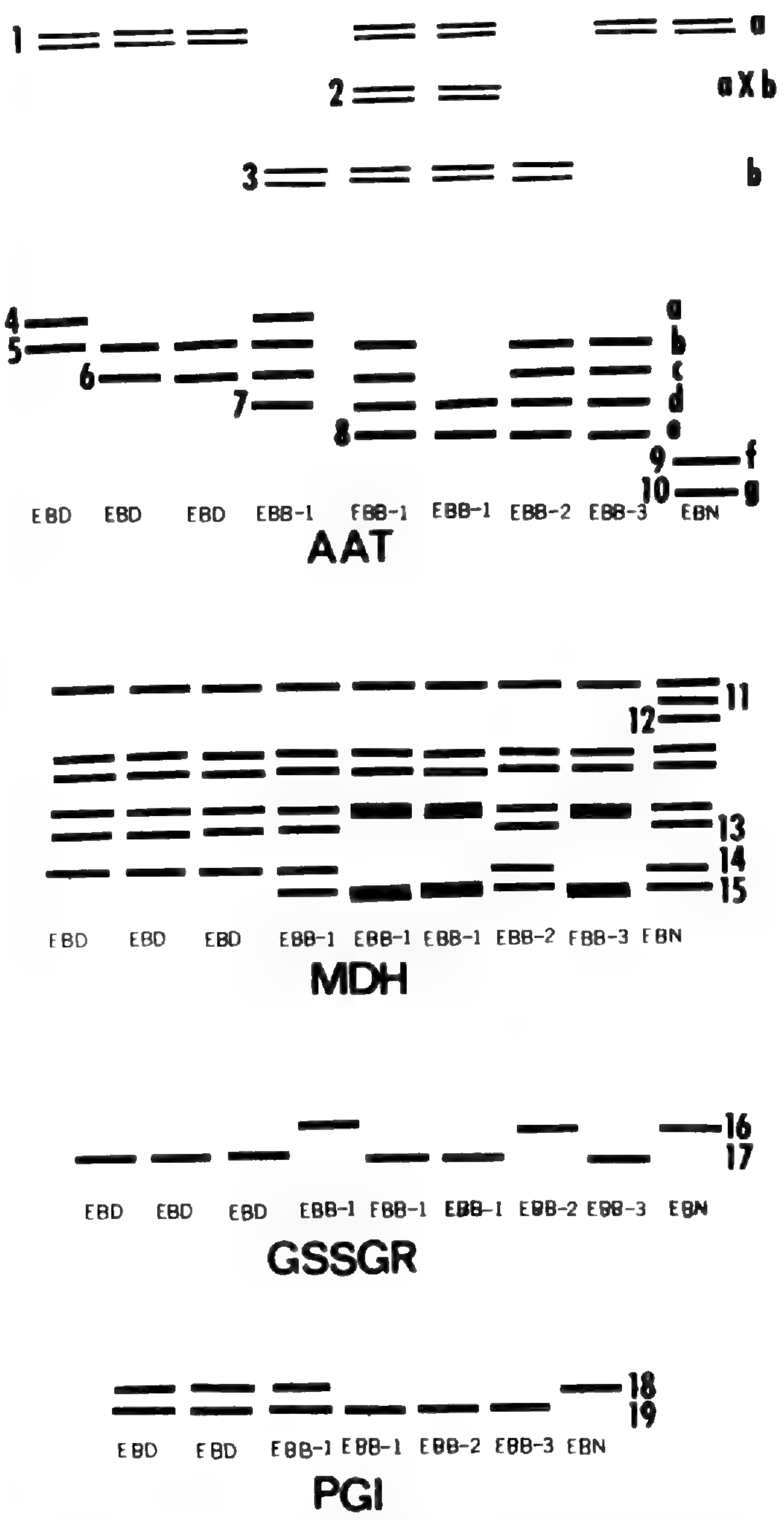


FIGURE 14. Electrophoretic phenotypes at all polymorphic loci in the *Eucharis bouchei* complex. Anodal end at top. Lower case letters to right refer to putative alleles discussed in text. Numbers refer to bands coded in presence/absence data matrix. Refer to Table 4 for population designations. AAT = aspartate amino transferase, MDH = malate dehydrogenase, GSSGR = glutathione reductase, PGI = phosphoglucoisomerase.

Eucharis bouchei var. *bouchei,* as presently conceived (Meerow, 1986), is diverse in floral morphology, chromosome morphology, and patterns of isozyme polymorphisms. Cladistic relationships based on the isozyme data indicate that this polymorphic variety may even be polyphyletic. Morphologically EBB3 is similar to "typical" El Valle var. *bouchei* (Fig. 1Aii). Though floral morphological differences exist between the El Valle and Cerro Brujo populations of var. *bouchei* (Fig. 1Aiii), they are not discontinuous

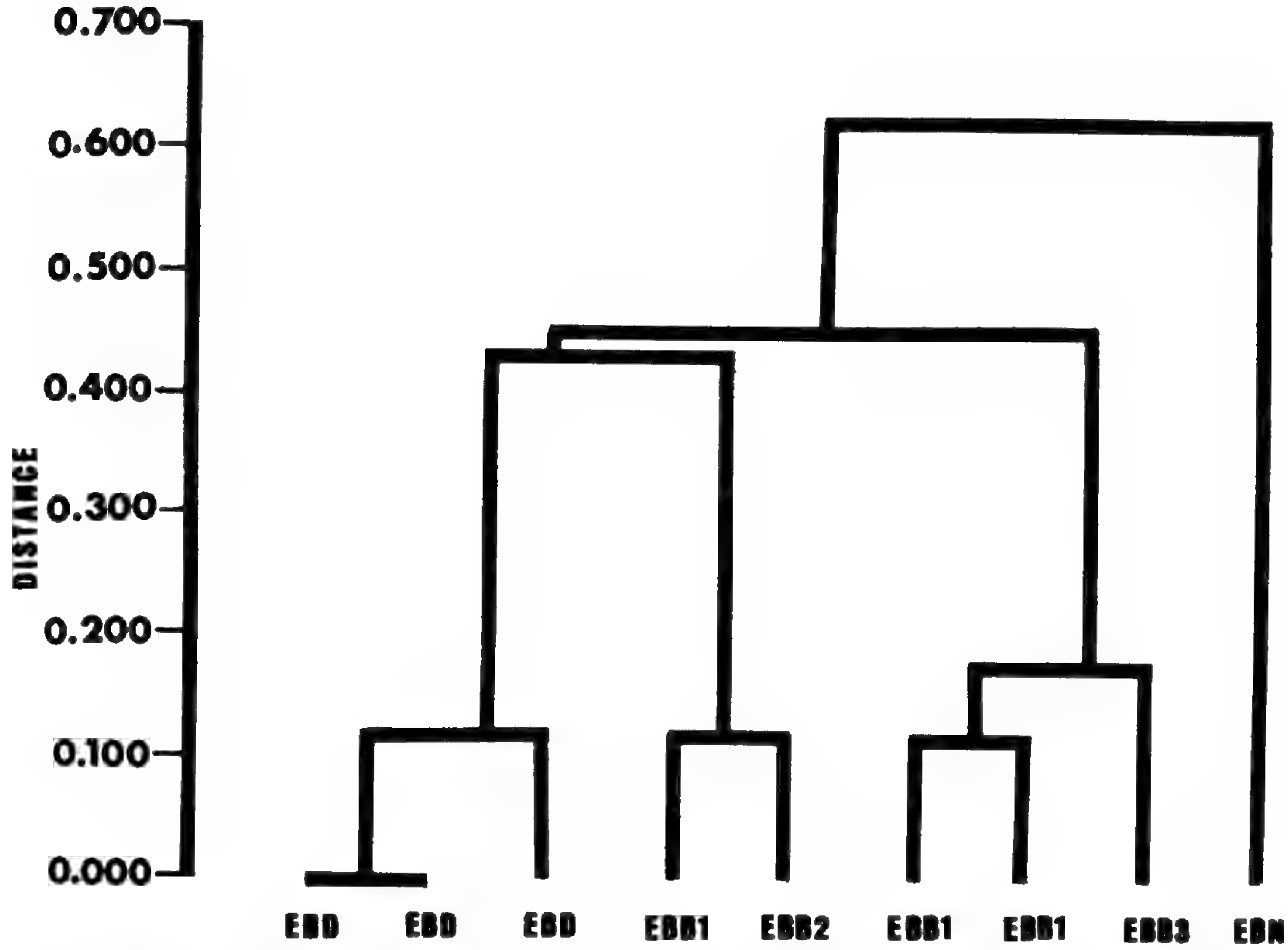


FIGURE 15. UPGMA dendrogram of tetraploid *Eucharis* isozyme phenotypes. Refer to Table 4 for population designations.

enough to warrant a clear differentiation of a fourth variety in the species. The two individuals representing different populations from Colón Province each have closer isozyme relationship to Coclé var. *bouchei* than they have to each other, while the Coclé population itself appears isozymically diverse. Cladistic relationships based on this data imply that Coclé populations of var. *bouchei* may be of heterogeneous ancestry. The cladogram (Fig. 16) also points to Colón Province as the likely origin of those ancestors. Divergence between and among the Coclé populations and those in Colón Province, presumably mediated by geographic isolation, may thus be an ongoing process.

On the basis of staminal cup morphology, I hypothesize that *Eucharis bouchei* has been steadily migrating away from the Colombian border (Meerow, 1986). The Cerro Brujo population of *E. bouchei* var. *bouchei* may represent an intermediate point in the divergence of a new geographical race of *E. bouchei*. The best test of this hypothesis would be the results of isozyme analysis of *E. bouchei* var. *darienensis*, the one variety for which material is not presently available. Variety *darienensis* occurs closer to the Colombian border than any other population of *E. bouchei* and has the most generalized staminal cup morphology relative to *Eucharis* as a whole. If my hypothesis is correct, var. *darienensis* should have the lowest genetic identity with populations of either var. *bouchei* or var. *dressleri* from Coclé Province, and higher identity with populations of var. *bouchei* from Colón Province.

Colón populations of *E. bouchei* are geographically intermediate between most populations of var. *darienensis* and the Coclé populations of var. *bouchei* (Meerow, 1986). The two varieties come into close proximity in the Cerro Campana area in Panamá Province. Colón populations may therefore also be genetically intermediate between the two varieties. Segregating genotypes in such a case could produce populations exhibiting a mosaic of varying genetic identity, some close to Coclé var. *bouchei*, others perhaps closer to var. *darienensis*. Further testing of this hypothesis with var. *darienensis* and larger numbers of populations and individuals is necessary.

Eucharis bouchei var. *dressleri* occurs sympatrically as a rare morph with populations of var. *bouchei*. The origin of var. *dressleri* may be the first step in sympatric speciation. This variety shows greatest isozyme relationship with certain individuals of the Coclé population of var. *bouchei*. In this regard, the presence of a second band for PGI in certain individuals of var. *dressleri* and El Valle var. *bouchei* may be significant (Fig. 14), but a larger number of individuals must be assayed to confirm this observation. This va-

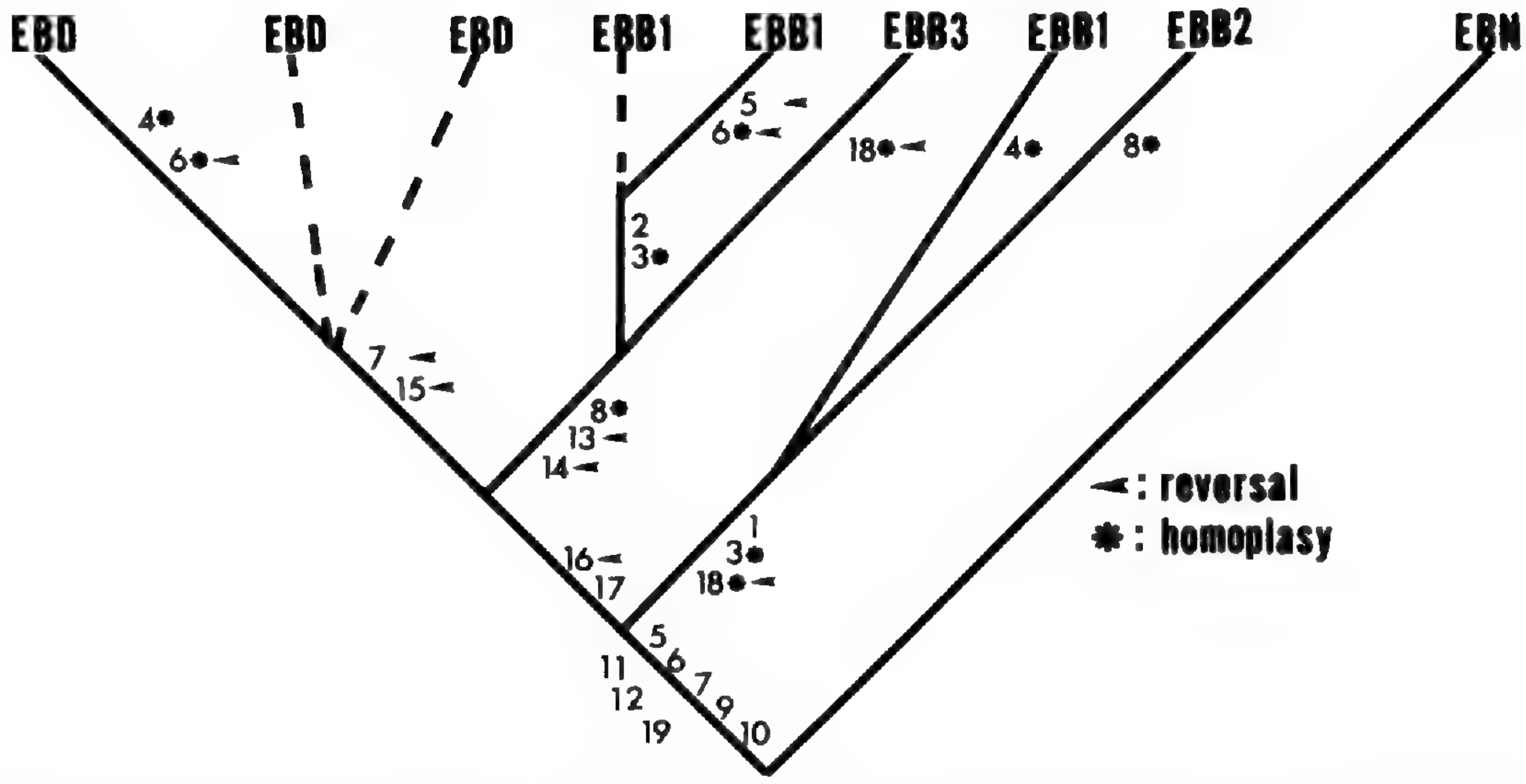


FIGURE 16. Cladogram based on isozyme phenotypes of tetraploid *Eucharis*. Refer to Table 4 for population designations. Broken line indicates zero-length branch.

riety is also an unstable tetraploid. Fifty percent of all chromosome counts of root tip cell mitotic metaphase configurations have $2n = 46$, the typical diploid chromosome number in *Eucharis*. Variety *dressleri* lacks the additive banding patterns or heterozygote phenotypes observed in both loci of AAT in all other populations of *E. bouchei*, a factor, perhaps, of this karyotypic instability. Additive enzyme banding patterns have been observed in a number of tetraploid taxa of *Gossypium* (Cherry et al., 1972), *Nicotiana* (Reddy & Garber, 1971; Sheen, 1972; Smith et al., 1970), *Triticum aestivum* (Hart, 1970, 1979; Jaaska, 1978; Torres & Hart, 1976), and *Stephanomeria* (Gottlieb, 1973), and are usually interpreted as indicative of allopolyploid origins (Crawford, 1983; Gottlieb, 1983; Soltis & Rieseberg, 1986). Pollen stainability of var. *dressleri* is 100% with Alexander's (1969) stain, suggesting that gamete formation is not impaired by the chromosome number instability. Nonetheless, I have not successfully crossed this variety with El Valle populations of var. *bouchei*.

The rare Colombian tetraploid *E. bonplandii* also lacks either heterozygote or additive banding patterns for AAT. This may indicate an autopolyploid origin for this species (Crawford, 1985; Soltis & Rieseberg, 1986), or at least a lower degree of heterozygosity than in *E. bouchei*. The rarity of this species, in relative contrast to *E. bouchei*, fits Stebbins's (1980) model of the "unsuccessful" autopolyploid. The difficulty in obtaining successful meiotic figures from bulbs of *Eucharis* (microsporogenesis occurs completely inside the bulb) blocks investigation of this question. *Eucharis bonplandii* exhibits large distance on the basis of isozyme phenotypes from all individuals of *E. bouchei*. The question of whether these two species represent a monophyletic group on the basis of their tetraploid origin is not conclusive.

Increased heterozygosity is an expected consequence of allopolyploidy (Crawford, 1983, 1985; Gottlieb, 1981a; Soltis & Rieseberg, 1986). A certain degree of fixed heterozygosity would also be expected in an allopolyploid (Gottlieb, 1981a; Soltis & Rieseberg, 1986), due to the presence of two genomes in the allotetraploid. Although it is premature to assess the degree of heterozygosity present in tetraploid *Eucharis*, their morphological diversity and isozyme polymorphisms indicate that it may be high.

There is insufficient information on the breeding system and pollination biology of *Eucharis* to support more than ad hoc hypotheses of the origin of most species in the genus. The characteristically small population sizes that are encountered throughout its range may indicate that founder effects (Mayr, 1954; Templeton, 1980a, 1980b) have played an important role in the movement of *E. bouchei* across the Isthmus of Panama, with subsequent isolation restricting gene flow between localized populations. The putatively allotetraploid genotype and karyotypic polymorphy of *E. bouchei* would favor the "hybrid recombination" type of "genetic transilience," a mode of speciation hypothesized by Templeton (1980a, 1980b). This is consistent with the distribution of *E. bouchei*, most populations of which are geographically isolated from each other (Meerow, 1986). Additional support comes from the morphological novelties expressed within each geographical variety (or race, in the case of var. *bouchei*). Templeton's model of speciation requires a period of successful inbreeding after the initial founding event. Though *Eucharis* are primarily out-crossing, evidence from greenhouse studies indicates only partial self-incompatibility (Meerow, 1986). At least one Amazonian species of subg. *Eucharis* [*E. castelanaena* (Baillon) Macbride] is autogamous (Meerow, 1986).

EUCHARIS IN CENTRAL AMERICA

Gentry (1982) suggested that two major opportunities, widely spaced in time, existed for floristic interchange between Central and South America. The first, occurring during the Late Cretaceous, was limited to a series of volcanic islands (the proto-Antilles; Dengo, 1975; Lillegraven et al., 1979). The degree to which this island arc remained above water is unknown. At the beginning of the Tertiary, however, this link between the continents was disrupted as the proto-Antilles began a northward displacement. It was not until the late Tertiary that the second opportunity for floristic interchange began to coalesce, as formation of the Central American trench and new volcanic activity gave rise to a new series of islands. These islands eventually formed lower Central America, with a land bridge across the Isthmus of Panama firmly established in the Pliocene, only ca. 3 million years ago (Keigwin, 1978; Marshall et al., 1982). Gentry (1982) concluded that only very well-established Cretaceous taxa would have been able to take advantage of the earlier connection via island-hopping. Entries into Central America dating from this earlier connection would be expected to show strong taxonomic differentiation in Central America. Gentry (1982) cited tribe Crescentieae of the Bignoniaceae as a putative example of early colonization of Central America by island-hopping, followed by taxonomic differentiation. On the contrary, any migration dating from the Pliocene or Pleistocene would not be expected to show much differentiation at the specific or at the generic level. I have characterized the *Eucharis bouchei* complex as a semispecies complex of geographically isolated races or varieties not yet strongly differentiated. Patterns of isozyme variation, chromosome cytology, and morphological variation in this group suggest that entry of *Eucharis* into Central America was fairly recent.

The species of subg. *Eucharis* geographically closest to *E. bouchei* is *E. bonplandii*, a rare species of central Colombia, and also tetraploid. It is inconclusive whether these two species represent a monophyletic tetraploid group. Nonetheless, the congruence of phytogeography with chromosome number in these two species suggests that this may indeed be the case. It is tempting to wonder if tetraploid *Eucharis* were at one time more common in northern Colombia, and if *E. bouchei* and *E. bonplandii* represent the remnant populations of a once more widespread, ancestral tetraploid complex. Prance's (1982) most recent distribution of Pleistocene refugia based on phytogeographic patterns includes both a Río Magdalena refuge in northern Colombia (most collections of *E. bonplandii* are from the Río Magdalena valley south of Prance's proposed refuge), and a Darién refuge in southwestern Panama. *Eucharis bouchei* var. *darienensis* is most common in the area of the Darién refuge and is putatively the least derived variety of the species. The absence of collections of *Eucharis* subg. *Eucharis* from northern Colombia is something of a mystery but may indicate that extinction of intervening populations between *E. bonplandii* and *E. bouchei* was widespread in the recent geological past.

CONCLUSIONS

The Central American *E. bouchei* complex is a tetraploid, putatively alloploid, possibly highly heterozygous, semispecies complex (sensu Grant, 1981) still actively evolving. Discrete patterns of isozyme divergence have not yet solidified between morphologically distinct and geographically isolated populations of *E. bouchei* var. *bouchei*. Founder effects and geographic isolation probably were, and still are, important forces influencing the continued evolution of *E. bouchei*. In one case (*E. bouchei* var. *dressleri*) sympatric divergence may be in process.

The unprecedented degree of variation in *E. bouchei* is thus likely the result of two main factors: (1) tetraploidy, accompanied or followed by structural rearrangement of chromosomes, and (2) a geologically recent colonization of Central America by this primarily northern Andean and Amazonian genus. The wide variation present in *E. bouchei* likely represents the segregating phenotypes of a richly diverse genetic base. On the basis of known distributions, it appears that substantial geographic barriers exist between groups of populations, probably restricting gene flow between them. Left undisturbed, as is *not* the case in the Neotropics today, these aggregates could conceivably one day each justify specific recognition.

The fact that *E. bonplandii* is the northernmost species of *Eucharis* subg. *Eucharis* in South America, and is also tetraploid, lends at least circumstantial credence to the hypothesis that *E. bouchei* and *E. bonplandii* diverged from a common tetraploid ancestor. The rare occurrence of polyploidy in *Eucharis* strengthens this possibility.

Stebbins (1985), in a recent review of polyploidy, found a correlation between high frequency of polyploidy and patchy geographical (or ecological) distributions, coupled with the occurrence of secondary contact between these differentiated populations. Levin (1983) discussed how chromosome doubling may " 'propel' a population into a new adaptive sphere." Though *E. bouchei* does not exhibit any noticeably novel ecological adaptations, its success in colonizing the Isthmus of Panama may have been aided by its polyploid-related genetic diversity. The heterogeneous isozyme patterns characteristic of El Valle var. *bouchei* may indicate either multiple ancestry for this population or that secondary contact has occurred between it and populations in Colón or Panama provinces to the east.

Eucharis bouchei offers an excellent opportunity for detailed study of the evolution of a tropical rainforest organism. Future work should seek to quantify in greater detail the genetic variation present within and among populations of this actively evolving complex. Meiotic pairing figures from dissection of bulbs may help confirm the nature of the polyploid origins of this species.

Paleotropical genera of "infrafamily" Pancratioidinae characteristically have $2n = 22$ or 20 chromosomes (Ponnamma, 1978; Zaman & Chakraborty, 1974), while almost all neotropical genera have $2n = 46$ (Di Fulvio, 1973; Flory, 1977; Meerow, 1987a, 1987b; Williams, 1981). The latter number is likely derived through fragmentation or duplication of a single chromosome, followed by doubling of the genome (Lakshmi, 1978; Sato, 1938). Increased heterozygosity may therefore have accompanied a tetraploid origin of the neotropical tribes of the Pancratioidinae from an ancestor with $2n = 22$ [the somatic number characteristic of *Pancratium* L., the largest paleotropical genus of the subfamily (Ponnamma, 1978)]. The high generic diversity of neotropical pancratioids (ca. 15 genera) in comparison with the paleotropical taxa (4 genera) itself may be partially a consequence of greater genetic variability. Comparative analysis of isozyme phenotypes between paleotropical and neotropical genera is planned and may provide insight into the evolution of the Pancratioidinae.

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THE SHRUBBY GENTIAN GENUS *MACROCARPAEA* IN PANAMA

KENNETH J. SYTSMA[1]

ABSTRACT

A single species of the lisianthoid genus *Macrocarpaea* had been known from Panama. Recent explorations of previously inaccessible cloud forest peaks in western, central, and eastern Panama have turned up additional species previously known only from Costa Rica and Colombia. Three species are now recorded from Panama: *M. browallioides*, *M. macrophylla*, and *M. subcaudata*. Evidence is provided to merge the Costa Rican *M. valerii* into *M. macrophylla*.

The shrubby gentians of the Neotropics are some of the most conspicuous elements of higher elevation tropical forests. This complex of about 16 genera comprised Grisebach's (1838) tribe Lisyantheae. These lisianthoid genera are notoriously difficult to separate taxonomically with the consequence that they have often been treated as synonyms of *Lisianthius* (or its orthographic variant "*Lisianthus*"). The taxonomic difficulties are compounded by their remote montane habitat which makes them poorly collected. Only *Lisianthius* sensu stricto (Weaver, 1972a) and *Macrocarpaea* (Ewan, 1948) have been adequately monographed. Other genera of the tribe Lisyantheae are now being taxonomically revised in a multidisciplinary study (Maas et al., 1984; Maas, 1985).

Macrocarpaea (Griseb.) Gilg is one of four lisianthoid genera in Panama (Elias & Robyns, 1975). *Symbolanthus pulcherrimus*, *Irlbachia alata* subsp. *alata* (formerly *Chelonanthus alatus*), and seven species of *Lisianthius* (Sytsma, 1987) also occur in Panama. These four genera can be separated in Panama by the following characteristics:

1a. Main stem terete; stigma capitate; old placentae visible as whitish bands along margins of mature capsules; pollen grains as monads .... *Lisianthius*
1b. Main stem usually quadrangular; stigma bifurcate; old placentae not visible on mature capsules; pollen grains as monads or tetrads.
  2a. Flowers 6–10 cm long; corolla funnelform; more or less distinct, membranaceous; corona scalelike; pollen grains as tetrads .... *Symbolanthus*
  2b. Flowers to 5 cm long; corolla usually campanulate; corona absent; pollen grains as monads or tetrads.
    3a. Leaves sessile; bracteoles never leafy; calyx 4–6 mm long; pollen grains as tetrads .... *Irlbachia*
    3b. Leaves petiolate; bracteoles leafy; calyx 6–20 mm long; pollen grains as monads .... *Macrocarpaea*

The genus *Macrocarpaea* is centered in the Andes of northern South America but extends into the Amazon Basin and the Guayana Highland. Of the approximately 30–50 species in the genus, only eight are known from Central America and adjacent West Indies. *Macrocarpaea domingensis* Urban & E. Ekman and *M. thamnoides* (Griseb.) Gilg are restricted to the Dominican Republic and Jamaica, respectively. Cuba has two endemic species, *M. pinetorum* Alain and *M. pauciflora* Alain. Three species have been described from Costa Rica (Weaver, 1972b): *M. subcaudata* Ewan, *M. valerii* Standley, and *M. acuminata* Weaver. A single species, the endemic *M. browallioides* (Ewan) Robyns & S. Nilsson, has been known from Panama near the border of Costa Rica (Elias & Robyns, 1975). The type specimen had represented the only collection for this apparently epiphytic shrub prior to 1975.

Recent explorations of cloud forest habitats in central regions of the Cordillera Talamanca, a ridge extending from the border of Costa Rica to near Panama City, and in the Cordilleras of the Darién near Colombia have provided additional sites for the previously known *Macrocarpaea* and new *Macrocarpaea* species for Panama. These explorations were conducted under the auspices of the Missouri Botanical Garden through the Flora of Panama Project (funded by NSF grant BSR-8305425). *Macrocarpaea subcaudata*, an epiphytic shrub known previously from only two collections in one region of Costa

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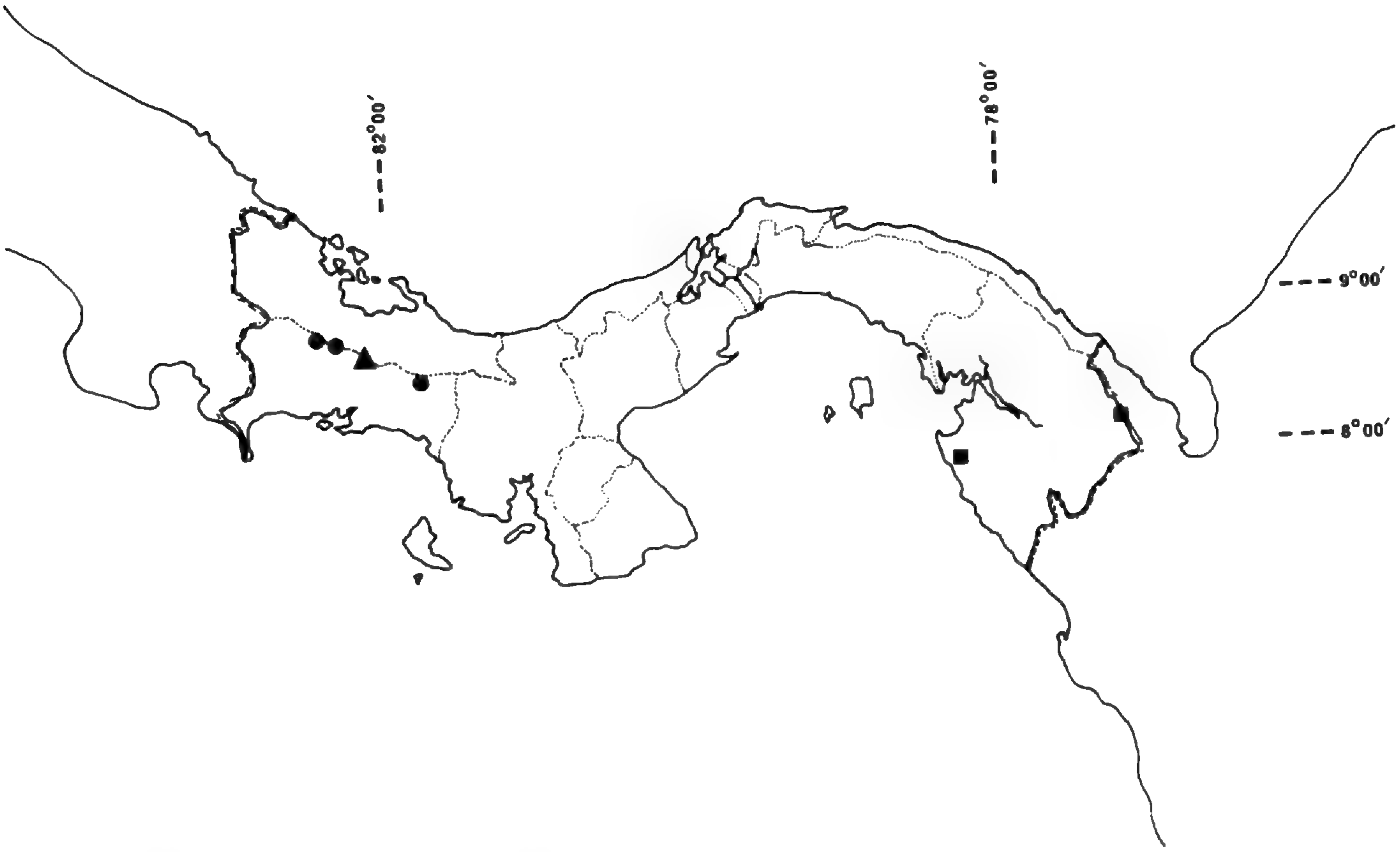

FIGURE 1. Geographical distribution of the genus *Macrocarpaea* in Panama. Circle = *M. browallioides*; square = *M. macrophylla*; triangle = *M. subcaudata*.

Rica, occurs in one cloud forest region in the mountains of central Panama. Recent additional collections of *M. browallioides* now extend the range of this distinctive epiphytic shrub. Several populations similar to both the Costa Rican *M. valerii* and the Colombian *M. macrophylla* (Kunth) Gilg are now known from the Darién. Analysis of morphological variation among the Costa Rican, Panamanian, and Colombian populations provides a basis for merging *M. valerii* with the now more widespread *M. macrophylla*.

KEY TO *MACROCARPAEA* IN PANAMA

1a. Calyx 6–14 mm long, lobes ovate-oblong, rounded at apex.
  2a. Epiphytic viny subshrub, leaves narrowly lanceolate, to 18 cm long and 5 cm wide .... 1. *M. subcaudata*
  2b. Terrestrial shrub to 4 m, leaves broadly elliptic, to 45 cm long and 26 cm wide .... 2. *M. macrophylla*
1b. Calyx 15–18 mm long, lobes triangular, acute to cuspidate at apex .... 3. *M. browallioides*

1. **Macrocarpaea subcaudata** Ewan, Contr. U.S. Natl. Herb. 29: 224. 1948. TYPE: Costa Rica: [San José] La Palma, *Wercklé 16492* (holotype, US; isotype, NY).

Epiphytic, viny subshrub. Leaves essentially glabrous except for small scattered hairs, somewhat thickened, narrow-lanceolate, to 18 cm long and 5 cm wide; petioles to 23 mm long. Inflorescence terminal or axillary from upper nodes, dichasium bi- or tri-ternately compound, often long-stalked. Calyx campanulate, greenish, glabrescent, 6–9 mm long; lobes slightly unequal, ovate-oblong, rounded or ciliolate at tips, 5–7 mm long, 3–4 mm wide. Corolla greenish yellow, to 3 cm long; tube to 2.3 cm long; lobes slightly recurved (incurved when dried), narrowly triangular, to 9 mm long, to 6 mm wide. Stamens inserted near middle of corolla tube; filaments to 17 mm long, just surpassing corolla lobes; anthers yellow, 4–5 mm long. Style just surpassing anthers. Capsules woody, 10–12 mm long ex. persistent beak of 3 mm. Flowering period at least mid-April through May.

Distribution. 1,500 m in mountains east of San José, Costa Rica and between 1,150–1,260 m near continental divide between Chiriquí and Bocas del Toro provinces in central Panama (Fig. 1).

Additional specimens examined. PANAMA. BOCAS DEL TORO: Continental divide on carretera del oleoducto ca. 1 km N of Quebrada Arena, IRHE Hydroelectric Project, *Knapp 5089* (MO), *McPherson 8613* (MO). CHIRIQUÍ: Along road between Gualaca and IRHE Hydroelectric Project, 10.1 mi. NW of Los Planes de Hornito, *Antonio 4190* (MO).

Macrocarpaea subcaudata occurs only in central Costa Rica and northcentral Panama. Determining whether this disjunction is real or not must await further collecting in as yet inaccessible cloud forest regions of both countries. Relationships of *M. subcaudata* to other species of *Macrocarpaea* are unclear. *Macrocarpaea browallioides* of Panama shares the epiphytic habit with *M. subcaudata*, but the two are clearly unrelated. Ewan (1948) considered *M. cerronis* Ewan and *M. salicifolia* Ewan from the tepuis of the Guayana Highland to be the closest relatives of *M. subcaudata*. The former two species (with related *M. arborea* (Britton) Ewan, *M. quelchii* (N.E. Br.) Ewan, and *M. tepuiensis* (Gleason) Steyerm.), however, differ from all other species of *Macrocarpaea* in having pollen in tetrads (Nilsson, 1968, 1970). Maas (1985) combined these six *Macrocarpaea* species with pollen in tetrads into *Irlbachia quelchii* (N.E. Br.) Maas. Weaver (1972b) cited *M. acuminata* Weaver and two West Indian species as the closest relatives of *M. subcaudata*. The Costa Rican *M. acuminata* is almost certainly related to, if not conspecific with, *M. macrophylla* (including *M. valerii*). *Macrocarpaea acuminata* and *M. macrophylla* share with *M. subcaudata* similar calyx features and might be close relatives of *M. subcaudata*.

2. **Macrocarpaea macrophylla** (Kunth) Gilg, Nat. Pflanzenfam. 4(2): 94. 1895. *Lisianth(i)us macrophyllus* Kunth, Nov. Gen. & Sp. 3: 183. 1819. TYPE: Colombia: trail over paramillo to Almaguer between Pansitara and Río Ruiz, 8,400 ft., *Humboldt & Bonpland* (Willd. Herb. 3561 fide Grisebach; MO photo 37455, of collection in Humboldt Herbarium at Paris).

Macrocarpaea valerii Standley, Publ. Field Mus. Bot. 18: 928. 1938. TYPE: Costa Rica: La Hondura de San José, *Valerio 692* (F).

Erect shrub or subshrub to 4 m tall. Leaves essentially glabrous, except for scattered small hairs, venation strongly prominent, broad-elliptic, to 45 cm long and to 26 cm wide, blade acute or abruptly acuminate; petioles to 3 cm long. Inflorescence terminal or axillary from upper nodes, dichasium simple or bi- or tri-ternately compound, long-stalked. Calyx campanulate, fleshy, 8–14 mm long; lobes strongly unequal, ovate-oblong, hyaline-margined, 3–6 mm long and wide. Corolla greenish-white or cream, narrowly to openly campanulate, to 3.5 cm long; tube 2.5–3.0 cm long; lobes recurved, broadly triangular, 6–8 mm long and wide. Filaments to 18 mm long, included in or surpassing corolla tube; anthers yellow, 3–5 mm long. Style to 15 mm long; stigma bilobed, the lobes 2 mm long. Capsules woody, to 20 mm long, persistent-beaked. Flowering period at least May through July.

Distribution. 1,000–1,800 m in mountains of Central Costa Rica; 1,000–1,400 m in Serranía del Sapo and Serranía del Darién of Darién Province, Panama (Fig. 1); and common at 1,500–2,500 m in the western and central Cordilleras of Colombia.

Additional specimens examined. PANAMA. DARIÉN: NE slope of Summit, Cerro Sapo, approach from Garachiné, *Hammel 7263* (MO); top of Cerro Mali, 10-year-old second growth on site of old helipad, Serranía del Darién, Panama/Colombia frontier, Cerro Tacarcuna expedition, *Gentry & Mori 13655* (MO), *Gentry et al. 16975* (MO).

Macrocarpaea macrophylla is distinctive as a tall erect shrub with large round leaves and prominent venation. As here defined, *M. macrophylla* ranges from Colombia to Costa Rica. Standley originally described the Costa Rican *M. valerii* based only on the type specimen. Ewan (1948) reiterated the differences between the two species based on only two Costa Rican collections. These differences were confined to size and shape of leaves and to corolla shape. Both sets of characters are subject to sampling error depending on how the plants were collected and pressed. Subsequently, additional collections of "*M. valerii*" in Costa Rica indicated that these features were not consistent, causing Weaver (1972b) to state that "the two are virtually identical, except the calyx of *M. valerii* is glabrous, while that of *M. macrophylla* is spiculate." Colombian, Panamanian, and Costa Rican specimens of these two taxa at MO and WIS showed considerable variation in the degree of surface ornamentation on the calyx. No consistent calyx differences or other foliar and floral differences were seen among specimens described as *M. macrophylla* and *M. valerii*. This necessitates the inclusion of these Colombian, Panamanian, and Costa Rican specimens into *M. macrophylla* (Kunth) Gilg, the name with priority.

3. **Macrocarpaea browallioides** (Ewan) Robyns & S. Nilsson, Bull. Jard. Bot. Natl. Belgique 40: 13. 1970. *Lisianth(i)us browallioides* Ewan, Proc. Biol. Soc. Washington 64: 132. 1951. TYPE: Panama. Bocas del Toro: northern slopes of Cerro Horqueta, Robalo Trail, *Allen 4932* (MO).

Epiphytic shrub to 1.5 m tall. Leaves glabrous, ± coriaceous, dark green and black-punctate above, gray-green below, elliptic to ovate-elliptic, to 11 cm long and to 5 cm wide; petioles to 25 mm long. Inflorescence a compound dichasium, ± long-stalked. Calyx campanulate, light green, 15–20 mm long; tube short; lobes ovate-triangular, strongly overlapping, 12–16 mm long, acute to long-acuminate at apex. Corolla fleshy, yellow-green to cream yellow, infundibuliform, 3.0–4.0 cm long; lobes subequal, ovate-triangular, acute at apex, to 1.2 cm long. Stamens inserted ca. 6 mm above base of corolla tube, ± exserted; anthers yellow, 5–6 mm long. Style just surpassing anthers. Capsule woody, to 14 mm long, excluding persistent beak of 6–8 mm. Flowering in February, May, August, and late November.

Distribution. 1,690–2,200 m, cloud forests of cerros Horqueta, Pate Macho, and Colorado, provinces of Chiriquí and Bocas del Toro.

Additional specimens examined. PANAMA. BOCAS DEL TORO: forest along trail from end of Río Palo Alto road to Chiriquí/Bocas del Toro border near peak of Cerro Pate Macho, *Hammel 5781* (MO). CHIRIQUÍ: Cerro Pate Macho, ca. 5 mi. NE of Boquete, trail to continental divide leading to Finca Serrano, *Antonio 2654* (MO); Cerro Colorado, along mining road 31.6 km beyond bridge over Río San Felix, 10.6 km beyond turnoff to Escopeta, *Croat 37155* (MO); Cerro Pate Macho, along the continental divide, on trail which leads to Finca Serrano, NE of Boquete, *Croat 48537* (MO); NW of Pate Macho, *Hammel 6112* (MO); NW ridge of Cerro Pate Macho from summit to Finca Serrano, *Sytsma et al. 4900* (MO).

Macrocarpaea browallioides is easily distinguished from the other Central American species of *Macrocarpaea* by its large calyx and long-acuminate calyx lobes. Like *M. subcaudata* it is epiphytic, but unlike *M. subcaudata* it is erect rather than viny. Several of the collectors do not mention an epiphytic habit. However, the distinction between an epiphytic and terrestrial habit is tenuous on an extremely wet, peatlike soil as is encountered on Cerro Pate Macho. True epiphytic as well as free-standing (although on mats of living roots or trunks) individuals of *M. browallioides* were seen on this cloud forest peak. The relationship of this species to other members of *Macrocarpaea* is unclear. Neither Ewan, who first described the species as a *Lisianthius,* nor Robyns and Elias, who transferred it to *Macrocarpaea,* gave any indication as to its likely relatives. Only three known species approach *M. browallioides* with its distinctive short calyx tube and long, overlapping, and acuminate-tipped lobes: *M. cochabambensis* Gilg of Bolivia; *M. glabra* (L.f.) Gilg endemic to paramo vegetation above Bogotá, Colombia; and *M. guttifera* Ewan of Amazonia, Brazil.

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MONOECY AND SEX CHANGES IN *FREYCINETIA* (PANDANACEAE)[1]

HANS-HELMUT POPPENDIECK[2]

ABSTRACT

In cultivation, two species of the basically dioecious genus *Freycinetia* (Pandanaceae) have produced pistillate and staminate inflorescences both sequentially and simultaneously on individual plants. These findings are discussed, together with other cases of occasional deviations from dioecy.

According to most textbooks and general reference works the genus *Freycinetia* is considered to be dioecious (Warburg, 1900; Heywood, 1979; Dahlgren et al., 1985; Stone, 1984), although some exceptions have been noted (Stone, 1972; Cox, 1981; Cox et al., 1984), drawing attention to the significance of these presumably rare exceptions to the dioecious condition. In *Freycinetia reineckei* Warb., Cox has observed functionally bisexual spikes, and both pistillate and staminate inflorescences on the same branch in *Freycinetia scandens* Gaudich., and Stone (1972) has noted the same in *Freycinetia negrosensis* Merr. and *F. imbricata* Blume.

The following observations made in the tropical greenhouses of the Hamburg Botanical Garden confirm and extend these earlier observations and, by adding some new pieces to the puzzle, seem to indicate that sex expression in this genus is to a considerable extent under environmental control. Both *Freycinetia funicularis* (Savigny in Lam.) Merr. and *F. cumingiana* Gaudich. (synonymous with *F. luzonensis* Presl, according to Stone) have been observed to show monoecy.

Both of the species mentioned above are easily cultivated from cuttings, and the material in cultivation probably represents single clones of each, so that the observations made at different places relate to genetically identical plants. *Freycinetia funicularis* is comparatively widely distributed in German botanic gardens, but its origin cannot be ascertained; however, it is a native of Indonesia, and probably was introduced from the Botanic Gardens in Bogor (formerly Buitenzorg), where it has been in cultivation for perhaps a century and still is common.

Freycinetia cumingiana (*F. luzonensis*) is a Philippine species which came to Hamburg from the Bonn Botanic Garden, and according to the curator there, Dr. K. Kramer (pers. comm.), it was introduced to Europe via Tübingen from a source in the U.S.A., initially under the name "*F. cunninghamiana.*" It has been possible to trace this clone back to its original source. Apparently it had been sent by E. D. Merrill from the Philippines to the New York Botanical Garden, from there to Puerto Rico, and to the Fairchild Tropical Garden in Miami, Florida, where it caught the attention of Dr. R. A. Howard of Harvard University, who reported his observations to Dr. B. C. Stone (see Table 1). Eventually this species found its way to Europe, perhaps from the Fairchild Tropical Garden.

OBSERVATIONS ON GROWTH AND SEX EXPRESSION

Observations on both species are summarized in Table 1. It is remarkable that despite the pronounced differences in shoot architecture (see Fig. 1), the two species have produced staminate and pistillate inflorescences, both sequentially and simultaneously. *Freycinetia cumingiana* apparently produces different kinds of shoots, predetermined to form either staminate or pistillate inflorescences. The latter are stouter and less ramified (Fig. 3). However, as shoot diameter decreases with age, the initially pistillate shoots convert to the production of staminate inflorescences. Evidently, shoot diameter and sex expression are correlated in this species. The qualitative "jump" may occur when the shoot diameter decreases to less than 4 mm (Fig. 2; Table 2). Perhaps this is also the diameter range wherein mixed inflorescences may form. In *Frey-*

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[1] My thanks to Dr. B. C. Stone for encouragement, to Dr. K. Kramer for details on *Freycinetia cumingiana*, J. Bogner on *F. funicularis*, Dr. M. Fallen and Prof. Dr. K. Kubitzki for advice, and Mrs. H. Schwob-Tonn and our greenhouse staff for expert cultivation.

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TABLE 1. Comparison of growth and flowering of two species of *Freycinetia* in the Hamburg Botanic Gardens, 1982–1986.

	Freycinetia funicularis	*Freycinetia cumingiana*
Morphology	Large climber ("rooter") with horizontal clinging roots and vertical roots; inflorescences lateral on at least one-year-old, still leafy shoots, often penetrating the leaf-bases.	Rhizomatous "leaner" with perennial shoots which may flower in 2nd year; inflorescences terminal on main axis or on rather elongated lateral shoots; shoots dimorphic, diam. ca. 5–6 mm in staminate shoots and 15–18 mm in pistillate shoots.
Flowering particulars		
1982	Abundant (ca. 50) inflorescences.	Several vegetative shoots; one fertile, with about 12 pistillate inflorescences.
1983	Abundant but exclusively pistillate inflorescences.	Only staminate inflorescences observed.
1984	Numerous staminate inflorescences plus a single pistillate inflorescence at the base of the plant; viable seeds and offspring obtained after hand-pollination.	Not recorded; allegedly staminate, but presence (or not) of pistillate inflorescences uncertain.
1985	Twelve staminate inflorescences, most produced later than usual after severe pruning had reduced the shade made by the plant itself.	Two ramified shoots with staminate inflorescences which had probably flowered the year before; 3 pistillate shoots, at least 2 flowering for the first time (Fig. 1); several fruits formed (no viable seed).
1986	No inflorescences on the old plant. Young plant (4 yr. old) with 12 staminate inflorescences mostly on vertical axes, 5 pistillate inflorescences on subapical parts of horizontally trained shoots, and one mixed inflorescence on a vertical shoot. Pollination yields fruits.	Staminate shoots continue to form staminate inflorescences; a pistillate shoot begins to produce staminate inflorescence on the distal parts (Fig. 2). Since 1984, only stout, apparently pistillate-determined shoots have been formed. New shoot formed in 1985 (diam. 6.2 mm) is pistillate.
Additional observations	Similar observations by J. Bogner in Munich Bot. Gard. Younger plants from cuttings first produced pistillate then both pistillate and staminate inflorescences in the next and subsequent years. Encke's account (1958) of "*Freycinetia insignis*" probably refers to *F. funicularis.*	A somewhat different sequence of flowering has been observed by Dr. K. Kramer (Bonn Bot. Gard.): the first inflorescences were staminate; later, also pistillate inflorescences were produced on basal parts of the branches. Eventually also mixed inflorescences were observed. Attempts to pollinate were not successful; no karyogamy had occurred. Same sequence observed by Dr. R. A. Howard, noted in a letter to Dr. B. C. Stone: "Sexes are a problem. I recall seeing pollen from one 'flower' but all I have are pistillate" (March 1969). "I assume the plant reproduced vegetatively and was completely female until this February, when I found an inflorescence producing pollen" (April 1969).

cinetia funicularis, this shoot differentiation is lacking, so that the synchronized formation of exclusively pistillate inflorescences in 1983 is unexplained. However, it seems to indicate that an adjustment over the whole vegetative body can take place, which may be hormonally (or nutritionally) determined. Observations made in the Munich Botanical Garden by Josef Bogner (pers. comm.) suggest that larger and vigorous plants of *F. funicularis* may develop inflorescences of both sexes.

It is difficult to assign these *Freycinetia* species

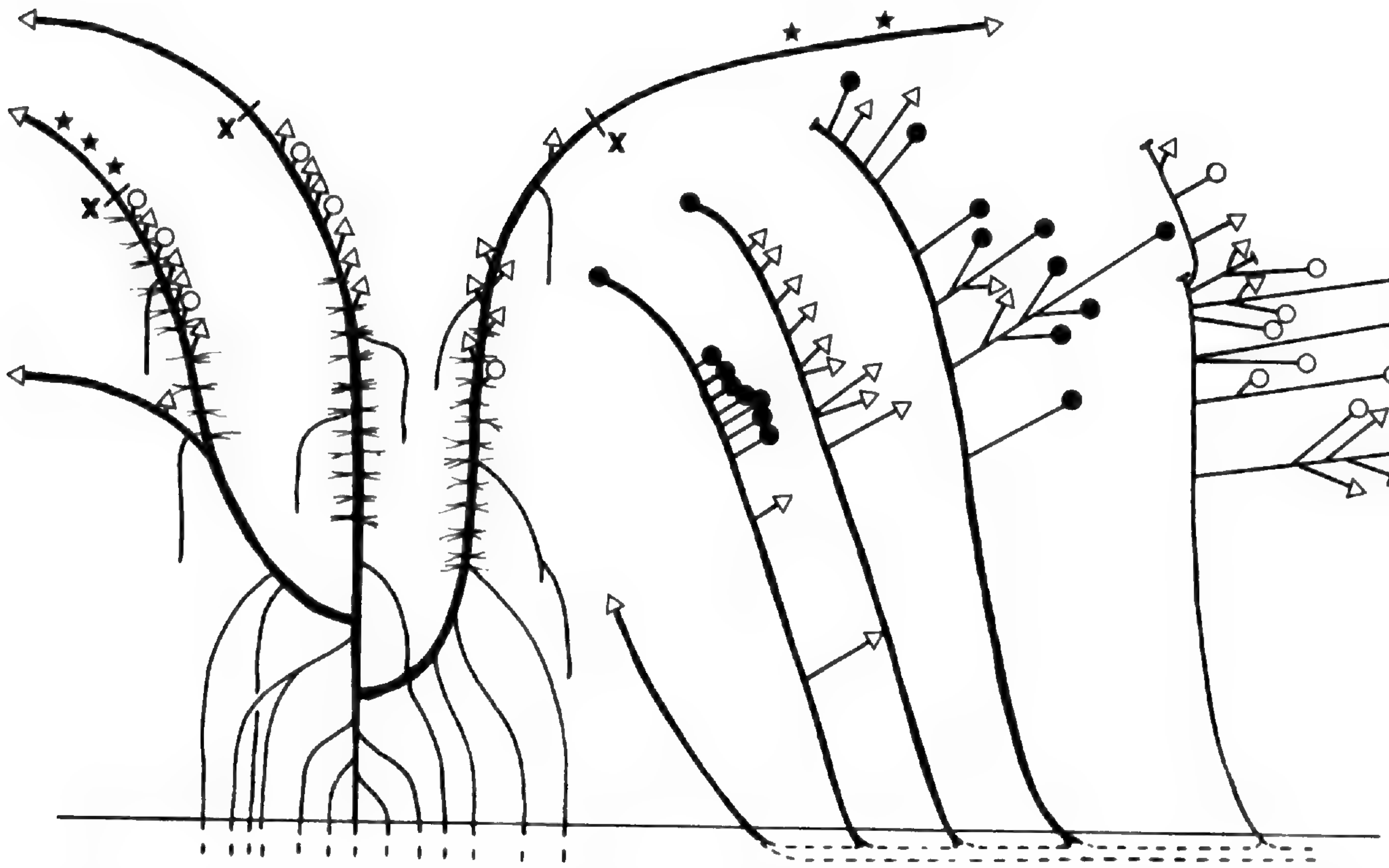

FIGURE 1. Diagrammatic sketch of shoot architecture in two species of *Freycinetia*. Pistillate inflorescences—black circles; staminate inflorescences—open circles; vegetative shoots—open arrows. Left: *Freycinetia funicularis*, an approximately three-year-old plant raised from a cutting, flowering for the first time; inflorescences, adventitious shoots, and clinging roots formed on at least one-year-old parts of the main shoots. X—plant trained horizontally from this point. ★—pistillate inflorescences formed here in the year to come. Right: *Freycinetia cumingiana*, showing (left to right) shoot of present year, two pistillate shoots formed during previous year, flowering for the first time, a two-year-old pistillate shoot, and a (probably) three-year-old staminate shoot. Note acrotonous ramifications, and "opportunistic" distribution of inflorescences and vegetative shoots probably influenced by different degrees of shading.

to one of the architectural models of Hallé et al., although some species have been so assigned by Castro dos Santos (1981). This is because the "opportunistic" growth of these lianas with easily formed accessory shoots makes it difficult to distinguish between homogeneous vs. heterogeneous axes and orthotropic vs. plagiotropic growth. In *F. cumingiana*, inflorescences are always terminal on the main shoot as well as on the lateral shoots, so that branching in the floral region is monopodial, except for occasional vegetative shoots. In *F. funicularis*, the inflorescences are lateral on short shoots.

When the staminate and pistillate inflorescences were produced simultaneously, hand-pollination of the latter resulted in fruit formation; in *F. funicularis* seeds from such fruits germinated to produce viable seedlings. In *F. cumingiana*, attempts to pollinate by hand were unsuccessful in both Hamburg and Bonn Botanic Gardens. Although the pistillate heads enlarged considerably and were not aborted, fertilization apparently did not occur; at least the pollen was able to trigger development. It may be noted that in the related genus *Pandanus*, no pollen stimulus is necessary, at least in some species, and parthenocarpy is normal. It must be remembered that attempts to pollinate tropical plants in temperate-zone greenhouses are chancy, for even if the basic aspects of the breeding system and the receptive period of the stigmas are understood, it may be impossible to obtain fertilization. An example of this difficulty is *Cinnamomum verum* (*C. zeylanicum*), the true cinnamon, as recounted by Kurz (pers. comm.). On the other hand, if pollination is successful, the possibility of pseudogamous agamospermy cannot be ruled out (Gadella, 1983). These observations are casual but may serve as the basis for some speculations, if only for the purpose of stimulating further experiments (which cannot be performed with scarce material in cultivation).

The evolutionary significance of dioecy has received recent attention, as in a symposium volume (Ann. Missouri Bot. Gard. 71: 243–296. 1984) where a survey of the subject and further

TABLE 2. Branch diameter and sex expression in *Freycinetia cumingiana.*

The axis was measured ca. 3 cm below the inflorescence (to avoid the expansion immediately below it). The pistillate shoot measure is that shown in Figure 2. The respective means are $m_a = 3.98 \pm 0.38$ mm for pistillate inflorescences, $m_b = 3.08 \pm 0.35$ mm for staminate inflorescences on pistillate shoots, and $m_c = 2.76 \pm 0.26$ mm for staminate inflorescences on staminate shoots. Branch diameter for pistillate inflorescences differs significantly from that for staminate inflorescences.

Branch Diam. (in mm)	Pistillate Inflorescences	Staminate Inflorescences	
		♀ Shoots	♂ Shoots
1.6–2.0			1
2.1–2.5		1	4
2.6–3.0	1	4	11
3.1–3.5	2	2	3
3.6–4.0	12	2	
4.1–4.5	5		1
4.6–5.0	4		

references may be found. Discussion centers around the question of whether the so-called benefits of dioecy (Willson, 1983) are genetically or ecologically determined, i.e., whether the promotion of outcrossing or ecological constraints on reproduction are evolutionarily decisive. This matter need not be resolved here, but our concern is with occasional departures from dioecy, a phenomenon that has been termed "leaky dioecy" by Baker & Cox (1984). Such leaky dioecy may be considered as one prerequisite for successful colonization of remote islands, since propagation by selfing becomes possible. Apomixis is another kind of solution to this problem, as is the parthenogenesis observed in some insular animal populations (e.g., Cox in White, 1985; Mau, 1978).

Rohwer & Kubitzki (1984) recently reported an interesting example of leaky dioecy in the neotropical riverine willow *Salix martiana* Leyb., which was found to produce regularly mixed catkins with staminate, pistillate, and perfect flowers. This was attributed to the difficulty of producing offspring after a probable long-distance dispersal and in an unstable environment. Mixed catkins are not uncommon in *Salix* (Velenowsky, 1904; Toepffer, 1925) but the high incidence in a tropical species, certainly much less studied than its temperate congeners, suggests that here it is a more or less regular phenomenon. Although hermaphroditic flowers are unknown in *Freycinetia,* the two genera may be taken as parallel cases for the evolution of monoecy (which may be a reversal of a previous evolutionary trend from monoecy to dioecy). Another aspect of this possible parallelism will be discussed next.

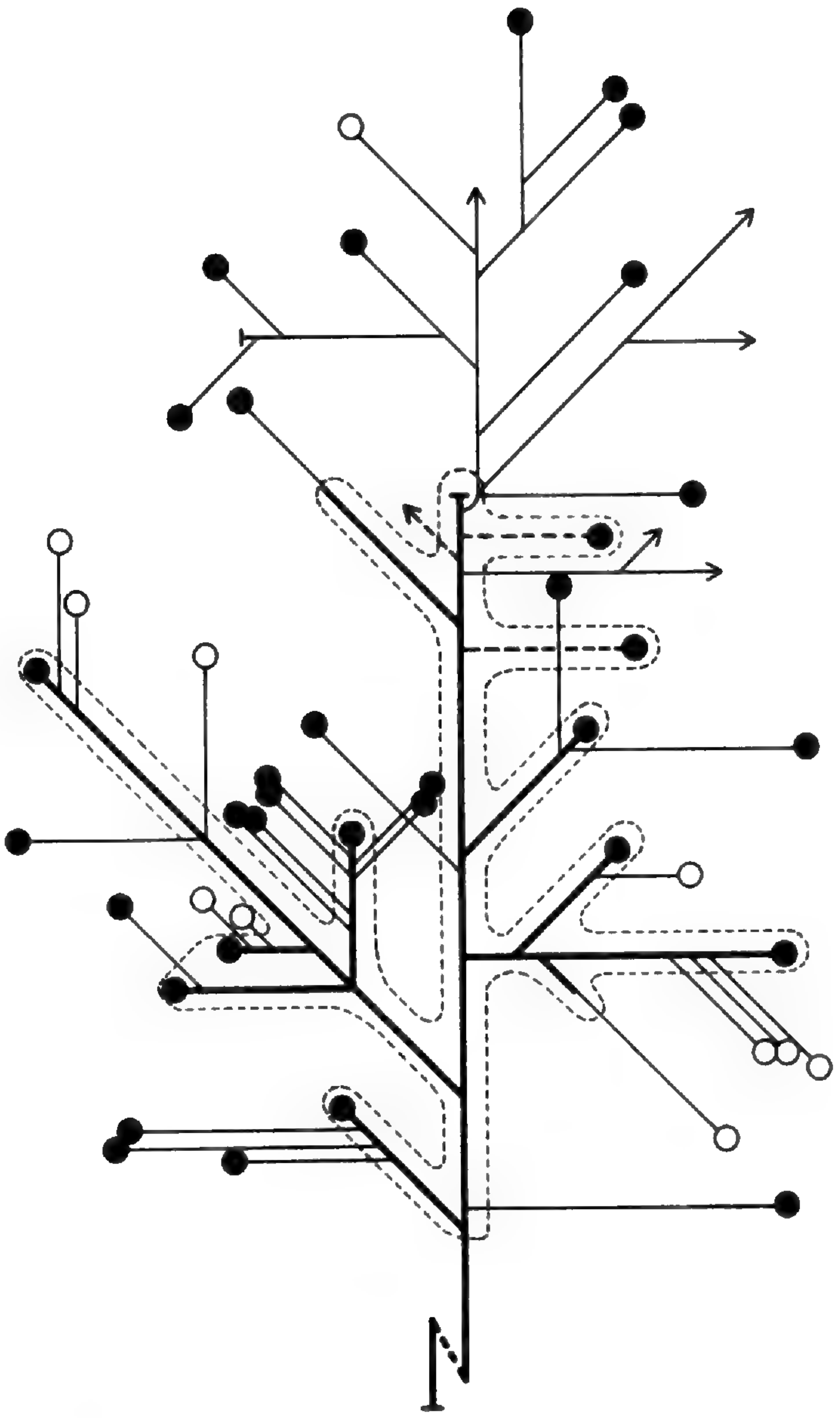

FIGURE 2. Diagrammatic sketch of sex expression on an initially pistillate shoot in two successive years. The broken line marks the state in spring, 1985; compare with the shoot second from left in Figure 1, but note that due to the straggling habit and the necessity of training the climber, some shoots may have been removed. Note further that the staminate inflorescences (open circles) formed on the distal parts of the shoot in 1986.

Developmental plasticity is one of the characteristics of liana species, as exemplified by their "opportunistic" shoot architecture in comparison with trees (Etifier, 1981). This plasticity is needed to adjust to a temporarily very heterogeneous habitat, where, for instance, light intensity encountered by juvenile plants is drastically different than that encountered by adults. In

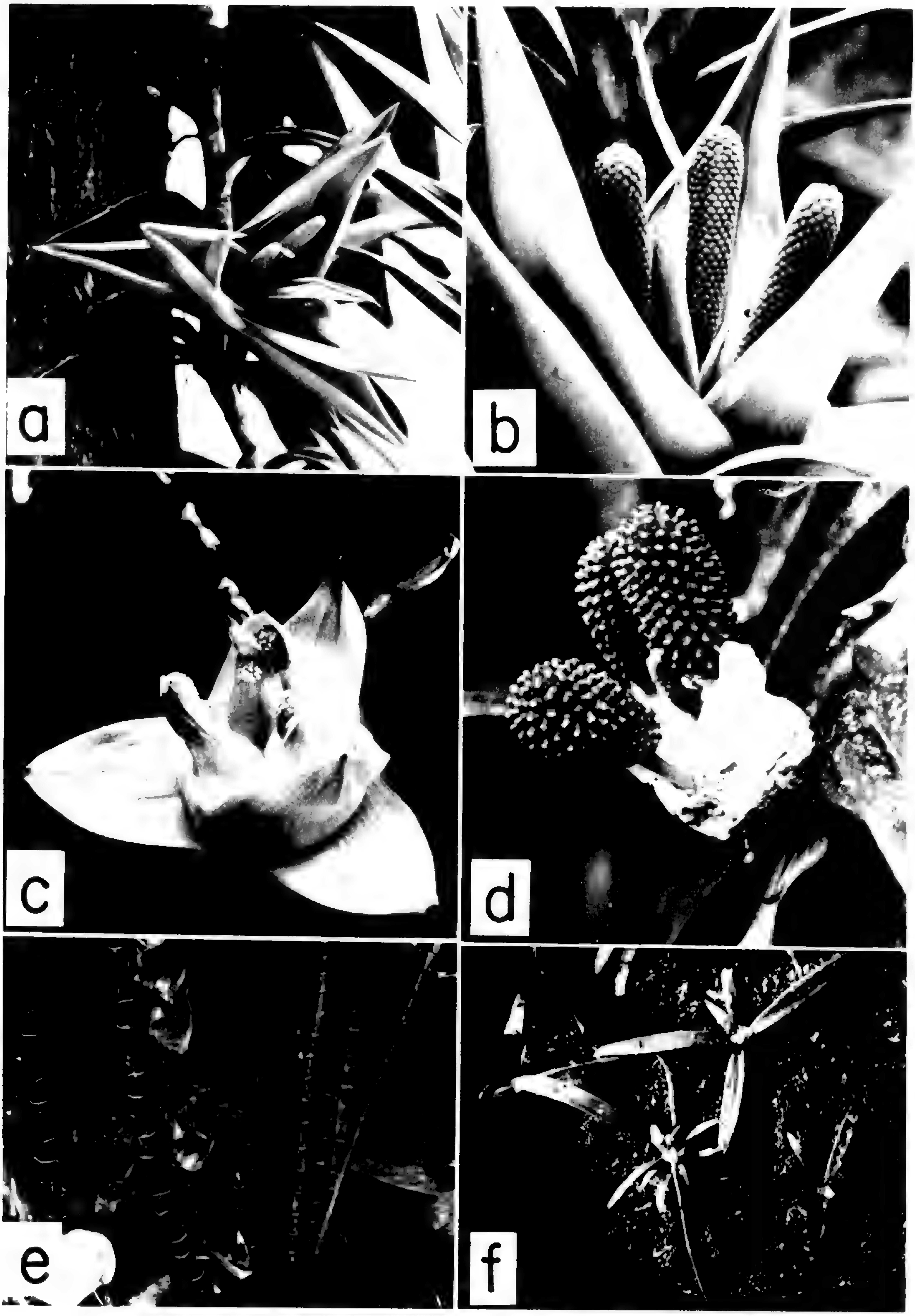

FIGURE 3. Aspects of growth of two *Freycinetia* species. a, b. *Freycinetia funicularis.*—a. Staminate inflorescence on a vertical shoot, ca. 18 cm diam.—b. Pistillate inflorescence at anthesis (spikes 8 cm long). c–e.

Freycinetia, at least in the two species observed for this study, such plasticity extends to sex expression. This is not surprising since environmentally determined sex expression has several selective advantages for species living in a "patchy" environment (Charnov & Bull, 1977; Willson, 1983), and sequential hermaphroditism has been reported for many species. The factors invoked include light intensity (e.g., *Catasetum*; Dodson, 1962), hormonal and nutritional status (e.g., *Elaeis guineensis*; Williams & Thomas, 1970), or disturbance of vegetative parts (e.g., *Arisaema*; Schaffner, 1921), all of which may interact variously, and all of which may be applicable to the present cases. Thus, in *F. funicularis,* horizontal training of the branches may have altered the hormonal balance toward the production of pistillate inflorescences; exhaustion of nutrient reserves, self-shading of shoots, or pruning may have been responsible for the switch back to staminate inflorescence production. Experimental proof for this would be difficult to obtain. At least, the size-correlated sex expression in plants of *F. cumingiana* will permit further study. Cuttings have been made from the differently determined axes and their fate will be observed in coming years.

Clearly it should not be too difficult to find plausible explanations for the adaptive values of dioecy, monoecy, or plasticity in sex expression in a given situation. However, the phenomenon of leaky dioecy is still puzzling. Why is it restricted to certain genera and absent in others? Why, for instance, are no such cases known in *Populus* or in *Pandanus,* which are the sister genera of *Salix* and *Freycinetia,* respectively? In *Populus* and *Pandanus* pollination is believed to be chiefly by wind (Toepffer, 1925; Cox, 1982). A possible explanation is that in anemophilous plants, the staminate and pistillate functions must suit quite different needs and, as a result, tend to evolve divergently. Such divergence seems improbable in zoophilous groups, where a high degree of similarity is advantageous (in overall form, size, color, odor, and perianth details, though not in the details of staminal and gynoecial form). The correlation of leaky dioecy with change from anemophily to zoophily is a possibility worth investigating.

To obtain evidence bearing on these questions, many more observations are needed, preferably on the same specimens over a number of years. The statement by Cox et al. (1984) about the value of living collections for this kind of study may be emphasized again. Phenomena such as these tend to escape the notice of both purely field- and herbarium-oriented workers, but botanic gardens provide an excellent location in which to study such things as "leaky dioecy."

VOUCHER MATERIALS

Herbarium material of both *Freycinetia* species discussed is deposited in PH and HBG, and the behavior of *F. funicularis* is also documented in M (*Bogner 1783*). Additional prints for photographic documentation are on deposit in PH and HBG.

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Freycinetia cumingiana.—c. Staminate inflorescence ca. 6 cm diam.—d. Pistillate inflorescence after anthesis, spikes 1.5–2 cm long.—e. Basal parts of shoots (from left to right, two old pistillate shoots, current pistillate shoot with caducous bracts, three pistillate shoots interspaced with two staminate shoots, the latter much thinner).—f. *F. funicularis* seedlings ca. six months old, their leaves about 2 cm long.

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A GUIDE TO COLLECTING LECYTHIDACEAE[1]

SCOTT A. MORI AND GHILLEAN T. PRANCE[2]

ABSTRACT

Because of their arborescent habit and unique flowers and fruits, Lecythidaceae present specialized collection problems. Instructions for the preparation of more informative collections of Lecythidaceae for use in taxonomy are provided.

The Lecythidaceae sensu lato are a pantropical family of small to very large trees. The family includes four subfamilies: Planchonioideae with 55 species in six genera distributed through tropical Asia, Malaysia, northern Australia, and the Pacific Islands; Foetidioideae, with five species in a single genus distributed in Madagascar, India, and Malaysia; Napoleonaeoideae, with 11 species in two genera distributed in West Africa and one species in the upper Rio Negro of Amazonia; and the Lecythidoideae, with about 206 species in ten genera distributed through tropical America from Veracruz, Mexico to southern Brazil (Kowal et al., 1977; Prance & Mori, 1979). Because our collecting experience has been mostly in the Neotropics, this essay emphasizes the Lecythidoideae. However, the methods described are applicable not only to other subfamilies of Lecythidaceae but to tropical trees in general.

General collections of plants provide the data upon which the monographic and floristic treatments of plant taxonomists are based. A single collection of a species usually does not provide sufficient data for its taxonomic description. Consequently, collections are needed that represent: (1) all parts of the plant used in classification (bark, wood, chromosomes, etc. as well as leaves and reproductive structures), (2) all stages of the life cycle of the plant (flowers, fruits, seeds, and seedlings), (3) individuals from distinct habitats in which the plant grows, (4) individuals from throughout the geographic range of the species, and (5) intra- and interindividual variation.

Many recent collections of neotropical Lecythidaceae have added little to what was already known about the species collected. These collections usually provide inadequate information about those features of the plant, such as habit and bark, that are not preserved on the herbarium sheet. Careful notes on habitat are usually lacking and even flower color is often not recorded in a manner that can be interpreted by taxonomists. Worst of all, flowers are often dried under such extreme heat and pressure that they become so carbonized that their structure is impossible to determine. Even fruits are collected in such a way that their taxonomic features and morphological variation are difficult to interpret. Finally, few collections of flowers and fruits are unequivocally documented as having come from the same tree.

Another problem is the continued collection of herbarium material of the same taxa from the same area by the same collectors. However, some duplication is necessary to voucher ecological studies of tropical forest structure and composition. Collections of some Lecythidaceae, such as *Gustavia augusta* L. and *G. hexapetala* (Aublet) J. E. Smith, continue to accumulate without augmenting the information needed for understanding the species. These collections do not merit the cost of their processing or the valuable space they occupy in herbaria. This same lack of selectivity in collecting occurs in almost all woody tropical families, for example, the Chrysobalanaceae (Prance & Campbell, in press).

If further progress is to be made in the taxonomy of tropical woody groups, more careful and selective collections by more sophisticated collectors are needed. The purpose of this article is to provide the information needed for making these collections. While we emphasize Lecythidaceae, similar needs pertain to almost all rainforest woody plant families.

TREE CLIMBING

Because of their large size, many species of Lecythidaceae can be collected only by felling or

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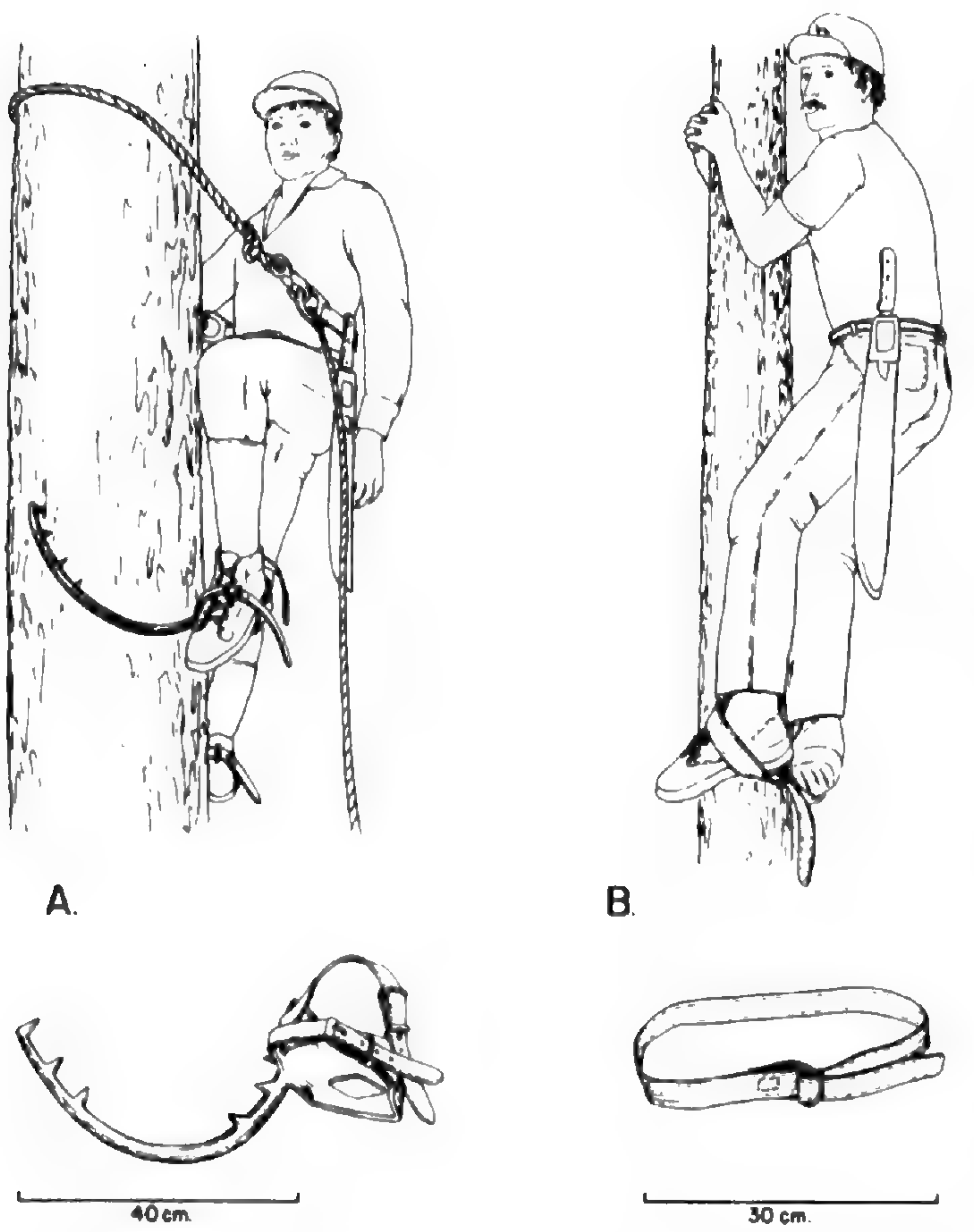

FIGURE 1. Climbing methods used to collect Lecythidaceae.—A. French tree climbing spikes ("griffes").—B. Brazilian belt used by native climbers ("peconha"). Reprinted with permission from the *Memoirs of the New York Botanical Garden.*

climbing. As a general rule, trees should be felled only if they face imminent destruction by road construction, agricultural clearing, dam construction, etc. Forest clearing provides an excellent opportunity for making collections from felled trees. The taxonomic information gathered from a herbarium specimen often does not warrant the sacrifice of a tree. This is especially true when collecting near Indian villages or settlements where trees may have economic value or cultural significance to natives. Boom (1985) has shown that 82% of the species of trees surrounding a Chácobo Indian village in Bolivia are used in one way or another by the Indians.

We have found climbing to be the most satisfactory method of obtaining specimens of Lecythidaceae. Although numerous methods are used for gaining access to tropical trees, we have employed (1) native climbers, (2) "Swiss Tree Grippers" (Mori, 1984; available from Forestry Suppliers, Inc., 205 West Rankin St., P.O. Box 8397, Jackson, Mississippi 39204-0397), and (3) French tree climbing spikes (Fig. 1).

Native climbers are becoming increasingly difficult to find. We have employed them most effectively to collect Lecythidaceae in Brazil, especially in eastern Amazonia where climbers are still common because of the custom of gathering edible fruits from *Euterpe* and *Oenocarpus* palms. The Brazilian climbers can efficiently scale trees under 35 cm DBH by using an adjustable canvas loop called a "peconha" (Fig. 1). A climber can be hired for about $10 per day.

For trees from 50 to 72 cm DBH we have used "Swiss Tree Grippers." To use them, lianas and epiphytes have to be cleared from the trunks before the trees can be ascended, but the trees themselves, in contrast to those scaled with spikes, are not damaged. The weight, bulk, and high price of the grippers often counterbalances the advantage of being able to climb the few additional trees not climbable with spikes.

We have found French climbing spikes (Fig. 1) to be the most efficient method for collecting Lecythidaceae. Smaller spikes (24 cm diam.) are used for trees from 10 to 25 cm DBH, whereas larger ones (35 cm diam.) are employed for trees from 26 to 50 cm DBH. The advantage of these spikes over the single spur spike preferred by some climbers is the ease with which trees can be climbed. The climber's weight and safety belt secures him to the tree in such a fashion that his hands are free for using clipper poles, capturing insects for pollination studies, etc. The advantage of the single spike apparatus is that trees of all sizes can be ascended with one pair of spikes. The French spikes are available from Ets Lacoste, 24160 Excideuil, France for about $50 a pair, not including shipping.

All climbs should be made with the climber secured to the tree with a safety belt. We prefer the Klein nylon protective belt with two D rings in combination with the Klein nylon adjustable lanyard (both available from Forestry Suppliers, Inc.). The use of two lanyards insures that the climber is attached to the tree at all times. When the climber reaches a branch, one lanyard remains around the trunk below the branch while the other is secured around the trunk above the branch to be passed. The belt around the main trunk beneath the branch can then be released and the climber is free to move above the branch.

We have climbed several thousand trees using the French spikes without any falls. Nevertheless, the climber should be extremely careful before and during any climb. Before climbing, the tree should be carefully inspected to insure that it is in good enough condition to support the weight of the climber, and for the presence of stinging and biting animals. Special attention should be paid to swarms of bees, as they may be made up of the particularly aggressive African honey bee, which has been responsible for the death of at least one biologist. The bases of tropical trees often serve to house creatures that vary from sand flies that carry the protozoan disease of leishmaniasis to snakes that can inflict painful and deadly bites. The tree itself may be occupied by bees, wasps, biting ants, and the deadly snake *Bothrops bilineata* (an arboreal fer-de-lance). The last is more frequent in fruiting trees, where it lies in wait to prey upon visiting frugivores. Extreme care should be used when reaching over branches or when climbing past epiphytes. Nearby trees should also be examined so that wasp and bee nests are not disturbed during manipulation of the clipper pole. Finally, the condition of the climbing gear should be constantly monitored and any frayed or defective parts should be immediately replaced. The recent fatal fall of a young botanist in Venezuela is a shocking reminder of the danger involved in making tropical tree collections.

Collection of specimens from the tree's canopy by a collector on the ground or in the tree itself is greatly facilitated by the use of a tree pruner attached to a series of aluminum poles. We have found the poles developed by botanists of the Missouri Botanical Garden staff to be the most efficient. This system includes three sets of two telescoping aluminum poles attached to one another by a spring activated button that passes from a hole in one pole into that of the next. Each pole is 1.8 m long so that when all six poles are joined nearly 11 meters plus the height of the collector can be attained. However, when more than four poles are joined it is very easy to bend the poles. In order to avoid this, it is best to cut with the poles in the most vertical position possible and to wrap the cutting rope around the poles several times in order to insure that the cutting force is directed along the poles. We find the best tree pruner to be the Snap-cut model 33 (available from Forestry Suppliers, Inc.) which fits exactly onto the end of one of the smaller aluminum poles. This head is light enough to allow maneuverability yet strong enough to cut most branches to about 4 cm in diameter.

LEAF VARIATION

Normal collection for herbaria does not adequately sample intra- and interindividual variation in leaf morphology. Collections which include shade and sun leaves, young and old leaves, and extremes in leaf size are invaluable in helping to solve taxonomic problems. In *Couroupita*, for example, there was much taxonomic confusion due to differences in leaves from the crown versus those that appear on the cauliflorous inflorescence. These leaves differ in shape, texture, and pilosity and were sometimes described as different species, though they in fact represent variation within the same species. Consequently, it is important to document leaf variation, even if more than one herbarium sheet is needed to do so.

FLOWERS AND FRUITS

The remarkable variation in the floral and fruit morphology of Lecythidaceae can often be related to pollinators and seed dispersers. The two principal floral types in neotropical Lecythidaceae differ in the structure of the androecium. One type is radially symmetrical (actinomorphic) and the other is bilaterally symmetrical (zygomorphic, Fig. 2). The actinomorphic androecium consists of a fused basal portion, the staminal ring, which is surmounted by free stamens (Fig. 2). In the zygomorphic androecium, the staminal ring is prolonged on one side into a stamen-free area called the ligule, which terminates in an appendage-bearing hood (Fig. 2). The hood may be open (with a space between it and the summit of the ovary) or closed and tightly appressed to the summit of the ovary. New World genera with the former type of androecium are *Asteranthos, Gustavia, Grias,* and *Allantoma,* whereas the latter type is found in *Couroupita, Corythophora, Bertholletia, Lecythis, Eschweilera,* and *Couratari* (Fig. 3). The flowers of *Cariniana* are intermediate between these two types (Fig. 3).

Pollinator rewards are produced exclusively by the androecium. In actinomorphic species the reward is always pollen. Moreover, the pollen collected by pollinators from actinomorphic flowers is the same kind of pollen that affects fertilization, i.e., no nectar or specialized pollen are produced. In the zygomorphic species either pollen or nectar may serve as the pollinator reward. However, the pollen collected by pollinators differs physiologically, and sometimes even morphologically (e.g., *Couroupita guianensis* Aublet: Mori & Boeke, 1987; Mori et al., 1980), from that which affects pollination. This specialized or fodder pollen is found in the anthers of the hood or in a group of stamens of the stam-

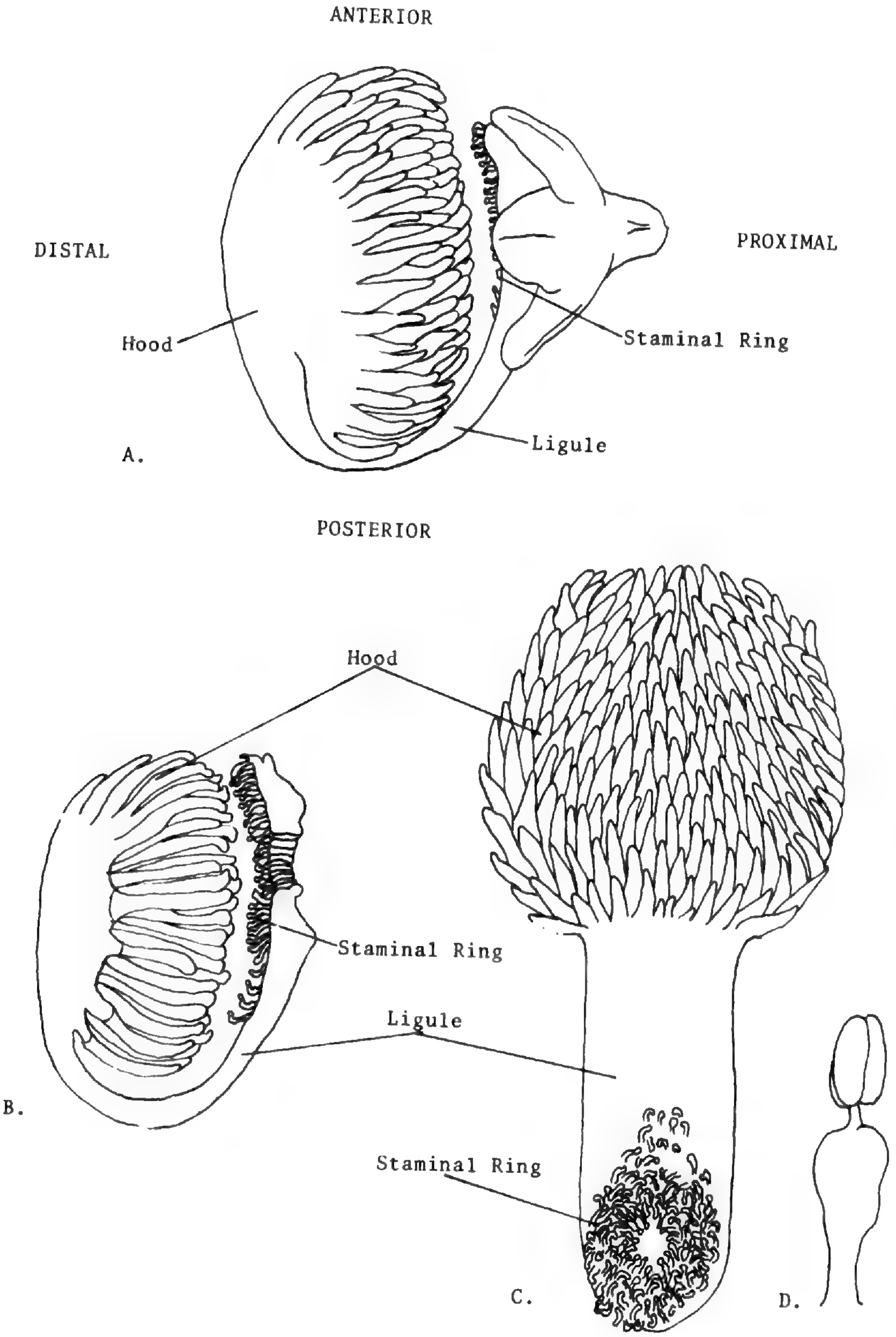

FIGURE 2. Androecial structure of a zygomorphic-flowered New World Lecythidaceae.—A. Side view of flower with petals removed, showing terminology used in describing floral orientation and in describing the androecium.—B. Medial section of the androecium.—C. Artificially opened androecium.—D. Stamen from staminal ring. Reprinted with permission from *Flora Neotropica*.

inal ring adjacent to the ligule. Color differences help to separate the two types of pollen. For example, in *Lecythis pisonis* Cambess. the fodder pollen, located in the hood, turns black after 24 hours, whereas the pollen in the staminal ring remains yellow. In *L. corrugata* Poit. subsp. *corrugata* the fodder pollen, located in a row of stamens on the ligular side of the staminal ring, is yellow in contrast to the white pollen of the remainder of the stamens. Nectar is the principal pollinator reward in those zygomorphic species with coiled androecial hoods.

The aforementioned androecial structures as well as other floral characteristics provide features useful in the classification of Lecythidaceae. Unfortunately, most collections do not ade-

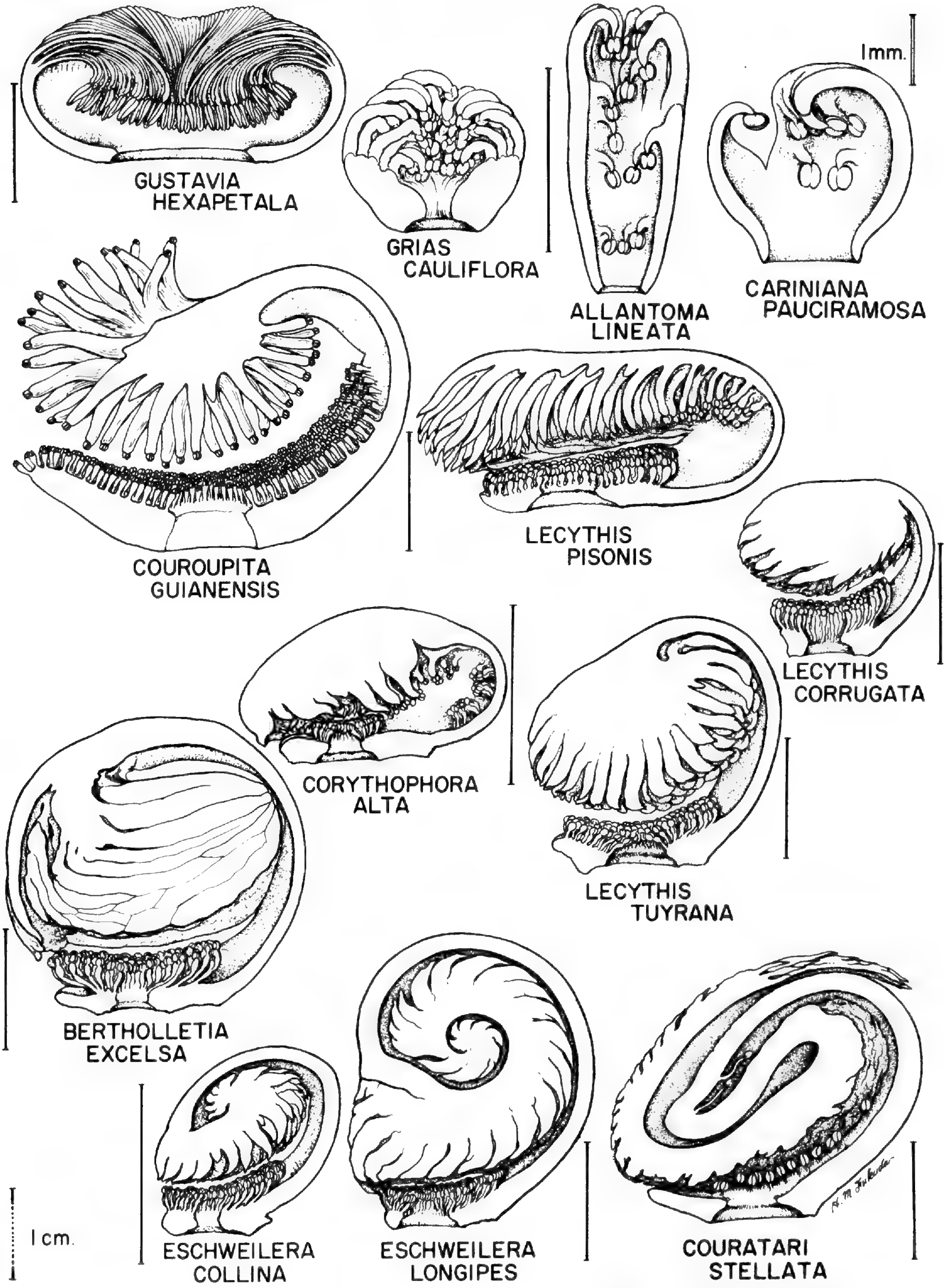

FIGURE 3. Variation in androecial structure of New World Lecythidaceae. In all cases the androecium has been removed from the flower and cut in medial section. *Gustavia, Grias,* and *Allantoma* are actinomorphic, whereas the remaining genera display varying degrees of zygomorphy. Reprinted with permission from *Flora Neotropica*.

quately preserve or describe these features. The most common error in the collection of flowers of Lecythidaceae is the use of excessive heat and pressure in the drying process. It is useful to dry at least some of the flowers outside the press in a paper bag over low heat and to preserve flowers in F.A.A. or 70% ethanol. Structure of the androecial hood can also be recorded by photographing a medial section of it. The photographs should subsequently be attached to the herbarium sheet.

Flower color and size are also useful features that have not been adequately considered in the classification of Lecythidaceae because they are seldom properly recorded. After drying, it is very difficult to determine flower size, and therefore the maximum diameters of several flowers from the same tree should be measured and stated on the label. It is also important to record the color of all the separate floral parts. It is not sufficient to state that the flowers are white, yellow, or some other color. If indeed they are entirely of a single color, this is unusual and should be clearly indicated. In many species of Lecythidaceae, the petals and androecial hood are different colors and this should be noted. In addition, the color and position of differently colored anthers should be recorded, as this indicates whether one or two types of pollen are produced within the same flower.

The fruits and seeds of neotropical Lecythidaceae have evolved a variety of forms in response to pressures exerted by different seed dispersal agents, fruit and seed predators, and environmental constraints. Major trends caused by these selective pressures are (1) indehiscence versus dehiscence; (2) retention of the fruit on the tree until the seeds have been released versus drop of fruits with the seeds inside; (3) fleshy versus woody pericarps; (4) development of mucilage within the pericarp; (5) lateral versus basal fleshy arils; (6) development of arils that completely surround the seeds; (7) loss of arils; (8) development of membranous, winglike arils; (9) development of plano-convex cotyledons as in *Gustavia*; (10) development of leaflike cotyledons as in *Cariniana, Couratari,* and *Couroupita*; (11) lack of well-developed cotyledons as in *Allantoma, Bertholletia, Corythophora, Eschweilera, Grias,* and *Lecythis*; and (12) terminal versus lateral seed germination. These characters have coevolved with animal and wind seed dispersers and environmental factors throughout a long history under rainforest conditions (Prance & Mori, 1978, 1979, 1983; Mori & Prance, 1981). The terminology used to describe the fruits and seeds of Lecythidaceae is illustrated in Figure 4.

A particularly difficult problem in the taxonomy of Lecythidaceae has been the determination of the extent of intraspecific fruit variation. Unfortunately, earlier monographers of the family (Miers, 1874; Knuth, 1939) did not have a concept of intraspecific fruit variation. They simply named all fruit variations as separate species. However, beginning with Dugand (1947), botanists have become aware that the fruits of Lecythidaceae can display considerable variation within the same species (Mori & Prance, 1981). In *Allantoma,* fruit morphs representing as many as six of Miers's species have been found on a single tree (Prance & Mori, 1979).

Collectors can help in the description of fruit and seed features of Lecythidaceae. They can also gather material that adequately shows fruit variation within and between individuals. It is especially important that the developmental state of the fruits is recorded. Under heat, young fruits may dehisce and thereby appear to be mature. Because it is often very difficult to open up dried fruits, some should be cut lengthwise through the middle and seeds removed from the fruit with the arils and funicles intact. The features mentioned earlier should be recorded at the time of collection.

It is extremely useful to have flowers and fruits from the same tree. Therefore, resident collectors can provide a useful service by periodically returning to the same trees to gather representative material from all stages of the plant's life cycle. This is especially critical in *Eschweilera,* where the similarity of the leaves of many species can lead to falsely relating fruits of one species with flowers of another. Collectors can also contribute to the proper correlation of flowers and fruits by always searching in the canopy and under flowering trees for old fruits. If the fruits are too rotten to collect, a photograph should be made and subsequently affixed to the herbarium collection. However, care must be taken to avoid attributing fruits from the ground to an incorrect tree. If any doubt exists, the fruits should be given a separate collection number.

Local collectors can contribute much to our knowledge of Lecythidaceae by becoming experts on the family in their areas. On-site studies of taxonomy, ecology, pollination biology, population dynamics, and ontogenetic development in species-rich areas will add much to our knowl-

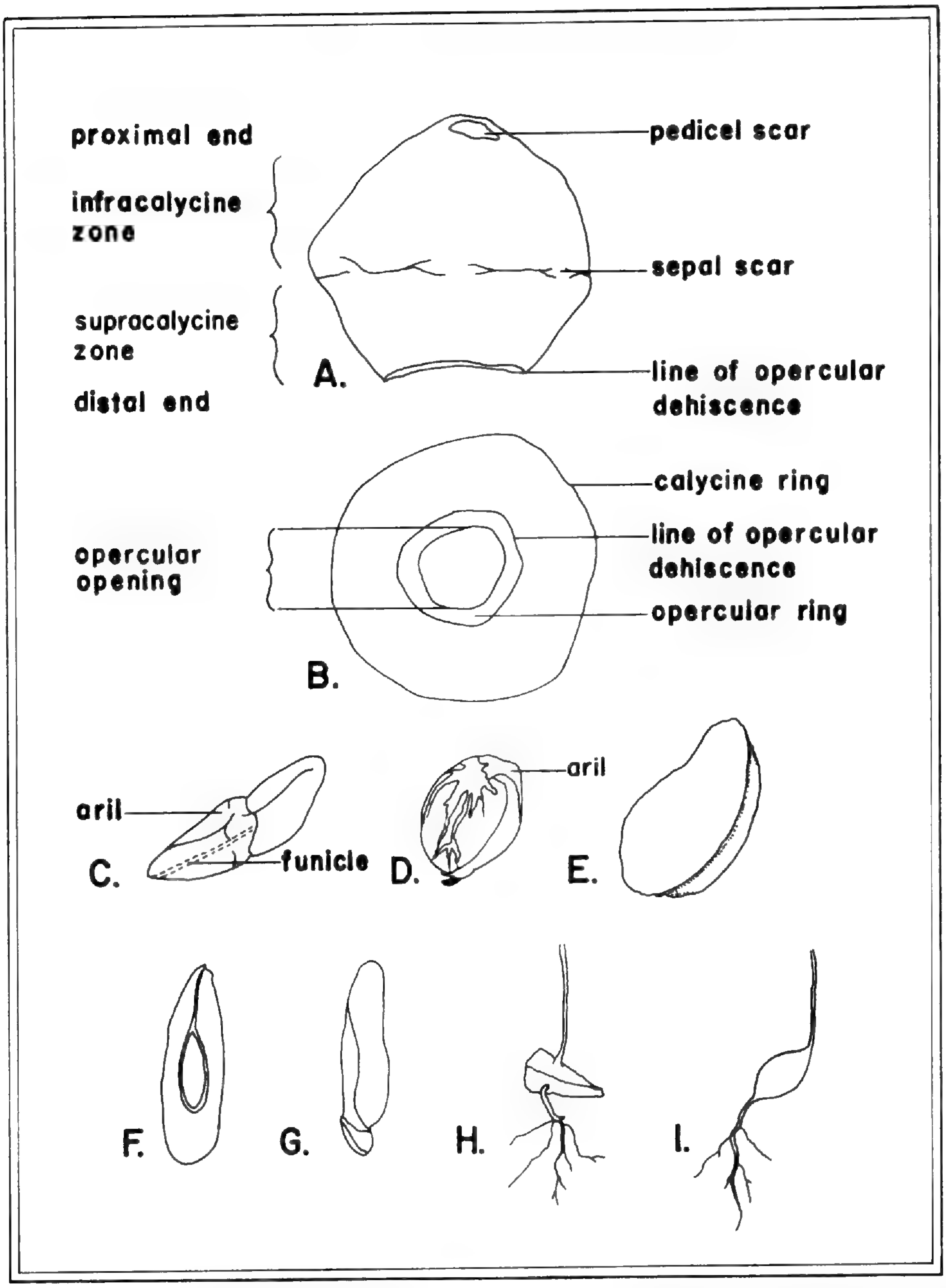

FIGURE 4. Fruit, seed, and seedling features of New World Lecythidaceae.—A–C. *Lecythis ampla* Miers. Note the basal aril in C.—D. *Eschweilera* sp. Seed with lateral aril.—E. Seed of *Bertholletia excelsa* Humb. & Bonpl. Note that this species lacks an aril.—F. Winged seed of *Couratari stellata* A. C. Smith. Note that the wing entirely surrounds the seed.—G. Unilaterally winged seed of *Cariniana micrantha* Ducke.—H. Lateral germination of *Eschweilera tenuifolia* (Berg) Miers.—I. Apical germination of *E. pittieri* R. Knuth. Modified with permission from *Flora Neotropica.*

edge of the family. These studies are needed because many features that allow recognition of species in the field are not apparent in herbarium specimens. For example, in French Guiana, where the senior author has recently completed a detailed study of the 27 species of Lecythidaceae in the proposed national park surrounding Saül (Mori & collaborators, 1987), we were able to resolve a number of taxonomic problems that could not be understood with herbarium material alone. Similar studies would be especially useful in central and western Amazonia and in the Chocó of Colombia.

ADDITIONAL NOTES

Collectors generally do not provide enough information on habitat, habit, and bark to aid in the identification and classification of Lecythidaceae. These features are valuable in separating species of Lecythidaceae and should be recorded by the collector.

Species of Lecythidaceae are primarily found in lowland moist forests. Nevertheless, a few species have invaded savanna habitats [e.g., *Cariniana rubra* Gardner ex Miers and *Eschweilera nana* (Berg) Miers of central Brazil and *L. schomburgkii* Berg of Roraima, Brazil], and 14 species of *Eschweilera* are known to occur at elevations above 1,000 m (Prance & Mori, 1979). Within lowland habitats, some species of Lecythidaceae are restricted to the periodically inundated *várzea* habitat where they may be among the most conspicuous elements of the vegetation [e.g., *Allantoma lineata* (Mart. ex Berg) Miers, *Couratari oligantha* A. C. Smith, *C. tenuicarpa* A. C. Smith, *Eschweilera ovalifolia* (DC.) Niedenzu, *E. parvifolia* Mart. ex DC., and *E. tenuifolia* (Berg) Miers]. However, Lecythidaceae are most diverse in the nonflooded, or *terra firme*, habitat. Even within *terra firme* some species appear to prefer ridge tops, others hillsides or valley bottoms (Mitchell & Mori, 1987). Consequently, it is important that collectors make very careful habitat notes, indicating the vegetation type, altitude, and slope from which collections are made. It is especially useful to note whether the plant grows near a stream or other body of water, and if the water is white, black, or clear.

Although all species of Lecythidaceae are trees (some may occasionally grow as shrubs), the collector should be aware of and note differences in habit. Some species (e.g., *Gustavia monocaulis* Mori) are unbranched pachycauls, others [e.g., *G. grandibracteata* Croat & Mori and *G. superba* (Kunth) Berg] are branched pachycauls, and others [e.g., *G. hexapetala* (Aublet) J. E. Smith and most other species] are leptocauls.

Species of Lecythidaceae are found as understory, canopy, and emergent trees. In order to communicate this information, the collector should record the height and DBH of collections as well as note the stratum to which this and other individuals of the species belong. Only reproductive individuals should be considered when determining the tree stratum in which the species belongs. For detailed studies of Lecythidaceae, diameter versus height diagrams should be prepared. The graphs will level out at the stratum in which the species reaches reproductive maturity. In his study of Surinam forests, Schulz (1960) has prepared such graphs for a number of species of Lecythidaceae as well as for species of other families.

The base of the trunk should also be described. Some species (e.g., *Lecythis idatimon* Aublet) have cylindric trunks to the very base, others (e.g., *L. chartacea* Berg) have basally swollen trunks, and others (e.g., *L. zabucaja* Aublet) have well-developed buttresses. The height, width, and thickness of the largest buttress should be measured. An undescribed species from French Guiana has pneumatophores.

An important but infrequently described feature of Lecythidaceae is the bark. There are four types of external bark morphology in the family. In the first, the bark is very deeply fissured (e.g., *Bertholletia excelsa* Humb. & Bonpl., *Corythophora rimosa* W. Rodr., and *Lecythis zabucaja* Aublet); in the second it is nearly smooth (e.g., *Eschweilera collina* Eyma); in the third it is more or less smooth, but shallow vertical cracks and lenticels may be present [e.g., *Eschweilera pedicellata* (Richard) Mori and *L. corrugata* Poit.]; and in the last it may be markedly scalloped or dippled [e.g., *E. micrantha* (Berg) Miers and *E. apiculata* (Miers) A. C. Smith]. The thickness of the outer and inner barks as well as the color of the inner bark should also be recorded. The bright yellow inner bark of *Lecythis poiteaui* Berg or the flesh pink inner bark of *Eschweilera apiculata* are excellent aids in field identification. Heartwood color should also be recorded when possible.

One of the best ways to communicate habit and external bark features is with photographs. The photograph should include a scale and the number of the collection and should eventually be affixed to the herbarium sheet.

SPECIALIZED COLLECTIONS

Known chromosome counts of Lecythidaceae are summarized in Kowal et al. (1977). Additional counts are needed for *Allantoma, Cariniana, Corythophora,* and *Couratari* of the New World Lecythidoideae, for most of the Old World genera, for *Asteranthos brasiliensis* Desf. (the only member of Napoleonaeoideae in the New World), and for species of *Gustavia* to determine the extent of polyploidy. Collections of buds of all sizes should be fixed in either Farmer's (3 ethanol : 1 glacial acetic acid, v/v) or Jackson's (4 ethanol : 2 methanol : 2 chloroform : 1 proprionic acid : 1 acetone, v/v). The best results have been obtained with fixation in Jackson's solution (Kowal, pers. comm.). If possible, the buds should be left on the inflorescence, as this facilitates location of buds in the proper stage for counting. In addition, because of their thickness, buds should be slit open to allow penetration of the fixative. After 12 hours of fixation the buds should be transferred to 70% ethanol and stored in a freezer when possible.

For anatomical studies, collections of leaves, twigs of several sizes (newly flushing ones are especially useful), and bark should be fixed in F.A.A. (10 ethanol : 7 distilled water : 2 formalin : 1 glacial acetic acid, v/v). They may be stored in F.A.A. or in 70% alcohol. The bark sample should consist of a block ca. 2 cm square and should include a portion of the outermost sapwood to insure that all layers of the bark are included in the sample.

Wood samples may be chisled from standing trees or cut from felled trees. In the former case, the block should be about 10 cm square by 10 cm deep and the bark should be left attached to the wood sample. Smaller blocks can be removed but, because of splitting of the sample upon drying, they are not as desirable. The wound left by the removed block should be painted over with a sealer to minimize infection. In the case of felled trees, larger blocks of wood or segments of trunk that can later be cut into specimens about 10 cm long (parallel to the long axis of the trunk) by 5 cm wide (tangentially) by 2 cm thick (radially) should be collected. Specimens should be taken from breast height and from the bole itself rather than from large branches or from the buttresses. The specimens should be dried over low heat to insure that a minimal amount of cracking occurs.

There have been no detailed studies of any aspect of the chemistry of neotropical Lecythidaceae (Prance & Mori, 1987). If collecting material for study of flavonoids, the collector should remember that the preservatives used in tropical fieldwork (i.e., aqueous mixtures of formaldehyde or paraformaldehyde, pentachlorophenol in alcohol, or alcohol) may remove these and other compounds and thus render the specimens useless for chemical study. Therefore, if material is collected for chemical study, it should be kept free of field preservatives and air dried. Moreover, all field preserved specimens should have the treatment indicated on the label so that the specimens are not subsequently screened for compounds soluble in the preservatives (Coradin & Giannasi, 1980).

It is now known that bees play a major role in the pollination of most neotropical Lecythidaceae. A recent review of pollination in neotropical members of the family is provided by Mori & Boeke (1987). Nevertheless, in order to understand the complex interactions of bees and Lecythidaceae, many carefully documented collections of bees visiting Lecythidaceae are still needed. Especially useful are detailed studies of the pollination of individual species of Lecythidaceae. Collections should be made at all times of the day when flowers are open. Fortunately, most species of Lecythidaceae open their flowers at daybreak and drop them late in the same afternoon. However, some species either flower entirely at night or open their flowers during the night. For example, the bat-pollinated *Lecythis poiteaui* Berg opens its flowers at dusk and drops its petals and androecia at about 0300, and the bee-pollinated *Gustavia augusta* L. opens its flowers during the night and drops its petals and androecia by late afternoon the next day. During the day, a French Guianan individual of *G. augusta* was visited mostly by trigonid bees, whereas the night-flying bee *Megalopta genalis* visited its flowers before daybreak. Consequently, it is necessary to determine floral longevity before a pollination study is begun, and once this is established, the plant must be observed and pollinators collected at all times when flowers are open. In addition, the species should be studied and pollinators collected throughout its entire flowering cycle. The pollinators at peak flowering may not be the same as those visiting the plant at the onset or the end of the flowering period. For example, Mori & Boeke (1987) have collected completely different species of *Trigona* dominating the flowers of *G. augusta* during the day at different times during its flowering cycle.

We have collected bees visiting Lecythidaceae by simply climbing into the crown and waiting by flowers until insects enter them. Random capture of all insects that approach flowers of Lecythidaceae will often give erroneous ideas of the pollinating species because many species of insects, such as wasps, visit flowers of Lecythidaceae to prey upon other insects, not to collect pollen or nectar. In species with zygomorphic flowers, it is especially important to observe the position and behavior of the bee in the flower, since this will indicate what type of pollinator reward the bee is after. Euglossine bees are best captured after they have completely entered the flower; otherwise, they often are quick to spot the movement of the net and escape.

We use the chlorocresol method described by

Tindale (1962) to preserve our insect collections in the field. This method keeps the insects moist and free of mold and allows them to be pinned directly upon their removal from the storage container. In this method, a teaspoonful of chlorocresol is placed on the bottom of a plastic container. It is held in place by a layer of cotton or tissue followed by a tightly fitting layer of cardboard or blotter paper. The bees are then placed in layers separated by tissue paper. Labels with the collection data are inserted in each layer. The plastic container is tightly sealed so that the moisture of the insects' bodies keeps them supple. If the collections are too dry, a little water may be sprinkled into the container before it is sealed. The insects should be pinned soon after removing from the container as they dry out relatively quickly upon removal. If the container is properly sealed, the insects will remain in good condition for months. Chlorocresol can be purchased from BioQuip Products, P.O. Box 61, Santa Monica, California 90406.

CONCLUSIONS

A complete understanding of the taxonomy and biology of neotropical Lecythidaceae must be based, to a large extent, on adequately prepared and documented herbarium specimens. It is not good practice to simply collect Lecythidaceae without giving consideration to the proper preservation of the structures used in the classification of the family. Moreover, it is essential that more detailed descriptions of structures not preserved on herbarium sheets, such as flower color and bark characteristics, be noted by the collector. Better descriptions of the phenological state of the plant and its habitat are needed as well. Specialized collections for the study of chromosomes, anatomy, chemistry, and pollination biology will add greatly to our knowledge of Lecythidaceae. It is also important that local collectors become more selective in the species they collect. Some species have already been adequately collected from a given locality, and, therefore, their continued collection adds no new information to our herbaria and only causes undue expense and takes up valuable space in herbaria.

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CHROMOSOME CYTOLOGY OF *OLDENBURGIA* (ASTERACEAE–MUTISIEAE)[1]

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Abstract

As determined from root tip mitoses, three of the four species of the endemic Cape genus *Oldenburgia* have the same diploid chromosome number, $2n = 36$, and a similar karyotype of small submetacentric to metacentric chromosomes. Base number in the genus is presumed to be $x = 9$, and *Oldenburgia* is probably a paleotetraploid relict. It has no close relatives in Africa, and it seems to be most closely related to a group of arborescent South American genera of Gochnatiinae, perhaps the most primitive subtribe of Mutisieae.

Oldenburgia is a distinctive and taxonomically isolated, southern African genus of Asteraceae tribe Mutisieae. It is currently being revised by Pauline Bond, and this cytological study was undertaken in conjunction with her work, the genus being unknown cytologically until now. *Oldenburgia* consists of four species, all of which occur in the Cape Province of South Africa, between Grahamstown in the east and the Tulbagh district in the west. All species are restricted to the nutrient-poor, sandstone-derived soils of the Cape geological system. All species are woody and *O. grandis* (syn. *O. arbuscula*) is a small tree. Mutisieae are poorly represented in Africa, but richly developed in South America, where several genera are arborescent.

Materials and Methods

Counts were obtained from root tips harvested from germinating seeds. The root tips were treated in 0.003 M hydroxyquinoline for six hours at refrigerator temperatures, then fixed in 3 : 1 absolute ethanol-glacial acetic acid for two to five minutes, and stored in 70% ethanol. The roots were squashed in FLP orcein (Jackson, 1973) after a six-minute hydrolysis in 10% HCl at 60°C. Vouchers are cited in Table 1.

Observations

The three species examined have a diploid number of $2n = 36$ and similar karyotypes with relatively small chromosomes, 1.5–3 μm long. The chromosomes are too small to be easily characterized, but submetacentric pairs predominate and there are a few distinct metacentrics.

Discussion

Oldenburgia is a member of the basal tribe Mutisieae of Asteraceae and is usually regarded as belonging to Gochnatiinae, possibly the most primitive of the four subtribes of Mutisieae (Cabrera, 1977). The genus is characterized by thick, coriaceous, spirally arranged leaves, large radiate capitula, and bilabiate florets with a well-developed pappus. Its affinities within Gochnatiinae are at present obscure. It appears to have no close relationships to other African members of the subtribe (Bond, in prep.), which include *Erythrocephalum, Achyrothalamus, Pasaccardoa, Dicoma,* and *Ainsliaea.* The last two genera lack ray florets (unlike *Oldenburgia*); *Erythrocephalum* and *Achyrothalamus* lack or have a reduced pappus (well-developed in *Oldenburgia*). *Pasaccardoa,* which comprises a few annual species, comes closest to *Oldenburgia* in floral characters but is unlike it in vegetative features. It seems likely that *Oldenburgia* is most closely related to a group of largely arborescent South American genera that includes *Chimantaea, Cnicothamnus, Pleiotaxis, Gongylolepis,* and *Wunderlichia,* as well as *Gochnatia,* which also occurs in southeast Asia. There are no counts for any of these genera. Counts for African genera of Gochnatiinae include $n = 12$ and 11 for *Ainsliaea* (Arano, 1957), and there is only a single count for *Dicoma,* $n = 11$, for an Indian member of the genus (Bhandari & Singh, 1977). These genera appear distantly related to *Oldenburgia* on cytological as well as morphological grounds.

Basic chromosome number for Asteraceae is probably $x = 9$ (Raven, 1975; Solbrig, 1977) and the same number is most likely basic for Muti-

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TABLE 1. Chromosome numbers in *Oldenburgia*. All counts are original in this paper. Localities are in the Cape Province, South Africa.

O. grandis (Thunb.) Baillor (syn. *O. arbuscula* DC.): $2n = 36$; cultivated at Kirstenbosch Botanic Gardens, probably from plants from Grahamstown, *Galpin s.n.* (National Botanic Gardens 984/13 in NBG).

O. papionum DC.: $2n = 36$; Wangenheim farm, Rawsonville, rock crevices, *Bond 1722* (NBG).

O. paradoxa Less.: $2n = 36$; Robinsons Pass, Outeniqua Mts., *Bond 1726* (NBG).

sieae and Gochnatiinae as well. *Oldenburgia* appears on present evidence to be a paleotetraploid genus probably allied to a group of South American genera, mostly of the Guayana Highlands, and geographically isolated in Africa. Its basic chromosome number is possibly the same as for the family and tribe.

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NOTES ON *CIPURA* (IRIDACEAE) IN SOUTH AND CENTRAL AMERICA, AND A NEW SPECIES FROM VENEZUELA[1]

PETER GOLDBLATT[2] AND JAMES E. HENRICH[3]

ABSTRACT

Cipura is a small genus of Iridaceae—Tigridieae that is widespread in tropical South and Central America, Mexico, and the West Indies. It comprises at least five species and is at present poorly understood. The type species, *C. paludosa* Aublet, is often treated as including the similar *C. campanulata* Ravenna (syn. *C. inornata* Ravenna), and the differences between the two are detailed. A new species, *C. rupicola,* is described from Territorio Federal Amazonas, Venezuela. It is closely allied to the only other known yellow-flowered species, *C. xanthomelas* Martius ex Klatt (syn. *C. flava* Ravenna), of interior Brazil. The basic chromosome number in *Cipura* is $x = 7$ and chromosome numbers have been established here for *C. xanthomelas* and *C. rupicola,* both tetraploid, $2n = 4x = 28$.

During preparation of treatments of Iridaceae for three regional floras, *Flora Mesoamericana, Flora de Nicaragua,* and *Flora of the Venezuelan Guayana,* the genus *Cipura* Aublet posed several problems in typification and delimitation of species. As a result we studied this small genus in some detail. Our conclusions relate to the genus as a whole and are presented in the form of a review. A new species, *C. rupicola,* is described from western Venezuela, and two more undescribed species are included in a key to the genus but are not published as new species here for reasons given below. A complete revision of *Cipura* is being prepared by P. Ravenna as part of a treatment of Iridaceae for *Flora Neotropica.*

Cipura is one of a distinctive group of New World Iridaceae comprising tribe Tigridieae (Goldblatt, 1982), which is characterized by a bulbous rootstock, plicate leaves, and a basic chromosome number of $x = 7$. The first genus in the alliance to be described (Aublet, 1775), it was based on *C. paludosa,* from what is now French Guiana. *Cipura* comprises five or probably a few more species, distributed from southern Mexico in the north to Bolivia, southern Brazil, and Paraguay in the south (Fig. 1). *Cipura paludosa* occurs over almost the entire range of the genus, but the other species have narrower and sometimes very restricted ranges.

Cipura is closely related to the larger genus *Cypella* Herbert from which it differs in having erect inner tepals that partly conceal the stamens and style-stigma apparatus and a large cauline leaf inserted at the flowering stem apex just below the single or few and closely set rhipidia (spathe-enclosed inflorescence units). As in *Cypella* and several other genera of Tigridieae, the fugacious flowers have broadly clawed outer tepals; inner tepals with an adaxial nectariferous area on the limb (usually concealed by a fold in the tepal surface); free stamens with weak filaments; and anthers adhering to the style branches.

The style divides above into three thickened branches. In the less specialized species there are one or two pairs of erect appendages (crests) which exceed each transverse stigma lobe. Such elaborate style branches are probably basic in *Cipura* and the apparently simpler structure in *C. paludosa* and *C. campanulata,* in which the style branches are not developed and the crests are absent or reduced, is derived.

The species of *Cipura* currently recognized are *C. xanthomelas* Martius ex Klatt, of which *C. flava* Ravenna is almost certainly a synonym; the new *C. rupicola*; *C. paludosa* Aublet; and *C. campanulata* Ravenna. In addition, there are two undescribed species: *Cipura* sp. 1, a large and violet-flowered species, some herbarium specimens of which have been annotated *C. formosa* Ravenna by P. Ravenna; and *Cipura* sp. 2, also with violet flowers, from southwestern Venezuela and adjacent Colombia.

In the review we include the following: 1) typification of *Cipura paludosa,* which involves the delimitation of *C. campanulata,* a largely Central American species often confused with *C. palu-*

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FIGURE 1. Geographical distribution of the species of *Cipura*. The occurrence of *C. paludosa* in Nicaragua, Honduras, El Salvador, Guatemala, and the Yucatán Peninsula has not been established. Some specimens from western Mexico are difficult to determine, owing to absence of properly preserved flowers. Both *C. campanulata* and *C. paludosa* appear to occur there but more and better preserved material is needed to establish accurately the distribution of *Cipura* in this area.

dosa; 2) description of *C. rupicola* and a discussion of its differences from the closely related *C. xanthomelas*; 3) brief discussion of the two violet-flowered species; 4) key to the species; and 5) synonymy and description of *C. paludosa.*

TYPIFICATION AND DELIMITATION OF *CIPURA PALUDOSA*

Cipura paludosa, described by Aublet in 1775 from plants growing near Cayenne, is the most widespread and common species in the genus. It has pale bluish, or sometimes white, flowers with a cylindric-fusiform ovary included in the spathes and non-clawed, broad, closely imbricate inner tepals about half as long as the outer tepals (Fig. 2A). They conceal, except from above, the stamens, style, and stigma. The style branches are hardly differentiated but the style is thickened above and weakly three-lobed apically (Fig. 2A). The stigmas are simply expanded lobes located opposite and above the anthers which form a tube enclosing the upper part of the style. Obscure crestlike appendages extending above the stigmas can sometimes be seen, but they are often microscopic. The inner tepals of *C. paludosa* are concave below and have a conspicuous central zone of yellow nectariferous tissue outlined in violet.

Identification of the type of *Cipura paludosa* with living populations is not without problems. The type collection was made by Aublet in wet savannas at the foot of Mt. Kourou in what is now French Guiana. The illustration accompanying the description conforms best with blue-flowered plants that are fairly widespread in the Guianas and Brazil, which generally have short stems, relatively broad leaves, and 2–3 flowers in each rhipidium. The flowers are clearly illustrated by Aublet as having erect and imbricate inner tepals and a style with short stigmatic lobes (flowers are not present on the specimen that we have designated lectotype in the Rousseau Collection in the Paris Herbarium). In the type figure the stigmatic lobes are also most unusual. They are drawn as large, ascending and acute structures, quite unlike those in any living plants of any species of *Cipura.* We assume that these strange structures were included in error.

A species described by Kunth (1816) from eastern Colombia, *Cipura graminea,* is regarded here as conspecific with *C. paludosa.* The type specimen lacks flowers but has comparatively narrow leaves and elongate included capsules, of which there are two in some rhipidia. The Bolivian species *Cipura major,* described by Rusby (1910), and a plant from Peru, *C. goodspeediana* (Vargas) R. Foster (1962), based on *Cypella goodspeediana* Vargas (1945), with pale blue flowers and short flowering stems 7–10 cm long, also conform with *C. paludosa.* Following Foster (1946), we regard both as synonyms of *C. paludosa. Cipura major* differs mainly in having very narrow leaves, but similar leaves are known on some specimens of *C. paludosa.*

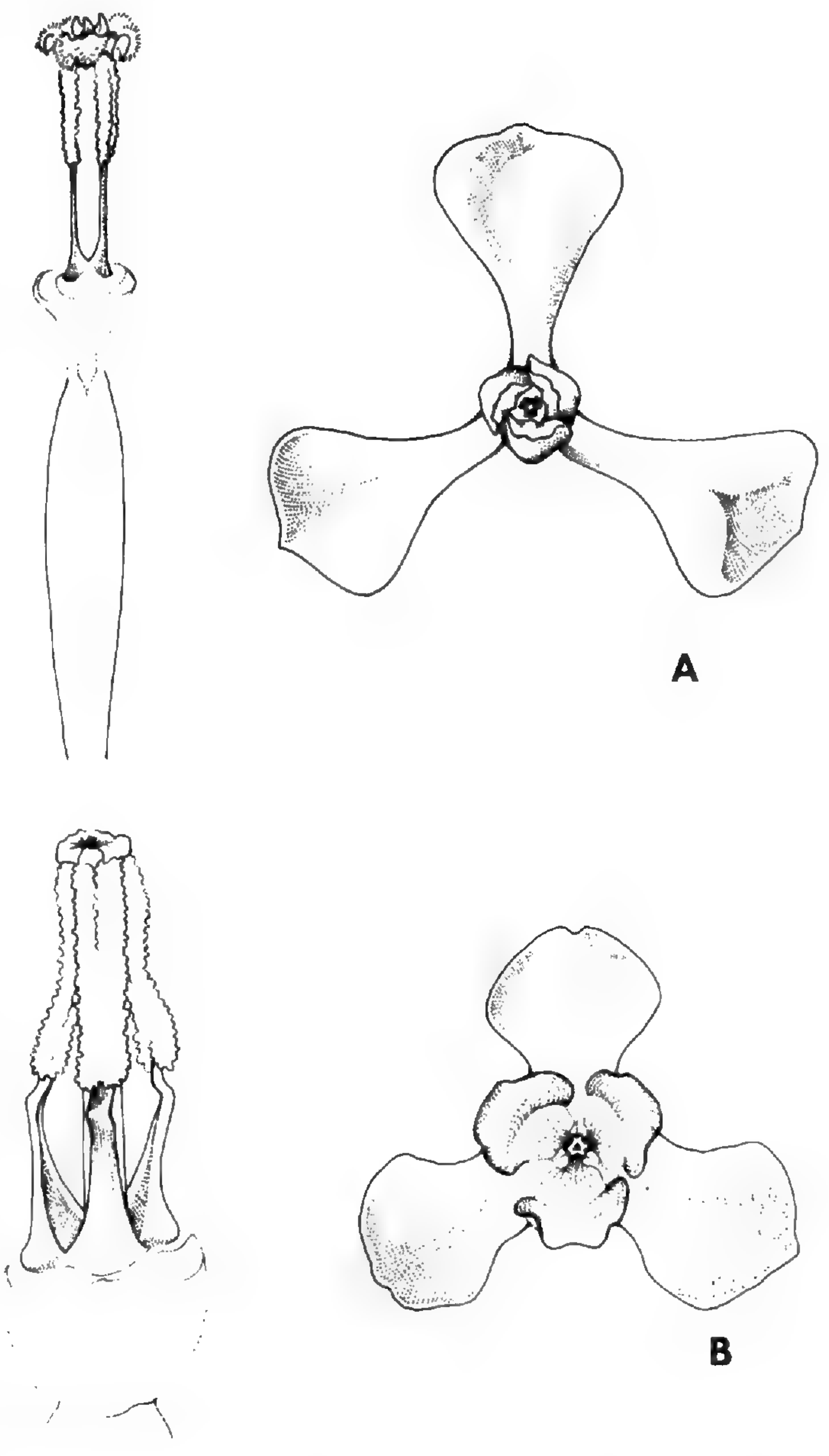

FIGURE 2. Dorsal views of the flowers (×2) and detail of the stamens and style from the side (×6), of *Cipura paludosa* (A), and *C. campanulata* (B).

Similar and closely related is a species common in Mesoamerica which almost always has white flowers. When dried it is difficult to distinguish from the often violet- or pale blue-flowered *Cipura paludosa,* with which it was included or confused in the several local and national floras for Mesoamerica. Living plants that we examined display some important differences not apparent in most dry specimens. The inner tepals are initially more or less erect but soon become semipatent and are held well away from the stamens and style-stigma apparatus (Fig. 2B). Also, the inner tepals lack nectariferous tissue and, at least to the unaided eye, have no glands. In addition the Mesoamerican species almost always has only one flower in each rhipidium (two or three in *C. paludosa*), and the flower emerges laterally from the spathes and is thus somewhat secund. The leaves are often very narrow, and the flowers have comparatively short pedicels 5–7 mm long. Names in the literature that appear to apply to this species are *C. campanulata* Ravenna (1964), the type of which is from Yucatán, and *C. inornata* Ravenna (1984) from Caracas, Venezuela. We have been unable to see the types of either of the species described by Ravenna. Holotypes are in the private herbarium of P. Ravenna who is unwilling to loan them to us. An isotype of *C. campanulata,* cited as at the Kew Herbarium (Ravenna, 1964), has not yet been received there.

From the description, *Cipura inornata* appears to differ hardly at all from *C. campanulata* and is reduced to synonymy here. Ravenna distinguished it, although not expressly, by the absence of style appendages but these are also lacking in *C. campanulata.* Ravenna (1964) explicitly distinguished *C. campanulata* from *C. paludosa* by its cernuous (i.e., secund) rather than erect flowers and by the inner tepals being nearly equal to the outer, his measurements being 19 mm long for the inner tepals and 21 mm for the outer.

We have four living collections of the white-flowered Mesoamerican *Cipura* and thus are able to assess, to some extent at least, its floral variation. The size, shape, and orientation of the inner tepals are most like the outer tepals of any of the species of *Cipura* and are about three-quarters as long (Fig. 2B), thus usually shorter by some 4–5 mm and are reasonably close to the dimensions given by Ravenna for *C. campanulata.* Moreover, the flowers are nearly always displaced to one side because they emerge laterally from the spathes rather than apically. Thus, there seems little to distinguish this plant from *C. campanulata* and, despite not having seen the type material, we feel that the name applies to the widespread Mesoamerican species. We must note, however, that several specimens from Yucatán that we have seen are somewhat more robust and have broad, strongly plicate leaves that are distinctly striated when dry. Nevertheless, we prefer not to recognize this form as a distinct taxon.

Cipura cubensis Griseb., based on *Wright s.n.,* anno 1865, is also white-flowered (Grisebach, 1866) and is sometimes regarded as separate from *C. paludosa.* We have been unable to locate the type, and it is impossible to tell from the protologue whether *C. cubensis* corresponds better with *C. campanulata* or *C. paludosa,* the presence of only the latter being established in Cuba. The name *C. cubensis* must for the present be excluded. We note, incidentally, that *C. paludosa* sensu Grisebach which is based on the cited collection, *Wright 3256,* is a species of *Cypella.*

Cipura paludosa and *C. campanulata* are probably the most specialized and least representative species of *Cipura.* They are distinct in their linear to fusiform ovaries, included in the rhipidia, and inner tepals lacking distinct claws. Both species are autogamous, unlike other members of *Cipura,* and have broad inner tepals, style branches represented by short stigmatic lobes, and anthers coherent around the thickened upper part of the style. The thickened part of the style probably represents fused style branches, which are present and free in other species of *Cipura. Cipura paludosa* is apparently a diploid species (Goldblatt, 1982), $2n = 14$, although structural heterozygosity and derived numbers of 13 and 12 have been recorded in plants of horticultural origin. The only count for *C. campanulata* is tetraploid, $2n = 28$ (reported by Goldblatt in 1982 as *C. paludosa*).

Cipura paludosa is the most widespread species in the genus, extending from northern Bolivia in the south to the Caribbean, Mesoamerica, and the West Indies in the north (Fig. 1). It varies in vegetative features. The stem is often quite short, reaching less than 8 cm from the ground, but in some plants may be up to 15 cm long. The leaves are usually relatively broad, 4–10 mm wide, but they may occasionally be only 1–2 mm wide. Its most distinctive features seem to be the number of flowers (and hence capsules) produced in each rhipidium, usually two or three, rarely more or fewer, and the closely imbricate inner tepals with conspicuous nectar guides.

In contrast, *Cipura campanulata* has pure white or rarely pale blue flowers without yellow nectar guides, and the inner tepals are initially erect (parallel to the axis of the flower) but later become somewhat outcurving. The style branches and stamens are similar to those of *C. paludosa* but always lack appendages. *Cipura campanulata* occurs in seasonally wet or marshy sites from Nayarit and Vera Cruz, Mexico through Mesoamerica to northern Venezuela and Colombia (Fig. 1).

YELLOW-FLOWERED SPECIES

A yellow-flowered species of *Cipura, C. xanthomelas,* was described by Klatt in 1882, based on collections made by Martius and Regnell in Brazil. It is characterized by globose, exserted capsules and yellow flowers. The relatively large yellow flowers have outer tepals 30–35 mm long. The inner tepals are about half as long as the outer, ca. 14 mm long, and have distinct claws ca. 8 mm long with red striations on the inner surface and dark markings on the knee and apex. The style branches are long and have well-developed crests ca. 2.8 mm long. *Cipura flava* (Ravenna, 1964) appears to be conspecific and pending examination of the type, deposited in the private herbarium of P. Ravenna, we are provisionally regarding it as a synonym. Bulbs of *C. xanthomelas* are quite large, usually 2–2.5 cm in diameter, with blackish resinous tunics, the spathes are (2.5–)3–5 cm long, and the nearly globose capsules are exserted and typically 12–14 mm long. The species is known to us from numerous herbarium specimens mostly with poorly preserved flowers and from a living collection grown at the Missouri Botanical Garden. The diploid chromosome number in this collection (*Plowman et al. 9306,* MO) is $2n = 28$, and the species thus appears to be tetraploid. Details of the karyotype of this and the following species will be reported elsewhere. The flowers of our living collection appeared to differ significantly from other material in having partly united filaments, a feature that we have not seen in other specimens. *Cipura xanthomelas* is centered in the Brazilian state of Goiás (Fig. 1) and extends into the neighboring states of Mato Grosso, Minas Gerais, Maranhão, and possibly Piauí, while an unusual variant is recorded from western Pernambuco, adjacent to Piauí.

A similar yellow-flowered species, here described as *Cipura rupicola,* has come to our attention from Venezuela. It has pale yellow flowers with unusual inner tepals having slender claws, between which the anthers can be seen, but the long style branches are partly concealed by the erect tepal limbs (Fig. 3). *Cipura rupicola* differs from *C. xanthomelas* in being less robust, in its non-resinous bulbs 1.5–2.5 cm in diameter, and shorter spathes 2.6–3.6 cm long. The flowers are also smaller and lack the markings on the inner tepals and the red striations on the claw characteristic of *C. xanthomelas.* The outer tepals are 25–28 mm long and the inner tepals have claws ca. 9 mm long and limbs ca. 8 mm long. The style branches lack crests. Like *C. xanthomelas, C. rupicola* has exserted capsules, globose in shape and usually 8–11 mm long, thus somewhat smaller than its relative. Chromosome number in *C. rupicola* is $2n = 28$ and it thus appears to be tetraploid like *C. xanthomelas.*

Cipura rupicola Goldblatt & Henrich, sp. nov. TYPE: Venezuela. T.F.A., Dept. Atures: near Puerto Ayacucho, *Davidse & Miller 26437* (holotype, MO; isotypes, COL, K, NY, VEN). Figure 3.

Plantae 12–40 cm altae, tunicis nigribus non resinosis, floribus flavis, tepalis exterioribus 25–28 mm longis, interioribus ca. 18 mm longis unguibus angustis, filamentis liberis 3 mm longis, antheris 3.5 mm longis, ramis styli 5 mm longis sine cristis, capsulis obovoideis 8–11 mm longis exsertis.

Plants 12–40 cm tall. *Bulb* 1.5–2.5 cm diam.; tunics dark brown to blackish, brittle-papery but not noticeably resinous. *Leaves* 3–5, all but one basal, strongly plicate, narrowly lanceolate, about as long to slightly longer than the flowering stem, (6–)9–14 mm wide; subterminal cauline leaf solitary (second smaller leaf occasionally present), smaller than the basal, 7–15 cm long, about 12 mm wide. *Flowering stems* 1–3 per plant, erect, lateral to the basal leaves, 8–20(–35) cm long, bearing 2–several crowded rhipidia either sessile or on short branches. *Inner spathes* 2.6–3.5 cm long; *outer* ½–⅔ as long. *Flowers* bright yellow, with a more or less distinct perianth tube ca. 2 mm long; *outer tepals* 25–28 mm long, oblong, tapering slightly near the base, somewhat distally twisted from horizontal, weakly divided into limb and claw, the claw ascending, plane, the margins becoming transparent, the limb horizontal, channeled, ca. 20 mm long, to 10 mm wide; *inner tepals* ca. 18 mm long, the claws ca. 2.5 mm wide, narrower towards the base, ascending and widely separated from one another and thus forming broad windows making the anthers visible, curving inwards above to become horizontal at the apex, the limbs erect, imbricate, the apex rolled abaxially, ca. 8 mm long, ca. 8 mm wide, bearing a small circular yellow zone at the base, running on to the apex of the claw. *Filaments* free, erect, thickened below, 3 mm long; *anthers* ca. 3.5 mm long, free from the style, latrorse, with a broad connective wider than the anther lobes; pollen yellow. *Ovary* included in the spathes at anthesis, ca. 4.5 mm long; *style* ca. 4 mm long, dividing into 3 erect branches, these hidden laterally by the inner tepal limbs; *style branches* 5 mm long, plane, truncate, without apical appendages, expanded apically into bilobed papillose stigmas. *Capsules* exserted from the spathes, obovoid, 8–11 mm long; *seeds* angular, to 2 mm at the longest axis. *Chromosome number* $2n = 28$. *Flowering time* June–July.

Distribution. Venezuela, T.F.A., Dept. Atures, in the vicinity of Puerto Ayacucho, growing on shallow soils of granite hills and outcrops and on the surrounding dry stony savannas (Fig. 1).

Additional specimens examined. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: DEPT. ATURES: alrededores de Puerto Ayacucho, *Huber & Tillett 932* (MO, VEN); between Puerto Ayacucho and airport, laja and adjacent flats, *Gentry & Berry 14430* (MO); alrededores de las rocas, Puerto Ayacucho, *Williams 13099* (K, US, VEN); se abren en medio de las rocas, Puerto Ayacucho, *Williams 12967* (F, VEN); medio y alto Orinoco, *Pannier & Schwabe 926* (VEN); prope Mayapures, ad flumen Orenoco, *Spruce 3596* (BM, K, NY); bords de l'Orenoque, *Gaillard 118* (P); Oripopos, 3.5 km N of Puerto Ayacucho, *Romero 1254* (MO).

VIOLET-FLOWERED SPECIES

There are two violet-flowered species known to us. One, *Cipura* sp. 1, fairly well represented

FIGURE 3. *Cipura rupicola.* Habit (×0.5), lateral view of the flower (×1), and detail of the stamens and style branches from the side including a dorsal view of the stigmatic region (×4).

in some herbaria, is native to Brazil, occurring in Bahia, Goiás, and Mato Grosso. It is easily recognized by the unusually large bulbs with resinous tunics, relatively broad rigid leaves, a short cauline leaf which is typically shorter than the spathes, and only one or sometimes two rhipidia. The flowers are unusual in their violet color and large size. The outer tepals are ca. 40–45 mm long and 30 mm wide, and the inner tepals are ca. 22 mm long, with a long ascending claw to ca. 18 mm long and a limb that curves forward over the claw and then is rolled outwards distally. The style branches are flattened and petaloid but fairly narrow and have two pairs of crests, the adaxial ca. 5 mm long and the abaxial about half as long. The species is known to us only from dry specimens and details of the inner tepals and style branches are not completely clear.

The second violet-flowered species, *Cipura* sp. 2, of which we have seen only two specimens, is from southwestern Venezuela (*Huber 5711*, VEN) and adjacent eastern Colombia (*Vincelli 1230*, MO). It also has resinous bulb tunics, but is taller than *C.* sp. 1, ca. 45 cm high, and has two to five rhipidia at the stem apex subtended by a cauline leaf about three times as long as the spathes. The flowers are much smaller than those of *C.* sp. 1 with outer tepals ca. 18 mm long. They are comparable with those of *C. paludosa* and *C. campanulata*, and it is probably most closely related to these two species. Floral details are obscure owing to poor preservation.

KEY TO THE SPECIES OF *CIPURA*

1a. Flowers yellow; capsules globose and exserted from the spathes.
  2a. Inner tepals yellow with blackish markings on the knee and at the apex, less than half as long as the outer tepals, to 14 mm long .... *C. xanthomelas*
  2b. Inner tepals entirely pale yellow; somewhat more than half as long as the outer, to 18 mm long .... *C. rupicola*
1b. Flowers shades of blue to violet or white; capsules cylindric-fusiform or nearly globose; included in the spathes.
  3a. Rhipidia solitary or two and subtended by a cauline leaf shorter than or about as long as the spathes .... *C.* sp. 1
  3b. Rhipidia usually more than one and subtended by a cauline leaf usually at least twice as long as the spathes.
    4a. Bulbs 15–20 mm in diameter, with tunics not or only slightly resinous.
      5a. Flowers white, rarely pale blue; inner tepals without yellow nectar guides or a zone of nectariferous tissue; flowers solitary in each rhipidium; inner tepals about ¾ the length of the outer and not imbricate .... *C. campanulata*
      5b. Flowers usually pale bluish to violet, rarely white; inner tepals with a yellow nectar guide and a zone of nectariferous tissue, often outlined in violet; flowers (1–)2–3 in each rhipidium; inner tepals closely imbricate, about half as long as the outer .... *C. paludosa*
    4b. Bulbs about 30 mm in diameter, with tunics heavily resinous .... *C.* sp. 2

NOMENCLATURE AND DESCRIPTION OF *C. PALUDOSA*

Cipura paludosa Aublet, Hist. Pl. Guiane 38–39. 1775. TYPE: French Guiana: near Mt. Kourou (as Courou), *Aublet s.n.* (lectotype, P—Herb. Rousseau, designated here). Figure 2.

Cipura graminea Kunth, Nov. Gen. Sp. 1: 320. 1816. TYPE: Colombia: ripa Orinoco propter urbem Santo Thomas del Angostura, *Humboldt & Bonpland s.n.* (lectotype, P, designated here; isolectotype, P—Herb. Bonpland).

Cipura major Rusby, Bull. New York Bot. Gard. 6: 493. 1910. TYPE: Bolivia: Tamupasa, 1,800 ft., *Williams 546* (lectotype, NY, designated here; isotypes, BM, K).

Cypella goodspeediana Vargas, Revista Univ. Cuzco 33: 171. 1944. TYPE: Peru. Convencion: Hda. Potrero, *Vargas 2509* (holotype, CUZ, not seen; isotype, GH); *Cipura goodspeediana* (Vargas) R. Foster, Rhodora 64: 311. 1962.

Cipura paludosa subsp. *mexicana* Ravenna, Phytologia 56: 195–196. 1984. TYPE: Mexico. Sinaloa: *Ravenna 278* (holotype, Herb. Ravenna, not seen).

Plants 16–27 cm tall. *Bulb* 12–20 mm diam.; tunics dry and brittle-papery, rarely slightly resinous. *Leaves* finely plicate, linear-lanceolate, 1–3 basal, 16–27 cm long, 2–5 mm wide; subterminal cauline leaf single, largest, clasping the spathes below, 16–23 cm long. *Flowering stem* 3.5–8(–15) cm long, bearing several crowded rhipidia, either sessile or on short branches. *Inner spathes* 30–35 mm long; *outer* ca. ⅔ as long as the inner. *Flowers* pale to bright blue, or white, the tepals connate into a distinct tube ca. 2 mm long; *outer tepals* fading to white at the base, oblanceolate, ascending to nearly horizontal, distally twisted ca. 30°, the margins rolled outward, the right more so than the left, 2.5–2.8 cm long, 1.3–1.5 cm wide, with a white nectary in a central zone ca. 1 cm above the base; *inner tepals* 1.5 cm long, 8–10 mm wide, light blue with a white apex, darkest at the margins, more or less obovate, erect and imbricate, the apex rolled outwards, strongly concave, with a yellow nectary in a median band extending ca. 2 mm from apex to 2–3 mm from the base, broadening to 4 mm at the widest, surrounding a white to light blue, raised nonglandular area, sometimes with semiparallel dark blue bands extending at right angles to the nectariferous zone. *Filaments* 2–3 mm long, thickened and sometimes contiguous at the base for up to 1 mm, free and threadlike above; *anthers* adhering to the style, 3.5–4 mm long, latrorse with a slender connective broadest at the base and tapering to the apex, pollen white. *Ovary* included in the spathes, 6–10 mm long; *style* 6–8 mm long, cylindric, 3-lobed above, the lobes usually emarginate, 1 mm long, 1 mm wide, distally papillose, with 1–2 obscure (often microscopic) erect, crestlike appendages at the base. *Capsules* oblong-cylindric, 12–18 mm long, included in the spathes; *seeds* angular, ca. 1.3–1.8 mm long. *Chromosome number* $2n = 14$.

Distribution. Bolivia and Paraguay, through southern Brazil to Central America, southern Mexico, and the West Indies (Fig. 1).

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ITHOMIINAE (LEPIDOPTERA: NYMPHALIDAE): SUMMARY OF KNOWN LARVAL FOOD PLANTS[1,2]

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Abstract

The known interactions between the larvae of ithomiine butterflies and their host plants (about 400, 90% in the Solanaceae) are described in a table, illustrated, and briefly discussed.

The widespread and diversified use of plants in the family Solanaceae by man is reflected in the large number of applied scientific papers published on these plants (see the taxonomic index of any issue of *Biological Abstracts*). The alkaloidal nature of most plants in this family has led to their extensive use in folk and proprietary medicine, consciousness expansion, and recently as a source of pharmaceutical intermediates. Other important uses include fodder, fencing, support, insecticide, ornament, and perfume.

In tropical America, the most important groups of herbivores of Solanaceae are grasshoppers, chrysomelid and meloid beetles, and larvae of butterflies in the nymphalid subfamily Ithomiinae. These insects overcome the considerable physical and chemical defenses of these plants and turn them to their own use, at least as recognition cues, if not necessarily as protection against predation (Brown, 1987). Useful Solanaceae frequently attacked by Ithomiinae include *Lycopersicon, Cyphomandra, Solanum* sect. *Lasiocarpa,* and solasodine-producing or tobacco-substituting *Solanum.* Also regularly eaten are *Solanum tuberosum, S. melongena* and relatives, as well as *Capsicum* and *Physalis.* Many ornamental and medicinal Solanaceae (*Brunfelsia, Cestrum, Solandra, Markea* s.l., *Juanulloa, Brugmansia, Acnistus, Solanum pseudocapsicum* and *Solanum* sect. *Jasminosolanum*) are heavily damaged by ithomiine larvae. *Nicotiana* and *Petunia* seem to be immune to these herbivores.

This paper lists the known interactions (to mid-1985) between ithomiine butterflies and their larval food plants, 90% in the Solanaceae (Table 1). It is the data base for papers by Drummond (1985), Brown (1985), and Brown & Drummond (in prep.). The 40 butterfly genera for which food plants are known or inferred are placed in phylogenetic order in the Table, grouped into tribes as first proposed by Fox (1961), followed basically by Mielke & Brown (1979), and modified by recent studies of early stages leading to a numerical phylogeny by Brown (in prep.). Nomenclature for the butterflies follows Mielke & Brown (1979) except in a few cases in which recent studies, especially of chromosomes, indicate changes in status. Nomenclature of the plants follows the thesis of Mary Fallen (1983, Hamburg) for Apocynaceae, recent compendia of the Solanaceae, and the *Index Kewensis.* We believe that identifications of both insect and plant taxa are accurate to the generic level in all cases, to the subgeneric level for *Solanum* in essentially all cases, and to the species level where given in the vast majority of cases. Many older records, either not confirmed or regarded as unlikely in view of broader recent studies, have been excluded from the list; these include especially those in the agricultural literature of Brazil, compiled in D'Araújo e Silva et al. (1968) and continuing up to the present day [such as a recent report of *Mechanitis lysimnia nesaea* Hübner as a pest of *Passiflora edulis* Sims. in northeastern Brazil, clearly a misidentification of *Heliconius ethilla narcaea* (Godart) or *Eueides isabella dianasa* (Hübner), common in the area]. Doubtful records are marked with a question mark in parentheses,

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whereas sure records with tentative (unconfirmed) plant identifications are indicated by a simple question mark after the name. Localities and sources are coded and given at the end of the table. Numbers or letters in parentheses after a plant name are voucher symbols for that species.

The following genera (with number of species in parentheses) of Ithomiinae have yet to be observed or suspected as larvae on any plants; from preliminary field observations, they are predicted to use the solanaceous genera indicated in each case: *Roswellia* (1) (*Capsicum ciliatum*), *Patricia* (2) (*Dunalia*), a new genus near *Hyposcada* (1) (*Lycianthes*), *Paititia* (1) (*Cyphomandra*), *Aremfoxia* (1) and *Pagyris* (1) (*Witheringia, Dunalia, Brugmansia,* and relatives), and *Dygoris* (1) and *Veladyris* (1) (*Solanum* sect. *Geminata, Cestrum*).

The following genera of Solanaceae, with one or more species available to Ithomiinae in their tropical or subtropical moist habitats (genera restricted to dry habitats or temperate zones not included), have not yet been seen to be used by any species of Ithomiinae. Solanoideae: *Jaltomata, Athenaea* (expected for *Epityches* and *Ithomia*), *Larnax, Saracha, Iochroma, Deprea* (Solaneae); *Jaborosa, Salpichroa* (Jaboroseae); *Lycium, Grabowskia* (Lycieae); *Trianaea* (Solandreae). Cestroideae: *Sessea, Metternichia* (Cestreae); *Nicotiana, Petunia, Fabiana, Nierembergia, Bouchetia* (Nicotianeae); *Schwenkia, Protoschwenkia, Melananthus* (Schwenkieae); *Parabouchetia* (Parabouchetieae); *Leptoglossis, Browallia, Streptosolen* (Salpiglossideae); *Heteranthia* (tribal position unclear). While some of these genera may be found to be used by Ithomiinae with more observation, members of others have been watched for years within large Ithomiinae communities and have not been seen to support the larvae; in a few cases, ovipositions were followed by larval death (e.g., in Campinas, SP, *Mechanitis polymnia casabranca* Haensch has oviposited on both *Capsicum annuum* and *Nicotiana* sp., but the larvae died without feeding or developing).

The complete picture of the known food plant relationships of the Ithomiinae, based on the data in the table, is presented in Figure 1, in which plant genera (from top to bottom) and butterfly tribes (from left to right) are arranged in phylogenetic order based on currently accepted evolutionary sequences (the vertical position of butterfly genera represents only convenience in presentation of the figure; details are given in the phylogeny of Brown, in prep.). The complexity of the relationships illustrated in the figure indicates that strong ecological influences may outweigh the presumed evolutionary history of the interactions. See papers by Drummond (1986) and Brown & Drummond (in prep.) for discussion of these aspects.

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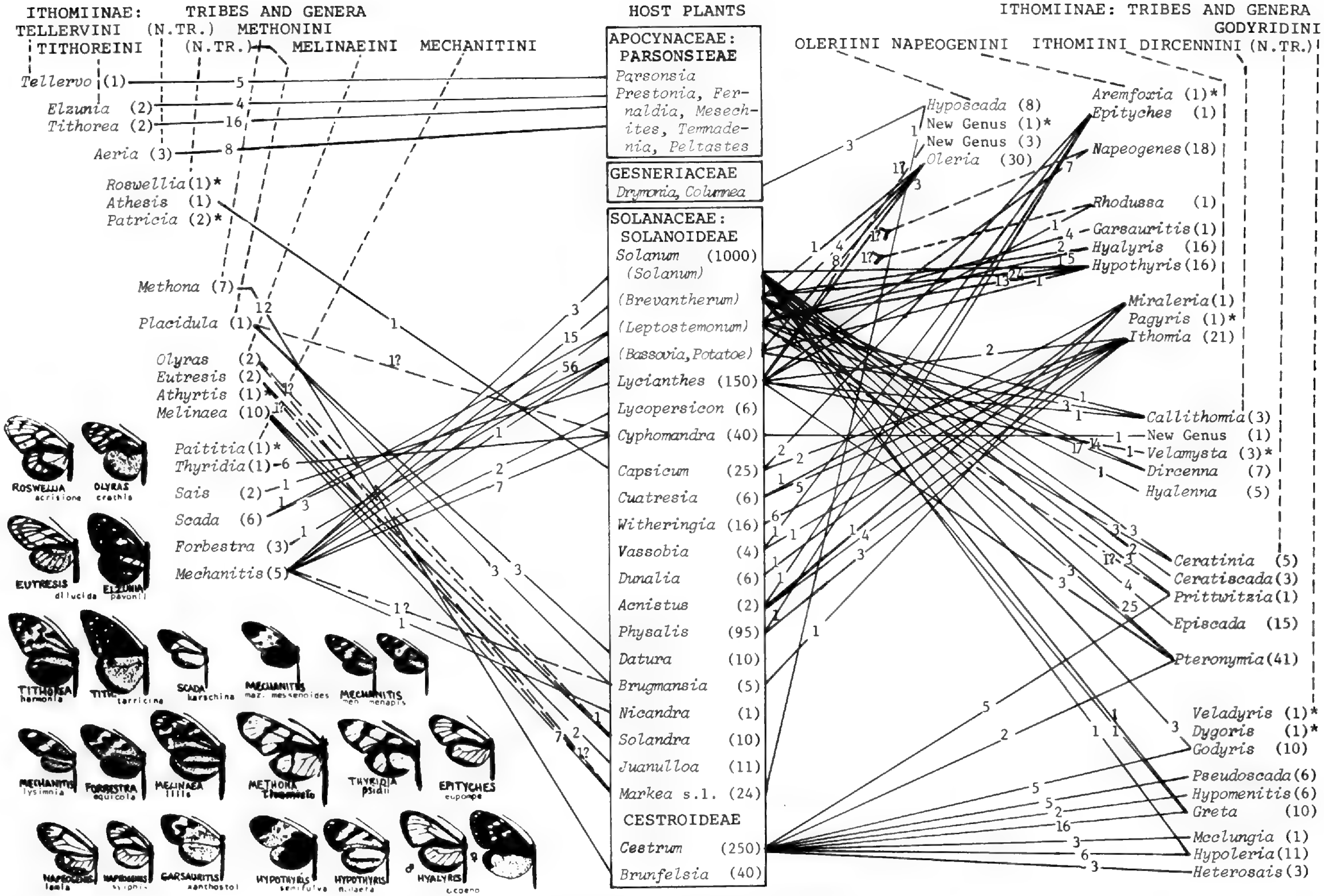

FIGURE 1. The Ithomiinae/Solanaceae interface. Numbers in parentheses refer to species in genus. Numbers on lines quantify interspecific interactions. Doubtful records followed by question mark. No host plants have been recorded for genera with asterisks.

TABLE 1. Ithomiine larval food plants.

Ithomiinae: Tribe, Genus, Species, and Subspecies	Host Plants[1]: Genus (Subgenus or Section) and Species	Locality[2]	Source[3]
A) APOCYNACEAE FEEDERS			
TELLERVINI (Old World)		Queensland, New Guinea, Solomons	JAE
Tellervo zoilus (Fabricius)	*Parsonsia* (5 species)		
TITHOREINI			
Elzunia humboldt bomplandii (Guérin)	"Echitoid vine"	Col	KB
pavonii (Butler)	*Prestonia* sp.	SEc	SK
	"Echitoid vine"	NPer	KB/LG
	"Echitoid vine"	NPer	KB
	Apocyne	NPer	GL
Tithorea tarricina pinthias Godm. & Salv.	"*Echites*" (? = one of following)	CR	MF
	Prestonia portobellensis (Buerl.) Woodson	CR	WH
	Prestonia guatemalensis Woodson	ElS, CR	AM, LG
harmonia salvadoris Staudinger	*Fernaldia pandurata* (A. DC.) Woodson	ElS	AM
	Prestonia guatemalensis Woodson	ElS	AM
helicaon Godm. & Salv.	*Prestonia portobellensis* (Buerl.) Woodson	CR	WB
furia Staudinger	"Echitoid vine"	Ven	KB
megara (Godart)	"*Echites*" (? = following species)	Trin	JLG, MB
	Mesechites trifida Muell. Arg.	Trin	LG
moppa Bryk	"*Echites*"	Belém	MF
lateflava Haensch	"Echitoid vine"	Rond	KB
pseudonyma Staudinger	*Prestonia acutifolia* (S. Moore) Woodson	MTN	KB
pseudethra Butler	*Prestonia coalita* (Vell.) Woodson	Mogi	KB
	Prestonia dusenii (Malme) Woodson	Camp	KB
	Prestonia acutifolia (S. Moore) Woodson	Mogi	KB
	Peltastes peltatus (Vell.) Woodson	Camp	KB
	Temnadenia violacea Miers	Sum	KB
	"Echitoid vine"	Goiás	KB
caissara Zikán	*Prestonia coalita* (Vell.) Woodson	SNegra	KB
neitha Hopffer	*Prestonia acutifolia* (S. Moore) Woodson	Peru	KB
NEW TRIBE	Apocyne (?)	Ven	KB
Aeria eurimedia agna Godman & Salvin	"*Echites*" (? = following species)	Trin	JLG
	Mesechites trifida Muell. Arg.	Trin	LG, MB

TABLE 1. Continued.

Ithomiinae: Tribe, Genus, Species, and Subspecies	Host Plants[1]: Genus (Subgenus or Section) and Species	Locality[2]	Source[3]
	Prestonia portobellensis (Buerl.) Woodson	CR	WH
	Prestonia sp.	CR	AY
olena Weymer	*Prestonia coalita* (Vell.) Woodson	Camp	KB
	Prestonia dusenii (Malme) Woodson	Camp	KB
elara elara (Hewitson)	Apocynaceae	Goiás	KB
	"*Echites*"	Rond	KB
	"*Echites*"	MTN	KB
B) SOLANACEAE FEEDERS			
NEW TRIBE			
Athesis clearista Doubleday	*Capsicum ciliatum* (Kunth) Kuntze	Ven	KB
METHONINI			
Methona confusa confusa Butler	*Brunfelsia amazonica* Morton	Man	GL
confusa ssp. nov.	*Brunfelsia dwyeri* D'Arcy	Pan	GS
confusa psamathe Godm. & Salv.	*Brunfelsia grandiflora* D. Don	San-Ec, Barn	KB
	Brunfelsia sp. (7330)	Lim	BD
	Brunfelsia pauciflora (Cham. & Schldl.) Benth.	Lim	BD
megisto (Felder & Felder)	*Brunfelsia mire* Monachino	Rond	KB
	Brunfelsia martiana Plowman	Man	KB
	Brunfelsia grandiflora D. Don	Man	KB
singularis (Staudinger)	*Brunfelsia uniflora* (Pohl) D. Don	Pnb	GL
themisto (Hübner)	*Brunfelsia australis* Benth.	RGS, Camp	GL, KB
	Brunfelsia pauciflora (Cham. & Schldl.) Benth.	Camp, Arg	KB, KH
	Brunfelsia uniflora (Pohl) D. Don	Rio	KB
NEW TRIBE			
Placidula euryanassa (Felder & Felder)	*Datura stramonium* L.	UR	CB
	Datura metel L.	UR	CB
	Datura fastuosa L.	UR	CB
	Brugmansia suaveolens (Willd.) Sweet	RGS	CB
	Brugmansia candida Pers.	Rio	RFD
	Brugmansia arborea (L.) Lagerheim	RGS	CB
	Cyphomandra crassicaulis (Ortm.) Kuntze (?)	RGS	CB

TABLE 1. Continued.

Ithomiinae: Tribe, Genus, Species, and Subspecies	Host Plants[1]: Genus (Subgenus or Section) and Species	Locality[2]	Source[3]
MELINAEINI			
Olyras crathis staudingeri Godm. & Salv.	*Solandra grandiflora* Swartz (?)	CR	WH
crathis Doubl. & Hewitson (reared on *Juanulloa mexicana*)	*Markea* (*Schultesianthus*) *megalandra* (Dunal) D'Arcy (?)	Ven	KB
Eutresis hypereia theope Godm. & Salv.	*Solandra grandiflora* Swartz (?)	CR	WH
hypereia Dblday. & Hew. (oviposited on *Juanulloa mexicana*)	*Markea* (*Schultesianthus*) *megalandra* (Dunal) D'Arcy (?)	Ven	KB
Melinaea mneme mneme (Linnaeus)	*Markea coccinea* Rich. (?)	Man	KB
mauensis Weymer	*Markea coccinea* Rich.	Marajó	KB
ludovica ludovica (Cramer)	*Markea* sp.	Belém	MF
paraiya Reakirt	*Markea* (*Dyssochroma*) *viridiflora* (Sims) Miers	Rio, SV	KB
lilis imitata Bates	*Juanulloa mexicana* (Schldl.) Miers	Mex, CR	LG
	Markea (*Merinthopodium*) *neurantha* Hems.	CR	WH, LG
	Solandra grandiflora Swartz	CR	LG
parallelis Butler	*Markea* (*Schultesianthus*) *leucantha* F. D. Smith	Pan	KB
marsaeus pothete D'Almeida	*Markea* (*Hawkesiophyton*) *ulei* (Dammer) Cuatrec.	Rond	KB
menophilus menophilus (Hewitson)	*Juanulloa mexicana*? (Schlecht.) Miers	Lim	BD
ssp. nov.	*Markea* (*Hawkesiophyton*) *ulei* (Dammer) Cuatrec.	Rond	KB
MECHANITINI			
Thyridia psidii melantho (Bates)	*Cyphomandra hartwegii* (Miers) Dunal	CR	WB, WH
	Cyphomandra crassicaulis (Ortm.) Kuntze	CR	BL
aedesia (Doubleday)	*Cyphomandra diversifolia* (Dunal) Bitter	Ven	FA-Mar
	Cyphomandra crassicaulis (Ortm.) Kuntze	Ven	RMF
ino (Felder & Felder)	*Cyphomandra hartwegii* (Miers) Dunal	Lim	BD
cetoides (Ros. & Talbot)	*Cyphomandra divaricata* Sendtner	Camp	JVN, RM
	Cyphomandra fragrans (Hook.) Sendtner	Camp	KB
	Cyphomandra sciadostylis Sendtner	SNegra	KB
	Cyphomandra crassicaulis (Ortm.) Kuntze	Camp	KB
Sais rosalia brasiliensis Talbot	*Lycianthes* sp. (decumbent)	Goiás	KB
Scada zibia xanthina (Bates)	*Solanum* (*Bassovia*?) *enchylozum* Bitter	CR	WH
	Solanum (*Micracantha*) *siparunoides* Ewan	CR	WH
batesi batesi Haensch	*Solanum* (*Bassovia*?) sp.	Lim	BD
reckia nr. *theaphia* (Bates)	*Solanum* (*Bassovia*) nr. *trizygum* Bitter	Rond	KB

TABLE 1. Continued.

Ithomiinae: Tribe, Genus, Species, and Subspecies	Host Plants[1]: Genus (Subgenus or Section) and Species	Locality[2]	Source[3]
Forbestra olivencia juntana (Haensch)	*Solanum* (*Bassovia*) *anceps* Rich.	Lim	BD
Mechanitis polymnia isthmia Bates	*Solanum* (*Brevantherum*) *schlechtendalianum* Walp.	CR	WH
	Solanum (*Brevantherum*) *asperum* Rich.	CR	WH
	Solanum (*Leptostemonum*) *ochraceoferrugineum* (Dunal) Fern.	CR	AY/M
	Solanum (*Leptostemonum*) *hispidum* Pers.	CR	WH, AY/M
	Solanum (*Leptostemonum*) *jamaicense* Miller	CR	WH
	Solanum (*Micracantha*) *lancaeifolium* Jacq.	CR	LG, WH
veritabilis Butler	*Solanum* (*Leptostemonum*) *melongena* L.	Ven	FA-Mar
	Solanum (*Lasiocarpa*) *hirtum* Vahl.	Ven	R/P
	Solanum (*Lasiocarpa*) *sessiliflorum* Dunal	Ven	FA-Mar
kayei Fox	*Solanum* (*Leptostemonum*) sp.	Trin	MB
dorissides Staudinger	*Solanum* (*Solanum*) sp.	Lim	BD
	Solanum (*Lasiocarpa*) *sessiliflorum* Dunal	Lim	BD
	Solanum (*Lasiocarpa*) *quitoense* Lam.	Lim	BD
	Lycopersicon esculentum Miller	Lim	BD
	Cyphomandra hartwegii (Miers) Dunal	Lim	BD
eurydice Haensch	*Solanum* (*Brevantherum*) sp.	Peru	RMF
angustifascia Talbot	*Solanum* (*Brevantherum*) *goodspeedii* Roe	Bol	KB
	Solanum (*Lasiocarpa*) *stramoniifolium* Jacq.	Rond	KB
polymnia (Linnaeus)	*Solanum* (*Brevantherum*) sp.	Bra	DS
	Solanum (*Leptostemonum*) sp.	Belém	KB
	Solanum (*Leptostemonum*) *sisymbriifolium* Lam.	Bra	DS
	Solanum (*Leptostemonum*) *crinitum* Lam.	Man	KB
	Solanum (*Acanthophora*) *aculeatissimum* Jacq.	Sur	JS
casabranca Haensch	*Solanum* (*Brevantherum*) *concinnum* Schldl. ex Sendter	Camp	KB
	Solanum (*Brevantherum*) *megalochiton* C. Martius	Sum	JVN
	Solanum (*Brevantherum*) *mauritianum* Scop.	Sum	JVN
	Solanum (*Brevantherum*) *granuloso-leprosum* Dunal	Mogi	RM
	Solanum (*Leptostemonum*) sp.	Brsl	KB
	Solanum (*Leptostemonum*) *variabile* C. Martius	Sum	JVN
	Solanum (*Leptostemonum*) *paniculatum* L.	Sum	JVN
	Solanum (*Leptostemonum*) *melongena* L.	Camp	KB
	Solanum (*Leptostemonum*) *robustum* Wendl.	Sum	JVN
	Solanum (*Leptostemonum*) *incarceratum* Ruiz & Pavón	Bra	DS
	Solanum (*Leptostemonum*) *torvum* Swartz	Rio	KB

TABLE 1. Continued.

Ithomiinae: Tribe, Genus, Species, and Subspecies	Host Plants[1]: Genus (Subgenus or Section) and Species	Locality[2]	Source[3]
	Solanum (*Leptostemonum*) *asperolanatum* Ruiz & Pavón	Camp	KB
	Solanum (*Lasiocarpa*) *sessiliflorum* Dunal	Rio	JFZ
	Lycopersicon esculentum Miller	Camp	KB
	Cyphomandra velutina Sendtner	Rio	NM
	Cyphomandra fragrans (Hook.) Sendtner	Camp	KB
	Cyphomandra sciadostylis Sendtner	Rio	NM
menapis saturata Godm. & Salv.	*Solanum* (*Leptostemonum*) *hispidum* Pers.	CR	WH
	Solanum (*Micracantha*) *siparunoides* Ewan	CR	WH
	Solanum (*Lasiocarpa*) *quitoense* Lam.	CR	WH
	Solanum (*Acanthophora*) *acerifolium* Humb. & Bonpl. ex Dunal	CR	WH
	Solanum (*Acanthophora*) *capsicoides* All.	CR	WH
	Solanum (*Acanthophora*) nr. *aculeatissimum*	CR	LG
mantineus Hewitson	*Solanum* (*Lasiocarpa*) *quitoense* Lam.	WEc	BD
	Solanum (*Acanthophora*) *mammosum* L.	WEc	BD
mazaeus mazaeus Hewitson	*Solanum* (*Leptostemonum*) sp. (7326) Jacq.	Lim	BD
	Solanum (*Leptostemonum*) sp. (7333)	Lim	BD
	Solanum (*Micracantha*) nr. *lancaeifolium*	Lim	BD
	Solanum (*Lasiocarpa*) *sessiliflorum* Dunal	7Lg	KB
deceptus Butler (& hybrids)	*Solanum* (*Lasiocarpa*) *sessiliflorum* Dunal	Lim	BD
	Solanum (*Lasiocarpa*) *pectinatum* Dunal	Lim	BD
	Solanum (*Lasiocarpa*) *quitoense* Lam.	Lim	BD
doryssus doryssus Bates	*Solanum* (*Brevantherum*) *rugosum* Dunal	CR	LG
	Solanum (*Brevantherum*) *umbellatum* Miller	CR	LG, WH
	Solanum (*Micracantha*) *siparunoides* Ewan	CR	WH
lysimnia elisa (Guérin)	*Solanum* (*Solanum*) *macrotonum* Bitter	Lim	BD
	Solanum (*Solanum*) sp. (7334)	Lim	BD
	Solanum (*Brevantherum*) *riparium* Pers.	Arg	KH
	Solanum (*Lasiocarpa*) *pectinatum* Dunal	Lim	BD
	Cyphomandra crassicaulis (Ortm.) Kuntze	Arg	KH
lysimnia (Fabricius)	*Solanum* (*Brevantherum*) sp. (fumo branco)	Bra	DS
	Solanum (*Brevantherum*) sp. (Maria branca)	Bra	DS
	Solanum (*Brevantherum*) *mauritianum* Scop.	RGS	CB
	Solanum (*Leptostemonum*) *incarceratum* Ruiz & Pavón	Bra	DS

TABLE 1. Continued.

Ithomiinae: Tribe, Genus, Species, and Subspecies	Host Plants[1]: Genus (Subgenus or Section) and Species	Locality[2]	Source[3]
	Solanum (*Leptostemonum*) *sisymbriifolium* Lam.	RGS	CB
	Solanum (*Leptostemonum*) *agrarium* Sendtner	Bra	DS
	Solanum (*Leptostemonum*) *robustum* Wendl.	Bra	DS
	Solanum (*Leptostemonum*) sp. (joá manso)	Bra	DS
	Solanum (*Leptostemonum*) brusquense Lyman B. Smith & Downs	Sum	JVN
	Solanum (*Leptostemonum*) *arcuatum* Sendtner	Camp	KB
	Solanum (*Leptostemonum*) *fastigiatum* Willd.	PCal, SV	KB
	Solanum (*Leptostemonum*) *variabile* C. Martius	Sum	JVN
	Solanum (*Leptostemonum*) *paniculatum* L.	Sum	JVN
	Solanum (*Leptostemonum*) sp.	Brsl	KB
	Solanum (*Leptostemonum*) *torvum* Swartz	Rio, SV	KB
	Solanum (*Leptostemonum*) sp.	Rio	KB
	Solanum (*Acanthophora*) *aculeatissimum* Jacq.	Rio	RFD
	Solanum (*Acanthophora*) *jatrophifolium* Sch.	Sum	JVN
	Solanum (*Acanthophora*) *atropurpureum* Schrank	Sum	JVN
	Solanum (*Acanthophora*) *capsicoides* All.	Sum, MG	JVN, KB
	Solanum (*Acanthophora*) *acerosum* Sendtner	PCal	KB
	Solanum (*Acanthophora*) *viarum* Dunal	Sum	JVN
	Solanum (*Potatoe*) *tuberosum* L.	Bra	CB
	Lycopersicon esculentum Miller	Bra	CB, KB
	Cyphomandra velutina Sendtner	Bra	DS
	Cyphomandra fragrans (Hook.) Sendtner	Camp	KB
	Cyphomandra sciadostylis Sendtner	Rio	NM
	Cyphomandra crassicaulis (Ortm.) Kuntze	Itat	KB
	Brugmansia arborea (L.) Lagerheim	RGS	CB
	Nicandra physaloides (L.) Gaertn.	PCal	KB
OLERIINI			
Hyposcada egra (Hewitson)	*Markea coccinea* Rich. (?) (reared to adult on *Juanulloa mexicana*)	Man	KB
virginiana evanides Haensch (Gesneriaceae feeder?)	*Columnea consanguinea* Hanst.	CR	WH
	Columnea grata Morton	CR	WH
	Drymonia conchocalyx Hanst.	CR	WH

TABLE 1. Continued.

Ithomiinae: Tribe, Genus, Species, and Subspecies	Host Plants[1]: Genus (Subgenus or Section) and Species	Locality[2]	Source[3]
New genus *canilla* (Hewitson)	*Lycianthes* sp. (?)	Peru	KB
Oleria victorine paula (Weymer)	*Lycianthes* nr. *multiflora* Bitter	CR	WH
vicina (Salvin)	*Lycianthes multiflora* Bitter	CR	WH
	Solanum (*Bassovia*) *trizygum* Bitter	CR	WH
makrena (Hewitson)	*Solanum* (*Bassovia*) *trizygum* Bitter	Ven	FA-Mar
agarista (Felder)	*Lycianthes maxonii* Standley	Lim	BD
	Solanum (*Potatoe*) *evolvulifolium* Greenman	Lim	BD
	Solanum (*Bassovia*) sp. (7319)	Lim	BD
	Solanum (*Micracantha*) sp. (7310)	Lim	BD
janarilla (Hewitson)	*Solanum* (*Bassovia*) sp.	Peru	SK
zelica pagasa (Druce)	*Solanum* (*Potatoe*) *evolvulifolium* Greenman	CR	AY
rubescens (Butler & Druce)	*Solanum* (*Micracantha*) *siparunoides* Ewan	CR	WH
astrea ssp. nov.	*Solanum* (*Potatoe*) nr. *chacoense* Bitter	Rond	KB
burchelli (Sanders)	*Solanum* (*Leptostemonum*) *insidiosum* C. Martius	Rond	KB
thiemei (Oberthür)	*Solanum* (*Lasiocarpa*) *stagnale* Moric.	BA	KB
aquata (Weymer)	*Solanum* (*Lepidota*) *swartzianum* Roemer & Schultes	MG	KB
crispinilla (Hopffer)	*Solanum* (*Potatoe*) nr. *chacoense* Bitter	Peru	KB
NAPEOGENINI			
Epityches eupompe (Geyer)	*Capsicum mirabile* C. Martius ex Sendtner	Rio	FM
	Capsicum flexuosum Sendtner	Japi	KB
	Vassobia breviflora (Sendtner) Hunziker	RGS	KB
	Acnistus arborescens (L.) Schldl.	Camp	KB
	Physalis neesiana Sendtner	RGS	KB
Napeogenes tolosa amara Godman	*Lycianthes* nr. *multiflora* Bitter	CR	WH
	Lycianthes sp.	CR	WH
	Solanum sp. (?)	CR	WH
duessa jamariensis D'Almeida	*Lycianthes* sp.?	Rond	KB
sylphis caucayaensis Fox & Real	*Lycianthes* sp.? (7325)	Lim	BD
acreana D'Almeida	*Lycianthes* sp.	Rond	KB
inachia johnsoni Fox & Real	*Lycianthes* sp.?	Col	KB
avila Haensch	*Lycianthes howardiana* D'Arcy	Lim	BD
sulphurina Bates	*Lycianthes* sp.?	Pnb	KB
Rhodussa cantobrica nundina D'Almeida	*Solanum* (*Jasminosolanum*) sp.	Rond	KB
	Lycianthes sp.	Acre	KB

TABLE 1. Continued.

Ithomiinae: Tribe, Genus, Species, and Subspecies	Host Plants[1]: Genus (Subgenus or Section) and Species	Locality[2]	Source[3]
Garsauritis xanthostola xanthostola (Bates)	*Solanum* (*Leptostemonum*) *insidiosum* C. Martius	Man	KB
	Solanum (*Leptostemonum*) sp.	Faro	KB
	Solanum (*Micracantha*) *lancaeifolium* Jacq.	Man	KB
desmora (Haensch)	*Solanum* (*Micracantha*) *coriaceum* Dunal	Rrpl	KB
Hyalyris oulita cana (Haensch)	*Solanum* (*Lasiocarpa*) *hirtum* Vahl.	Ven	FA-Mar
ssp. nov.	*Solanum* (*Brevantherum*?) sp.	San-Ec	KB
metella (Hopffer)	*Solanum* (*Leptostemonum*) nr. *variabile* C. Martius	Peru	KB
	Solanum (*Brevantherum*) *appressum* Roe	Peru	KB
excelsa decumana (Godm. & Salv.)	*Solanum* (*Leptostemonum*) *accrescens* Standley & Morton	CR	WH
	Solanum (*Micracantha*) *siparunoides* Ewan	CR	WH
ssp. nov.	*Solanum* (*Lasiocarpa*) *hirtum* Vahl	Ven	KB
Hypothyris ninonia completomaculata (Zikán)	*Solanum* (*Lasiocarpa*) *sessiliflorum* Dunal	7Lg	KB
completa (Haensch)	*Solanum* (*Brevantherum*) *schlechtendalianum*	Man	KB
neimyi (Riley)	*Solanum* (*Lepidota*) sp. A	Rond	KB
	Solanum (*Lepidota*) sp. B	Rond	KB
daeta (Boisduval)	*Solanum* (*Jasminosolanum*) *flaccidum* Vell.	Mogi	KB
	Solanum (*Lepidota*) *murinum* Sendtner	Camp	JVN
	Solanum (*Indubitaria*) sp.	RCl	KB
	Solanum (*Brevantherum*) *concinnum* Schott ex Sendtner	Camp	KB
	Solanum (*Brevantherum*) *gemellum* C. Martius ex Sendtner	Itat	KB
	Solanum (*Brevantherum*) *megalochiton* C. Martius	Sum	JVN
	Solanum (*Lepidota*) *argenteum* Dunal ex Poiret	Rio	RFD
	Solanum (*Lepidota*) *swartzianum* Roemer & Schultes	Camp	JVN
	Solanum (*Brevantherum*) *mauritianum* Scop.	Sum	JVN
	Solanum (*Leptostemonum*) *racemiflorum* Dunal	Rio	JFZ
	Solanum (*Leptostemonum*) *insidiosum* C. Martius	Camp	KB
	Solanum (*Leptostemonum*) *variabile* C. Martius	Camp	JVN
	Solanum (*Leptostemonum*) *robustum* Wendl.	Sum	JVN
	Solanum (*Leptostemonum*) *paniculatum* L.	Sum	JVN
	Solanum (*Leptostemonum*) *torvum* Swartz	Rio	KB
	Solanum (*Leptostemonum*) *brusquense* Lyman B. Smith & Downs	Sum	JVN
fluonia berna (Haensch)	*Solanum* (*Micracantha*) sp. (7311)	Lim	BD
semifulva satura (Haensch)	*Solanum* (*Brevantherum*) *schlechtendalianum* Walp.	Lim	BD

TABLE 1. Continued.

Ithomiinae: Tribe, Genus, Species, and Subspecies	Host Plants[1]: Genus (Subgenus or Section) and Species	Locality[2]	Source[3]
daphnis amapaensis Brown	*Solanum* (*Brevantherum*) *asperum* Rich.	Amp	KB
	Solanum (*Brevantherum*?) sp.	Ror	KB
daphnoides D'Almeida	*Solanum* (*Brevantherum*) *rugosum* Dunal	Car	KB
daphnis D'Almeida	*Solanum* (*Brevantherum*) *rugosum* Dunal	Rond	KB
mamercus ssp. nov.	*Solanum* (*Leptostemonum*) *insidiosum* C. Martius	Rond	KB
leprieuri ssp. nov.	*Solanum* (*Micracantha*) *coriaceum* Dunal	Ror	KB
	Solanum (*Micracantha*) *lancaeifolium* Jacq.	Rond	KB
Hypothyris euclea leucania (Bates)	*Solanum* (*Brevantherum*) *rugosum* Dunal	CR	LG, AY
	Solanum (*Brevantherum*) *umbellatum* Miller	CR, Pan	LG, KB
euclea (Godart)	*Solanum* (*Brevantherum*) *asperum* Rich.	Ven	FA-Mar
	Solanum (*Brevantherum*) sp. ("tabacote")	Ven	FA-Mar
intermedia (Butler)	*Solanum* (*Brevantherum*) *bicolor* Willd. ex Roemer & Schultes	Lim	BD
tenna (Haensch)	*Solanum* (*Brevantherum*) nr. *asperum* Rich.	San-Ec	KB
barii (Bates)	*Solanum* (*Brevantherum*) *asperum* Rich.	Man, Amp	JVN, KB
	Solanum (*Brevantherum*) *rugosum* Dunal	Tuc	KB
nr. *barii* (Bates)	*Solanum* (*Brevantherum*) *asperum* Rich.	Rond	KB
	Solanum (*Brevantherum*) *rugosum* Dunal	Rond	KB
	Solanum (*Lasiocarpa*) *stramoniifolium* Jacq.	Rond	KB
laphria (Doubleday)	*Solanum* (*Brevantherum*) *asperum* Rich.	Linh	KB
	Solanum (*Brevantherum*) *rugosum* Dunal	Linh	KB
laphria × *nina* (Haensch)	*Solanum* (*Brevantherum*) *mauritianum* Scop.	Camp	KB, JVN
	Solanum (*Brevantherum*) *granuloso-leprosum* Dunal	Mogi	PCM
ITHOMIINI			
Miraleria cymothoe cymothoe (Hewitson)	*Cuatresia riparia* (Kunth) Hunziker	Ven	FA-Mar
	Dunalia solanacea Kunth	Ven	KB
	Acnistus arborescens (L.) Schldl.	Ven	FA-Mar
	Brugmansia suaveolens (Willd.) Sweet	Ven	FA-Mar
Ithomia diasia hippocrenis Bates	*Lycianthes* sp.? (6)	CR	LG
	Witheringia asterotricha (Standley) Hunziker	CR	WH
	Witheringia solanacea L'Her.	CR	WH
patilla Hewitson	*Lycianthes multiflora* Bitter	CR	WH
	Witheringia solanacea L'Her.	CR	LG, WH
lichyi D'Almeida	*Capsicum lucidum* (Moricand) Kuntze	MG	KB
	Capsicum flexuosum Sendtner	Japi	KB
	Capsicum villosum Sendtner (?)	Japi	KB

TABLE 1. Continued.

Ithomiinae: Tribe, Genus, Species, and Subspecies	Host Plants[1]: Genus (Subgenus or Section) and Species	Locality[2]	Source[3]
amarilla Haensch	*Cuatresia* sp. (7327)	Lim	BD
celemia plaginota Butler & Druce	*Cuatresia riparia* (Kunth) Hunziker	CR	WH
iphianassa iphianassa Dbldy. & Hew.	*Cuatresia riparia* (Kunth) Hunziker	Ven	FA-Mar
	Witheringia solanacea L'Her.	Ven	FA-Mar
heraldica Bates	*Cuatresia riparia* (Kunth) Hunziker	CR	WH
	Witheringia morii D'Arcy	CR	WH, LG
	Acnistus arborescens (L.) Schldl.	CR	WH
xenos (Bates)	*Cuatresia riparia* (Kunth) Hunziker	CR	WH
	Witheringia cuneata (Standley) Hunziker	CR	WH
	Acnistus arborescens (L.) Schldl.	CR	WH
drymo drymo Hübner	*Acnistus arborescens* (L.) Schldl.	Camp	KB
agnosia agnosia Hewitson	*Vassobia breviflora* (Sendtner) Hunziker	Camp	KB
	Acnistus arborescens (L.) Schldl.	Camp	KB
	Physalis pubescens L.	Lim	BD
	Physalis angulata L.	Rond	KB
derasa salapia Hewitson	*Physalis angulata* L.	Lim	BD
DIRCENNINI			
Callithomia hezia hezia (Hewitson)	*Lycianthes sanctae-clarae* Greenman & Donn.	CR	WH
	Solanum (*Androceras*) nr. *granelianum* D'Arcy	CR	WB
lenea travassosi D'Almeida	*Solanum* (*Jasminosolanum*) *pensile* Sendtner	Rond	KB
	Solanum (*Leptostemonum*) *grandiflorum* Ruiz & Pavón	MTN	KB
xantho (Felder)	*Solanum* (*Jaminosolanum*) *flaccidum* Vell.	Mogi	KB
New genus *lonera* (Butler & Druce)	*Cyphomandra hartwegii* (Miers) Dunal	CR	LG, WH
Velamysta cruxifera (Hewitson)	*Lycianthes* sp.	B-Ec	KB
Hyalenna pascua (Schaus)	*Solanum* (*Brevantherum*) nr. *schwackeanum* Lyman B. Smith & Downs	Japi	KB
Dircenna adina marica (Felder & Felder)	*Solanum* (*Brevantherum*) nr. *hazenii* Bitter	Ven	KB
lorica (Weymer)	*Solanum* (*Brevantherum*) nr. *asperum* Rich.	San-Ec	KB
loreta acreana D'Almeida	*Solanum* (*Leptostemonum*) *grandiflorum* Ruiz & Pavón	Rond	KB
	Solanum (*Leptostemonum*) *insidiosum* C. Martius	Rond	KB
	Solanum (*Lasiocarpa*) *stramoniifolium* Jacq.	Rond	KB
	Solanum (*Lasiocarpa*) *sessiliflorum* Dunal	Rond	KB
Dircenna klugii (Geyer)	*Solanum* (*Brevantherum*) sp. (22)	CR	LG
	Solanum (*Brevantherum*) nr. *rugosum* Dunal	CR	LG

TABLE 1. Continued.

Ithomiinae: Tribe, Genus, Species, and Subspecies	Host Plants[1]: Genus (Subgenus or Section) and Species	Locality[2]	Source[3]
	Solanum (*Brevantherum*) *umbellatum* Miller	CR	WH
	Solanum (*Leptostemonum*) *hispidum* Pers.	CR	WH
	Solanum (*Leptostemonum*) *ochraceo-ferrugineum* (Dunal) Fern.	CR	WH
	Solanum (*Leptostemonum*) *torvum* Swartz	Mex	DM
	Solanum (*Micracantha*) *lancaeifolium* Jacq.	CR	LG
relata Butler & Druce	*Solanum* (*Brevantherum*) *cordavense* Sessé & Moc.	CR	WH
	Solanum (*Brevantherum*) nr. *rugosum* Dunal	CR	LG
	Solanum (*Brevantherum*) *umbellatum* Miller	CR	WH
	Solanum (*Leptostemonum*) *hispidum* Pers.	CR	AY
olyras (Felder & Felder)	*Solanum* (*Brevantherum*) *cordavense* Sessé & Moc.	CR	WH
	Solanum (*Brevantherum*) *umbellatum* Miller	CR	WH
jemima ssp. nov. ("*chiriquensis*")	*Solanum* (*Micracantha*) *siparunoides* Ewan	CR	WH
jemima (Geyer)	*Solanum* (*Brevantherum*) *hazenii* Bitter	Ven	KB
dero euchytma (Felder & Felder)	*Solanum* (*Leptostemonum*) *ochraceo-ferrugineum* (Dunal) Fern.	CR	LG, WH
celtina Burmeister	*Solanum* (*Brevantherum*) *megalochiton* C. Martius	Sum	JVN
	Solanum (*Brevantherum*) *mauritianum* Scop.	Sum	JVN
	Solanum (*Leptostemonum*) *variabile* C. Martius	Sum	JVN
	Solanum (*Leptostemonum*) *robustum* Wendl.	Sum	JVN
	Solanum (*Leptostemonum*) *paniculatum* L.	Sum	JVN
	Solanum (*Leptostemonum*) *torvum* Swartz	Rio	KB
	Solanum (*Leptostemonum*) *incarceratum* Ruiz & Pavón	RGS	CB
	Solanum (*Leptostemonum*) *sisymbriifolium*	RGS	CB
NEW TRIBE			
Ceratinia neso zikani D'Almeida	*Solanum* (*Leptostemonum*) *insidiosum* C. Martius	Rond	KB
	Solanum (*Lasiocarpa*) *stramoniifolium* Jacq.	Rond	KB
	Solanum (*Leptostemonum*) sp.	Bel	KB
poecila poecila (Bates)	*Solanum* (*Geminata*) *antillarum* Schulz	Lim	BD
tutia dorilla (Bates)	*Solanum* (*Geminata*) *antillarum* Schulz	CR	WH
tutia (Hewitson)	*Solanum* (*Geminata*) sp.	Ven	FA-Mar
Ceratiscada canaria Brown & D'Almeida	*Solanum* (*Geminata*) *laxiflorum* Sendtner	ES	KB
hymen (Haensch)	*Solanum* (*Geminata*) sp. (7336)	Lim	BD
Prittwitzia hymenaea hymenaea (Prittwitz)	*Solanum* (*Geminata*) *caavurana* Vell.	Camp, Japi	KB
	Solanum (*Geminata*) sp.?	Rio	KB
	Solanum (*Pseudocapsica*) *pseudocapsicum* L.	Camp	KB
	Solanum (*Leptostemonum*) *sisymbriifolium* Lam. (?)	RGS	CB

TABLE 1. Continued.

Ithomiinae: Tribe, Genus, Species, and Subspecies	Host Plants[1]: Genus (Subgenus or Section) and Species	Locality[2]	Source[3]
	Cestrum nocturnum L.	RGS	CB
	Cestrum parqui L.	RGS	CB
	Cestrum sendtnerianum C. Martius	Camp	KB
	Cestrum schlechtendalii G. Don	Camp	KB
	Cestrum laevigatum Schldl.	Camp	KB
Episcada salvinia (Bates)	*Solanum* (*Geminata*) *antillarum* Schulz	CR	WH
	Solanum (*Geminata*) *nudum* Humb. & Bonpl. ex Dunal	CR	WH
	Solanum (*Geminata*) sp. (?)	Col	KB
clausina striposis Haensch	*Solanum* (*Geminata*) *caavurana* Vell.	Rio	KB
Pteronymia artena artena (Hewitson)	*Lycianthes multiflora* Bitter	CR	WH
	Lycianthes escuitlensis (Coult.) D'Arcy	CR	WH
	Lycianthes synanthera (Sendtner) Bitter	CR	WH
beebei Fox	*Solanum* (*Geminata*) sp.?	Ven	FA-Mar
simplex simplex (Salvin)	*Solanum* (*Geminata*) *antillarum* Schulz	CR	WH
	Solanum (*Geminata*) *arboreum* Humb. & Bonpl. ex Dunal	CR	WH
	Solanum (*Geminata*) *brenesii* Morton & Standley	CR	WH
	Solanum (*Geminata*) sp. (A)	CR	WH
	Solanum (*Geminata*) sp. (B)	CR	WH
	Solanum (*Geminata*) sp. (C)	CR	WH
	Solanum (*Geminata*) sp. (D)	CR	WH
	Solanum (*Geminata*) sp. (E)	CR	WH
cotytto (Guérin)	*Solanum* (*Geminata*) *nudum* Humb. & Bonpl. ex Dunal	CR	WH
agalla Godman & Salvin	*Solanum* (*Geminata*) *brenesii* Morton & Standley	CR	WH
notilla Butler & Druce	*Solanum* (*Geminata*) *roblense* Bitter	CR	LG
	Solanum (*Geminata*) *arboreum* Humb. & Bonpl. ex Dunal	CR	WH
	Solanum (*Geminata*) *brenesii* Morton & Standley	CR	WH
	Solanum (*Geminata*) sp.	CR	WH
	Solanum (*Geminata*) sp.	CR	WH
	Cestrum megalophyllum Dunal	CR	AY
carlia Schaus	*Solanum* (*Geminata*) *caavurana* Vell.	Camp	KB
	Solanum (*Pseudocapsica*) *pseudocapsicum* L.	Camp	KB
	Solanum (*Lepidota*) *argenteum* Dunal ex Poiret	RGS	CB
	Solanum (*Lepidota*) *swartzianum* Roemer & Schultes	Camp, RCl	RM, KB
	Cestrum laevigatum Schldl.	Camp	KB
	Solanum (*Geminata*) sp.	Japi	KB

TABLE 1. Continued.

Ithomiinae: Tribe, Genus, Species, and Subspecies	Host Plants[1]: Genus (Subgenus or Section) and Species	Locality[2]	Source[3]
fulvescens Godm. & Salv.	*Solanum* (*Geminata*) *brenesii* Morton & Standley	CR	WH
fulvimargo Butl. & Druce	*Solanum* (*Geminata*) nr. *Antillarum* Schultz	CR	WH
latilla (Hewitson)	*Solanum* (*Geminata*) nr. *ripense*	Ven	KB
vestilla sparsa Haensch	*Solanum* (*Geminata*) nr. *nudum* Humb. & Bonpl. ex Dunal	Lim	BD
hemixanthe (Feld. & Feld.)	*Solanum* (*Brevantherum*) sp.?	BA	KB
euritea (Cramer)	*Solanum* (*Geminata*) *pseudoquina* St. Hil.	ES	KB
	Solanum (*Geminata*) *laxiflorum* Sendtner	ES	KB
GODYRIDINI			
Godyris zygia (Godman & Salvin)	*Cestrum nocturnum* L.	CR	WH
	Cestrum sp. (13)	CR	LG
gonussa caesiopicta (Niepelt)	*Solanum* (*Geminata*) *brenesii* Morton & Standley	CR	AY
zavaleta matronalis (Weymer)	*Cestrum* sp. (7334)	Lim	BD
	Cestrum laevigatum Schldl.	Lim	BD
ssp. nov.	*Solanum* (*Geminata*) sp.?	Acre	KB
ssp. nov.	*Cestrum* sp. (decumbent)	Rond	KB
kedema kedema (Hewitson)	*Solanum* (*Geminata*) nr. *ripense*	Ven	KB
Pseudoscada timna (Hewitson)	*Cestrum* sp. (7324)	Lim	BD
erruca (Hewitson)	*Cestrum schlechtendalii* G. Don	Camp	KB
	Cestrum laevigatum Schldl.	Camp	JVN, KB
	Cestrum corymbosum Schldl.	Japi	KB
	Cestrum sp.	MG	KB
Hypomenitis alphesiboea (Hewitson)	*Cestrum* sp.	San-Ec	KB
libethris (Felder & Felder)	*Cestrum* sp.	Col	KB
Greta polissena (Hewitson)	*Cestrum fragile* Francey	CR	WH
	Cestrum megalophyllum Dunal	CR	WH
	Cestrum nocturnum L.	CR	WH
	Cestrum rugulosum Francey	CR	WH
	Cestrum lanatum C. Martius & Gal.	CR	WH
	Cestrum sp.	CR	WH
	Cestrum sp.	CR	WH
morgane oto (Hewitson)	*Cestrum* sp.	CR	WH
	Cestrum lanatum C. Martius & Gal.	CR	WH
andromica lyra (Salvin)	*Cestrum* sp. (13)	CR	LG
andromica (Hewitson)	*Solanum* (*Geminata*) nr. *ripense*	Ven	KB

TABLE 1. Continued.

Ithomiinae: Tribe, Genus, Species, and Subspecies	Host Plants[1]: Genus (Subgenus or Section) and Species	Locality[2]	Source[3]
cubana (Herrich-Schaeffer)	*Cestrum* sp.	Cuba	JG
nero (Hewitson)	*Cestrum* sp.	CR	WH
	Cestrum standleyi Francey	CR	AY
annette annette (Guérin)	*Cestrum* sp.	CR	AY
	Cestrum fragile Francey	CR	WH
	Cestrum sp.	CR	WH
	Solanum (*Brevantherum*) *cordavense* Sessé & Moc.	CR	WH
McClungia salonina salonina (Hewitson)	*Cestrum sendtnerianum* C. Martius	Sum	JVN
	Cestrum schlechtendalii G. Don	Camp	KB
	Cestrum laevigatum Schldl.	Sum	JVN
Hypoleria cassotis (Bates)	*Cestrum megalophyllum* Dunal	CR	WH
	Cestrum sp.	CR	WH
	Solanum (*Geminata*) sp.?	CR	AY
ocalea (Doubleday & Hewitson)	*Cestrum latifolium* Lam.	Trin	MB
orolina (Hewitson)	*Cestrum* sp. (7353)	Lim	BD
adasa (Hewitson)	*Cestrum sessiliflorum* Schott ex Sendtner	MG	KB
	Cestrum sp.	Japi	KB
Heterosais nephele (Bates)	*Cestrum* sp. (7324)	Lim	BD
	Cestrum sp. (decumbent)	Rond	KB
edessa	*Cestrum amictum* Schldl.	MG	KB

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[1] In the genus *Solanum*, sections *Micracantha*, *Lasiocarpa* and *Acanthophora* are in the subgenus *Leptostemonum*; sections *Androceras* and *Jasminosolanum* are in subgenus *Potatoe*, which some feel could also include *Lycopersicon* and *Lycianthes* as sections (here treated as genera); and sections *Geminata* (= *Leiodendra* auct. or *Leiodendron* auct., see S. Knapp, Taxon 32: 635–636, 1983), *Indubitaria*, *Lepidota* and *Pseudocapsica* are for the time being placed next to each other in subgenus *Solanum*.

[2] Alphabetical list of locality codes:
Acre = near Rio Branco, Acre, SW Brazil, 50 m.
Amp = Lourenço, Amapá, extreme N Brazil, 100–300 m.
Arg = Argentina, various localities in northern part of country.
BA = Ubatã and Catu, eastern Bahia, Brazil, 20–100 m.
Barn = Barinitas, Barinas, Venezuela, 800–1,500 m.
Belém = Region of Belém and Bujaru, Pará, Brazil, 20 m.
Bol = Region of Caranavi, La Paz, Bolívia, 800 m.
Bra = Brazil, various regions, mostly southeastern.
Brsl = Brasília, Distrito Federal, Brazil, 1,000–1,200 m.
Camp = Region of Campinas, São Paulo, Brazil, 600–800 m.
Car = Serra dos Carajás, southern Pará, Brazil, 200–700 m.
Col = Colombia, mostly Villavicencio area, Meta, 400–1,500 m.
CR = Various localities in Costa Rica, sea level to 1,600 m.
Cuba = Probably eastern part of the island of Cuba.
ElS = El Salvador, mostly western sector.
ES = Northern Espírito Santo, eastern Brazil, 20–800 m.
Faro = Faro, western Pará, Brazil, 20 m.
Goiás = Santo Genoveva, Goiânia, and Goiás Velho, state of Goiás, Brazil, 600 m.
Itat = Parque Nacional de Itatiaia, Rio de Janeiro, SE Brazil, 1,000–2,000 m.
Japi = Serra do Japi, Jundiaí, São Paulo, SE Brazil, 800–1,200 m.
Lim = Limoncocha, eastern Ecuador, 280 m.
Linh = Linhares, Espírito Santo, eastern Brazil, 20 m.
Man = Region north of Manaus, Amazonas, Brazil, 50–100 m.

Marajó = Central part of Ilha de Marajó, mouth of Amazon, Pará, Brazil, 10 m.
Mex = Tuxtlas and Sierra de Juárez, Veracruz, México, 200–1,600 m.
MG = Mongaguá, coastal São Paulo, SE Brazil, sea level to 300 m.
Mogi = Fazenda Campininha, Mogi-Guaçu, São Paulo, SE Brazil, 400–550 m.
MTN = Western part of the state of Mato Grosso (do Norte), western Brazil, 200–500 m.
NPer = Jaén, Pucará, and Tumbes, northern Peru, 600–2,000 m.
Pan = Panamá, various localities, sea level to 2,000 m.
PCal = Poços de Caldas, Minas Gerais, Brazil, 1,000–1,800 m.
Peru = Central Peru.
Pnb = Pernambuco, NE Brazil, 50–250 m.
RCl = Rio Claro, São Paulo, SE Brazil, 600 m.
RGS = Rio Grande do Sul, extreme southern Brazil, sea level to 1,000 m.
Rio = Region of Rio de Janeiro, SE Brazil, sea level to 800 m.
Rond = Rondônia, SW Brazil: Colorado, Jaru, Theobroma, Ariquemes, 200–600 m.
Ror = Roraima, extreme northern Brazil, 50–200 m.
Rrpl = Rurópolis, Pará, Brazil, 100 m.
San-Ec = Upper Santiago river basin (Macas to Gualaquiza and Zamora), east Ecuador, 800 m.
SEc = Southern Ecuador.
7Lg = Sete Lagos, northeast of San Gabriel de Cachoeira, upper Rio Negro, Amazonas, NW Brazil, 100–200 m.
SNegra = Serra Negra, São Paulo, SE Brazil, 900–1,400 m.
Sum = Sumaré, São Paulo, Southeast Brazil, 550–600 m.
Sur = Suriname coast, sea level.
SV = São Vicente, coastal São Paulo, SE Brazil, 20–300 m.
Trin = Trinidad, sea level to 800 m.
Tuc = Tucuruí, Rio Tocantins, Pará, Brazil, 30 m.
UR = Uruguay, various localities.
Ven = Northern Venezuela, various localities, sea level to 2,000 m.
WEc = Coastal plain of Western Ecuador, sea level to 700 m.

[3] Alphabetical list of reference codes, sources of data:
AM = Muyshondt, A. 1976. Rev. Soc. Mex. Lep. 2: 77–90.
AY = Young, A. M., see 1980. Acta Biotheoretica 29: 37–64 for bibliography.
AY/M = Young, A. M. & M. W. Moffatt. 1979. Dtsch. Ent. Z., N.F. 26: 21–38.
BD = Drummond, B. A., III. 1976. Ph.D. Thesis, University of Florida, Gainesville, and further observations and corrections through 1984.
BL = Ballou in Costa Rica, reported by Lamas, G. 1973. Ph.D. Thesis, Universidade de São Paulo, Brazil.
CB = Biezanko, C. M. various publications, especially 1957 (with collaborators). Rev. Fac. Agron. Montevideo 46: 1–152, and 1960. Arq. Entom. Rio Grande do Sul III, A: 1–6 and B: 1–6. Doubtful records have been eliminated, and those presented here require confirmation.
DM = de la Maza, J. 1980. Bol. Inf. Soc. Mex. Lep. 6: 3–9.
DS = D'Araújo e Silva et al., 1968, mostly untrustworthy older records from agronomical literature, needing confirmation.
FA-Mar = Information in the collection of the Facultad de Agronomia, Maracay, Venezuela, including extensive notes by Avril Fox on material deposited mostly in the British Museum (Natural History).
FM = Müller, Fritz. 1886. Zool. Jahrb. 1: 1–225, probably trustable.
GL = Unpublished information from Gerardo Lamas M., Lima, Peru, and also 1976. Rev. Per. Ent. 18: 2.
GS = Observations of Gordon B. Small in Panamá.
JAE = Published and unpublished observations by John A. Edgar, especially in 1982. J. Zool. London 196: 385–399, and (with collaborators) 1974. Nature 250: 646–648.
JFZ = Unpublished records of J. F. Zikán in SE Brazil, many questionable.
JG = Gundlach, J. 1881. Contribución a la Entomologia Cubana. Havana.
JLG = Guppy, J. L. 1894. J. Trinidad Field Nat. Club 2: 170–174; 1904. Trans. Ent. Soc. London 52: 225–228.
JS = Sepp, J. 1828–1855. Surinaamsche Vlinders, 3 volumes. Amsterdam.
JVN = Vasconcellos-Neto, J. 1980. M.Sc. Thesis, Universidade Estadual de Campinas, São Paulo, Brazil.
KB = Mostly unpublished records of Keith Brown, recently with much participation of Renata S. C. Dias, also 1976. Acta Amazonica 7: 75–137. 1977. Syst. Ent. 2: 161–197. 1980. J. Lep. Soc. 32: 152–172. (With R. F. D'Almeida) 1970. Trans. Amer. Ent. Soc. 96: 1–17. (With W. W. Benson) 1974. Biotropica 6: 205–228.
KH = Hayward, K., information in various catalogues of Argentinian Lepidoptera.
LG = Unpublished information of L. E. Gilbert, mostly in a 1968 OTS report, with later corrections of plant names and more recent observations.
MB = Barcant, M. 1970. Butterflies of Trinidad and Tobago. Collins, London.
MF = Drawings of Margaret Fountaine, deposited in the British Museum (Natural History), also 1913. Entomologist 46: 189–194, 214–219.
NM = Moreira, N. 1881. Arch. Mus. Rio de Janeiro 4: 1–13, probably trustable.
PCM = Paulo Cesar Motta, Central São Paulo.
RF = Fox, R. M. 1967. Mem. Amer. Ent. Soc. 22: 1–190.
RFD = D'Almeida, R. Ferreira, 1922. Mélanges Lepidopterologiques. Berlin. 1938. Mem. Inst. Oswaldo Cruz 33: 381–394. 1944. Arq. Zool. Est. São Paulo 4: 33–72, many records requiring verification.
RM = Monteiro, R. F. 1981. M.Sc. Thesis, Univ. Estadual de Campinas, SP, Brazil.
R/P = Rathcke, B. J. & R. W. Poole. 1975. Science 187: 175–176.
SK = Unpublished recent observations of S. Knapp and J. Mallet, Guyana and Peru.
WB = Unpublished observations of Woodruff W. Benson.
WH = Haber, W. 1978. Ph.D. Thesis, University of Minnesota, and more recent observations and updates of this large data set from Costa Rica.

CHEMISTRY AT THE SOLANACEAE/ITHOMIINAE INTERFACE[1,2]

KEITH S. BROWN, JR.[3]

ABSTRACT

The secondary chemical constituents of 42 species in sixteen genera of Solanaceae, of five species in three genera of Apocynaceae-Parsonsieae, and of 142 species in 45 genera of Ithomiinae (Lepidoptera: Nymphalidae) whose larvae feed on these plants, have been analyzed and compared in a standardized manner. Large orb spiders (*Nephila clavipes*), which cut field-caught adult Ithomiinae out of their webs, were used to assay fractions for defensive substances eventually present in or derived from larval food plants; the fractions were applied externally to the palatable nymphaline butterfly *Biblis hyperia.* All extracts and fractions from Solanaceous plants were inactive, not defending *Biblis* against predation by *Nephila.* The principal defensive compounds of adult Ithomiinae (also found in eggs and occasionally in Apocynaceae used by some Ithomiinae larvae) are dehydropyrrolizidine alkaloid (PA) monoesters and their N-oxides, stored in up to 20% of dry weight. These compounds are obtained from a variety of natural sources by the adults after emergence from the pupa (freshly hatched individuals of both sexes in 26 genera were readily eaten by *Nephila*), especially from decomposing Boraginaceae-Heliotropoideae and flowers of Compositae-Eupatorieae, for which they serve as pollinators. *Trichogonia, Adenostemma,* and many *Eupatorium* flowers were confirmed as rich sources of the alkaloids, showing characteristics indicating long periods of coevolution in obligatory mutualism with the ithomiine pollinators. The highly diversified and variable Solanaceae toxins seem not to be stored and used for defense by the Ithomiinae, but may be important in mediating larval feeding preferences and oviposition in the butterflies, which show appreciable chemical specificity in host plant preference. Patterns of ithomiine larval use of the Solanaceae at the generic level, however, do not indicate parallel phylogenetic diversification of the two groups. An alternative hypothesis points to sequential adaptation by radiating lines of Ithomiinae to different classes of chemical toxins in the already diversified Solanaceae. By obtaining their PAs, necessary for their defense and reproduction (pheromone synthesis), from a source stabilized by mutualism, the Ithomiinae avoid dependence on the Solanaceae chemicals, constantly destabilized by divergent selection in the antagonistic system. Quantitative determination of PA concentrations in parts of different Ithomiinae and Eupatorieae permits the drawing of a diagram for the flow of these substances in natural ecosystems.

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[1] Presented in part at the Second International Symposium on the Biology and Systematics of the Solanaceae (Missouri Botanical Garden, August 1983), at the Second Gordon Research Conference on Chemical Aspects of Plant-Herbivore Interactions (Ventura, California, January 1983), at the Jardim Botânico do Rio de Janeiro (April 1983), at the 35th and 36th Annual Reunions of the Sociedade Brasileira para o Progresso da Ciência (Belém, Pará, July 1983 and São Paulo, July 1984), and at the first meeting of the International Society of Chemical Ecology (Austin, Texas, June 1984). For a preliminary communication, see Brown (1984); detailed analysis of the insect side of the interface is presented in Brown (1985).

[2] I am especially grateful to Prof. João Vasconcellos-Neto for providing the fundamental biological background for the analysis of the interface and the testing of chemical fractions with *Nephila clavipes.* An earlier version of this paper was read and criticized by T. M. Lewinsohn, W. W. Benson, L. E. Gilbert, M. Rothschild, and J. A. Edgar. R. F. D'Almeida, O. H. H. Mielke, and Gerardo Lamas M. stimulated my interest in the Ithomiinae, and special attention to the interface with Solanaceae was infused by W. W. Benson, L. E. Gilbert, and B. A. Drummond III. W. G. D'Arcy, M. Nee, M. Whalen, D. Costich, L. A. F. de Carvalho, and especially S. Knapp were most helpful with systematic aspects of the Solanaceae, and H. F. Leitão F♀ with the Compositae. Silvana Aparecida Henriques assisted greatly in extraction and fractionation (Table 3), and José Roberto Trigo and Renata S. C. Dias helped in field study of the Ithomiinae/Solanaceae interaction. T. Eisner provided information and reprints about the *Utetheisa*/PA/*Nephila* interaction first studied by him and his students in Florida. R. Forster and D. A. Monteiro facilitated access to field sites in the Fazenda Santa Elisa, Instituto Agronômico de Campinas. A. and C. Kascheres provided important services in NMR and mass spectra at the Instituto de Química, UNICAMP, and I. Valio and L. Sodek permitted extensive use of the Micronal colorimeter in the Departamento de Fisiologia Vegetal, UNICAMP. Chemistry of the Solanaceae was lucidly presented to me by W. Evans, K. Schreiber, D. Lavie, and J. G. Roddick. I especially thank L. P. Brower, J. A. Edgar, and M. Rothschild for help in understanding chemical ecology, pyrrolizidine alkaloids, and bioassay techniques. FAPESP contributed to the original installation of the Laboratório de Ecologia Química (project 74/0544) and Rhodia S. A./FUNCAMP to its reinstallation. The CNPq provided a research fellowship.

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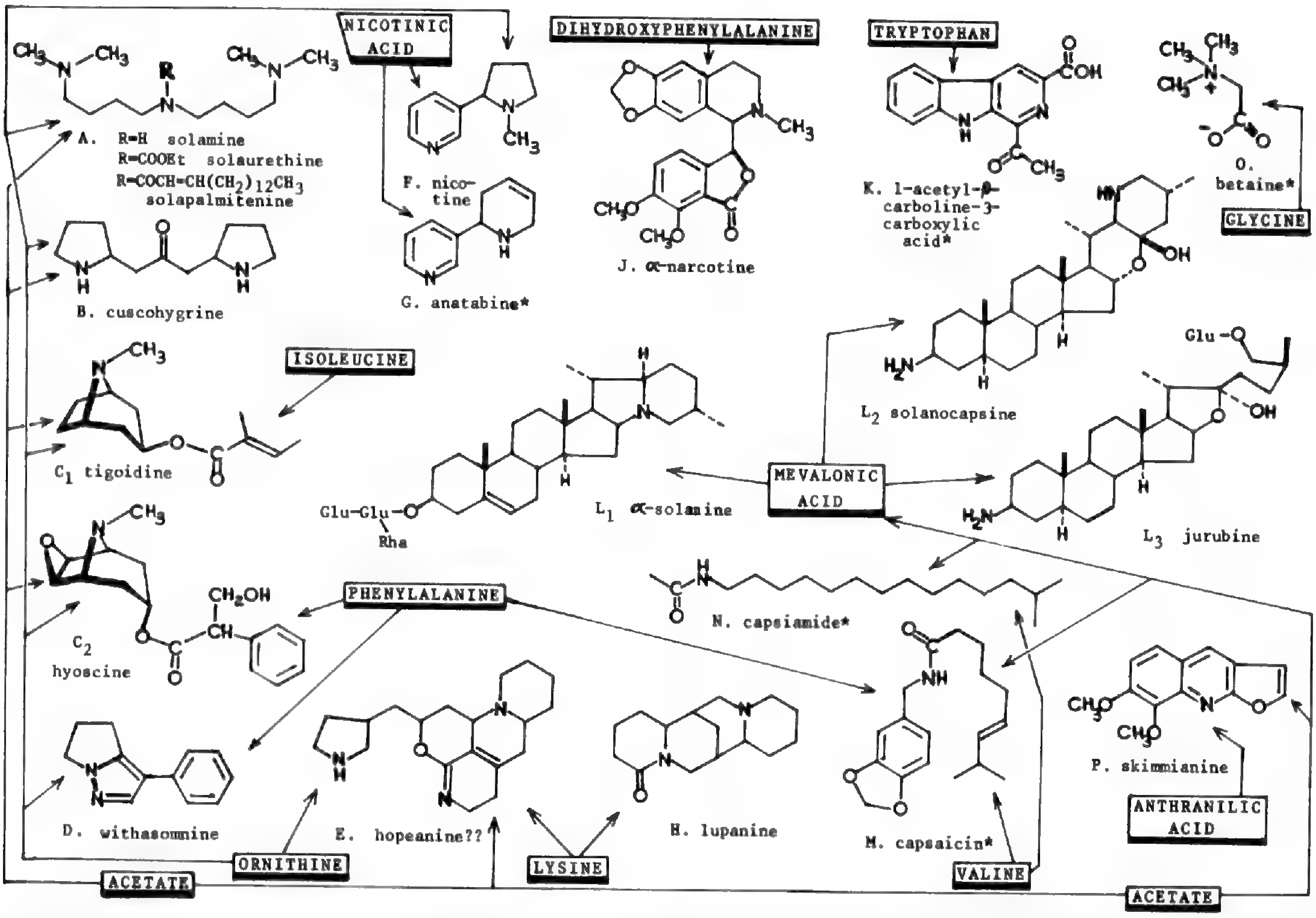


FIGURE 1. Representative alkaloids known from the Solanaceae, with probable biosynthetic pathways; see Table 2 for occurrence in genera. Asterisked alkaloid types are not known yet in leaves of natural Ithomiinae host plants.

Plants in the cosmopolitan family Solanaceae are widely known for their toxic qualities derived from an exceptionally diverse suite of alkaloids (Fig. 1) and steroidal bitter principles, terpenes, saponins, and phenolic glycosides (Fig. 2; Evans, 1979; Schreiber, 1979; Harborne & Swain, 1979; Kirson & Glotter, 1982). Such a rich larder of potential poisons could be expected to repel, deter, or intoxicate almost all herbivores while causing a few to become specialists; the specialists might be predicted to sequester the Solanaceae poisons and use them in their own defense against predators. In fact, the herbivorous insects found on Solanaceae leaves in the Neotropics are often restricted to the family and some of them are brightly colored as if to suggest unpalatability (Table 1). These form ideal systems for the investigation of biochemical ecology and coevolution (Brown, 1980).

One of the most important groups of Solanaceae herbivores in the Neotropics is butterfly larvae of the nymphalid subfamily Ithomiinae (Drummond & Brown, 1987). The brightly colored adults are regarded as prime distasteful movers in regional insect mimicry complexes (Brown, 1979, 1987; Brown & Benson, 1974). They even pull in other less abundant and perhaps less protected, but typical aposematic butterflies such as Heliconiini (Brown, 1972a; Brown & Benson, 1974), Danainae-Itunini (Brown, 1987), Acraeinae (Brown & Benson, 1974), and Troidini (which are usually central models of their own mimicry rings), as well as myriad Batesian mimics (Satyrinae, Nymphalinae, Charaxinae, Riodininae, Pierinae, Dismorphiinae, Hesperiidae, Castniidae, Geometridae, Dioptidae, Arctiinae and Pericopinae—the last two possibly distasteful Müllerian mimics—and members of other insect orders such as Odonata and Homoptera). Adult Ithomiinae were involved in the original proposals of Batesian and Müllerian mimicry and have been shown to be rejected by a variety of vertebrate predators (Bates, 1862; Belt, 1889; Brower & Brower, 1964; Haber, 1978; Coimbra-Filho, 1981). One known exception (Brown & Vasconcellos-Neto, 1976) involves complex learning behavior by a single tanager population (*Pipraeidea melanonota*), which squeezes out fatty abdominal contents of individuals in winter reproductive diapause dur-

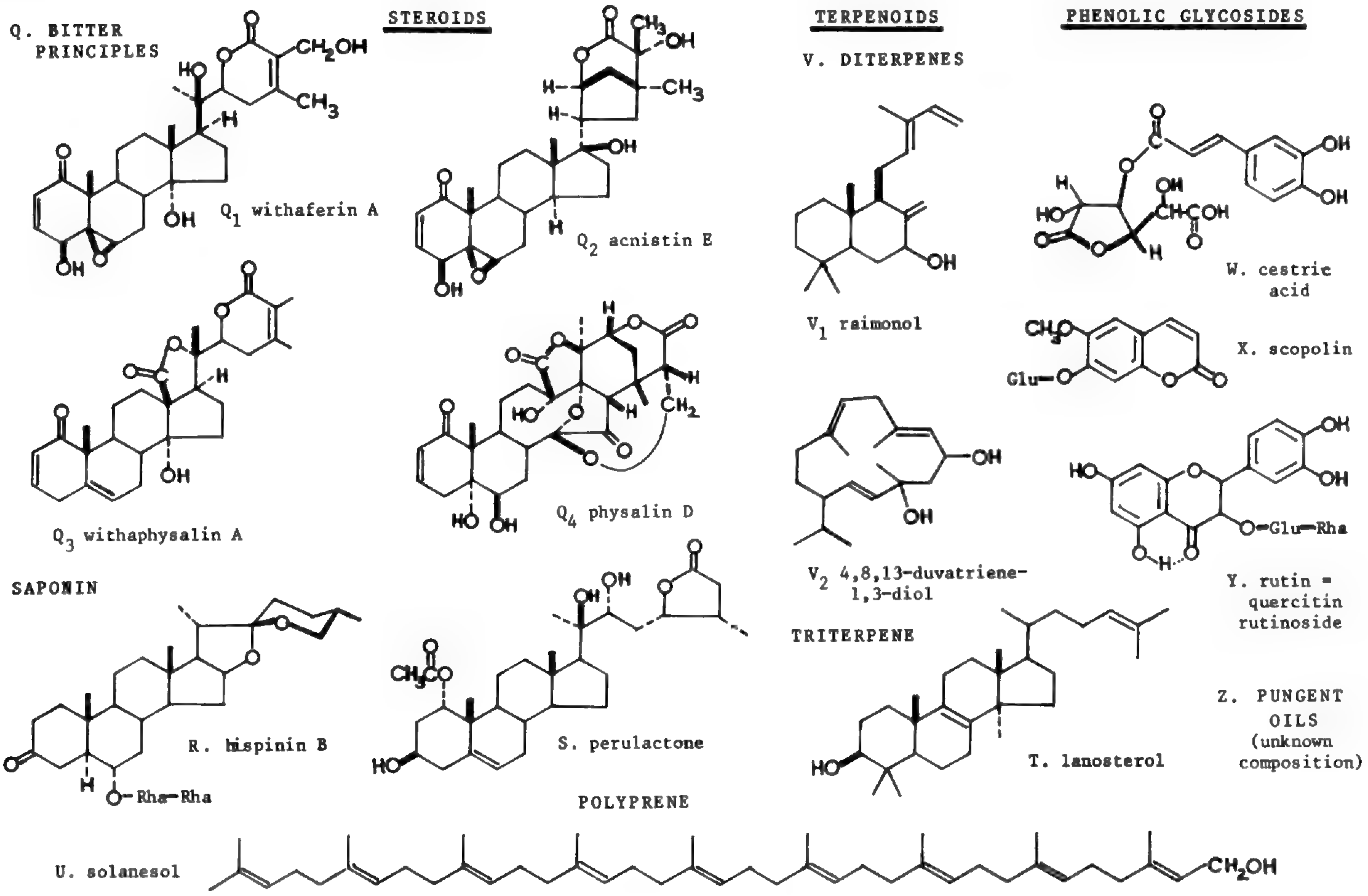


FIGURE 2. Examples of non-nitrogenous secondary compounds found in Solanaceae used as larval hosts by Ithomiinae. Carotenoids and other pigments are not included; for flavonoids, see Harborne & Swain (1979). See Table 2 for distributions.

ing the cold of early morning, treating them as it does fruits with a bitter rind. Similar learned behavior has been observed in jays (Corvidae) eating ithomiines in Costa Rica (R. Hagen, pers. comm.), as well as in orioles and grosbeaks attacking wintering monarchs (*Danaus plexippus*) in central Mexico (Calvert et al., 1979; Fink & Brower, 1981). Like most aposematic insects, Ithomiinae have tough and resilient bodies; surviving individuals squeezed by the tanager were often captured in flight one or more days after attack. They often remain on the forest floor for weeks after death, avoided by predatory and scavenging ants. Even the giant tropical orb spider *Nephila clavipes*, which often clutters the airspace of ithomiine colonies with broad sticky webs and takes most aposematic butterflies with typical rapaciousness (Vasconcellos-Neto & Lewinsohn, 1982, 1984), cuts out all Ithomiinae from its web rapidly (10 sec.–2 min.) after contact with any part of the body or wings. Other spiders, especially flower-frequenting Thomisidae (crab spiders), may take Ithomiinae regularly, however (Drummond, 1976; pers. obs.).

It has been suggested frequently that the protection of adult Ithomiinae against predators is due to alkaloids or other toxic chemicals sequestered and stored by the larvae from Solanaceae and passed on to the adult (Brower & Brower, 1964, p. 154; Young, 1972, p. 291; Drummond, 1976, p. 268, 1981, p. 63; Brown, 1980). A good precedent for this suggestion exists in the storage of cardiac glycosides (Fig. 3A) by larvae of Danainae—sister-group to the Ithomiinae (Ackery & Vane-Wright, 1984)—which are transmitted to adults and help protect them against avian and other predators (Brower et al., 1967; Brower, 1969; Brower & Glazier, 1975). Nevertheless, no evidence has been obtained yet for the presence of any Solanaceae secondary chemical sequestered naturally into the tissues of any herbivore. Indeed, all results reported by Rothschild (1973) showed metabolism and excretion of Solanaceae alkaloids by specialist herbivores; a later experiment showed retention of tropanes in *Manduca sexta* (tobacco hornworm) (Rothschild et al., 1979), but this herbivore does not normally encounter these insecticidal compounds in nature. Since Solanaceae alkaloids and steroids are relatively stable compounds, abundantly available to Ithomiinae through the larval food plant and toxic enough to be eminently suit-

TABLE 1. Important herbivores specialized to Solanaceae (other than *Nicotiana*) in Brazil. (Source: personal observations and A. G. d'Araújo e Silva et al., Quarto Catalog dos Insetos que Vivem nas Plantas do Brasil (1968).)

Insect Order	Family and Subfamily	Genera	Occurrence on Solanaceae	Degree of Specialization (Sp. Level)	Damage to Plants	Aposematic?
ORTHOPTERA	Acrididae: Romaleinae	*Chromacris* and others	Frequent	Low to moderate	Heavy	Many are
THYSANOPTERA	Various families		Infrequent	Low to moderate	Moderate	Rarely
HEMIPTERA	Miridae		Frequent	High	Moderate	Some are
	Coreidae	*Phthia, Hypselonotus*	Frequent	High	Moderate	Most are
	Lygaeidae + Pyrrhocoridae		Infrequent	Moderate to high	Light	Yes
	Pentatomidae[a]	*Runibia*	Infrequent	High	Light	Yes
	Tingidae	Many genera	Infrequent	High	Light	Some are
HOMOPTERA	Cicadellidae	Many genera	Infrequent	Moderate	Moderate	Many are
	Membracidae	Several genera	Infrequent	Moderate	Light	Some are
	Aleyrodidae		Moderate	Low	Moderate	Not
	Aphididae	Several genera	Frequent	Moderate	Moderate	Rarely
	Coccoidea: various families		Moderate	Low	Moderate	Not
LEPIDOPTERA	Hepialidae	*Phassus*	Rare	Moderate	Heavy (borer)	Unlikely
	Geometridae	*Hammaptera*	Rare	High	Light	Probably
	Arctiidae (including Ctenuchinae)	Various genera	Infrequent	Moderate	Moderate	Yes
	Noctuidae	*Gonodonta*	Rare	High	Moderate	Yes
	Pyralidae: Chrysauginae	Several genera	Rare	High	Light	Some are
	Sphingidae	*Manduca, Hyles*	Infrequent	High	Heavy	Adults + Larvae
	Nymphalidae: Ithomiinae	Over 30 genera	Frequent	High	Heavy	Adults yes
COLEOPTERA	Chrysomelidae: eight subfamilies	About 20 genera	Frequent	Usually high	Heavy	Most are
	Coccinellidae	*Epilachna*	Infrequent	Moderate	Moderate	Yes
	Curculionidae: Brachyderinae, Cleoninae	6 genera	Infrequent	Moderate	Light	Rarely
	Scarabeidae	Many genera	Rare, flowers	Low	Moderate	Rarely
	Meloidae	*Epicauta, Lytta*	Frequent	Moderate	Heavy	Some are
DIPTERA	Agromyzidae and others	Several genera	Rare	Moderate	Light	Not

[a] Many Pentatomid predators are often found patrolling Solanaceae; they do not attack the plants, but the herbivores.

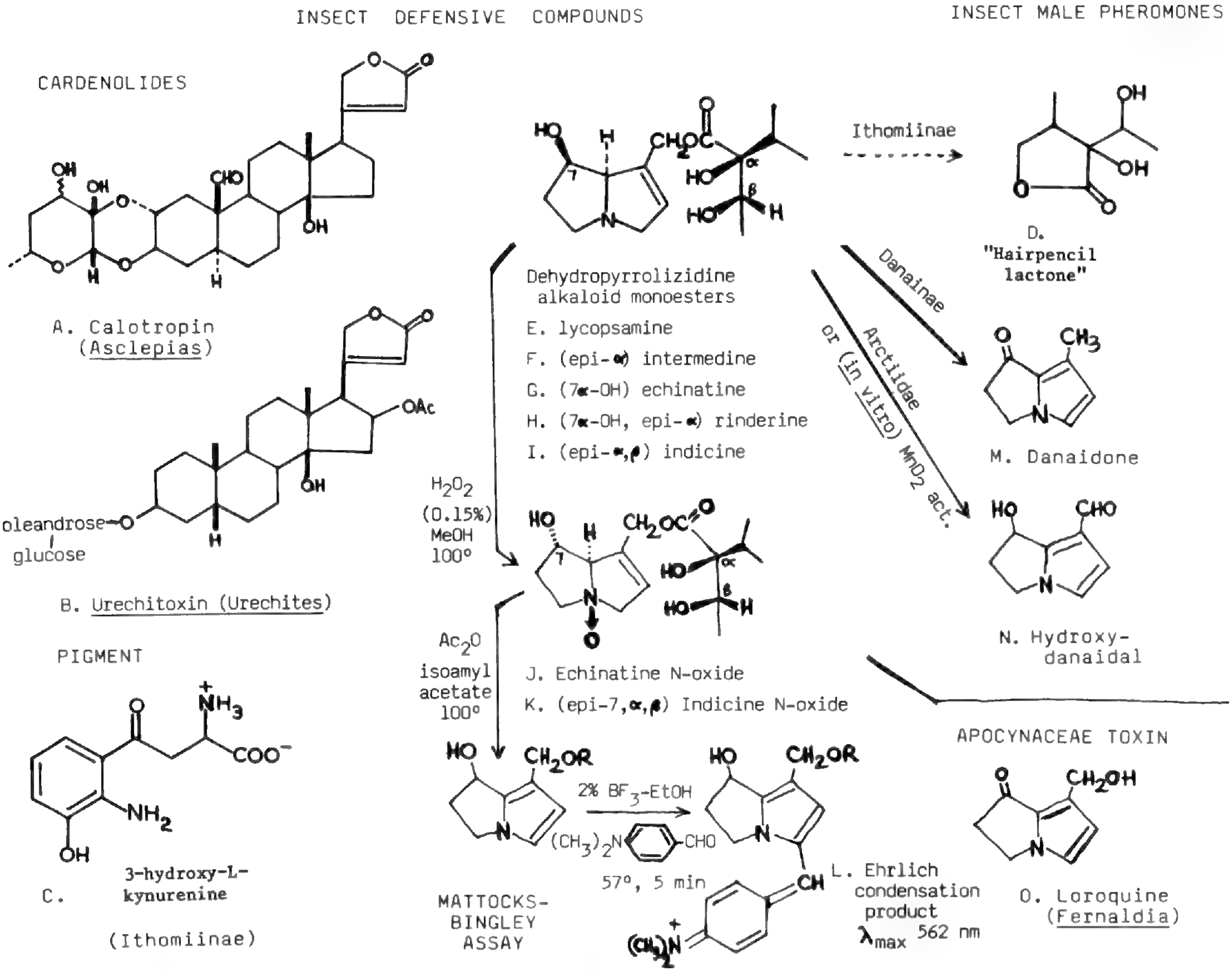


FIGURE 3. Danaine and ithomiine pheromones and defensive compounds, including cardiac glycosides (A, B), a pigment (C), male sex pheromones (D, M, N), dehydropyrrolizidine alkaloids (E–I) and their N-oxides (J, K), the reaction sequence and final product (L) of the Mattocks-Bingley assay, and Apocynaceae toxins (B, E, O). Compounds M, N, O are dihydropyrrolizines with carbonyl conjugation. See text for explanations.

able for protection against predators, their absence in Solanaceae-feeding insects was quite a disappointment (Rochschild, 1973). The only known "secondary chemicals" isolated from the Ithomiinae before this work were the amino-acid yellow pigment 3-hydroxy-*L*-kynurenine (Fig. 3C; Brown, 1967; Brown & Domingues, 1970) and a pheromonal lactone related to some esterifying acids of pyrrolizidine alkaloids (Fig. 3D), as well as the presumed precursors of the latter (Fig. 3E, F) (Edgar et al., 1976).

Especially interesting to find in adult Ithomiinae were these latter compounds (dehydropyrrolizidine alkaloids, or PAs, Fig. 3E–K), since they have been shown to be very important in both defense and reproduction of the butterflies in the sister group Danainae (Edgar & Culvenor, 1974; Schneider et al., 1975; Schneider, 1977; Rothschild & Marsh, 1978; Boppré, 1978; Edgar et al., 1979; Edgar, 1982). Unlike the rather sporadically stored cardenolides (Rothschild et al., 1975; Dixon et al., 1978; Malcolm & Rothschild, 1983; Fig. 3A, B), PAs are universally present in field-captured adult Danainae, which actively seek them out and sequester them (Boppré, 1984) from flower nectar, plant exudates, and even other insects (Bernays et al., 1977). Some danaines (*Euploea*) also obtain PAs from apocynaceous larval food plants (Parsonsieae: *Parsonsia*; Edgar, 1982). Larvae of a primitive ithomiine isolated in the New Guinea region, *Tellervo zoilus,* feed on these same plants; adults contain PAs presumably derived from *Parsonsia* (Edgar, 1982), as do adults of a primitive Central American ithomiine (*Tithorea tarricina*) whose larvae feed on *Prestonia* (Apocynaceae: Parsonsieae) containing the same PA found in the butterflies (Fig. 3E; Edgar, 1982; Edgar & Harvey, in prep.).

The purpose of this paper is to examine in detail, by chemical analysis and field bioassay, three basic questions related to the specific interaction between Neotropical Ithomiinae and their Solanaceae larval host plants. These questions derive from conventional aspects of insect-plant coevolutionary theory, especially as applied (with much success) to aposematic insects on poisonous plants (Ehrlich & Raven, 1965; Benson et al., 1976; Brown, 1980):

(1) To the extent that host plant specificity may exist in the Ithomiinae/Solanaceae relationship at generic and specific levels, how does it relate to chemical mediation of cues for oviposition and larval feeding?

(2) How might such chemical specificity reflect mutual interaction of these two groups over long evolutionary time, leading to diversification in both groups as a function of reciprocal selective pressures—that is, what is the evidence for coherent patterns of biochemical or "parallel diversification" coevolution?

(3) To what extent do the Ithomiinae use the poisonous secondary chemicals of their Solanaceae larval hosts for their own defense against predators in any stage of their life cycle?

A preliminary phylogenetic (Brown, in prep.) and chemical (Brown, 1984, 1985) survey of the Solanaceae/Ithomiinae interface, accompanied by an efficient spider bioassay for predator-defense compounds, has indicated surprisingly that, while the first question seems to merit an affirmative response, the other two questions must be answered by "little or no evidence in favor." The Ithomiinae apparently colonized the Solanaceae well after the generic diversification of this plant family in the New World, tolerating and using the diverse secondary chemicals (Figs. 1, 2) for oviposition cues to regulate specificity, but not for defense. Efficient chemical protection of adult Ithomiinae is generally unrelated to toxins encountered by larvae but not stored; instead, the adults seek out PAs in flower nectar and decomposing leaves, using them not only in pheromone synthesis (Fig. 3D) but also in defense, exactly as in the Danainae. The results of this survey are reported here, along with details of chemistry, bioassay, host plant specificity, and alternative ecological and physiological factors in the relationship.

MATERIALS AND METHODS

STUDY SITES

Field observations of interactions between Solanaceae and their herbivores were undertaken principally in two very different artificial tropical forest systems in the Fazenda Santa Elisa, Instituto Agronômico de Campinas, São Paulo (600 m elevation): Monjolinho (a forest garden of native plants) and Amarais (an old eucalyptus forest with natural under- and middlestory) (see Brown et al., 1981, for photos, maps, and description). Supplementary observations were made in Sumaré, SP (similar to Amarais, 550 m); Martinho Prado, SP (floodable riverine forest, 400 m); Serra do Japi, Jundiaí, SP (native seasonal and montane forest on rocky soils, 850–1,150 m); Serra Negra, SP (humid montane forest, 1,000 m); Bertioga, São Vicente and Mongagua, coastal São Paulo (perhumid tropical forest, near sea level); Poços de Caldas, Minas Gerais (montane forest, 1,200 m); coastal Rio de Janeiro and Espírito Santo (disturbed tropical rain forest, sea level to 800 m); Goiânia, Goiás (riverine thicket, 800 m); various parts of Rondônia, SW Brazil (seasonal forest on rich soils, 100–650 m); various parts of NE and S Pará, Brazil (tropical forest, sea level to 800 m); the region north of Manaus, Amazonas, Brazil (disturbed tropical rain forest on poor soils, 50 m); and in northern Venezuela (deciduous and cloud forest, sea level to 1,400 m). Some limited data have also been obtained in Mexico, Panama, Colombia, Ecuador, and Peru.

JUVENILE BIOLOGY

Ecological observations in the field were conducted with the aid of binoculars and suitable recipients for living adults and larvae (for details see Brown & Benson, 1974, and Brown, 1972b). Identification is secure for adult ithomiines, at least 90% certain for juveniles, and secure for Solanaceae host plants at the genus or section level but still uncertain in a few cases at the species level. Early stages of ithomiines were brought into the laboratory when necessary and reared to adults in glass or plastic dishes on separated leaves of natural or experimental host plants, kept subhumid. At least one fertile egg could usually be expressed from any field-captured reproductive female ithomiine by careful pressure on the abdomen with thumb and forefinger, working backwards slowly from the fourth segment. Such eggs were kept with expected or potential food plants until hatching (3–9 days). A large number of potential food plants could be found in Monjolinho or other areas in Campinas; many others were cultivated as available in my garden.

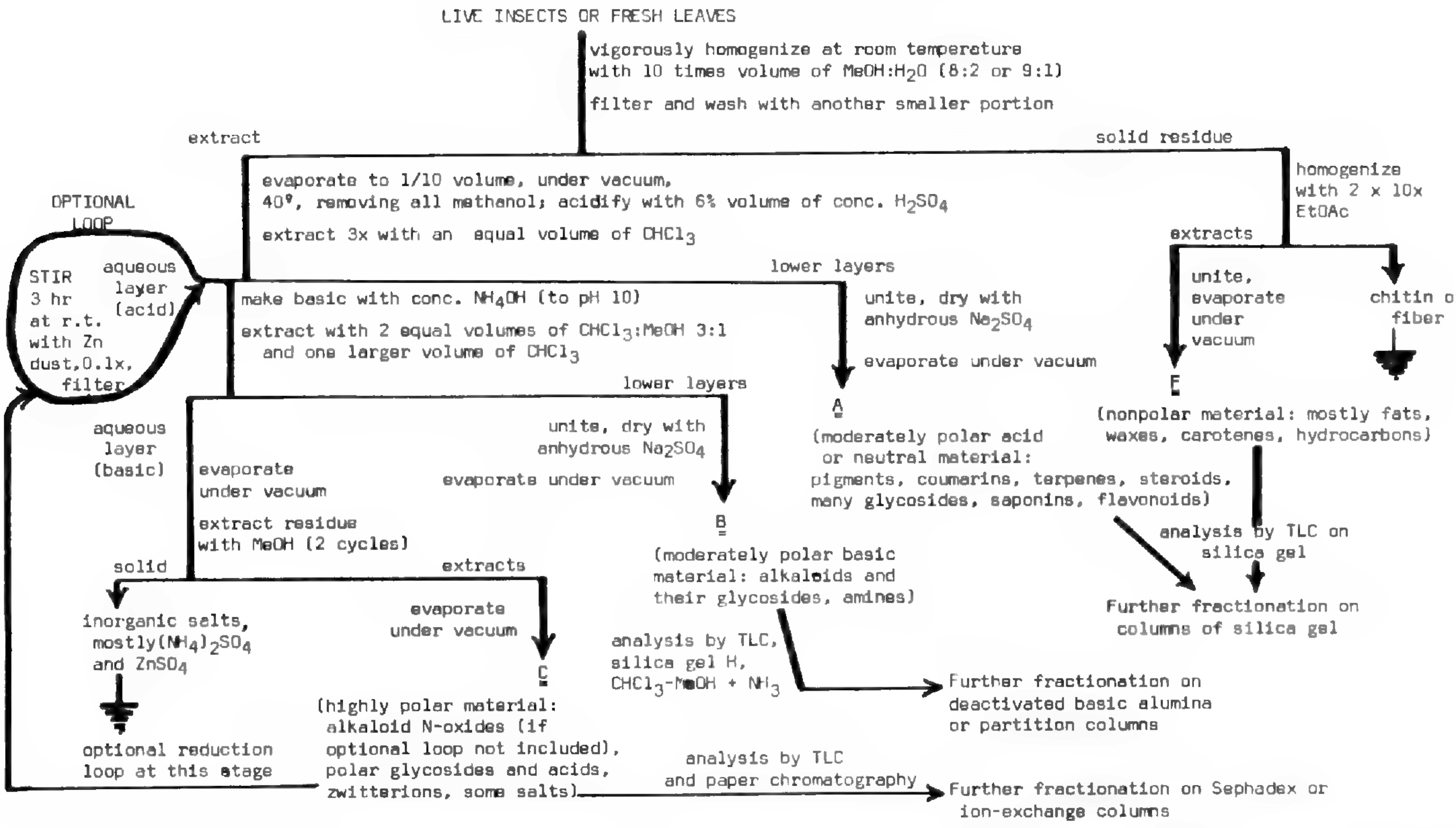


FIGURE 4. Mild and rapid standardized fractionation scheme for fresh leaves, flowers or insects, adapted to alkaloid-containing materials, giving fractions for chemical and ecological analysis and assay.

CHEMICAL FRACTIONATION

A standard extraction and fractionation was developed for all plant or animal material (Fig. 4). Leaves or flowers of plants observed to be used by Ithomiinae larvae or adults were separated from petioles or peduncles and maintained fresh until extraction; juvenile and adult Ithomiinae were kept alive in dishes or envelopes until the moment of extraction. Thus, all extractions were performed on fresh and recently functioning living tissues. The method was adapted to rapidly remove all organic substances of moderate to high polarity and at the same time deactivate enzymes in the living material; stable nonpolar compounds were removed afterwards. The initial use of heat, aeration, acids, bases, or acetone (which can condense with primary amines) was avoided. Exhaustive extraction was sacrificed in favor of rapidity; the more labile polar compounds (especially glycosides) were immediately and efficiently dissolved by vigorous maceration in the first extracting solvent added to fresh material. The leaves, flowers, or insects were divided if necessary into pieces of no more than 2 cm maximum linear dimension by scissors, already under or falling directly into methanol-water 8 : 2 (usual for leaves to extract less chlorophyll) or 9 : 1 (for adult insects), using about ten times the volume in milliliters as the fresh weight of material to be extracted. The extraction was immediately completed with scissors (if less than 40 ml) or with a kitchen homogenizer (Braun "Mini-Pimer" with a two-blade metal propellor) introduced into the suspension from above. Within a minute, leaves were reduced to tiny fragments and insects to pieces of chitin, partly coated with a fatty layer. The extract was homogenized for 1–3 minutes and filtered under suction; the insoluble material was washed and stirred with a further amount of aqueous methanol, up to half the original volume. Nonpolar compounds (fats, waxes, carotenes, some terpenes, and free flavonoids), insoluble in aqueous methanol, were immediately extracted from the residue with two portions (each 5 × original fresh weight) of ethyl acetate, giving a "fat fraction" (F) and leaving only polymeric organic fiber or plaque (cellulose, lignin, chitin).

The filtered and united aqueous-methanolic extracts were evaporated under vacuum at less than 40°C until all the methanol was removed. The resulting aqueous suspension (at times after filtration, giving a chlorophyll or nonpolar fraction F′) was acidified with conc. sulfuric acid (roughly 6% of the total volume, making it about 2 N = 1 M in acid) and extracted three times with an equal volume of chloroform. If occasional emulsions encountered at this or later stages (especially in some plant extracts) did not separate after 6 hours, they were filtered or broken with MeOH. The organic layers were united, dried with anhydrous granular sodium sulfate, filtered, and evaporated under vacuum to dryness to give a relatively more polar but nonalkaloidal fraction (A), often including some chlorophyll from leaves (usually little soluble in aqueous methanol) plus terpenoids and steroids (including most cardiac glycosides, withanolides, and saponins), flavonoids, coumarins, and organic acids (Fig. 2). Half or all of the aqueous phase was then made strongly basic (pH above 10) with conc. ammonium hydroxide and extracted with two equal volumes of chloroform-methanol 3 : 1 and one to three volumes (1.5 ×) of chloroform; this gave effective partition between water-methanol 8 : 1 and chloroform-methanol 6 : 1, obviating salting out of polar organic constituents from the upper layer. The organic layers were combined, dried, and evaporated as above to give a moderately polar alkaloid fraction (B) containing glycoalkaloids, tropanes, pyrrolizidines, and simpler bases (Figs. 1, 3). The remaining aqueous phase retained alkaloid N-oxides, very polar glycosides, more polar acids, and salts and sugars; it was directly evaporated and extracted with methanol (two cycles with filtration) to give a polar extract (C) and leave insoluble organic salts, mostly ammonium sulfate. If the alkaloids corresponding to the N-oxides were desired, the other half of the acidic solution (after $CHCl_3$ extraction, 2 N in H_2SO_4) or fraction C after dissolution in 2 N H_2SO_4 was reduced by stirring for 2 hours at room temperature with an excess of zinc dust (usually in grams equal to one tenth of solution volume), filtered (paper cone, gravity funnel), alcalinized with an excess of conc. NH_4OH (until all zinc salts dissolved as the zinc-ammonia complex), and extracted as above with $CHCl_3$-MeOH (2 ×) and $CHCl_3$. If this gave a much greater weight of alkaloid than in unreduced extracts, significant amounts of N-oxide were indicated. The complete extraction and fractionation scheme is illustrated in Figure 4.

Crude or purified fractions were analyzed by NMR spectra in $CDCl_3$ + 1% TMS, on the Varian T-60 of the Instituto de Química, UNICAMP, or eventually by IR spectra (in $CHCl_3$ or KBr) on a Perkin-Elmer Infracord. Mass spectra were performed by Mrs. Concetta Kascheres on the Varian MAT 311A instrument of the Instituto de Química, at 70 eV, probe temperature 60–105°C. Chromatographic analysis on TLC plates (coated microscope slides) used silica gel H (no binder) and varying amounts of chloroform-methanol or benzene-ethyl acetate, plus 1% NH_4OH for alkaloidal fractions; other systems used ethanol, acetone, and amines. Separations on adsorption columns (silica gel or alumina activity III were usual) followed results of the TLC analysis and used careful gradient elution. Alkaloids were purified by partition chromatography with the system ethanol-chloroform-water (usually 1 : 9 : 1), stationary (upper) phase 0.75 × (V/W) on Celite 545 and including phenol red as indicator (Brown & Kupchan, 1962) or chloroform and buffer solutions.

DETERMINATION OF PAS

Dehydropyrrolizidine alkaloids (PAs) were quantitatively assayed in fresh plant or insect material (they are destroyed after death or drying), cut up under absolute methanol (at least 10 ×), and, after at least one day, colorimetric determination on aliquots (usually 1/20, preferably containing no more than 100 μg PA; 40 μg gave initial absorbance off scale (> 2.0) and the Beer's law curve became unreliable above 150 μg) with a modification of the Mattocks (1967, 1968)-Bingley (1968) method. The assay is very sensitive as modified (< 0.1 μg is easily seen), very accurate for N-oxides (± 1%), reasonably accurate for total PA (± 10%), and extremely specific and applicable on total plant or insect extracts with minimal interference by other components; the final product of Ehrlich condensation shows λ_{max} 561.5 nm (in isoamyl acetate-ethanol-acetone about 1 : 1 : 2 with 2% BF_3) with $\epsilon \sim 57{,}000$ (Fig. 3L). For total PA determination, the aliquot is treated with 0.5 ml of freshly prepared 0.15% methanolic H_2O_2 (from 200 : 1 dilution of 30% aqueous H_2O_2 stabilized with 5 mg/ml of $Na_4P_2O_7$) and heated in a boiling water bath for 30 minutes, followed by drying with hot air for 5 minutes. This procedure destroys about 40 ± 5% of the total alkaloid N-oxide formed, but milder methods of oxidation give incomplete reaction or difficulties in the following steps. The resulting completely dry N-oxide (or an aliquot of the original extract air-dried at 80°C) is taken up in 1.0 ml isoamyl acetate, treated with 0.125 ml acetic anhydride, and heated 2 minutes in the boiling water bath. After being cooled to room temperature, the solution is treated with 1.0 ml of a solution of absolute ethanol : 20% BF_3-methanol : *p*-dimethylaminobenzaldehyde (50 : 5 : 1) and heated at 56–59°C for five minutes. Absorbance is read against a blank which passed through all the reactions, at 561.5 nm, after dilution to 3.8 ml with anhydrous acetone; further dilution with acetone gives a linear decrease in absorbance. At room temperature absorbance reaches a maximum several hours after the last reaction, about 5% above the reading immediately after it, and then diminishes; it may be maintained for many days at 4°C. Each microgram of PA in the original aliquot contributes to the absorbance 0.05 (N-oxide) or 0.03 (total base) (standard curves with echinatine and lycopsamine samples, Fig. 3G or E, provided by J. A. Edgar). Determinations were routinely done in racks of 40 13 × 100 mm glass test tubes, always doing total base and N-oxide determinations in the same batch to equalize the initial aliquot sampling and give an internal control on abnormal results. Separate pipets and bulbs should be used for each reagent in the series; water must be rigorously eliminated from the test tubes before the Polonovski reaction (Ac_2O-isoamyl acetate).

PAs with a carbonyl group conjugated with the unsaturated ring (7-ketones, or 9-aldehydes or carboxylates, such as Fig. 3M–O) or with no double bond in the ring did not give any blue color with this method. Dihydropyrrolizines (with the nucleus of Fig. 3M, N) without carbonyl conjugation could be directly determined on aliquots to an accuracy of about ± 10% using the final reaction in the series. They were usually destroyed in the first reaction step (oxidation) if present in the extract.

NEPHILA BIOASSAY

Fractions were bioassayed for predator-defense compounds, following observations of Vasconcellos-Neto and Lewinsohn (1982, 1984), with natural populations of the giant tropical orb spider *Nephila clavipes* (L.). This predator, common from December through July in Campinas (the same period as that of maximum ithomiine density in the same places) and present in small numbers year round, cuts out of its web, alive and unharmed, any field-captured ithomiine that is introduced naturally or experimentally, after contact with any part of body or wings. If the butterfly struggles excessively (ithomiines generally remain quiet, awaiting liberation), it may be attacked or wrapped in silk, but the spider does not suck it (Vasconcellos-Neto & Lewinsohn, 1982, 1984). *Nephila* spiders are among the most abundant, effective, and aggressive potential predators of flying insects in Campinas and throughout the more seasonal Neotropics, and can be safely regarded as very important in the evolution of predator defense mechanisms in the Ithomiinae. Vertebrate predators have not been used yet in the bioassay, but they were shown to reject an ithomiine by Brower & Brower (1964), to reject almost all ithomiines by Haber (1978), to reject two ithomiines by Coimbra-Filho (1981), and to accept only fatty abdominal contents of ithomiines in Brazil by Brown & Vasconcellos-Neto (1976).

Living individuals of the palatable nymphaline butterfly *Biblis hyperia* (Cr.), readily attacked and eaten by the spider, were painted with aqueous solutions, suspensions, or emulsions of fractions or compounds (corresponding to 0.5–1.5 butterfly, 2 g fresh weight of leaves, or 0.2 g fresh weight of flowers), covering the entire body, legs, antennae, and wing bases to at least half the radius, and let dry. Still alive, they were thrown into part of the web of an adult, non-satiated, and healthy spider (as judged by web structure), from a distance of 0.5–1.5 m on the side opposite the spider, between 1200 hours and 1500 hours on a warm sunny day. The spider normally advanced immediately to attack the butterfly (delays of up to 5 minutes can occur if the spider is "dozing" or distracted). If the *Biblis* was punctured, sucked, and then cut out or wrapped in silk by the spider, or (to still its struggles) was bitten, wrapped in silk, cut out, and taken to another part of the web and sucked, the test was regarded as negative. All such tests were repeated at least twice with different spiders and different individuals of *Biblis*. A positive test consisted of the spider's drawing back from the animal, at times inspecting various parts with its sensory palps but not biting or sucking, and eventually cutting out the living butterfly by breaking all necessary strands (usually cutting them with the third pair of legs), manipulating the entire insect and letting it drop unharmed. This test, usually repeated at least three times with at least two *Biblis*, was regarded as strong evidence for effective predator-deterrent compounds in the extract.

Biblis is common year round in most parts of the Neotropics, not especially fast- or high-flying, and readily attracted to fermenting baits. It is brightly colored black and red, regarded as an "incipient mimic" by the Browers (1964; Brower, 1969; Brower et al., 1971). Its larva feeds upon *Tragia*, an urticant euphorbiaceous vine, and the adult possesses dorsal scent glands in the abdomen that it displays in evident defensive behavior when handled. Nevertheless, it is readily eaten by *Nephila* and thus is an ideal substrate for the bioassay of chemical fractions. Alternative organisms used with similar success in the bioassay include some pierids (*Eurema*) and *Heliconius erato*, also eaten by the spider (Vasconcellos-Neto & Lewinsohn, 1982, 1984).

CHEMICAL COMMUNICATION AND COEVOLUTION AT THE SOLANACEAE/ITHOMIINAE INTERFACE

HOST PLANT UTILIZATION PATTERNS

In the principal field sites around Campinas, SP, at least 42 species of Solanaceae are used (or potentially should be used, by analogy with other regions) by larval Ithomiinae (Figs. 5–8). A further four species have been inspected frequently but show no signs of usage: *Capsicum praetermissum* Heiser & P. G. Smith, *Lycianthes rantonnetii* Carr. ex Lescuyer, *Solanum wendlandii* Hook. f. and *Solanum americanum* Mill. Many additional species occur in nearby field sites (at least 15 more species of *Solanum*) or in gardens.

Six of the 25 species (in 17 genera and 11 of the 13 neotropical tribes) of Ithomiinae known from the Campinas region (Figs. 5, 9) can be regarded as only occasional visitors (the two *Melinaea*, *Episcada philoclea*, *Pseudoscada quadrifasciata*, and *Hypoleria adasa* and *goiana*); these possibly do not find enough adequate host plants available to establish permanent populations. At least 15 additional species in as many genera occur in healthy populations within 200 km of Campinas, often in different forest types, and may eventually be recorded in the region. Two of the 19 species regularly present feed only on Apocynaceae-Parsonsieae (Fig. 5). Thirty-six species of solanaceous food plants have been recorded for 14 of the remaining 17 species and may be confidently predicted for the rest (Fig. 5); no species is monophagous but only *Mechanitis* (and possibly *Pteronymia*) could be called polyphagous (the rest are best regarded as quite narrowly oligophagous, especially in the chemical sense, as will be shown below).

This pattern is a microcosm of the general picture of food plant usage by the Ithomiinae (see Drummond & Brown, 1987), comprising about 400 species × species interactions. Monophagy or narrow oligophagy is the rule at the present level of information, not only for local populations but also for whole genera. A summary of all these data (Table 2) with chemical information added from many sources in the literature (with preliminary verification in this work, see Table 3) shows a reasonable specificity in the interactions between Ithomiinae and Solanaceae, at least at the level of genera of ovipositing females and host plants. Most of the ithomiine genera are known at present from only one or two Solanaceae genera or subgenera of *Solanum*; even generalists like the common and ubiquitous *Mechanitis* show a strong preference for only two subgenera of *Solanum* in most sites.

The records are still incomplete, however. Ithomiine ovipositions are not commonly observed, and 23 of the 52 genera are still represented by three or fewer confirmed food plant records. The possibility cannot be discounted that the specificity patterns shown in Table 2 are primarily due to lack of adequate information. Confident patterns of food plant specificity are seen only in the well-documented interactions of the

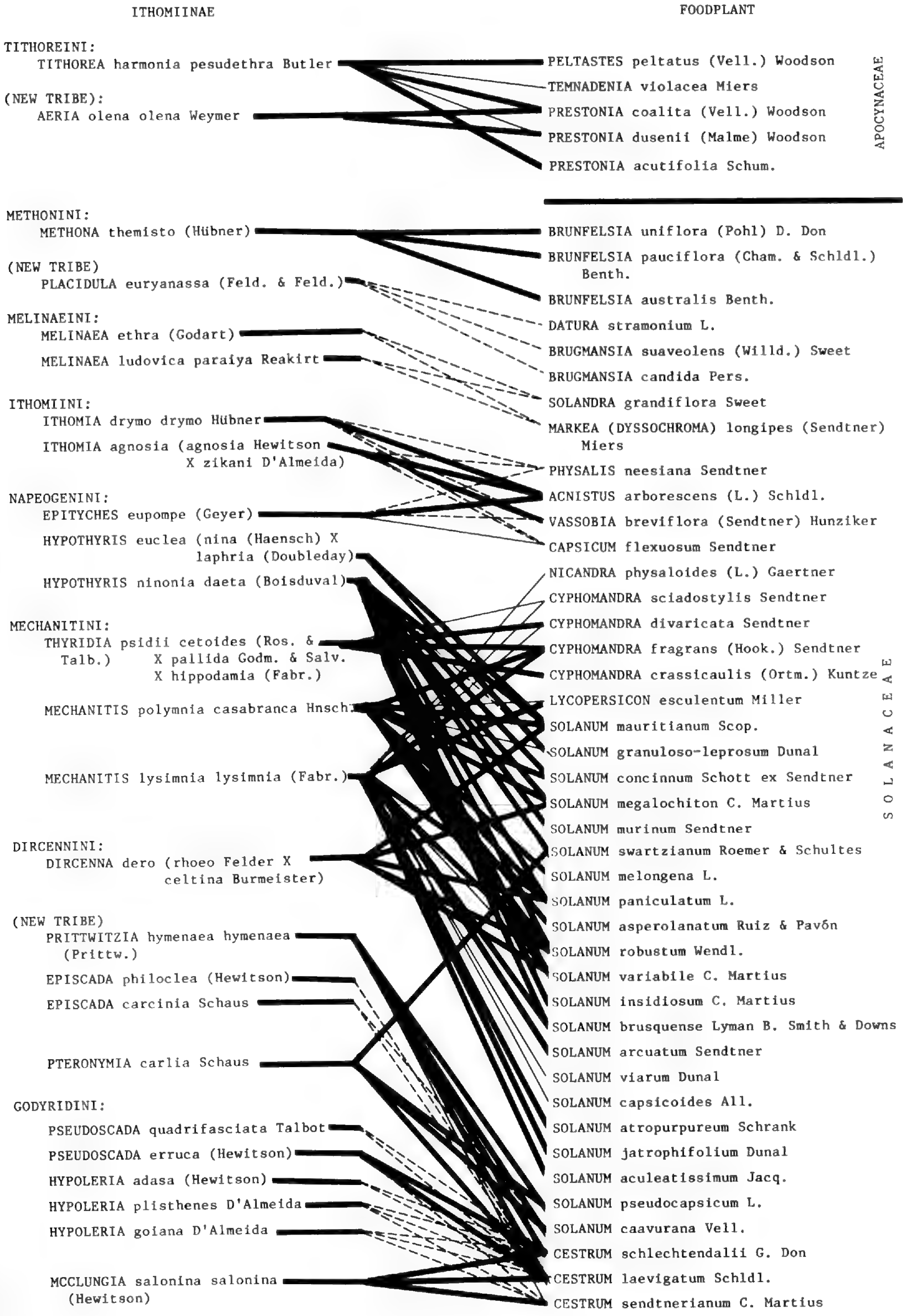
→

FIGURE 5. Known and expected food plant relationships of Ithomiinae in the Campinas region, São Paulo. Heavier lines have all been verified in interbreeding populations occupying various habitats within a 5-km diameter circle between Campinas and Barão Geraldo; note prevalence of oligophagy and some polyphagy (*Mechanitis, Prittwitzia, Pteronymia*). Neither Ithomiine tribes nor Solanaceae genera are in evolutionary order (see Table 2 for this), but have been arranged so as to simplify the figure.

FIGURE 6. Solanaceae of southeastern Brazil (photographed in Campinas, São Paulo unless otherwise indicated): *Solanum*.—A. *S. mauritianum*.—B. *S. swartzianum*.—C. *S. capsicoides*.—D. *S. aculeatissimum*.—E. *S. robustum*.—F. *S. atropurpureum*.—G. *S. paniculatum*.—H. *S. megalochiton*.—I. *S. pseudoquina* St. Hil. For authors' names, see Figure 5.

FIGURE 7. Solanaceae of southeastern Brazil (continued).—J. *Solandra grandiflora* (cultivated).—K. *Brugmansia candida* (cultivated; Jardim Botânico, Rio de Janeiro).—L. *Markea* (*Dyssochroma*) *viridiflora* (Sims.) Miers (Jardim Botânico, Rio de Janeiro).—M. *Brugmansia suaveolens*.—N. *Brunfelsia australis*.—O. *Vassobia breviflora*.—P. *Acnistus arborescens*.—Q. *Cestrum laevigatum*.—R. *Cestrum intermedium* (Joinvile, Santa Catarina).

Known (▬▬▬▬) and presumed (---------) food-plant records
for Ithomiinae in the region of Campinas, São Paulo, southeast Brazil
(23° S, 48° W, 600-1,000 m)

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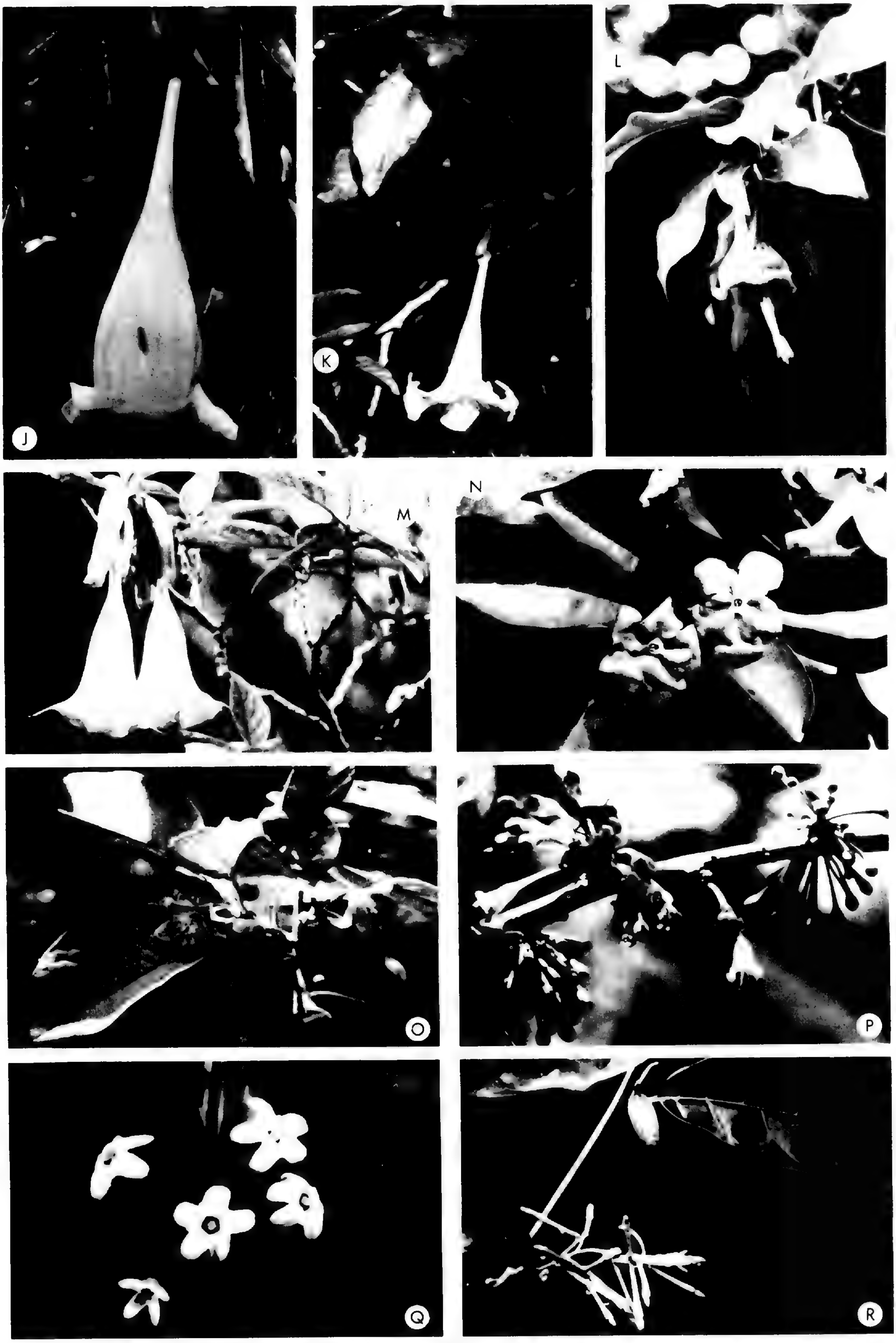
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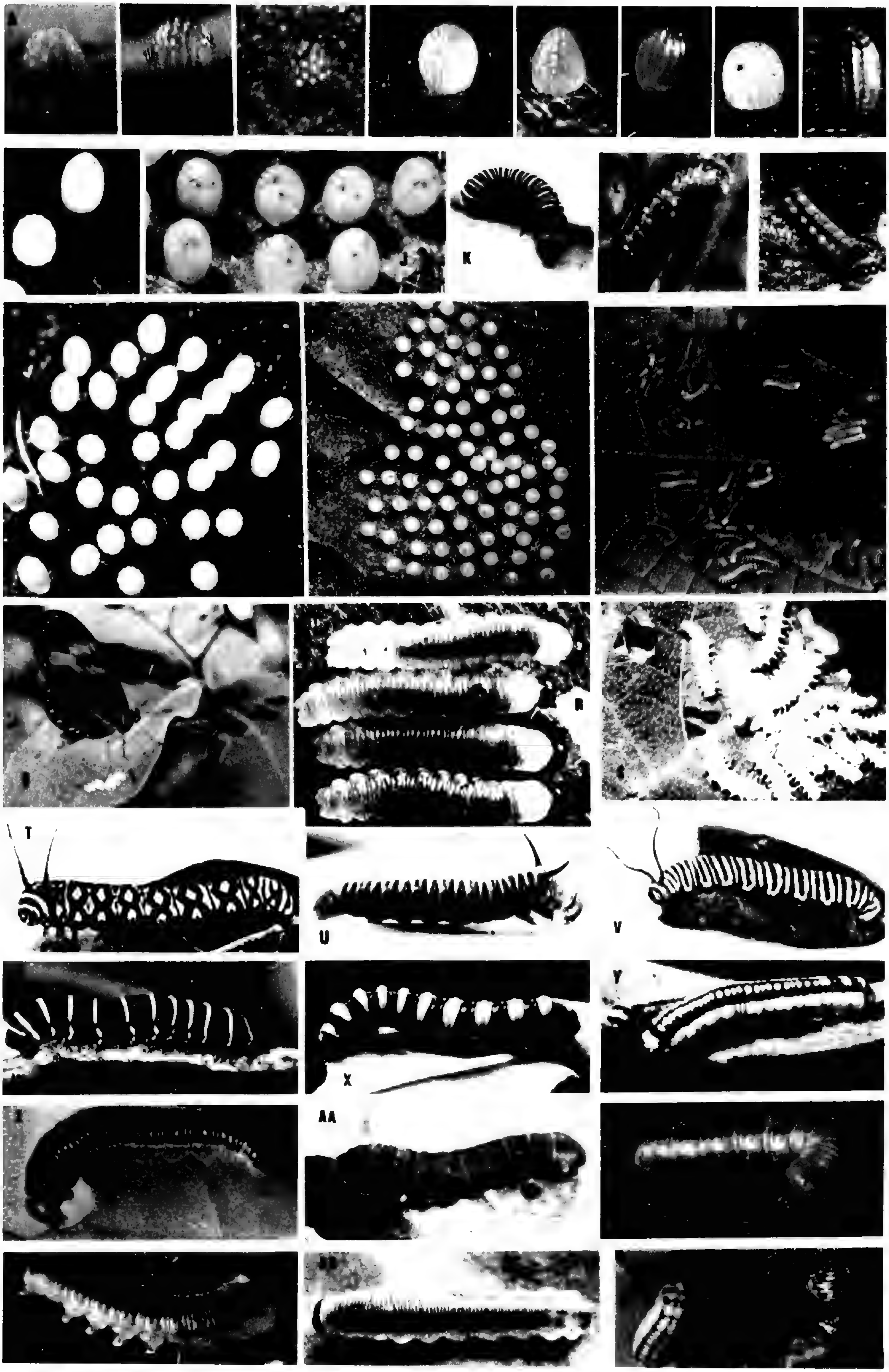
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genera *Tithorea, Elzunia,* and *Aeria* (with Apocynaceae: Parsonsieae), *Methona, Melinaea, Thyridia, Mechanitis, Hypothyris, Ithomia, Dircenna, Pteronymia,* and *Greta.* At a higher level, almost all members of the last two tribes show collectively a strong specificity to *Cestrum* and surprisingly also to the distant section *Geminata* of *Solanum.* It is probable that more work will provide more evidence of the restriction of *Napeogenes* to *Lycianthes* and confirm the nascent patterns in *Placidula, Scada, Epityches, Oleria,* and *Callithomia,* but this is mere speculation at this time.

At the species level, *Mechanitis* females tend to divide up the local *Solanum,* resulting in minimal overlapping of oviposition (see Drummond, 1976; Haber, 1978; Vasconcellos-Neto, 1980, 1986), but the divisions do not coincide with simple taxonomic lines in the plants. They also vary from area to area and are not correlated with larval choice or survivorship in experiments, indicating an unstable ecological determination of the partition.

Though the butterflies may be able to recognize their food plants, biologists have greater difficulty in Solanaceae identification, even to the genus level, which may result in some spurious patterns in Table 2. In 1969, a top Solanaceae taxonomist identified for me a specimen from near Rio de Janeiro as a *Capsicum* on the basis of its cleft anthers, but both S. Knapp (pers. comm.) and I regard this plant as *Solanum* (sect. *Geminata*) *caavurana.* The "diagnostic" trait in this case may have been an artifact of the drying method used for the specimen. If such evolutionarily distant and chemically distinct taxa could be potentially confusing to an experienced expert, how will they appear to the average field biologist who, having just observed a female ithomiine oviposit on a (presumably solanaceous) bush with glabrous entire leaves and no flowers, faces the maze of complex and confusing taxonomy in the family? This plant could be placed preliminarily in over 30 genera, five with over a hundred species and one with over a thousand. Thus the "solid" data base for host plant usage in Table 2, from which a number of completely unlikely records have already been purged, may yet suffer fundamental modifications with further work.

COEVOLUTION AND PHYLOGENETIC DIVERSIFICATION

An attempt to relate the phylogeny of the Ithomiinae with that of their larval food plants, such as was done with reasonable confidence and results for the nymphaline tribe Heliconiini (Benson et al., 1976), has met with very little success (Drummond, 1986; Brown & Drummond, in prep.; Drummond & Brown, 1987). Only the broadest pattern can be seen in the progression from Apocynaceae to Solanaceae (with Gesneriaceae in the middle to provoke the imagination). The most primitive ithomiine genera to use Solanaceae (*Athesis, Methona, Olyras,* and *Melinaea*) feed on the genera regarded as highly advanced in this family. Two large tribes (Mechanitini and Napeogenini) run their food plant

←

FIGURE 8. Juveniles of Ithomiinae with food plant and locality. A–J, N–O. Eggs, about 0.6–1.0 mm high.—K–M, P, R. Second instar larvae, about 4–7 mm long.—Q. Adult ovipositing (photo J. Vasconcellos-Neto).—S-DD. Fourth or fifth instar larvae, about 20–35 mm long.—EE. Prepupa and pupa. A. *Tithorea harmonia pseudethra* (*Prestonia*? sp.), Piracanjuba, Goiás.—B, U. *Aeria olena* (*Prestonia coalita*), Campinas, SP.—C, AA. *Napeogenes sulphurina* Bates (*Lycianthes* sp., a vine), Ipojuca, Pernambuco.—D, CC. *Garsauritis xanthostola* Bates (*Solanum* sp., note simple hairs), Faro, Pará.—E, BB. *Hypothyris daphnis amapaensis* Brown (*Solanum asperum*), Lourenço, Amapá.—F, DD. *Oleria astrea thiemei* (Oberthür) (*Solanum stagnale* Moricand), Catu, Bahia.—G, Z. *Ceratiscada canaria* Brown & D'Almeida (*Solanum laxiflorum* Sendt.), Santa Teresa, Espírito Santo.—H. *Pteronymia hemixanthe* (Feld. & Feld.) (*Solanum* subg. *Brevantherum*?), Ubatã, Bahia.—I, R. *Mechanitis lysimnia* (*Solanum* subg. *Leptostemonum*), Brasília, DF.—J, M, O, P, Y, EE. *Hypothyris euclea laphria* (*Solanum asperum*), Linhares, Espírito Santo.—K. *Melinaea menophilus* ssp. (*Markea ulei* (Damm.) Cuatr., originally reported as "*Forsteronia* sp."), Jaru, Rondônia.—L. *Mcclungia salonina* (*Cestrum sendtnerianum*), Sumaré, SP.—N, Q. *Mechanitis polymnia casabranca* (*Solanum* nr. *rugosum, Solanum variabile*), Brasília, DF and Sumaré, SP.—S. *Mechanitis polymnia angustifascia* Talbot (*S. goodspeedii*), Caranavi, Bolívia.—T. *Tithorea harmonia moppa* Bryk (*Prestonia*? sp.), Belém, Pará.—V. *Melinaea ludovica* (Cr.) (*Markea* sp.?), Belém, Pará.—W. *Methona themisto* (*Brunfelsia australis*), Campinas, SP.—X. *Methona confusa psamathe* Godm. & Salv. (*Brunfelsia grandiflora* D. Don), Barinitas, Venezuela. T and V are from watercolors by Emily Fountaine, preserved in the British Museum (Natural History). Solanologists are requested to photograph and rear through to the adult or to preserve in alcohol any eggs (with ridges as in A–J) or larvae of these types found on identifiable plants and send them to B. Drummond or K. Brown for identification and registry in the data bank for Table 2.

TABLE 2. Approximate number of known interactions (species × species) between Ithomiinae and their larval food plants, with data on plant chemistry (Figs. 1, 2) and on attraction to pyrrolizidine alkaloid sources.

	Attraction to:[c]		Plant Families: Genera[a,b] (no. species)																		
					Solanaceae																
					Solanum (1000)																
	Boraginaceae (withered plants)	Eupatorieae (flowers & plants)	Apocynaceae *Prestonia, Fernaldia, Mesechites*, etc.	Gesneriaceae *Drymonia, Columnea*	*Solanum* (incl. *Geminata, Pseudocapsica*)	*Brevantherum*	*Leptostemonum*	*Potatoe, Bassovia*	*Lycianthes* (150)	*Cyphomandra* (40)	*Lycopersicon* (6)	*Capsicum* (25)	*Cuatresia* (6), *Witheringia* (16)	*Physalis* (95)	*Vassobia* (4), *Dunalia* (6), *Acnistus* (2)	*Datura* (10), *Brugmansia* (5)	*Nicandra* (1)	*Solandra* (10)	*Markia* (24)[f], *Juanulloa* (11)[f]	*Cestrum* (250)	*Brunfelsia* (40)
	Chemical Constituents		Alkaloids (Fig. 1)																		
			Indoles, Steroids, PAs (3E–I)	?	------ ABFLH ------				BL	ABCL	BL	BC?L	C?	ABC	BC	BCP	C	BC	C?	LC	BCE
			Other Chemical Constituents (Fig. 2)																		
Ithomiinae: Tribes, Genera[d,e] (no. species)			Cardiac glycosides, XYZ	WY	-- RTUWXYZ --				R?	Z	RWXY	YQ?	Q	QSY	QY	QYZ	QR	XY	XY	RWXYZ	XY
A. Tellervini[g]																					
Tellervo (1)[g]	1	1	**5**																		
B. Tithoreini																					
Elzunia (2)	1	?	**4**																		
Tithorea (2)[h]	1	1	**16**															1?			
C. (New Tribe)																					
Aeria (3)[h]	2	3	**8**																		
D. (New Tribe)																					
Athesis (1)	1	1										**1**									
E. Methonini																					
Methona (7)[h]	1	1																			**12**
F. (New Tribe)																					
Placidula (1)	2	3								1?						**6**					
G. Melinaeini																					
Olyras (2)	2	2																1?	**1**		
Eutresis (2)	2	2																1?	**1**		
Melinaea (10)[h]	2	2																1	**9**		
H. Mechanitini																					
Thyridia (1)[h]	2	3								**6**											
Sais (2)	1	3							1												
Scada (6)	1	3					1	**3**													
Forbestra (3)	1	3						1													
Mechanitis (5)[h,i]	1	3			3	15	**56**	1		7	2					1?	1				
I. Oleriini																					
Hyposcada (8)	2	3		**3**														**1**			
New genus (3)	1	1							1												
Oleria (30)[h]	2	3				1	**4**	**8**	3												
J. Napeogenini																					
Epityches (1)	2	3										**2**		**1**	**2**						
Rhodussa (1)	2	3						1?	**1**												
Napeogenes (18)[h]	2	3						1?	**8**												
Garsauritis (1)	2	3					**4**														
Hyalyris (16)	2	3				**2**	**5**														
Hypothyris (16)[h]	2	3			**1**	**24**	**13**	1													
K. Ithomiini																					
Miraleria (1)	2	3											**1**		**2**	**1**					
Ithomia (21)[h]	2	3							2			**2**	**11**	3	**5**						
L. Dircennini																					
Callithomia (3)[h]	3	3					1	**3**	1												
Velamysta (3)	3	3							1												
New Genus (1)	2	?								1											
Dircenna (7)[h]	1	3				**14**	**17**														
Hyalenna (5)	3	3				**1**															
M. (New Tribe)																					
Ceratinia (5)	3	3			**3**		**3**														
Ceratiscada (3)	2	3			**2**																
Prittwitzia (1)	2	3			**3**		1?													**5**	
Episcada (15)[h]	2	3			**4**																
Pteronymia (41)[h]	3	3			**25**	**3**			3											2	

TABLE 2. Continued.

			Plant Families: Genera[a,b] (no. species)																		
					Solanaceae																
	Attraction to:[c]				*Solanum* (1000)																
Ithomiinae: Tribes, Genera[d,e] (no. species)	Boraginaceae (withered plants)	Eupatorieae (flowers & plants)	Apocynaceae *Prestonia, Fernaldia, Mesechites,* etc.	Gesneriaceae *Drymonia, Columnea*	*Solanum* (incl. *Geminata, Pseudocapsica*)	*Brevantherum*	*Leptostemonum*	*Potatoe, Bassovia*	*Lycianthes* (150)	*Cyphomandra* (40)	*Lycopersicon* (6)	*Capsicum* (25)	*Cuatresia* (6), *Witheringia* (16)	*Physalis* (95)	*Vassobia* (4), *Dunalia* (6), *Acnistus* (2)	*Datura* (10), *Brugmansia* (5)	*Nicandra* (1)	*Solandra* (10)	*Markia* (24)[f], *Juanulloa* (11)[f]	*Cestrum* (250)	*Brunfelsia* (40)
N. Godyridini																					
Godyris (10)[h]	3	3			3															**5**	
Pseudoscada (6)[h]	2	3																		**5**	
Hypomenitis (6)	2	3																		**2**	
Greta (10)	2	3			1	1														**16**	
Hypoleria (11)[h]	2	3			1															**6**	
Mcclungia (1)	2	3																		**3**	
Heterosais (3)[h]	3	3																		**3**	

[a] Families are in approximate order of advancement and genera of Solanaceae in order according to Hunziker (1979), from primitive to advanced.

[b] In addition to *Nicotiana* (see note i, below), important Solanaceae genera available to Ithomiinae in tropical America for which no food plant records are yet known include *Jaltomata, Athenaea* (but probably used by *Epityches* and *Ithomia*), *Larnax, Saracha, Iochroma, Salpichroa, Jaborosa, Lycium, Grabowskia, Trianaea, Sessea, Metternichia, Petunia, Fabiana, Nierembergia, Bouchetia, Protoschwenkia, Schwenkia, Melananthus, Parabouchetia, Leptoglossis, Browallia, Streptosolen,* and *Heteranthia.*

[c] 1—weak attraction usually including both sexes, 2—males strongly attracted, 3—males strongly and females regularly attracted.

[d] Tribes and genera follow the order of Mielke and Brown (1979) as modified by Brown (in prep.), from primitive to advanced (including genera within each tribe).

[e] No food plants have yet been recorded for the following genera of Ithomiinae (number of species in parentheses). * = Andean genera, usually of high-altitude cloud forests, though *Roswellia* extends out into the foothills.—Tribe D. **Roswellia* (1), **Patricia* (2).—Tribe G. *Athyrtis* (1).—Tribe H. *Paititia* (1).—Tribe I. *a new genus near *Hyposcada* (1).—Tribe J. **Aremfoxia* (1).—Tribe K. **Pagyris* (1).—Tribe N. **Dygoris* (1) and **Veladyris* (1). Total, 9 genera with 10 species.

[f] The recent divisions of these two genera into a number of smaller genera (Hunziker, 1979), most of them used by the same Ithomiinae, are here included under the collective older names.

[g] Restricted to the Old World tropics, regarded by some as closer to the Danainae than the Ithomiinae (see Ackery & Vane-Wright, 1984).

[h] Food plant patterns are constant from the northern to the southern extremes of the range of the genus, usually from Central America to southern Brazil (total of 18 genera).

[i] Ovipositions of *Mechanitis polymnia casabranca* were observed in Campinas, São Paulo, on cultivated *Capsicum annuum* L. and feral *Nicotiana* (rosette only), but the larvae did not grow on these plants.

[j] The published structure for "hopeanine" (1E) is biogenetically and chemically implausible and does not agree with the data presented in the original study (Iyer, 1978); the alkaloids of *Brunfelsia* are presently under investigation.

phylogeny backwards (more advanced butterflies use increasingly primitive plants). And although the most morphologically advanced ithomiine genera concentrate on the relatively advanced *Cestrum,* they use equally well the supposedly primitive section *Geminata* of *Solanum* (Table 2). That the neotropical Ithomiinae represent a widely diversified butterfly group (51 genera in 13 tribes) could help explain why a comparison of their host plant utilization patterns with those of the 65 rather homogeneous species in no more than ten genera of the single tribe Heliconiini does not lead to a fruitful parallel. The patterns for the Ithomiinae are complex, and the arrangement of the plant groups in Figure 5 so as to produce a maximum parsimony scheme (lowest number of crossing lines in the middle) has produced some strange and thought-provoking proximities between genera normally widely separated; note especially the positions of *Brunfelsia* and *Cestrum.*

While the Solanaceae indeed may have represented a new field for adaptive radiation of the Ithomiinae in the New World, it is probable that the plant family was already very diversified chemically and taxonomically before the butterfly subfamily began to move onto it. A large number of available genera (at least 24) are still not known to be attacked by Ithomiinae (see Table 2). Furthermore, the genus *Brunfelsia*, regarded as a relatively advanced member of the Solanaceae, apparently entered the Caribbean area and diversified greatly (as section *Brunfelsia*) before *Methona*, a relatively primitive ithomiine genus in a monotypic tribe, could evolve as a specialist herbivore on it (Plowman, 1979, p. 489). It is possible, however, that the extensive speciation verified in *Solanum* and *Cestrum* eventually may be related to their heavy use by a variety of Ithomiinae (Table 2). This can be investigated only by careful chemical analysis and bioassay with larvae, following in parallel two independently developing phylogenetic lines of species or populations that show specific interactions.

Further considerations of the incongruities between phylogenies of genera of Solanaceae and Ithomiinae are presented in Brown & Drummond (in prep.).

BIOCHEMICAL COEVOLUTION

The taxonomic diversification of the Solanaceae has been accompanied by an impressive diversification in secondary chemicals, leading some to suggest polyphyly for the family as presently constituted. Indeed, no other plant family can challenge the Solanaceae in having alkaloids representing all four major biosynthetic pathways (lysine-ornithine, phenylalanine-tyrosine, tryptophan, and steroid), an equal number of less important pathways (nicotinic acid, anthranilic acid, glycine, acetate), and a further set of aberrant or combined sources unique to the family (leading to capsaicins, solanines, withasomnine, and hopeanine) (Fig. 1), not to mention more common amines such as choline, noradrenaline, and hypoxanthine; some species also produce very toxic peptides. As is often the case, these alkaloid-rich plants are singularly poor in lower (volatile) terpenes, but some *Datura*, *Cyphomandra*, and especially *Cestrum* and *Solanum* section *Geminata* share a similar and abundant pungent oil that may include terpenes. Diterpenes and triterpenes abound in some Solanaceae, and nonalkaloidal steroids are represented as saponins (such as diosgenin glycosides) and withanolides/physalins, unusual steroidal lactones with marked biological activity (Fig. 2). Flavonoids and coumarins also are documented amply in diverse members of the family (Fig. 2; Harborne & Swain, 1979), and further phenolics and their glycosides (including tannins) are almost always found when sought in polar extracts. The C_{45} alcohol solanesol is an unusual unsaturated linear nonaprenol (Fig. 2). Lacking are reports of cyanogenic glycosides, cardenolides, glucosinolates, nonprotein amino acids, and iridoid glycosides, but their absence cannot be definitively affirmed because few phytochemists have specifically sought them in the Solanaceae.

Thus the plants in this family are well defended chemically and attacked by rather few insect herbivores other than Ithomiinae (Table 1). The only ones that seem to promote similar damage in natural systems are generalist grasshoppers and meloid beetles, perhaps molluscs in more calcium-rich areas, and specialist chrysomelid beetles. The plants also at times are defended admirably against vertebrate chewers by prickles (Symon, 1986) but these have very little effect on smaller invertebrates, who walk and chew around them or build silken pads over them. Other defenses (tough leaves, glandular trichomes) are more effective against invertebrates (Vasconcellos-Neto, 1980, 1986), as may be further quantitative defenses (tannins, amino-acids, and resins) and a host of ecological strategies such as phenology (see Vasconcellos-Neto, 1986) habitat, growth form, seed dispersal by chiropterochory, and encouragement of spiders and predatory pentatomids on the leaves, among others observed in Brazil.

When the generic preferences of the butterflies are analyzed in terms of plant chemicals (Table 2), the associations seem to show patterns, though the data are still chemically and biologically very incomplete. There appears to be a certain tendency toward chemical specificity, at times without reference to taxonomic relationship (as in the similarly potent-smelling *Solanum* sect. *Geminata* and *Cestrum*). It seems probable that female Ithomiinae search for and find specific chemical cues for oviposition on certain genera of Solanaceae and may be led to place eggs on unrelated plants with similar chemicals. What else would permit a *Mechanitis polymnia* female in Campinas in May 1981 to recognize a small *Nicotiana* plant in Monjolinho as a potential Solanaceae host, or to oviposit on *Capsicum annuum* in my garden, especially when the larvae survived on neither? (The first shares nicotine and the second steroidal glycoalkaloids with a usual host, *Solanum mauritianum.*) Based on the patterns in Table 2, some still unknown chemical may be predicted to set *Solanum* subgenera *Bassovia, Potatoe,* and *Lycianthes* apart from all other Solanaceae (see *Napeogenes, Oleria,* and *Callithomia*) and possibly associate *Lycianthes* with the withanolide-elaborating genera (see *Ithomia*) and even with *Solanum* sect. *Geminata* (*Pteronymia* uses both).

Further support for some degree of chemical mediation at the oviposition sector of the interface comes from the broad geographical consistency of the more specific relationships, at least from Mexico through Costa Rica and Ecuador to south Brazil for the 18 genera for which food plants are known over this range (Table 2; Drummond & Brown, 1987). This surely must have been established over long evolutionary time in developing phyletic lines of the butterflies. The chemical proximity of disparate taxonomic groups of plants, treated as interchangeable by ovipositing females, also supports a chemical mediation at the interface. In order to separate this possible evolutionary component in food plant usage from the ecological noise in the system, careful comparative tests with free-flying females must be performed under controlled conditions, coupled with larval feeding preferences in multiple-choice tests, and thorough chemical analysis of all potentially active compounds in the food plants chosen or rejected.

The patterns broadly reflected in Table 2 and supported on a local scale by Figure 5, however, do not support any easily envisioned hypothesis of mutual interaction and fine coevolutionary adjustment between the two groups at a taxonomic level. Although some regularity in chemical cues for oviposition and chemical specificity is suggested, the data are still very limited and give little support for parallel diversification in the two groups. Much more complete biological and chemical information will be necessary before any claims of biochemical coevolution can be advanced at this plant/herbivore interface. The present information already seems to falsify many attractive and conventional hypotheses.

In view of the fact that Ithomiinae populations probably are controlled principally by certain limiting adult resources (suitable humid open-understory "pockets" and sources of PAs, see below), they may exert very little, if any, selective pressure for chemical and phylogenetic diversification on their host plants. In any case, the specific choices seem to vary appreciably with local ecological conditions. Under a moderate degree of Ithomiinae attack, some Solanaceae even respond by vigorous new growth and flowering (especially in *Brunfelsia* and in section *Brevantherum* of *Solanum*). Under these conditions, it is difficult to establish the most basic prerequisites for "classical" coevolution between herbivores and host plants.

AN ALTERNATIVE HYPOTHESIS: SEQUENTIAL COLONIZATION BY CHEMICAL ADAPTATION (TABLE 4)

The results of chemical extraction, fractionation, and *Biblis/Nephila* bioassay of 48 ithomiine host plants are presented in Table 3. In the cases investigated so far the Solanaceae have shown in their leaves the compounds already reported or presumed for each species, in good quantities.

If these chemical characteristics of the host plants are combined with the utilization patterns in Table 2, a most suggestive picture emerges, as summarized in Table 4. Nothing is known of the paleophytochemistry of these plants beyond the global variation in secondary compounds seen in widespread geographical populations of each genus today, but it may be presumed that they were diversified generically before Ithomiinae began attacking them in the New World (since the most advanced genera were attacked first) and probably similarly protected chemically to modern species.

It then becomes possible to trace a series of small hypothetical advances in larval toleration of food plant chemicals, each facilitated by preadaptations on the existing host plants, which lead to a complete picture of chemical specificity as observed today (Tables 2, 4). The scheme is clearly oversimplified but is attractive as a hypothesis for the sequential colonization of plant hosts, already diversified taxonomically and chemically, by progressively adapting herbivores (Futuyma, 1983). It is in excellent agreement with the great diversity and apparent nonstorage by herbivores of the Solanaceae chemicals and the initial dependence of the Ithomiinae stock on PAs (see below).

Thus, Apocynaceae-feeding Ithomiinae dependent on PAs probably did not adapt sufficiently to the great chemical variability in the Parsonsieae (seen today also), which in some cases repelled or poisoned larvae, in others left adults unprotected against predators and deficient in

TABLE 3. Summary of chemical fractionation of Ithomiine larval food plants (leaves).

Larval Food Plant[a]	Source[b]	Weight Fresh	Weight Dry[c]	% H$_2$O	Fractions (as % of dry wt.)[d] A	B (% N-Ox.)[e]	C	F	Fibre	Probable Compounds[f]	Fractions Tested[d]	Bio-assay Re-sults[g]
SOLANACEAE												
1. *Solanum* (Sect. *Geminata*) *caavurana*	C	64	14.4	78	8.3	1.3 (0)	7.0	0.7	82.7	ABL$_1$L$_2$RWYZ	Ex, 2	–
2. *S.* (Sect. *Geminata*) *pseudoquina* St. Hil.	C	46	14.1	65	5.0	4.2 (0)	18.9	6.7	65.2	ABL$_1$L$_2$RWY		NT
3. *S.* (Sect. *Geminata*) nr. *ripense* Dunal	V	14.5	2.4	84	2.8	2.2 (0)	9.4	1.7	83.9	ABLWYZ	Ex	–
4. *S.* (Sect. *Pseudocapsica*) *pseudocapsicum*	C	40	9.5	76	4.9	3.5 (0)	7.7	6.7	77.2	ABL$_2$RWY	Ex, 2	–
5. *S.* (Sect. *Lepidota*) *murinum*	C	72	20.5	72	3.0	0.67 (0)	10.9	5.1	80.3	ABL$_1$RTWY	Ex	–
6. *S.* (Sect. *Indubitaria*) *megalochiton*	C	131	38.2	71	3.4	0.5 (0)	7.2	6.2	82.7	ABL$_1$L$_2$RWYZ	Ex	–
7. *S.* (Sect. *Anthoresis*) nr. *schwackeanum*	J	50	12.1	76	5.9	1.3 (0)	2.0	3.1	87.7	ABL$_1$RWY		NT
8. *S.* (Sect. *Anthoresis*) *concinnum*	C	107	33.4	69	4.8	0.99 (0)	4.9	4.6	84.6	ABL$_1$L$_2$RWY	Ex	–
9. *S.* (Sect. *Brevantherum*) *mauritianum*	C	100	28.3	72	5.9	0.2 (25)	5.6	4.5	83.8	ABFL$_1$L$_2$RTWY	Ex	–
10. *S.* (Sect. *Brevantherum*) *asperum* Rich.	M	–	9.8	–	3.5	2.2 (0)	9.7	1.3	83.3	ABFL$_1$L$_2$RTWY		NT
11. *S.* (Sect. *Melongena*) *melongena*	C	34	8.4	75	4.0	0.37 (0)	10.8	5.9	78.9	ABL$_1$RWY	Ex	–*
12. *S.* (*Leptostemonum*) *robustum*	C	60	10.4	83	5.6	0.4 (0)	7.3	2.9	83.8	AL$_1$RWY	Ex, A, B, F	–
13. *S.* (*Leptostemonum*) *variabile*	C	44	12.0	73	4.5	1.3 (0)	8.1	2.8	83.3	ABL$_1$RWY	Ex, 2	–
14. *S.* (*Leptostemonum*) *brusquense*	C	30	6.6	78	11.2	0.33 (0)	3.8	6.2	78.2	ABL$_1$L$_2$RWY	Ex	–*
15. *S.* (Sect. *Acanthophora*) *atropurpureum*	C	39	7.4	81	4.8	0.46 (0)	11.8	6.1	76.8	ABL$_1$L$_2$RWY	Ex, A, B, C	–*
16. *S.* (Sect. *Jasminosolanum*) *flaccidum*	MP	93	16.8	82	5.8	0.35 (0)	11.8	4.0	78.0	ABC?L$_1$L$_2$RWY		NT
17. *S.* (Sect. *Aculeigerum*) *wendlandii*	C	18	2.2	88	1.5	0.28 (35)	5.3	9.2	83.7	BC?L$_1$L$_2$WY	Ex	–
18. *Lycianthes rantonnetii* Carr. ex Lesc.	C	30	5.2	83	5.3	0.98 (0)	17.8	6.8	69.1	BC?L$_1$L$_2$WY		NT
19. *L.* sp. (Goiânia)	G	18	6.3	65	1.1	0.13 (0)	3.7	1.2	93.8	BC?L$_1$L$_2$WY	A	–
20. *Cyphomandra sciadostylis*	SN	60	15.5	74	5.2	0.17 (15)	5.6	3.9	85.1	ABCL$_1$WYZ	Ex	–
21. *C. fragrans*	C	55	9.8	82	6.4	0.84 (0)	10.2	4.0	78.6	ABL$_1$WY		NT
22. *Lycopersicon esculentum*	C	42	5.5	87	7.0	1.8 (0)	6.4	4.2	80.6	BL$_1$L$_2$WYZ	Ex	–
23. *Capsicum ciliatum* (Kunth) O. Kuntze	V	183	42.5	77	2.9	0.4 (10)	17.7	1.6	77.4	BCL$_1$QRWY		NT
24. *C. villosum* (Sendtner) (?)	J	10	1.4	86	10.0	1.4 (0)	16.8	2.3	69.5	BL$_1$QWY		NT
25. *C. flexuosum*	J	28	6.9	71	7.6	2.5 (0)	11.7	0.3	78.0	BL$_1$QRWY	Ex	–
26. *C. lucidum* (Moricand) O. Kuntze	RJ	40	10.0	75	11.2	1.7 (11)	16.8	4.1	66.2	BL$_1$QRWY	Ex	–
27. *C. mirabile* Sendtner	SL	120	26.3	78	7.6	0.95 (0)	13.9	2.2	75.4	BL$_1$RWY		NT
28. *Physalis neesiana*	C	65	9.3	86	5.3	1.05 (0)	4.2	4.2	85.2	ABCQRSWY	Ex, A, B	–*
29. *P.* sp. nr. *neesiana*	C	20	2.6	87	8.8	2.8 (0)	11.4	2.9	74.1	ABCQRSWY	Ex	–*
30. *Vassobia breviflora*	C	90	12.8	86	8.7	0.84 (0)	7.1	4.4	78.9	BCQRWY	Ex, A	–*
31. *Acnistus arborescens*	C	227	32.6	86	5.0	0.64 (0)	9.6	5.6	79.1	BCQRWY	Ex, A, B, C	–*
32. *Datura stramonium*	C	66	7.8	88	6.9	1.4 (0)	7.4	4.2	80.1	BCQWYZ	Ex, B	–

TABLE 3. Continued.

		Weight		%	Fractions (as % of dry wt.)[d]							Bio-assay
Larval Food Plant[a]	Source[b]	Fresh	Dry[c]	H_2O	A	B (% N-Ox.)[e]	C	F	Fibre	Probable Compounds[f]	Fractions Tested[d]	Re-sults[g]
33. *Brugmansia suaveolens*	C	50	6.7	87	5.2	1.8 (0)	9.2	3.5	80.3	BCQWY	Ex	–
34. *Nicandra physaloides*	PC	115	13.4	88	7.8	0.63 (0)	5.9	3.5	82.2	BCQRWY	Ex, A, B, C	–*
35. *Solandra grandiflora*	C	30	5.2	83	4.2	0.73 (0)	7.5	7.0	80.5	BCWY	Ex	–
36. *Markea (Dyssochroma) viridiflora* (Sims.) Miers	RJ	41	6.6	84	1.4	0.24 (40)	3.9	3.9	90.6	BCWY	B	–
37. *Juanulloa mexicana* (Schldl.) Miers	LG	17	2.7	84	2.4	0.33 (50)	2.6	6.7	88.1	BCWY	Ex	–*
38. *Cestrum schlechtendalii*	C	40	6.8	83	4.3	0.38 (15)	8.9	5.4	81.0	BC?L_1RWYZ	Ex, A, B	–
39. *C. laevigatum*	C	50	11.1	78	6.5	1.3 (0)	6.8	6.3	79.1	BC?L_1RWYZ	Ex	–
40. *C.* nr. *amictum*	SL	42	7.3	83	4.4	0.18 (0)	10.7	4.0	80.7	BC?L_1RWY		NT
41. *Brunfelsia australis*	C	40	10.4	74	3.4	0.21 (0)	5.2	3.3	87.9	BC?EWXY	Ex	–
42. *B. pauciflora*	C	45	9.1	80	3.5	0.36 (0)	5.6	2.9	87.6	BC?EWXY	Ex	–
APOCYNACEAE: PARSONSIEAE												
43. *Prestonia coalita*	C	36	5.3	85	1.7	0.45 (0)	5.2	6.0	86.6	3B?O?, YZ	Ex, A, B	–*
44. *P. dusenii*	SN	14	3.3	62	4.9	0.24 (0)	0.96	1.8	92.0	3B?O?, YZ	Ex	–
45. *P. acutifolia*	MP	59	12.7	78	5.8	0.49 (43)	16.4	3.2	74.1	3B?EN, Y		NT
46. *Peltastes peltatus*	C	54	9.0	83	4.3	0.17 (0)	5.9	3.1	86.6	3B?O?, Y	Ex	–*
47. *Temnadenia violacea*	C	128	28.1	79	2.4	0.27 (0)	12.2	6.4	78.7	3B?, WY		NT
GESNERIACEAE												
48. *Nematanthus fritschii* Hoehne	SL	175	19.4	89	3.6	3.8 (20)	19.8	2.0	70.8	C?, WY		NT

[a] Leaves extracted with MeOH-H_2O 4:1 as in Figure 4. Authors' names not given are in Figure 5. Additional genera of food plants used by Ithomiinae not yet investigated are *Witheringia, Dunalia, Cuatresia* (Solanaceae) and *Drymonia, Columnea* (Gesneriaceae, both quite close to *Nematanthus*).

[b] Codes for source localities (also applying to Tables 5 and 6): C = Campinas, São Paulo and vicinity. G = Goiânia, Goiás. J = Serra do Japi, Jundiaí, São Paulo. LG = *ex* Larry Gilbert, Austin, Texas (from Costa Rica). M = Manaus, Amazonas, and region to north. MP = Martinho Prado, São Paulo. PC = Poços de Caldas, Minas Gerais (with help of Renata S.C. Dias). RJ = region of Rio de Janeiro, including eastwards along coast. SL = coastal São Paulo (Bertioga, São Vicente, Mongaguá). SN = Serra Negra, São Paulo. V = northern Venezuela (with help from S. S. Tillett, Francisco Romero, and Roberto and Renato Mattei).

[c] Dry weight calculated as the sum of the fractions and fiber. The water content varies with collecting and transporting conditions.

[d] See Figure 4 for letters of fractions. Ex = total extract, freed of methanol. Most fractionations were performed by Silvana Aparecida Henriques.

[e] No dehydropyrrolizidine alkaloids were detected in any Solanaceae and only one Apocynaceae investigated showed appreciable quantities. *Brunfelsia, Brugmansia,* and *Juanulloa* may contain similar compounds acting as precursors or analogs. Presence of N-oxides may indicate tropanes or nicotine analogs.

[f] Based on literature references, plus preliminary investigation in this work. Much variation was often seen in the secondary compounds encountered in a plant species; detailed isolation and identification of principal chemical constituents is underway. The letters indicate structure types (not necessarily individual compounds) in Figures 1 and 2, unless otherwise indicated (Fig. 3 in Apocynaceae).

[g] + indicates positive (*Biblis* cut out), – negative, –* positive at high concentrations, becoming negative upon dilution. NT indicates not yet tested in the *Nephila* bioassay. A positive test at normal concentrations (at least 300 μg on the *Biblis*) sometimes became negative with less than 100 μg; this is indicated by the symbol +*.

PA-derived sex attractants and other pheromones (Fig. 3D). Adults increasingly exploited PA sources (Boraginaceae leaves, Compositae flowers) and may even have found some substitutes for PA precursors in Solanaceae (*Brunfelsia*?). Since they were preadapted to bicyclic 8-carbon monoester alkaloids and their N-oxides (both PAs and tropanes fall under this classification), the generally well-protected, tropane-rich Solanaceae represented an open niche. At least two separate radiations could have moved onto these plants (discussion of the move over onto the Gesneriaceae must await further biological and chemical study of *Hyposcada* and its food plants; the move onto *Brunfelsia,* whose alkaloids are still enigmatical, was probably a sidetrack of one of the radiations). The line that colonized the tropane-containing *Brugmansia* (represented by *Placidula* and *Miraleria* today) also encountered in these plants the steroidal bitter principles, to which they were also preadapted through their experience with cardenolides in the Apocynaceae. Tolerance of these bitter steroids permitted further colonization of the many genera defended by them, most of which also contain tropane alkaloids, sometimes with N-oxides. Utilization of *Capsicum* by this line also gave a gateway, through its steroidal glycoalkaloids and saponins (Table 2), to the immense and underutilized resource represented by *Lycianthes* and *Solanum,* on which the more advanced genera persist today.

The second radiation found tropanes initially in *Solandra* and relatives, and thence in *Cyphomandra,* on which it adapted to tolerate the steroidal glycoalkaloids also present there and initiated tolerance of pungent oils. This permitted a similar colonization of *Lycianthes* and *Solanum* (*Sais, Scada*). As a final step, adaptation to saponins and strong-smelling oils present in some *Solanum* (especially section *Geminata* and relatives) permitted exploitation of the abundant *Cestrum* in the forest understory. In all cases, tolerance of toxins encountered previously in the evolutionary history of each line could be maintained as new enzymes were developed to detoxify progressively more effective classes of plant defensive chemicals, in many cases not correlated strictly with taxonomy and evolution of the plants. Indeed, some of the more primitive genera—possibly with a broader range of biosynthetic capabilities, according to present concepts of biochemical evolution in plants—seem to have been the last to be colonized by the most advanced Ithomiinae.

Persuasive evidence for this hypothetical scenario (Table 4) can come only from extensive studies of female oviposition preferences and larval tolerance of food plants or chemical compounds. Preliminary data (Table 2) and some initial experiments are encouraging: *Placidula* cannot eat *Solanum,* nor does *Aeria* accept any Solanaceae, but *Mechanitis* can use tropane- and withanolide-containing plants (*Datura, Nicandra*), and some *Cestrum*-feeders continue to use *Solanum* and even *Lycianthes.* Experiments in this area inevitably will encounter problems related to individual and local adaptation, lateral radiation (as onto *Brunfelsia*), and loss of ancestral genes but should in the long run help to define the viability of this proposed sequential expansion of Ithomiinae through progressive chemical tolerance to Solanaceae food plants.

HERBIVORES AS PHYTOCHEMISTS

The chemosensory apparatus of the average insect is capable of detecting very small amounts of specific chemicals, either through smell (antennae) or taste (tarsal or buccal chemóreceptors). This highly specialized analytical instrument transforms chemical structures into recognizable electrical potentials through mechanical contact between compound and receptor and uses these potentials to stimulate a variety of response behavior sequences. It can be fooled at the receptor end by substances of different chemical composition but similar conformation and spatial relations among active binding sites. It is far more sensitive and accurate, however, than the majority of the instruments in the modern phytochemist's laboratory. Its specialization is selected over many generations of advantages accrued by those who could recognize a few chemical compounds and thereby compete better for higher quality food, defense, or mates.

To the extent that ovipositing female Ithomiinae seem to demonstrate an appreciable specificity in host plant recognition (Table 2), which involves use of chemoreceptors on the forelegs ("drumming" on leaves) and antennae, they can serve as precise analytical tools for the phytochemist. If some chemical patterns are already evident on a very rough scale in the food plant choices of the Ithomiinae (Table 2), these could be used to suggest analytical methods for still-uninvestigated Solanaceae and predict chemicals in others that have undergone only preliminary analysis.

TABLE 4. Possible scheme for sequential colonization of Solanaceae by Ithomiinae through progressive preadaptive tolerance of secondary chemical classes.

Step	Ithomiines (genera)	Plants Colonized	Substances Tolerated
1	*Tellervo, Elzunia, Tithorea, Aeria*	Apocynaceae: Parsonsieae (*Parsonsia, Prestonia,* etc.)	3E–K: PAs and N-oxides 3A–B: Cardenolides
2a	*Athesis, Placidula, Miraleria*	Solanaceae: *Brugmansia, Capsicum ciliatum*	1C: Tropane alkaloids and N-oxides
2b	*Olyras, Melinaea, Hyposcada*	*Juanulloa, Markea, Solandra*	2Q: Bitter steroids PA precursors?
2c	*Methona*	*Brunfelsia*	
3a	*Epityches, Ithomia*	*Acnistus, Physalis,* etc. further *Capsicum*	1C + much 2Q (varieties) Some 1L: steroid alkaloids
3b	*Thyridia*; New genus	*Cyphomandra*	1C, 1L, 2R: saponins
4a	*Napeogenes, Rhodussa, Oleria*	*Lycianthes*; *Solanum* subgen. *Bassovia, Potatoe* (sect. *Jasminosolanum*)	1L: glycoalkaloids
4b	*Scada, Sais, Forbestra*; *Callithomia*		2R; 1A; possible 1C
5a	*Garsauritis, Hypothyris, Hyalyris*	*Solanum* (subgenera *Leptostemonum* and *Brevantherum*)	1L, 2R, 1A; occasional nicotine, pungent oils
5b	*Mechanitis*; *Dircenna, Pteronymia*		
6b	*Ceratinia, Pteronymia, Godyris, Hypoleria, Pseudoscada, Greta*	*Solanum* (sect. *Geminata*), *Cestrum*	IL, 2R; 2Z: pungent oils

For example, it could be predicted that the *Solandra-Markea-Juanulloa* group of genera, which support the danaioid larvae of *Melinaea* (Fig. 8K, V), might have some protective chemicals similar to those of Apocynaceae-Parsonsieae; and these chemicals should be more storable by larval insects than the usual run of Solanaceae chemical compounds. These have yet to be identified (cardenolides are strongly suspected) and should be investigated. Similarly, the strong-smelling essential oil of *Solanum* sect. *Geminata* should be chemically very similar to the like-smelling oil of *Cestrum*; this also seems to have escaped chemical identification. *Witheringia* could have been predicted to show physalins by *Ithomia,* which also recognized these chemical components with withanolide-structures in *Physalis* and divided its specificity among *Acnistus* and these genera. Since both *Ithomia* and *Epityches* use wild *Capsicum* species, these should surely contain a withanolide-like compound; at least one major substance, possibly with this type of structure, is present in the neutral fraction (A) of two *Capsicum* species investigated (Table 3).

Do the genera *Deprea* and *Athenaea* contain withanolides also? Start by testing some cooperative females of *Ithomia* and *Epityches.* Are any other Solanaceae besides *Datura*/*Brugmansia* especially rich in scopolamine? One could begin with some *Placidula* females or perhaps even larvae. If the latter were found on a *Solanum* or *Cestrum,* I would bet on the presence of tropanes in the leaves. Are there glyco-alkaloids in *Dunalia*? I might start by asking *Hypothyris,* known only from *Solanum,* or perhaps even *Pteronymia,* which specializes on the high-alkaloid (Bradley et al., 1979; Table 3) *Geminata* section of *Solanum.* This analysis could be extended even to individual constituents once appropriately specialized populations of Ithomiinae have been identified. It may also give some false results, but these will hold even more interest than the expected ones, pointing out new types of plant components. As a preliminary survey, it should be strongly suggestive of certain types of chemicals.

CHEMICAL CONTRIBUTIONS OF THE SOLANACEAE TO PREDATOR DEFENSE IN THE ITHOMIINAE

ITHOMIINE CHEMISTRY

Chemical investigation of the passage of Solanaceae toxins to adult Ithomiinae started with

TABLE 5. Summary of PA content and distribution, and bioassay of adult Ithomiinae and Danainae.

		No. of spp.					
Tribe	Genus	In Genus	Analyzed	Typical Species[a]	Source[b]	Host Plants[c]	Number Analyzed
ITHOMIINAE[g]							
B	*Tithorea*[h]	2	1	*harmonia*[ij]	VB	45	21/16
C	*Aeria*[h]	3	3	*olena*[j]	C	43, 44	31/20
				elara	G	*43*	10/15
E	Methona[h]	7	5	*themisto*[ikj]	C	41, 42	36/27
F	*Placidula*[h]	1	1	*euryanassa*[k]	C, J, SL	33	24/17
G	*Olyras*[h]	2	1	*crathis*[k]	V	*37*	4/2
	Melinaea[h]	10	7	*mneme*	RO	*36*	5/4
				ludovica[k]	M	*36*	50/1
				menophilus	RO	*37*	15/15
H	*Thyridia*	1	1	*psidii*[i]	C	20, 21	10/10
	Sais	2	1	*rosalia*[i]	G	19	12/12
	Scada	6	2	*reckia*[k]	RO	*16*	35/13
				karschina	ES	*16*	15/4
	Mechanitis	5	5	*polymnia*[ikj]	C	6–13	44/37
					M	*14*	12/12
				lysimnia[ikj]	C	13–15	28/14
I	*Hyposcada*	8	4	*egra*[k]	M	*36*	11/1
	Oleria	30	13	*astrea*	BJ	*12*	4/12
					RO	*12*	13/7
J	*Epityches*	1	1	*eupompe*[k]	C	25–31	30/33
	Rhodussa	1	1	*cantobrica*	RO	*18*	17/9
	Napeogenes	18	8	*cyrianassa*	ES	*18*	10/8
				inachia	RO	*18*	10/11
	Garsauritis	1	1	*xanthostola*	M	*13–14*	48/20
	Hypothyris	16	13	*ninonia daeta*[k]	C	5–14	51/40
				euclea[hikj]	C	9	22/22
				(males attracted)	M	10	16/12
					V	*10*	17/14
K	*Ithomia*	21	7	*agnosia*[ik]	C	30, 31	29/38
L	*Callithomia*[h]	3	2	*lenea xantho*[k]	MP	16	18/21
	Dircenna	7	4	*dero*[k]	C	6–13	29/18
M	*Ceratinia*	5	4	*neso*[h]	BJ, RO	*13*	24/24
	Ceratiscada	3	2	*doto*	BJ	1?	6/7
	Prittwitzia	1	1	*hymenaea*[k]	C	1	10/12
	Episcada	15	5	*clausina*	ES	1	17/14
				carcinia	C	1?	25/29
	Hyalenna	5	1	*pascua*[k]	J	7	1/9
	Pteronymia[h]	41	10	*carlia*[k]	C	1	31/17
N	*Godyris*	10	3	*zavaleta*[k]	RO	*38*	10/9
	Pseudoscada	6	4	*erruca*[k]	C	39	31/28
	Greta	10	1	*andromica*[h]	V	*38*	4/4
	Mcclungia	1	1	*salonina*[k]	C	39	11/11
	Hypoleria	11	10	*arzalia*	G, VB	*39*	8/4
	Heterosais	3	3	*nephele*	VB, RO	*40*	16/11
				giulia	V	*40*	7/4
DANAINAE							
	Danaus (*Anosia*)[h]	2	2	*gilippus*[i]	C	*Oxypetalum*	25/16
	Danaus (*Danaus*)[h]	1 (S.A.)	1	*plexippus*	C	*Asclepias*	22/14
	Ituna[h]	1	1	*ilione*[i]	C	*Ficus*	6/5
	Lycorea[h]	2	2	*cleobaea*	C	*Ficus*	12/11

TABLE 5. Continued.

	Individual PA Analysis (♂/♀)[d]		Other Fractions[e]				
Average Dry wt. (mg)	Average PA conc. (% N-Ox.)	Maximum (% av. dry wt.)	(% average dry wt., ♂/♀)			Fract. Tested	Bioas. Re-sults[f]
			A (neut.)	C (polar)	F (fat)		
60/75	0.3/0.3 (48/45)	0.9/0.6	8.4	8.4	13.9	Ex	+
9/13	2.5/1.6 (55/55)	7.1/4.0	3.9/5.2	14.7/15.8	13.9/16.3	Ex	+
9/13	1.3/1.1 (61/57)	1.9/1.9					NT
100/120	0.06/0.1 (41/48)	1.6/0.9	3.2/1.9	7.2/7.0	10.8/26.6	Ex	+
54/65	0.2/0.2 (48/48)	1.6/0.9				Ex	+*
110/110	1.2/0.3 (54/49)	1.8/0.5					NT
55/60	6.3/1.2 (54/49)	10.5/1.5					NT
55/60	0.6/1.3 (57/59)	2.5/—	5.9/3.7	7.2/9.6	15.7/13.9	Ex	+
55/60	3.6/1.3 (50/49)	6.5/4.4					NT
64/70	2.7/2.2 (70/68)	5.1/3.9	3.5/4.3	9.3/7.1	12.3/20.7	Ex	+
25/27	3.6/1.6 (59/58)	6.8/3.6	7.0/7.2	12.7/7.4	20.7/21.6	Ex	+
6/7	9.7/3.2 (47/54)	20.6/5.3					NT
8/9	13.1/6.7 (61/65)	20.0/10.4					NT
33/45	1.8/2.4 (60/60)	5.8/4.0	8.9/5.8	6.4/6.7	14.1/23.8	Ex, B, C	+
		September:	5.6/6.1	5.4/3.0	9.7/18.9	A, F	−
35/45	4.4/2.9 (58/57)	7.6/4.7	6.2	8.3	10.7		NT
25/35	3.8/1.8 (50/55)	8.8/6.4				Ex	+
20/22	0.7/0.2 (51/48)	3.8/—					NT
13/15	2.0/1.9 (53/58)	4.5/4.0					NT
13/15	4.0/1.8 (50/43)	8.2/3.4					NT
24/26	6.9/3.2 (56/58)	11.4/4.3	2.3	11.4	11.9	Ex	+
18/20	3.1/3.3 (48/52)	8.6/6.1					NT
18/20	7.7/3.5 (55/56)	12.9/5.9					NT
13/14	5.4/3.6 (56/54)	11.7/6.2					NT
20/23	0.9/1.0 (53/53)	4.9/3.2					NT
25/27	3.3/2.8 (51/57)	9.2/6.5	3.5	6.3	21.8	Ex	+
22/25	2.2/1.5 (48/44)	9.3/5.4	4.2	10.3	12.2	Ex	+
20/23	0.8/1.5 (55/46)	2.9/4.5	5.3	10.8	10.4		NT
20/22	5.1/2.8 (58/60)	9.0/5.7					NT
14/16	5.4/2.0 (56/58)	12.9/7.1	1.9	10.6	23.2	Ex	+
24/28	0.5/0.4 (52/53)	2.6/1.5					NT
40/45	1.7/0.9 (65/69)	4.3/2.4	4.0	9.9	12.3	Ex	+
15/17	2.0/1.0 (55/56)	5.7/3.3				Ex	+
14/15	1.1/0.5 (52/48)	1.9/1.2					NT
14/16	2.8/1.7 (57/60)	5.8/3.5	4.6	7.4	19.5	Ex, B, C	+
16/17	5.7/5.3 (53/58)	10.0/7.0				A, F	NT
17/18	1.6/2.0 (51/58)	6.0/5.2				Ex	+
18/20	1.1/2.0 (47/52)	—/3.4					NT
14/17	7.8/3.6 (58/62)	13.3/5.8				Ex	+
33/33	1.5/1.4 (43/51)	2.9/3.1					NT
15/17	4.9/2.7 (57/54)	9.7/5.8	4.9	14.0	9.6	Ex	+
15/17	7.2/5.0 (56/52)	10.6/6.0					NT
16/17	1.7/1.1 (70/82)	3.3/2.2	5.2	7.5	15.5	Ex	+
14/15	1.1/0.5 (56/59)	2.3/0.9					NT
21/26	1.6/0.6 (55/53)	4.4/1.0					NT
20/24	2.7/0.8 (53/43)	5.3/1.7	4.8/—	9.6/—	8.2/—	Ex	+
80/75	2.1/1.8 (57/52)	4.5/4.5					NT
180/170	0.1/0.1 (50/51)	0.4/0.2					NT
160/140	1.1/1.2 (54/53)	2.5/2.1					NT
130/110	2.7/1.2 (58/55)	4.8/3.2					NT

TABLE 5. Continued.

ANALYSIS OF PARTS:[m]	WINGS				
Species & Sex	Basal	Hairpencil	Apical	Appendages (Legs, Anten.)	Rest of Head
Mechanitis polymnia casabranca (males)	1.13/88	**4.15**/64	0.14/100	0.26/77	0.60/70
	1.70/100	1.10/100	1.03/65	0.52/92	1.03/72
	1.03/58	**1.70**/58	0.83/51	0.98/97	1.43/75
	2.60/85	**4.40**/100	2.10/48	4.20/77	3.40/75
Ithomia agnosia agnosia (females)	4.50/81	—	1.38/78	7.50/68	**12.5**/69
	0.69/42	—	0.63/45	**1.60**/55	**2.00**/68
	0.70/67	—	0.75/48	0.72/100	**1.05**/44
Danaus gilippus (male)	3.10/63	“pockets” 1.00/55	0.73/49	2.00/57	1.75/55
(female)	1.45/50	—	0.47/42	1.20/46	1.50/51

	Displaying Male	
	Rest of Insect	Spermatophore
Mechanitis lysimnia	3.09/61	8.50/54
	3.32/59	8.85/55
	3.06/52	9.75/49
	0.78/54	2.40/64
	4.20/52	**25.3**/55
	6.40/56	**17.4**/54
Mechanitis polymnia	2.23/52	**8.60**/62
	0.26/46	1.05/54
	0.92/62	3.92/55
Aeria olena	3.00/50	**12.3**/67
	3.60/69	**10.0**/72

[a] Authors’ and subspecies names are in Figure 5 or Brown (1985).

[b] See Table 3, footnote b. Additional localities: BJ = Bujaru, Pará. ES = various parts of Espírito Santo. RO = various parts of Rondônia. VB = Vila Bela, western Mato Grosso.

[c] Numbers refer to the plants listed in Table 3. Italicized numbers indicate probable food plants or species near to that number.

[d] Just-captured butterflies were cut up under 2 ml absolute methanol (3 ml for heavier species) and after at least one day’s standing aliquots (usually 1/20, or 1/4 for component parts) were assayed directly for total PA and N-oxide, following Mattocks (1967, 1968) and Bingley (1968); see text for details.

[e] See fractionation scheme in Figure 4 for letters.

[f] See footnote g of Table 3 for bioassay codes.

[g] No secondary compounds from larval food plants have been found stored in adult Ithomiinae. Additional genera examined (few specimens) were (Tribe letter, genus and species, host plant): A *Tellervo zoilus, 45*; B *Elzunia humboldt, 45*; D *Athesis clearista,* 23 and *Patricia dercyllidas, 30?*; G *Eutresis hypereia, 37* and *Athyrtis mechanitis, 37?*; H *Forbestra equicola, 16* and *F. truncata, 16*; I (New genus) *canilla, 18*; J *Hyalyris coeno, 13* and *Hyalyris oulita metella, 13*; K *Miraleria cymothoe,* 31 + 33; L *Velamysta pupilla, 17*; N *Dygoris dircenna, 39* and *Hypomenitis dercetis, 39* and *H. libethris, 39.*

Rothschild (1973), who obtained only negative results. In August 1978, 3,200 dry bodies of *Mechanitis polymnia* (75 g, representing over 300 g fresh weight of insects) were mailed to Dr. Desiré Daloze of the Collectif de Chimie Bio-Organique in Brussels, where ant bioassays were used to follow repellent activity in the fractionation. No alkaloids, cardiac glycosides, or other interesting active compounds, or even their degradation products, could be found (D. Daloze, pers. comm., 1980). This along with the previous results suggested that the protective compounds of adult Ithomiinae might be labile, degraded after death or upon storage, and possibly unrelated to the larval food plant poisons.

Total MeOH-H_2O extracts of fresh ithomiines

TABLE 5. Continued.

THORAX		ABDOMEN				
Exoskeleton	Muscles	Exoskeleton	Fat	Reprod. Organs	Intestine	
0.29/75	0.21/100	0.21/92	0.49/65	0.12/91	0.02/100	NR
1.18/42	0.92/48	1.82/91	0.81/66	**2.54**/99	0.63/89	
1.02/66	0.63/65	0.50/100	0.19/69	0.60/100	0.14/56	
4.10/67	4.40/68	**6.60**/72	3.20/100	4.10/92	4.00/97	
						Eggs
1.06/79	3.56/50	4.45/65	1.76/65	**52.0**/45	0.13/91	**8.85**/78
0.35/45	0.47/20	0.47/38	0.42/54	**1.67**/40	0.28/14	1.00/30
0.62/48	0.40/33	**0.87**/100	0.26/18	0.34/100	0.15/60	NR
1.90/57	1.20/50	2.20/56	0.73/65	**4.20**/58	Hairpencil	3.50/55
1.60/52	1.10/48	1.40/62	**3.30**/59	0.90/62	Eggs	0.90/12

Pairs captured in copula

Male: Rest of Insect	Spermatophore	Female: Rest of Insect	Abdomen Ducts
2.12/52	**12.8**/65	6.26/52	3.50/59
2.23/64	**11.9**/54	0.40/74	0.35/57
3.71/54	**12.7**/66	2.26/62	0.83/100
0.44/56	**1.31**/78	3.00/62	3.30/60
1.29/50	**22.5**/60	3.30/51	3.51/65
0.25/54	4.70/48	3.58/63	5.10/62
0.87/52	9.10/61	2.52/48	3.26/58
0.38/48	**14.6**/72	2.06/72	7.20/88
2.96/59	**12.6**/72	5.06/61	**13.6**/63
2.26/51	2.32/57	3.90/58	**40.5**/64
8.90/62	**18.7**/77	4.10/54	5.40/59

[h] Larvae of these species may be considered as aposematic in color-pattern and behavior.

[i] Eggs of these subspecies contained up to 9% of dry weight as PAs.

[j] Larvae of these species feeding on the indicated plants did not contain any PAs nor did their extracts protect *Biblis* against predation by *Nephila*; possible exceptions are *Methona themisto, Aeria olena* and *Tithorea harmonia.*

[k] Recently emerged adults of both sexes of these species reared from larvae on the indicated food plants, were consumed without hesitation by *Nephila,* which in most cases had just cut out an adult of the same species and sex captured in the field. Notice that almost all Solanaceae genera and chemicals are included in the food plants.

[m] Data are given as percent of dry weight of part/% of PA as N-oxide. When the N-oxide value is high, it usually indicates appreciable PA present as dihydropyrrolizines (types 3MNO), usually confirmed. Especially noteworthy values are printed in boldface type.

(prepared as in Fig. 4), when applied to the edible *Biblis hyperia,* were at least as repellent to *Nephila* spiders as were the live butterflies. The repellency was then located in the alkaloid fraction B (Fig. 4) and also in the polar fraction C. When these fractions were compared with the corresponding fractions of the larval food plants, there appeared to be no compounds in common. Furthermore, all food plant extracts and fractions tested in the spider bioassay were negative (Table 3). To put the final nail in the coffin, both sexes of 30 species in 26 genera of Solanaceae-feeding Ithomiinae, reared from the larvae in the laboratory on fresh leaves of natural food plant, upon emergence from the pupa and introduction into *Nephila* webs were promptly and enthusiastically eaten (Table 5). In most cases, the *Nephila* had just as efficiently rejected a field-captured adult ithomiine of the same species and sex.

In all, 142 species of Ithomiinae in 45 genera and all 14 tribes were examined in parallel with 48 host plants in 16 genera of Solanaceae, three genera of Apocynaceae, and one of Gesneriaceae (see Tables 2, 3, 5), both in chemical analysis

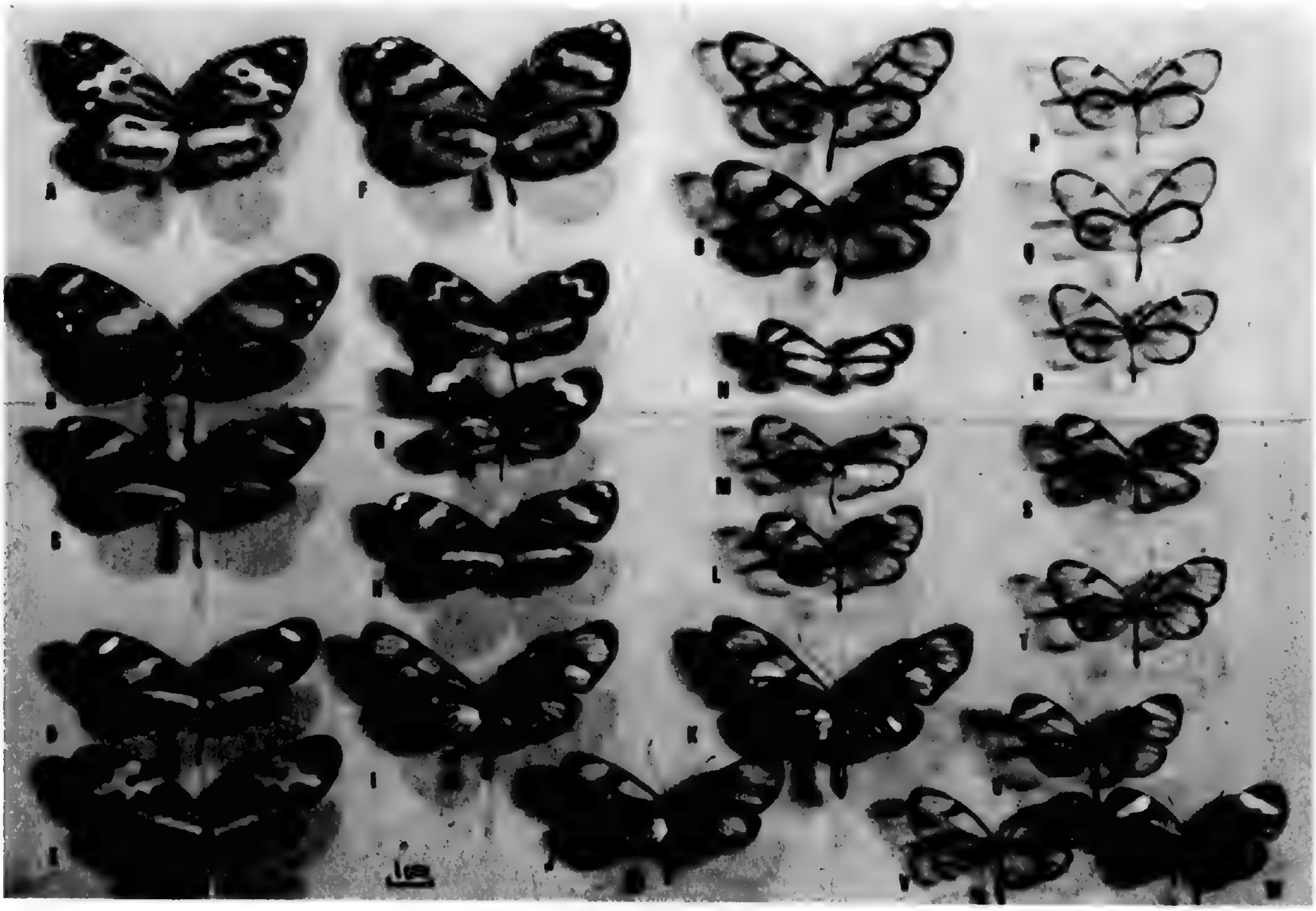

Figure 9. Ithomiinae found in the Campinas region, interior of São Paulo state, SE Brazil. Missing are **Episcada philoclea* (Hewitson) and *†Pseudoscada quadrifasciata,* very similar to U. * indicates rare visitors from the coastal mountains or plain, † rare visitors from the tropical Paraná valley to the west. Names follow in order of natural abundance in dry season assemblages.—E. *Mechanitis polymnia casabranca* (about 50% of all Ithomiinae, can increase to 75% in some seasons).—D. *Mechanitis lysimnia* (17%).—S. *Mcclungia salonina* (13%).—H. *Hypothyris ninonia daeta* (8%).—L. *Ithomia agnosia* (5.5%).—N. *Aeria olena* (2.5%).—P. *Prittwitzia hymenaea* (1.1%).—O. *Dircenna dero* (upper *D. celtina,* lower *D. rhoeo*) (0.8%).—G. *Hypothyris euclea* (*laphria* × *nina,* mixed population) (0.4% but can be common in some years).—A. *Tithorea harmonia pseudethra* (0.4%).—J. *Epityches eupompe* (sometimes common in September).—T. *Pseudoscada erruca* (common in some pockets, not in others).—U. *Hypoleria plisthenes.*—I. *Thyridia psidii cetoides.*—Q. *Episcada carcinia.*—K. *Methona themisto* (common on tree-lined city streets and in gardens).—R. *Pteronymia carlia.*—W. *†Hypoleria goiana.*—M. **Ithomia drymo* (sometimes moves through in numbers in September).—F. **Placidula euryanassa.*—V. **Hypoleria adasa.*—B. **Melinaea ludovica paraiya.*—C. **Melinaea ethra.* The ranking is based on over 20,000 captures, mostly for marking and recapture population studies. For systematic order of genera and species (primitive to advanced), see Tables 2 and 5; for authors' names, see Figure 5.

and bioassay. In terms of the hypothesis of sequestration of defensive chemicals by ithomiine larvae, these results were thoroughly disappointing; no important compounds were detected that were shared by butterflies and their larval food plants. All butterfly extracts were positive and all plant total extracts and fractions were negative in the *Nephila* tests. However, all butterflies showed a strong Mayer's test on the acidified total aqueous extract, suggesting the presence of some kind of alkaloids.

Since adult ithomiines, like danaines, are known to be strongly attracted to sources of dehydropyrrolizidine alkaloids (Pliske, 1975a, 1975b) and use these at least for pheromone synthesis (Edgar et al., 1976), the extracts were examined for these compounds, using on TLC plates the iodine/Ehrlich test (dehydrogenation followed by *p*-dimethylaminobenzaldehyde in conc. HCl/acetone). All butterfly species showed the presence of similar moderately polar PAs as the major components of the alkaloid fraction B; in all cases, this fraction was greatly augmented and often became over 90% of a single compound after the zinc-reduction loop in Figure 4, indicating that much of the PAs were present as a single alkaloid and N-oxide in the butterflies, the latter probably responsible for the activity seen in fraction C. Pure pyrrolizidine alkaloid fractions accounted for essentially all the activity

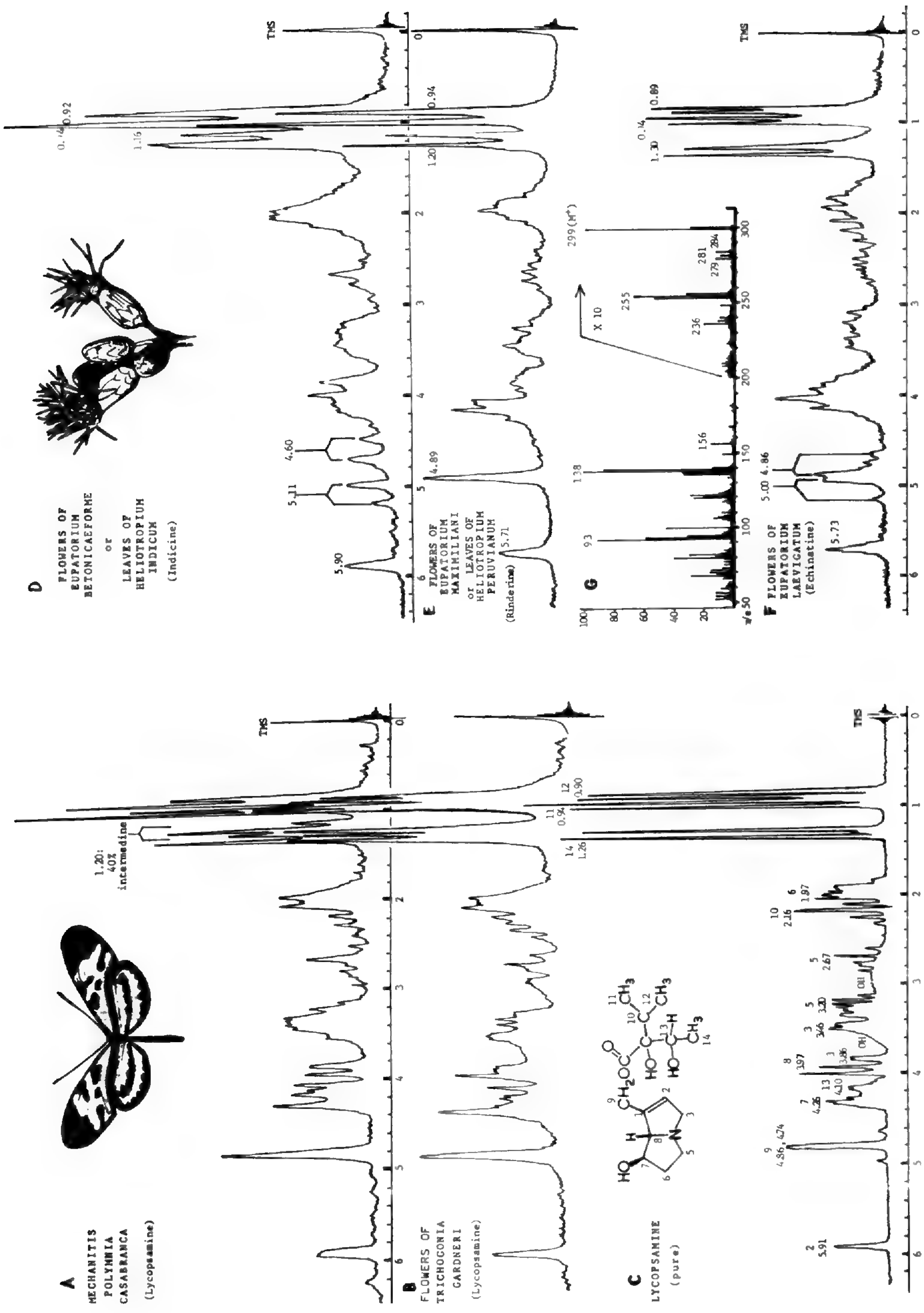

FIGURE 10. NMR spectra at 60 MHz in $CDCl_3$.—A. Crude total alkaloid from *Mechanitis polymnia* (lycopsamine/intermedine 6 : 4).—B. Crude total alkaloid from *Trichogonia gardneri* flowers, Amarais (same).—C. Pure lycopsamine (100 MHz, spectrum sent by J. A. Edgar).—D. Crude total alkaloid from *Eupatorium betonicaeforme* flowers (Bertioga) or *Heliotropium indicum* leaves (indicine).—E. Crude total alkaloid from *Eupatorium maximiliani* flowers or *Heliotropium peruvianum* leaves (rinderine, very easily crystallized).—F. Purified total alkaloid from *Eupatorium laevigatum* buds or flowers (isolated by J. R. Trigo).—G. Mass spectrum of echinatine (F) at 90 eV similar to that of all other isomers.

Figure 11. Feeding of Ithomiinae at PA sources.—A. *Mechanitis polymnia casabranca* on *Trichogonia gardneri* flowers, Amarais, Campinas, SP.—B. *Mechanitis lysimnia elisa* (Guérin) on *Eupatorium macrophyllum* flowers, Colorado, Rondônia.

seen in the *Nephila* bioassay, protecting the adults against predation by this spider.

The most common species in the Ithomiinae communities in the Campinas area, *Mechanitis polymnia casabranca* (Brown & Vasconcellos-Neto, 1976; Vasconcellos-Neto, 1980, 1986; Fig. 9), was chosen initially for detailed chemical investigation, using the fractionation scheme shown in Figure 4. The ethyl acetate extract (F) from 455 butterflies captured in Amarais in August 1982 (19.1 g dry weight, 13 of this as insoluble tegument) weighed nearly 5 g and readily solidified at 8°C to an off-white crystalline mass, indicating nearly pure saturated triglyceride; its exact composition is presently under investigation, but it was negative in the *Nephila* bioassay—probably quite nutritive, in fact. This extensive storage of high-energy fat (26% of dry weight at the height of the winter dry season) reflects the long (up to six months) reproductive diapause of these species (May–October; Vasconcellos-Neto, 1980) and also helps to explain the advantages of the learned predation behavior of the tanager (Brown & Vasconcellos-Neto, 1976), which squeezes this fat out of the abdomen of the butterflies. It is interesting that the fat reserves fell to only half of August levels in butterflies extracted in late September; the butterflies are long-lived and have few exogenous resources in September. Tanager predation usually ceases in September, probably from a combination of a lower reward (here confirmed) and more difficulty in capture as the days become warmer (Brown & Vasconcellos-Neto, 1976).

The total alkaloid extract B, isolated after the zinc reduction loop (which increased its weight from 60 to 260 mg equivalent yield from 19 g butterflies = 1.4% of dry weight) showed on TLC a single major spot (90%) that gave a positive I_2/Ehrlich test for PAs. The 60-MHz NMR spectrum of this noncrystallizable fraction (Fig. 10) showed it to be almost exclusively a 60 : 40 mixture of lycopsamine and intermedine (Fig. 3E, F) compared with a spectrum of pure reference lycopsamine contributed by J. A. Edgar (Fig. 10C). Very minor impurities due to other dehydropyrrolizidines could be seen in the NMR spectrum. The alkaloid fraction co-chromatographed with authentic lycopsamine (donated by J. A. Edgar) on TLC in four different systems, giving indications of latent separation of the isomers in some solvent mixtures.

The NMR spectrum of the total alkaloid fraction showed no signs of the "methylene envelope" or quaternary methyl signals typical of steroid alkaloids of *Solanum,* nor of the anomeric protons of glycosides, nor of the N-methyl groups of solanines, nicotine, and tropane alkaloids (Figs. 1, 10). This supports nonsequestration of alkaloids from the larval food plant. The spectrum also indicated that most of the butterflies obtained their alkaloid from a single source; the structure and the mixture strongly support flowers of *Trichogonia gardneri,* common in Amarais and intensively visited by *M. polymnia* (Fig. 11A; Table 6).

When the zinc reduction was not performed, the much diminished alkaloid fraction showed two spots, one corresponding to the lycopsamine/intermedine mixture and the other more mobile (probably the isomers echinatine/rinderine, Fig. 3G, H). The NMR spectrum of the whole fraction was rather complex, indicating several additional components of diverse structures including saturated PAs, but still showed no signs of the presence of other classes of alkaloids.

In expansion of the work on *M. polymnia* preliminary fractionation gave PAs representing various mixtures of the five isomers of a single structure (Figs. 3, 10) in up to 13%, and in *Scada* over 20% of dry weight in some individuals, in all 141 additional Ithomiinae species indicated in Table 5, many captured in the Campinas region but also sought in more distant places for comparison and to verify the generality of the phenomenon. No PAs were seen in the Zn-reduced extracts of any of the food plants tested (summarized in Table 3).

ITHOMIINE DEFENSE

That the protection of adult Ithomiinae against predation by *Nephila* is due to PAs was confirmed by feeding 200–400 μg of echinatine N-oxide (Fig. 3J) in dilute honey solution to newly emerged adults of *Mechanitis lysimnia* and *Pseudoscada erruca* (which normally were eaten by *Nephila*); within an hour, the butterflies were routinely rejected by the spiders (experiments performed together with J. R. Trigo). Reared butterflies kept alive for many days did not biosynthesize any protective chemicals; protection was lost within a day after death of a butterfly rejected by the spider, again indicating the instability of the PAs. Very fresh field-captured Ithomiinae often showed no PA and could be consumed by *Nephila*, but in general the adults seemed to be able to accumulate sufficient defensive compound from different sources in their environment within a very short period after emergence from the pupa.

The strong dependence of adult ithomiines on PA sources, including for their courtship pheromones, perhaps made it inevitable that they should also retain the PAs for their defense. The lack of storage of Solanaceae defensive compounds, already verified in early investigations, increased the probability of alternate defensive compounds in the Ithomiinae—labile compounds not detectable in dead insects. The universal rapid cutting out of Ithomiinae from *Nephila* webs suggested that such alternate defense substances did not derive from the widely variable larval foods but from a more homogeneous adult food source. In the only other reported case of a lepidopteran being cut out from spiders' webs—*Utetheisa ornatrix*, an aposematic day-flying arctiid whose larvae feed on *Crotalaria* and pass sequestered PA diesters on to the adults, where they are also used in pheromone synthesis—it has been shown that PAs are responsible for this deterrent activity (Conner et al., 1981; Eisner, 1982).

The Solanaceae poisons have thus been absolved, at least for the time being, from participation in the unpalatability of adult Ithomiinae to their most dangerous predators. It seems possible that exceptions will be found to this, especially as more predators are incorporated into the bioassays and more butterflies and food plants into the chemical analysis. However, the PAs and especially the biologically active (hepatotoxic, tumor-inhibiting) lycopsamine-group monoesters and their N-oxides should be regarded as the principal, perhaps nearly universal chemical protection for adult Ithomiinae.

PAs are also widespread in Danainae and Arctiidae moths (Ctenuchinae, Pericopinae, and Arctiinae), whose adults sometimes inherit them from the larvae but inevitably seek them out at the same sources visited avidly by the Ithomiinae, and similarly use them for defense and pheromone synthesis. Indeed, lycopsamine and its stereoisomers have been found in wild populations of essentially every species of Danainae and Ithomiinae investigated (Edgar, 1982; Table 5), though their presence is erratic in the moths. These compounds seem to represent a very effective "ancestral predator defense" that has been retained in diverging phyletic lines up to the present (Edgar, 1975) in spite of a variety of habitats, food plants, and behaviors.

Adult Ithomiinae sequester their PAs from a variety of sources: decomposing borages and composite flowers (Eupatorieae) especially, but also orchids, *Crotalaria*, apocynes, and less traditional PA-containing materials. These are inevitably abundant wherever Ithomiinae occur in numbers.

The proponderance of PAs in adult Ithomiinae defense could also help to explain the cryptic coloration and behavior observed in most ithomiine larvae (Fig. 8), notable exceptions being *Methona* on *Brunfelsia* (Fig. 8W, X), the feeders on Apocynaceae (Fig. 8T, U), *Melinaea* with similar larvae (Fig. 8K, V) feeding on *Markea*, *Juanulloa*, and related genera, and a few showy larvae scattered on other plants. Newly emerged ithomiine larvae eat their eggshells (which contain PA derived from their mother; see below) and immediately move to the underside of the same leaves (if not already there), usually acquiring a cryptic coloration. The fact that most ithomiine immatures are cryptic translucent green, closely matching their substrate, and feed

TABLE 6. Summary of PA content and distribution, and bioassay of food sources of adult Ithomiinae.

Adult Food Source[a]	Source[b]	Weight		%	Fractions (as % of dry wt.)[d]					PAs[f]	Fractions Tested[d]	Bio-assay Re-sults[g]
		Fresh	Dry[c]	H_2O	A	B (% N-Ox.)[e]	C	F	Fibre			
COMPOSITAE: SENECIONEAE (flowers)[h]												
Erechtites valerianaefolia (Wolf.) DC.*[h]	SL	6.5	1.7	64	1.9	0.47 (?)	11.2	3.8	82.6	?	Ex	+*
COMPOSITAE: EUPATORIEAE (flowers)[h]												
Mikania cordifolia Willd.	C	26	7.9	68	5.5	0.5 (?)	14.1	5.3	74.6	—	Ex, B, C	+*
Trichogonia gardneri A. Gray*[h]	C	14	3.8	72	5.0	1.4 (60)	15.2	7.3	71.1	E, (F)	Ex, B, C	+
Adenostemma involucratum King. & H. Robinson[i]*[h]	RJ	6.8	1.4	80	4.6	0.87 (70)	10.9	3.6	79.9	EH?	B	+
Adenostemma brasilianum Cass.[i]	I	17	3.5	79	7.9	3.4 (70)	14.2	3.1	70.8	EH?		NT
Adenostemma sp.[i]	ES	—	0.54	—	4.4	2.0 (?)	17.3	2.4	73.9	E?		NT
Eupatorium itatiayense Hieron.	J	160	54	66	7.4	0.98 (?)	19.2	7.6	64.8	F, (H)		NT
Eupatorium vauthierianum DC.	I	9.1	2.3	74	6.5	1.6 (60)	20.3	2.9	68.7	H?		NT
Eupatorium macrophyllum L.	AP	—	10.7	—	3.2	0.86 (35)	9.2	2.9	83.8	H	Ex	+
	ES	—	1.4	—	3.4	1.7 (46)	13.3	4.2	77.4	H		NT
	V	—	1.2	—	1.8	0.73 (?)	11.3	3.1	83.3	H		NT
Eupatorium odoratum L.	BJ	—	6.4	—	1.9	0.25 (30)	8.2	1.6	88.2	H?	Ex	+
Eupatorium maximiliani Schrad. ex DC.	C	13	4.1	69	1.6	0.73 (60)	10.0	2.1	85.6	H	Ex	+
Eupatorium laevigatum Lam.[j]	C	9.8	1.7	82	12.2	3.9 (60)	17.4	4.6	63.2	G	Ex, B, C	+*
Eupatorium macrocephalum Less.	PA	—	5.9	—	6.3	1.4 (?)	12.7	9.6	70.0	H		NT
Eupatorium betonicaeforme (DC.) Baker*[h]	SL	75	13.8	82	1.4	1.64 (60)	8.4	3.3	79.3	I		NT
	C	360	90	75	7.8	2.5 (60)	8.8	7.0	73.9	I + ??		NT
BORAGINACEAE: HELIOTROPOIDEAE												
Heliotropium indicum L. (aerial parts)	C	82	22.6	72	3.4	3.7 (49)	17.6	1.0	74.3	I	Ex, B	+
Heliotropium peruvianum L. (leaves)[j]	C	64	11.8	82	2.9	10.7 (64)	9.4	2.5	74.5	H	B	+
(stems)	C	35	7.0	80	2.3	6.7 (65)	25.4	1.6	61.7	H	Ex	+
Heliotropium transalpinum Vell. (leaves)	RC	130	26.5	80	5.1	0.44 (42)	12.1	2.6	79.6	HI	Ex, B	+
(whole plant)	C	—	3.5	—	4.4	0.77 (25)	13.2	0.6	81.0	HI		NT
Tournefortia breviflora DC. (flowers)	C	31	8.6	72	1.9	6.7 (55)	31.8	5.0	54.6	E + ??		NT
(leaves)	C	67	21	69	5.3	3.0 (58)	15.2	5.1	71.4	??		NT

TABLE 6. Continued.

ANALYSIS OF PLANT PARTS:[m] Eupatorieae Species (Source[b])		Young Leaves	Stems and Peduncles	Immature Buds		Mature Flowers				Seed Capsules		
				Involucre	Young Flowers	Involucre	Ovaries	Nectaries	Upper Part	Involucre	Seeds	Dry Flowers
Trichogonia gardneri (June)	C	3.50/12	0.24/18	1.70/73	2.20/77	1.16/79	**4.10**/60	**4.10**/32	2.90/49	0.94/87	2.13/49	1.04/46
(September)	C	1.82/19	0.93/13	2.86/38	4.93/48	2.67/47	2.48/76	**7.70**/60	5.03/52	0.60/38	0.80/37	0.38/21
Eupatorium maximiliani (June)	C	0.24/54	0.23/13	0.41/23	1.67/80	0.25/30	0.79/46	**2.20**/17	0.82/70	0.60/17		0.87/57
Eupatorium betonicaeforme (Oct.)	SL	0.59/46	0.07/88	1.67/46	**4.09**/58	0.61/42	**3.30**/40		1.64/47	0.72/49	2.95/50	1.07/61
(older parts[k]) (roots: 0.56/55)		0.00/—	0.004/—	1.01/49	**3.22**/57					0.18/52	0.38/22	0.29/44
(December)	C	0.13/23	0.23/8	1.26/50	2.64/55	0.80/40	1.24/67	**3.24**/56	1.22/54	0.33/33	1.16/47	0.67/42
(older parts[k]) (roots: 0.16/69)		0.02/53	0.005/—	0.78/32	**3.73**/53	0.36/37	1.35/46		0.68/40	0.30/48	0.71/53	0.92/59

[a] Whenever possible, food sources actually being used intensively by Ithomiinae adults were collected for extraction.

[b] See footnoes b of Tables 3 and 5. Additional localities: AP = upper Rio Amapari, Amapá. I = Serra de Itatiaia, Rio de Janeiro. PA = Porto Alegre, Rio Grande do Sul. RC = Rio Claro, São Paulo.

[c,d,e,g] See footnotes c, d, e and g of Table 3.

[f] See structures and stereochemical configurations in Figure 3.

[h] Also examined were *Eupatorium xestolepis* Rob.[i], probably containing 3E, *E. vitalbae* DC.[j], *E. squalidum* DC.[j], and *Ageratum conyzoides* L.[j], all showing PAs in good quantities. When an asterisk is used (*[h]), only the interior of the flowers (flowerlets, without involucres) was extracted.

[i] *Adenostemma* and some *Eupatorium* are fragile plants of the dark, humid forest understory, with isolated, small white flowers, typically and specifically pollinated by Ithomiinae and other PA-seeking Lepidoptera of this habitat (Pliske, 1975a, 1975b; Drummond, 1976; Haber, 1978).

[j] Collected and fractionated by José Roberto Trigo.

[k] The lower line of figures represents corresponding older parts: large leaves, lower stem, older flower bud, open flowers already pollinated, and dry seed capsules.

[m] See footnote m, Table 5.

on the underside of leaves (Fig. 8) may indicate rapid metabolism of the Solanaceae poisons (though cryptic and toxic insects are not rare); at least the poisons are not carried through to the adults, whom they would not protect in any case, and do not seem to be stored in the larvae. Aposematic but nontoxic insects are rare (except for obvious Batesian mimics that diverge from their taxonomic relatives), the main case being automimics in the Browerian sense (Brower et al., 1971; Rothschild, 1979). For this reason the strongly aposematic larvae in a few ithomiine genera may incorporate or synthesize some sorts of unpleasant substances that have yet to be identified.

In previous work reported without details, a lycopsamine/intermedine mixture was found in *Hypomenitis dercetis* and *Oleria makrena* from northern Venezuela (Edgar et al., 1976) and regarded as primarily precursorial to pheromones (only males were analyzed) rather than as defensive. Later work (Edgar, 1982) emphasized the potential defensive role of these compounds, here confirmed.

SELECTIVE PA STORAGE

When male and female *Mechanitis polymnia* were separately extracted in late September 1982, some interesting differences were observed, indicating that careful work on this chemical interaction should always maintain the sexes apart in analysis. At least in September, at the beginning of the reproductive season, the females contained much more fat and PA than males (Table 5). That this difference is closely related to the respective reproductive tasks is supported by the previous pheromone study (Edgar et al., 1976) and by analysis of *Mechanitis* eggs. A raft of 31 *M. polymnia* eggs, weighing 11 mg, was extracted with 2 N H_2SO_4 and directly reduced with zinc, alcalinized, and extracted with $CHCl_3$-MeOH. This showed on TLC the presence of abundant lycopsamine/intermedine mixture, perhaps as much as 1% of the fresh weight or 0.1 mg. All other Ithomiinae eggs analyzed also showed the presence of appreciable PA (Table 5). The bright white *Mechanitis* eggs, laid in rafts of 5–100 on top of the host plant leaves, with which they contrast vividly (Fig. 8I, N, Q), could be described as a true collective display of aposematic insects, just like the adult assemblages in dry season "pockets."

As shown in Table 5, male Ithomiinae generally accumulate more PAs than the females; indeed, in many species they are the principal or only sex found on the sources (Table 2; Pliske, 1975a, 1975b). The females of most species seem to get the majority of their PAs in the spermatophores received from males during mating, which is repetitious (Ehrlich & Ehrlich, 1978); these small sacs often have 20–50× the PA concentration as the rest of the male (Brown, 1984, 1985).

Both males and females are able to selectively distribute the collected PAs to different tissues, including tegument and wings (possibly by regurgitation with fat as a wetting agent) and especially to reproductive parts (pheromone glands, spermatophores, ovaries; Table 5), thence in females to the eggs.

Males attracted to *Heliotropium* baits placed in relatively PA-poor areas and females attracted to displaying males showed lower average and maximum PA content than random samples of the same populations, indicating an "appetite effect" that obviously would be highly adaptive in these organisms.

More complete information on PA storage, use, and distribution in Ithomiinae may be found in Brown (1985).

SOURCES OF DEHYDROPYRROLIZIDINE ALKALOID MONOESTERS

In the same paper in which he predicted that PAs would be used for defense in the Ithomiinae, Edgar (1982) predicted that they would be found in the nectar of Eupatorieae, in view of the heavy dependence of Ithomiinae on these plants and their characteristic occurrence in the Boraginaceae, also frequently visited by Ithomiinae and source of precursor for the pheromone (Fig. 3D) as well as of the most attractant esterifying acids for ithomiine males (Pliske et al., 1976). Indeed, many genera and most females are more strongly attracted to Eupatorieae flowers than to *Heliotropium* (Table 2), the difference being especially pronounced in *Mechanitis* and allies (Fig. 11).

Extraction of the flowers of 16 species in four genera of the Eupatorieae actively visited by Ithomiinae in the field led to the isolation and identification of a variety of PAs but usually only one isomer and structure in each species (Table 6; see Figs. 3, 10). Alkaloids of this structure were also found in *Heliotropium* and *Tournefortia* flowers (Boraginaceae-Heliotropoideae) often visited by Ithomiinae, as well as in the leaves of

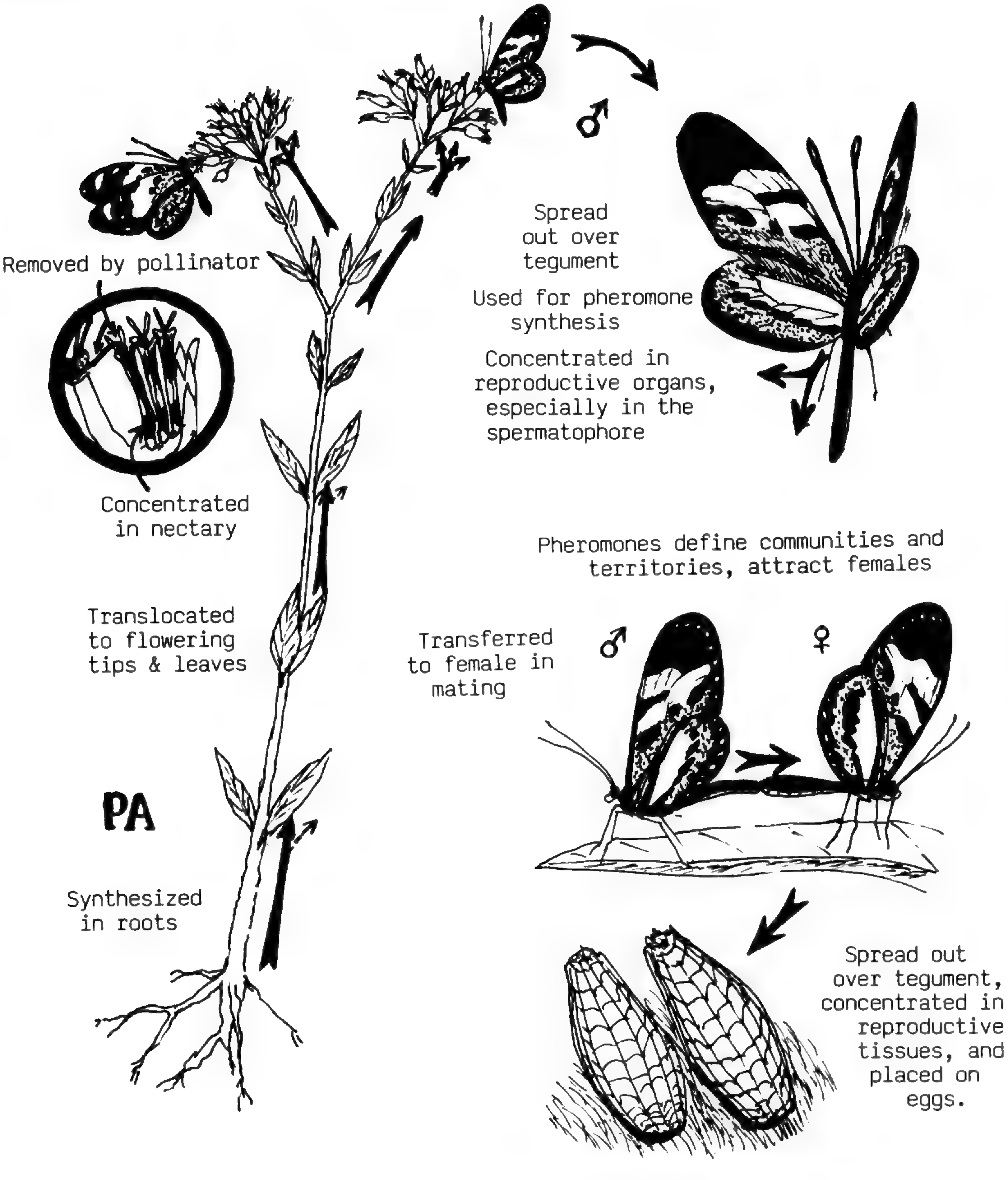

FIGURE 12. Flow of dehydropyrrolizidine alkaloid monoesters in natural ecosystems.

various *Heliotropium* species (Table 6), but not in *Mikania* (Eupatorieae), *Cordia* (Boraginaceae), or several other flowers sporadically visited by Ithomiinae. When the plants were analyzed for PAs by parts (Table 6), the highest concentrations always appeared in the nectaries of still unopened flowers, suggesting that they might be a reward to specific PA-seeking pollinators; the concentration was often 2–4% of dry weight of the whole flower.

In open vegetation or poor soil areas with few Ithomiinae present, Eupatorieae gave lower yields of less pure isomers in the flowers and showed dramatically reduced seed set, even though pollination was effected by other groups that also depend on PAs (Danainae and Arctiidae). Areas with few Eupatorieae or only very seasonal species showed scattered and transient Ithomiinae populations, whereas in areas with abundant Ithomiinae there were always common Eupatorieae in flower throughout the year, especially *Trichogonia* (Fig. 11A; see also Pliske, 1975a). It is evident that this mutualistic relationship, profoundly affecting the reproduction and abundance of both butterflies and plants, is of fundamental importance to both groups and has determined many adaptations on both sides of the interaction, in a coevolutionary picture probably much stronger and more stable than that of the Ithomiinae with the Solanaceae.

FLOW OF DEHYDROPYRROLIZIDINE ALKALOIDS IN NATURE (FIG. 12)

The analysis of PA monoesters in different parts of plants and butterflies in various physiological and reproductive states (Tables 5, 6; Brown, 1984, 1985), made possible by the selectivity and sensitivity of the Mattocks-Bingley assay (Fig. 3), permits a diagram to be drawn of the synthesis, flux, use, and eventual dissipation of these highly active compounds in ecological systems (Fig. 12). Thus the PAs are probably synthesized in the roots of Apocynaceae, Boraginaceae, and Compositae-Eupatorieae (diesters are also elaborated by Compositae-Senecioneae and Leguminosae: *Crotalaria*); young plants show highest concentrations in the roots and even mature plants show a bimodal concentration distribution between flower heads and roots. The compounds also may be concentrated in the leaves when this will give important protection against herbivores; in a few cases, these leaves are attacked by specific insects, including larvae of some Danainae, Ithomiinae, Ctenuchinae, Pericopinae, and Arctiinae among the Lepidoptera, and a variety of Hemiptera and Coleoptera. Many of these specific herbivores store and use the compounds directly for defense or adult reproduction, whereas others excrete them.

As the plant comes into flower the alkaloids are translocated to the flowering tips and then into the nectaries, where they guarantee attraction and relatively long visits of specific Lepidopteran pollinators in the same five subfamilies, the first three pantropical (with scattered species in north temperate areas), the fourth neotropical and the last cosmopolitan. The alkaloids are also retained in the seeds to deter predation.

In the frequent case of selective attraction of male butterflies to the PA sources, these spread the PAs over their tegument for predator defense and channel them into pheromone synthesis glands (Fig. 3), which sometimes are formed only with PA stimulation (Schneider et al., 1982), and other reproductive tissues, especially spermatophores. The spermatophores are transferred to females during mating and the PAs are similarly spread out over the tegument and channeled into reproductive tissues, eventually being deposited on the eggs for protection. Newly hatched larvae consume the eggshells but quickly lose their PAs unless they find themselves on leaves that contain them.

This chemico-ecological flow scheme (Fig. 12) opens ample perspectives for the localization, selection, and cultivation of PA-producing plants. Indicine N-oxide (Fig. 3K) and at least one isomer (Fig. 3J) are promising anticarcinogenic drugs now in advanced clinical testing; some *Eupatorium* in the right ecologico-evolutionary setting might become important sources for these compounds (Table 6). The free bases, however, and especially the diesters, are very hepatotoxic and carcinogenic, representing a serious problem in human and veterinary medicine. Knowledge of the flow of PAs in nature should be useful for the control of both plants and PA content in natural and agricultural systems. It may also help in the control and evaluation of medicinal plants such as comfrey (*Symphytum*, Boraginaceae), which surely should contain a minimum of PAs when used as herbal teas or fortifying salads, to avoid permanent liver damage to the unsuspecting consumers.

CONCLUSIONS, SYNTHESIS, AND PERSPECTIVES

The integrated ecological, phylogenetic, and biochemical investigation of the Solanaceae/Ithomiinae interface, with the collaboration of *Nephila clavipes*, a large spider that is a major potential predator of the butterflies, has shown that:

(1) Although there exists a reasonable and geographically widespread specificity in the usage of 19 genera of Solanaceae by Ithomiinae larvae, especially at the level of host plant secondary chemistry, there is very little evidence for parallel phylogenetic diversification of these interacting groups over evolutionary time; in general, advancing phyletic lines of butterflies use ever more primitive hosts. The New World Ithomiinae seem to have colonized the already generically diver-

sified Solanaceae through sequential preadaptation to, and encounter and toleration of progressively more toxic secondary chemicals in their food plants. This has undoubtedly affected the distribution, population structure, habit, habitat, phenology, and exceedingly diversified and variable chemistry of these plants, but it should not be called "coevolution."

(2) The variable and diversified Solanaceae toxins are not stored by larval Ithomiinae and do not protect newly emerged adults against the spider predator, which rejects field-caught individuals. Adult Ithomiinae depend heavily on dehydropyrrolizidine alkaloid monoesters for defense and reproduction. These are sought out and sequestered from decomposing Boraginaceae and especially from a constant source, stabilized by mutualistic interaction: flowers of Compositae-Eupatorieae, which place in their nectar a single chemical structure (usually as only one of five different stereoisomers) to attract the pollinators that need these alkaloids. This intimate relationship has undoubtedly determined many aspects of morphology, physiology, population structure, distribution, abundance, and the highly convergent chemistry of these plants and their pollinators.

Interesting additional problems that have arisen during this research, presently under active investigation with similar methodology, include:

(1) The special relationship of the Ithomiinae *Tithorea* and *Aeria* to Apocynaceae-Parsonsieae, which sometimes contain PAs that may be stored by the aposematic larvae of these genera (research under way with J. R. Trigo).

(2) The additional aposematic larvae of Ithomiinae, which feed mostly on tropane-containing plants and *Brunfelsia* (though some *Solanum* are also included), and which may be storing effective predator deterrents from the food plant and, in the case of *Methona* (which contains almost no PAs in the adults), possibly passing them on to the adult butterflies.

(3) Reasons for the apparent nonstorage (and perhaps nonstorability) of most Solanaceae toxins by herbivores.

(4) Possible participation of further compounds, volatile or unstable and derived from PAs or similar precursor, in defense of adult Ithomiinae.

(5) Physiological or behavioral mechanisms for the spreading out of PAs on the tegument of the butterflies and their use in synthesis of various pheromones.

(6) The great diversity and variability of toxins in both the Apocynaceae and the Solanaceae used by larval Ithomiinae and the importance of these in relation to evolution, oviposition, larval feeding, survivorship, and reproduction in their usual herbivores and in other potential enemies.

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NEW TAXA OF RUBIACEAE FROM VENEZUELA

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ABSTRACT

Four new taxa of Rubiaceae are described from Venezuela: *Coccocypselum apurense, Faramea cazaderensis, Psychotria buntingii,* and *Psychotria subimbricata.*

Coccocypselum apurense Steyerm., sp. nov. TYPE: Venezuela. Edo. Apure: Dtto. Pedro Camejo, Caño El Cabello, 16 airline km NW of Mata de Guanabana, between the Río Meta and Río Cinaruco, 6°19′N, 68°19′W, 75 m, 27 Feb. 1979, *Gerrit Davidse & Angel Gonzalez 15825* (holotype, MO; isotype, VEN).

Herba radicans, caulibus 1.5–2.5 mm diam. glabris; stipulis subulatis usque 6 mm longis glabris; foliis petiolatis, petiolis 8–13 mm longis marginibus superioribus adpresso-piloso-ciliatis ceterum glabris; laminis ovatis apice breviter acutis vel subacutis basi obtusis vel subobtusis majoribus 6–7 cm longis 3–4 cm latis, adultis supra costa adpresso-pilosa atque marginibus minute adpresso-ciliolatis, pilis 0.1–0.3 mm longis munitis, ceterum glabris, subtus glabris, juvenilibus subtus costa nervisque lateralibus pilosis, nervis lateralibus utroque latere ca. 7 adscendentibus subtus impressis; inflorescentia ca. 12-flora subcapitata pedunculata; pedunculo 4.5 mm longo glabro; calycis lobis inaequalibus lineari-lanceolatis 2–2.5 × 0.3–0.7 mm; corollis coeruleis 5 mm longis extus glabris.

Creeping herb with rooting glabrous stems 1.5–2.5 mm diam. Stipules subulate, to 6 mm long, glabrous. Leaves petiolate, appressed-pilosulous on upper margins, otherwise glabrous; leaf blades ovate, shortly acute or subacute at apex, obtuse or subobtuse at base, the larger ones 6–7 cm long, 3–4 cm wide; adult leaf blades appressed-pilose adaxially on midrib, minutely appressed-pilosulous on margins with hairs 0.1–0.3 mm long, elsewhere glabrous, abaxially glabrous; young leaf blades pilose abaxially on midrib and lateral nerves; lateral nerves ascending, 6 or 7 each side; petioles 8–13 mm long. Inflorescence ca. 12-flowered, subcapitate, the heads 8 mm wide, 5 mm high, pedunculate; peduncle 4.5 mm long, glabrous. Flowers sessile; bracts subtending flowers linear-ligulate, obtuse, 3 mm long, 0.5 mm wide, glabrous; hypanthium campanulate, 1.5 mm long, 1.1 mm wide, glabrous; calyx lobes unequal, linear-lanceolate, acute, the larger pair 2.5 mm long, 0.7 mm wide, the smaller pair 2 mm long, 0.3–0.5 mm wide, sparsely ciliolate to glabrescent; corolla blue, infundibuliform, 5 mm long, glabrous without, tube 2 mm long, 1.2 mm wide, glabrous within, the lobes ovate-oblong, subacute, 2 mm long, 1.5 mm wide, papillate-puberulent within. Anthers slightly exserted, linear, 2 mm long. Style exserted, 6 mm long.

This species resembles the newly described *C. croatii* Steyerm. but is readily distinguished from that taxon by the longer petioles, very short peduncles, less conspicuous, shorter hairs of the ciliate-margined leaf blades, shorter stipules, inflorescences with more flowers, and fewer lateral leaf veins that are less arcuate.

Faramea cazaderensis Steyerm., sp. nov. TYPE: Venezuela. Edo. Táchira: Dtto. Lobatera, La Cazadera, 2,000 m, 22 Jul. 1983, *H. van der Werff & R. Ortiz 5457* (holotype, MO; isotype, VEN).

Frutex 4-metralis, ramis juvenilibus quadrangularibus glaberrimis; foliis subsessilibus subamplexicaulibus oblongis vel ovato-oblongis apice abrupte obtuse acutis basi subcordatis vel rotundatis 6.5–13 cm longis 3.5–7 cm latis prominente nervatis, nervis lateralibus utroque latere 9–12 fere horizontalibus; inflorescentia terminali umbellatim cymosa, floribus pedicellatis, pedicellis 2.5–4 mm longis; calyce hypanthioque 5.5 mm longo, hypanthio urceolato 1 mm longo; calyce tubuloso 4.5 mm longo inaequaliter leviterque dentato, dentibus deltoideis acuminatis 0.3–1 mm longis, deinde uno latere fisso.

Shrub 4 m tall, glabrous throughout; branches quadrangular. Stipular sheath shallowly and broadly semilunar, 3 mm long, 2 mm wide, ending in an awn 2–3 mm long. Leaves subsessile, subamplexicaul, oblong or ovate-oblong, abruptly obtusely acute at apex, subcordate or rounded at base, 6.5–13 cm long, 3.5–7 cm wide, prominently nerved; lateral nerves 9–12 each side, nearly horizontal or widely spreading at an angle of 5–15°, elevated abaxially, impressed adaxially, anastomosing 3–6 mm before the margin, ter-

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tiary veins prominently reticulate, marginal nerves somewhat thickened; petioles 2–3 mm long. Inflorescence terminal, umbellately cymose, 2–2.5 cm wide, 1.5–1.7 cm high, 12–15-flowered, pedunculate; peduncle erect, 1.7–4 cm long, 1 mm wide; primary axes 4–5, ascending, 5–7 mm long, 0.7–0.9 mm wide, each bearing 3 flowers. Flowers on pedicels 2.5–4 mm long, 0.5–0.7 mm wide; bracts subtending axes and pedicels deltoid-ovate, acute, 0.5–0.8 mm long. Calyx and hypanthium 5.5 mm long; hypanthium urceolate, 1 mm long; calyx tubular, 4.5 mm long, shallowly and unequally dentate, teeth broadly deltoid, acute to acuminate, 0.3–1 mm long, eventually splitting on one side. Corolla purple (in bud), abruptly acute, 7 mm long.

Paratypes. VENEZUELA. EDO. TACHIRA: Dtto. Lobatera, La Cazadera, 7°55′N, 72°18′W, 1,600 m, 24 Jul. 1983, *van der Werff & Ortiz 5587* (MO, VEN); Parque Cazadero, Quebrada Cazadero, 16 km NW of San Cristóbal, 7°54′N, 72°18′W, 400–650 m, 2 May 1981, *Liesner & Guariglia 11668* (MO, VEN).

This species is well marked by the subamplexicaul leaves and relatively few-flowered umbellate inflorescence. It may be distinguished from *F. sessilifolia* (Kunth) A. DC. by the umbellately disposed, smaller inflorescence of 4 or 5 axes, each of which is only 3-flowered, the obtusely acute leaves with fewer pairs of lateral nerves, and by the tubular, longer calyx which becomes split on one side. Further, the habitat of the new taxon in the cooler montane forests of the Andes of Táchira is in contrast with that of *F. sessilifolia* in the lowlands of the Orinoco, Río Negro, and Madeira river basins.

Psychotria buntingii Steyerm., sp. nov. TYPE: Venezuela. Edo. Zulia: Dtto. Perijá, alrededores de la Estación Hídrológica Aricuaisá-Pie de Monte, 9°35′N, 72°53′55″W, en zona de bosque siempreverde, 100–250 m, 25 Feb.–3 Mar. 1982, *G. S. Bunting, G. Panapera & H. Lobo 10876* (holotype, MO; isotypes, JBM, VEN).

Suffrutex 0.3-metralis, ramis minute tomentellis; stipulis terminalibus lanceolatis acutis usque 5.5 mm longis; foliis elliptico-lanceolatis apice subfalcato-acuminatis basi acutate angustatis 4.5–8.5 cm longis 0.9–1.9 cm latis supra glabris subtus costa nervis lateralibusque minute puberulentibus, nervorum lateralium axillis domatiis barbellatis, ceterum glabris, subtus punctis brunneis minute notatis, marginibus sparsim ciliolatis; inflorescentiis axillaribus vel terminalibus pedunculatis cymoso-umbellatis gracillimis sub anthesi 0.4 cm alto 1.2 cm lato sub fructu 1.2 cm alto 2 cm lato, 12–17-floris, axibus primariis tribus filiformibus 3–7-floris; pedunculo filiformi 1.6–2 cm longo 0.5 mm lato dense puberulo; floribus pedicellatis, pedicellis 0.5–0.8 mm longis 0.3–0.4 mm crassis; calyce hypanthioque 1.5 mm longo, hypanthio turbinato 0.5 mm longo 0.5 mm lato; calyce 1.2 mm longo, tubo 0.5 mm longo 1 mm lato; corolla (immatura) 3.5 mm longa.

Slender subshrub; branches minutely tomentellose with numerous minute cystoliths. Terminal stipule and those on next lower node lanceolate, acute, up to 5.5 mm long, 1.5 mm wide, glabrous or glabrate except for the ciliate margins, prominently marked with pale cystoliths near margins, nodes below brown-fimbrillate on the stipular scar. Leaf blades elliptic-lanceolate, subfalcately acuminate at apex, acutely narrowed to the base, 4.5–8.5 cm long, 0.9–1.9 cm wide, 4¼–4½ times longer than broad, glabrous adaxially, minutely puberulent abaxially on midrib and main lateral nerves, otherwise glabrous, the surface minutely brown-dotted, axils of the nerves abaxially barbellate with domatia, margins sparsely ciliolate; lateral nerves 7–8 each side, ascending at an angle of 45°, faintly anastomosing 1.5–2 mm from margin; petiole very slender, 4–7 mm long, moderately tomentellose. Inflorescence axillary or terminal, cymosely umbellate with 3 main axes, 12–17-flowered, 0.4 cm high, 1.2 cm wide in anthesis, 1.2 cm high, 2 cm wide in fruit, pedunculate, the main axes with two additional shorter central axes 1 mm long; main axes filiform, the lateral 3–7-flowered. Peduncle 1.6–2 cm long, 0.5 mm wide, densely puberulent and conspicuously marked with cystoliths. Flowers pedicellate, pedicels filiform, 0.5–0.8 mm long, 0.3–0.4 mm thick; bract subtending pedicel subulate, 0.2 mm long. Calyx and hypanthium 1.5 mm long, the hypanthium turbinate, 0.5 mm long, 0.5 mm wide, tomentellose; calyx tube 0.5 mm long, 1 mm wide, lobes glabrous throughout except for ciliolate margins, longer than the tube. Corolla white (in bud) cylindric-infundibuliform, 3.5 mm long, glabrous without, sparsely pilose within the tube, sparsely marked with cystoliths, tube 1 mm long, lobes 2 mm long. Fruit (immature) elliptic-oblong, 3 mm long, 2 mm wide, sparsely puberulent.

This species resembles the pubescent *P. horizontalis* var. *glaucescens* (Kunth) Steyerm., from which it is readily distinguished by the minute calyx and hypanthium, shorter, filiform peduncles and pedicels, much smaller inflorescence, and narrowly elliptic-lanceolate leaf blades with barbellate domatia in the abaxial nerve axils.

It is a pleasure to associate this new taxon with the name of Dr. George S. Bunting, who has contributed greatly to our knowledge of the flora of the state of Zulia in Venezuela.

Psychotria subimbricata Steyerm., sp. nov. TYPE: Venezuela. Edo. Miranda: Parque Nacional Guatopo, laderas pendientes pedregosas a lo largo del Río Santa Cruz de Río Grande, lado occidental de la carretera, al sureste de Los Alpes, 10°4′45″N, 66°29′30″W, 400 m, 31 Oct. 1981, *Julian A. Steyermark & Bruno Manara 125483* (holotype, VEN).

Planta subherbacea 1.5-metralis; foliorum laminis subtus glabrescentibus, nervio medio subtus minute puberulo; inflorescentiae pedunculo 1–6 cm longo, bracteis bracteolisque subimbricatis glabris; hypanthio glabro.

Stem subherbaceous, simple, hollow, leafy below, 1.5 m tall. Stipule spreading with revolute margins, broadly ovate-oblong, subacute, 6–10 × 6–8 mm. Leaves broadly obovate or elliptic-obovate, abruptly and shortly acute to shortly acuminate or obtusely acute at apex, conspicuously narrowed to the decurrent base, the lamina 21–25 cm long, 10–15 cm wide; lower midrib microscopically appressed-puberulent, the middle and upper portion with two parallel lines of puberulence along the margins of the midrib; abaxial surface glabrous to glabrescent; adaxial surface glabrous; lateral nerves 13–16 each side, arcuate-ascending, arising at angle of 15–20°, strongly sulcate adaxially, elevated abaxially; decurrent petiole 3–8 × 5 mm. Inflorescence axillary in upper leafy axils and in leafless middle axils, fasciculate with 1–3 elongated peduncles 1–6 cm long, glabrous, trichotomously branched at maturity with the central longer axis up to 13 mm long and two lateral shorter axes up to 7 mm long, or the peduncle with two lower axes and an upper trichotomously branched portion; 2 bracts subtending the base of the principal axes naviculate, lanceolate to ovate-lanceolate, acute to acuminate, 7–9 mm long, 4–5 mm broad near base, glabrous. Flowers in small compact groups subspicately arranged, each group subtended by imbricate, ovate, obtuse, glabrous bracts 6.5 × 4 mm; flowers numerous in an inflorescence, 3 or 4 of them subtended by a larger, glabrous, ciliolate bract in each compact group. Calyx lobes 5, narrowly ligulate, unequal, subobtuse, ciliolate, 3–3.5 × 0.4–0.6 mm; calyx tube and hypanthium 2 × 1.5 mm, glabrous; 1 scale-like squamella, oblong-triangular or lanceolate, acute, in the sinus between 2 calyx lobes; corolla tubular, 7 mm long, glabrous except for the barbate orifice. Anthers exserted, oblong, 1.2 mm long. Style 3.5 mm long; style branches filiform, 1.3 mm long, puberulous.

The new taxon differs from *P. humensis* Steyerm. and *P. decurrens* Steyerm. in the glabrous hypanthium, more branched inflorescence with longer peduncules, glabrous, subimbricately arranged bracts and bracteoles, and minutely puberulent lower midrib of a glabrescent abaxial leaf surface.

SIX NEW SPECIES OF NEOTROPICAL LAURACEAE[1]

HENK VAN DER WERFF[2]

ABSTRACT

Among recent collections of Lauraceae and older collections received on loan from various herbaria, several undescribed species were found. Six of those, *Aiouea inconspicua* van der Werff, *Licaria bracteata* van der Werff, *Phoebe glabra* van der Werff, *Pleurothyrium costanense* van der Werff, *P. grandiflorum* van der Werff, and *P. westphalii* van der Werff, are described. Difficulties with the generic placements of these new species are discussed.

Lauraceae, comprising about 40 predominantly tropical genera, are rich in species in the Neotropics. The majority of the species have small, inconspicuous flowers. Genera are often hard to recognize and nearly all are in need of modern treatments.

During identification of the large number of unidentified Lauraceae in MO and among the various loans I received, several undescribed species were found. Of those, the following six are here described as new.

AIOUEA AUBLET

Aiouea, recently monographed by Renner (1982), comprises about 20 neotropical species and is best represented in Brazil, Venezuela, and the Guianas.

Having seen specimens of most species attributed to *Aiouea,* it seems quite likely to me that *Aiouea,* as circumscribed by Renner (1982) and accepted here, is polyphyletic. Most of the South American species (including the type species) have a typical aspect, with large, many-flowered inflorescences, flowers with rather long pedicels, leaves drying greenish, and twigs with smooth bark. The Central American species look quite different but key to *Aiouea* because of their nine 2-celled anthers; they do not fit in the other, better defined, neotropical genera with nine 2-celled anthers. Because some Central American species show a striking resemblance to sympatric *Ocotea* species, it is quite well possible that the Central American *Aiouea* species are derived from local *Ocotea* or *Nectandra* species which have lost two of their four anther cells. Variation in the number of anther cells in *Aiouea lundelliana* Allen, a species excluded from *Aiouea* by Renner (1982), has been reported earlier (van der Werff, 1984). A study of the wood anatomy could probably answer the question whether these *Aiouea* species share more characters with the South American *Aiouea* species or with Central American *Ocotea* or *Nectandra* species.

Aiouea inconspicua van der Werff, sp. nov. TYPE: Mexico. Vera Cruz: 0–2 km S del campamento Hnos. Cedillo, rumbo a Río Alegre, por la desviacíon al E, Hidalgotitlan, 140 m, 22 Apr. 1974, *Brigada Dorantes 2929* (holotype, MO; isotypes, MO, BM, UC). Figure 1.

Frutex vel arbor parva. Ramuli tenues, teretes, juniores minute tomentelli, vetustiores glabrescentes. Folia alterna, lanceolata (8–11 × 2–3 cm), chartacea, base acuta, apice acuminata vel caudata, subtus sub lente minute immersa punctata, penninervia, nervis arcuatis prominentibusque. Venatio camptodroma accedens brochidodroma. Laminae supra costam minute tomentellae vel glabrae, subtus praeter nervorum axillas barbellatas glabrae, sicco olivaceae praeter nervos virides. Inflorescentiae axillares, minute tomentellae, ad 4 cm longae, pauciflorae. Flores glabri, infundibuliformes. Tepala 6, aequalia, ovata vel transverse ovata, concava. Stamina fertilia 9, bilocellata, ca. 0.9 mm longa; 6 exteriora introrsa, 3 interiora extrorsa et basi filamentorum glandulis binis aucta. Staminodia absentia. Ovarium glaberrimum stigmate crasso sessilique. Bacca globosa, 1.5 cm diametro, basi cupulae planae, in pedicellum clavatim attenuatae insidens, tota exserta.

Shrub to 7 m tall. Twigs terete, glabrous; young twigs minutely tomentellous. Terminal buds slender, greyish pubescent. Leaves alternate, 8–11 cm long, 2–3 cm wide; lamina chartaceous, lanceolate, with numerous small gland dots, the base acute, plane, the apex acute or caudate, with a slender tip 1 cm long, the margin thickened

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[1] I thank the curators of A, BM, BR, GH, U, UC, US, and VEN for the often large loans that I received. Dr. J. Dwyer kindly checked the Latin. John Myers made the illustrations. The designation CORO is used for the herbarium of the Proyecto Flora Falcón in Coro, Venezuela.

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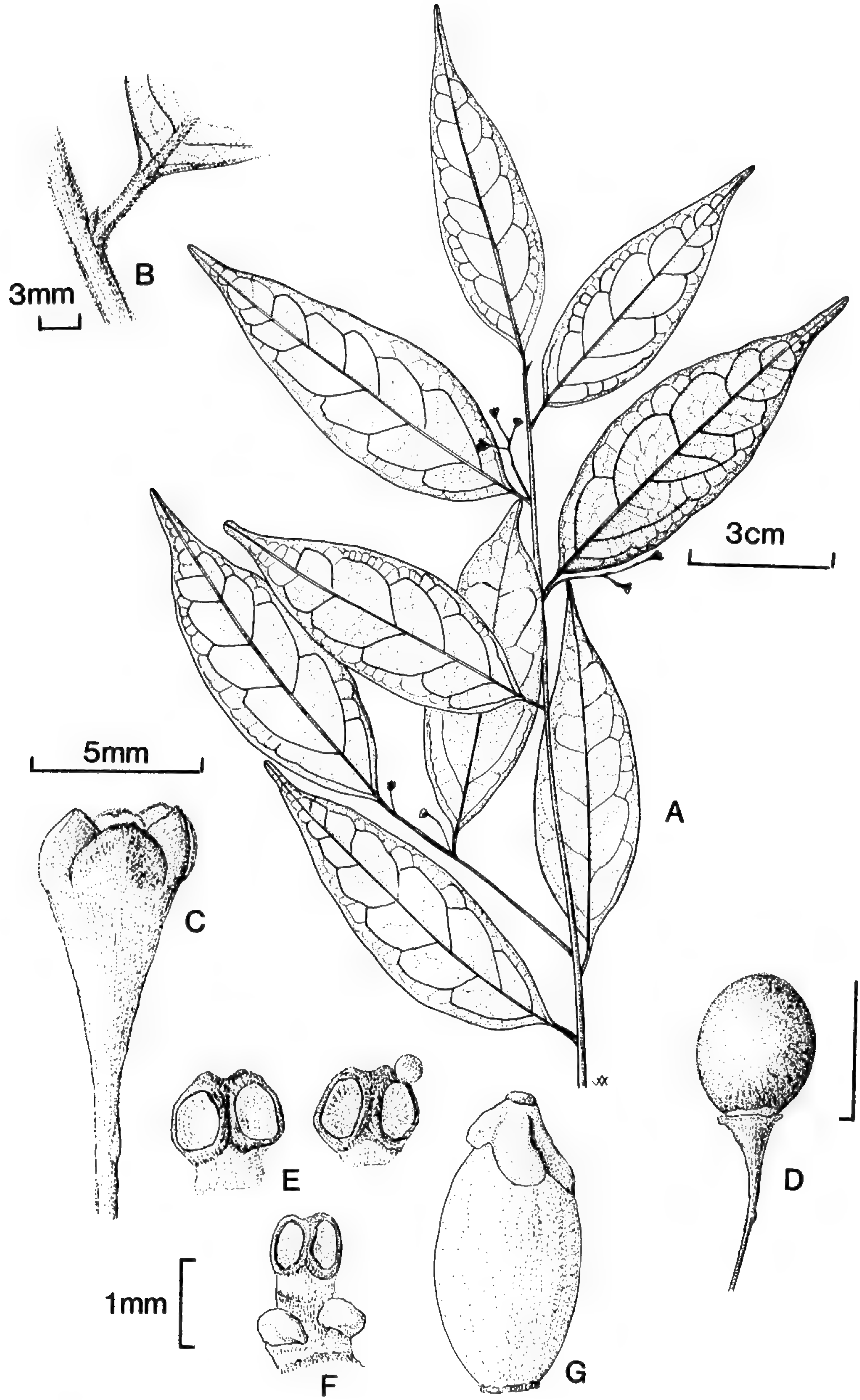

FIGURE 1. *Aiouea inconspicua.*—A. Habit.—B. Detail of twig.—C. Flower.—D. Fruit.—E. Two outer anthers.—F. Inner anther with basal glands.—G. Ovary and stigma.

and cartilaginous, glabrous below with the exception of small tufts of hair at the bases of the lowermost lateral veins, puberulous above on the midveins of young leaves, otherwise glabrous; lateral veins 4–6 pairs, slightly raised below and lighter than the leaf tissue, not reaching the margins but forming conspicuous arches ca. 3 mm from margin; tertiary venation reticulate, slightly raised on upper and lower surface. Inflorescences in axils of deciduous (rarely persistent) leaves, minutely tomentellous, to 4 cm long, few-flowered (4–7 flowers per inflorescence in material seen). Flowers greenish white, funnel-shaped, glabrous, with small terminal openings revealing the anthers, the pedicels 2–3 mm long. Tepals 6, equal or the outer 3 slightly shorter than the inner ones, roundish or slightly wider than long (0.9–1.2 × 1.2–1.4 mm), concave. Fertile stamens 9, ca. 0.9 mm long; anthers 0.3 mm long, with gland dots, all with 2 anther cells, these filling the entire anther; outer 6 anthers with introrse cells, the inner 3 with extrorse cells; filaments 0.6 mm long, as wide as anthers, pubescent; filaments of the inner 3 stamens with two basal glands. Ovary 1 mm long, elliptic, glabrous; style lacking, the stigma sessile, large, 0.4 mm wide. No staminodia seen. Fruit round, 1.5 cm diam. Cupule a shallow disc, ca. 8 mm diam., gradually narrowed into the pedicel.

Additional specimens examined. MEXICO. VERACRUZ: Hidalgotitlan, Río Solosuchil entre Hnos. Cedillo y la Escuadra, 11 Sept. 1974 (fl.), *Brigada Vazquez 1368* (MO); Hidalgotitlán, lomita pedregosa caliza al E de la estacíon de luz, 23 Feb. 1981 (fl, fr), *Wendt, Villalobos, Anguiano, Gonzâlez y Nararrete 2921* (MO). GUATEMALA. DEPT. ALTA VERAPAZ: Cerro Chinajá, 150–700 m, 1–2 Apr. 1942 (sterile), *Steyermark 45578* (A).

Aiouea inconspicua represents the first *Aiouea* species reported from Mexico. It resembles most closely *A. guatemalensis* (Lundell) Renner, known only from Guatemala. The most striking differences between the two species are listed in Table 1. In addition, *A. guatemalensis* has longer, wider leaves than *A. inconspicua*, and the leaves dry dark green with contrasting lighter venation in *A. inconspicua*, a feature lacking in *A. guatemalensis*.

TABLE 1. Selected characters of *Aiouea inconspicua* and *A. guatemalensis*.

	A. inconspicua	*A. guatemalensis*
Young twigs + terminal bud	puberulous	glabrous
Staminodes	lacking	present (teste Renner, 1982)
Axillary tufts of hairs in lowermost veins	present	absent
Leaf texture	chartaceous	chartaceous-coriaceous

An unusual feature of *A. inconspicua* is the absence of staminodia. In both earlier generic keys for Lauraceae (Kostermans, 1957; Hutchinson, 1964) and by Renner (1982) presence of staminodia was considered a characteristic feature of *Aiouea*, although Renner (1982) mentioned two exceptions. Because other lauraceous genera (*Ocotea, Nectandra*) include species with and without staminodia, I do not see the absence of staminodia in *A. inconspicua* as an obstacle for its inclusion in *Aiouea*.

Two of the collections were distributed by the Flora Veracruz project and may be present in several additional herbaria: *Brigada Dorantes 2929* was distributed as *Nectandra salicifolia* HBK and *Brigada Vazquez 1368* as *Nectandra sanguinea* Rolander ex Rottboel. The Steyermark collection was distributed as *Ocotea effusa* (Meissner) Hemsley.

LICARIA AUBLET

The genus *Licaria*, endemic to the Neotropics, was recently monographed by Kurz (1983), who recognized about 40 species ranging from southern Florida to southern Brazil. Among the neotropical Lauraceae, *Licaria* can be recognized readily based on its three 2-celled stamens, double-rimmed cupule, and alternate (rarely opposite, never clustered) leaves.

Licaria bracteata van der Werff, sp. nov. TYPE: Guatemala. Alta Verapaz: Sacté, large tree in dense humid forest, 900–1,050 m (fl), *I. Kunkel 7* (holotype, BR). Figure 2.

Arbor magna. Ramuli obtuse angulati, glabri. Folia alterna, glabra, chartacea, elliptica, 25–40 × 11–15 cm. Inflorescentiae e axillis bractearum ortae, breviter cinereo-pubescentes. Bracteae glabrae, nigrescentes, 1–1.5 cm longae. Flores 3–4 mm longi, 2.5–3 mm lati, urceolati, sparsim cinereo-puberuli. Tepala 6, inaequalia, 3 exteriora contingentia, 3 interiora minoria, magnopere tepalis exterioribus occulta. Stamina fertilia 3, 2-locellata, 2 glandulis basalibus munita, staminodia 9, 6 exteriora late lanceolata, ad 1 mm longa, 3 interiora lanceolata, ad 0.8 mm longa, staminibus

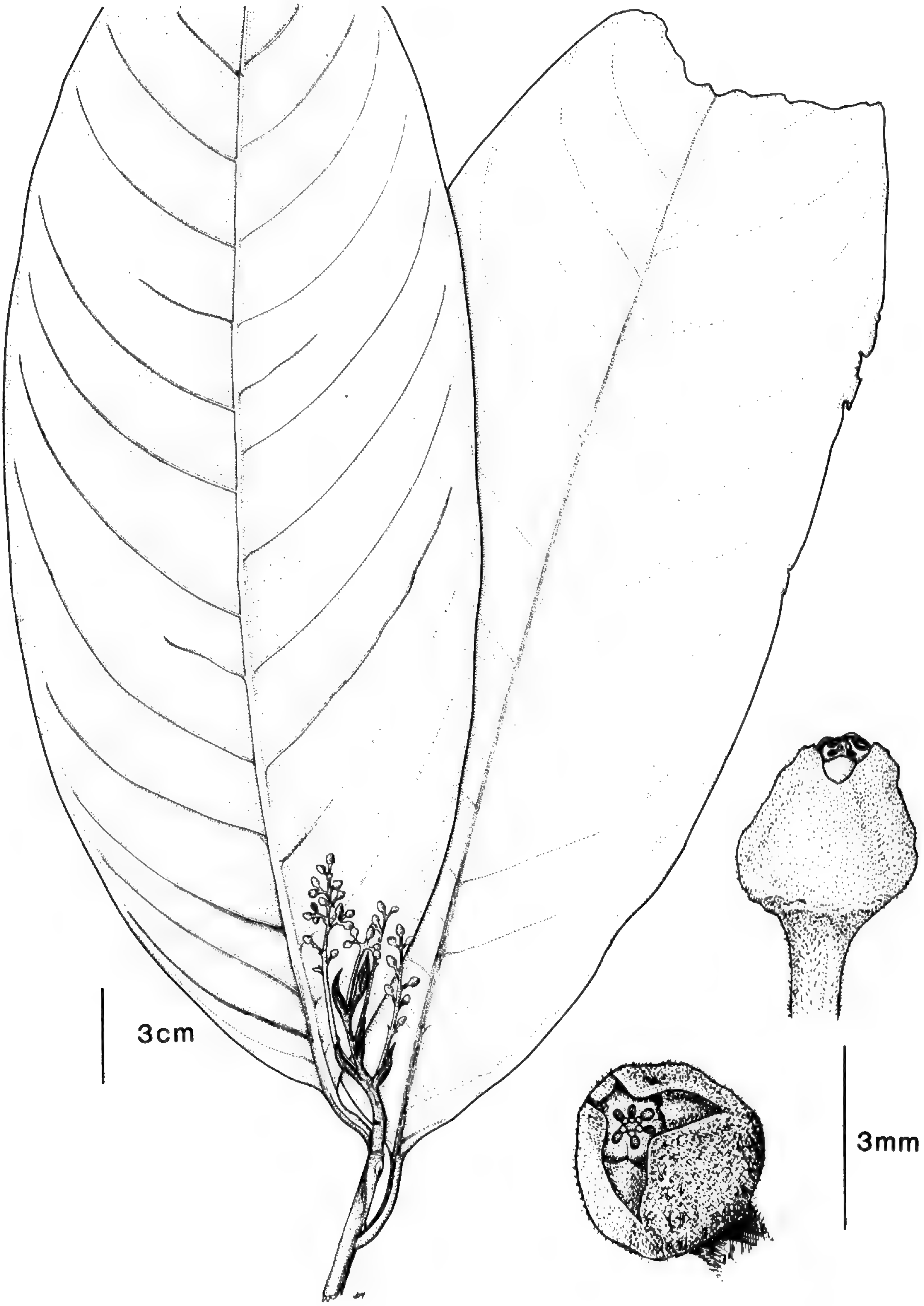

FIGURE 2. *Licaria bracteata*. Habit and flower seen from aside and above.

alternantia. Ovarium glabrum, tubo florale dense pubescente. Fructus ignoti.

Large tree. Twigs roundly angled, glabrous, with small, light-colored lenticels, the terminal bud drying black, glabrous. Leaves alternate, chartaceous, glabrous on both surfaces (only a small part of the lower leaf surface visible on specimens seen), elliptic, the apex not seen, the base acute, 25–40 × 11–15 cm, the upper surface opaque, the midvein and lateral veins (11–15 pairs) sunken, the tertiary venation slightly raised, the lower surface opaque, with midvein, lateral veins, and tertiary venation raised. Inflorescences in the axils of bracts, these ultimately deciduous but present in young inflorescences, up to 5 cm long, very short grey-pubescent, with 10–20 flowers per inflorescence. Inflorescences inserted near the tips of the twigs above the leaves or along short, leafless spurs in the axils of persistent leaves. Bracts at bases of inflorescences black, glabrous, 1–1.5 cm long. Flowers 3–4 mm long, 2.5–3 mm wide, sparsely grey-puberulous, urn-shaped, abruptly widened at the base and gradually narrowed towards the tip. Tepals 6, erect or somewhat incurved, unequal, the outer 3 triangulate, ca. 1 mm long, touching each other and largely obscuring the inner 3 tepals, these ca. 0.6 mm long, 1.1 mm wide. Fertile stamens 3, ca. 1.4 mm long, each with 2 basal glands, 2-celled, the anther cells small, apical, opening towards the centers of the flowers. Staminodia 9, the outer 6 broadly lanceolate, ca. 1 mm long, the inner 3 lanceolate, alternating with the 3 fertile stamens, ca. 0.8 mm long, occasionally with minute anther cells. Ovary glabrous, the floral tube densely pubescent inside. Fruit unknown.

Additional specimen examined. GUATEMALA. ALTA VERAPAZ: Sacté, large tree in dense humid forest, 900–1,050 m (fl), *I. Kunkel 56* (MO).

In Kurz's treatment (1983) *L. bracteata* keys to the subgenus *Guianensis* (correctly: subg. *Licaria,* because it includes the type species of the genus) and within this subgenus to a small group of three Central American and West Indian species with unequal tepals. However, these species (*L. cubensis, L. urceolata* and *L. peckii*) have much smaller leaves, smaller flowers, fewer staminodia, and (with the exception of *L. urceolata*) pubescence on leaves and/or twigs. *Licaria urceolata,* which has glabrous leaves and twigs, lacks the pubescence of *L. bracteata* on the inflorescence. *Licaria bracteata* is an unusual species because of its large, rather persistent bracts, large flowers, and, uniquely in subg. *Licaria,* the presence of nine staminodia.

That Mrs. Kunkel-Westphal, who was not trained as a botanist, collected two interesting new species of Lauraceae in Guatemala, is both a compliment to her qualities as a collector and an indication that many surprises await the collector of large tropical trees.

PHOEBE NEES

A good set of characters to separate the genus *Ocotea* from *Phoebe* has unfortunately not yet been found. *Ocotea* is a particularly large and vaguely defined genus which includes various assemblages of species. *Phoebe* likewise is poorly understood. In the New World there are two main centers of *Phoebe* species: one in northern Central America and one in central-southern Brazil. In the intervening areas *Phoebe* is very poorly represented, and it is not clear yet whether the Brazilian and Central American species form a monophyletic group. An added difficulty is that the type of *Phoebe* is an Asian species and that, according to Kostermans (1961), the Asian *Phoebe* species are not congeneric with the neotropical *Phoebe* species. Kostermans (1961) transferred all neotropical *Phoebe* species to *Cinnamonum,* an Asian genus generally not considered native to the Neotropics. He did not discuss the difficulties in separating *Ocotea* from *Phoebe,* nor the heterogeneous assemblage of species classified in neotropical *Phoebe.*

Earlier authors relied on two characters to separate *Ocotea* from *Phoebe.* In *Ocotea* the staminodes were said to be inconspicuous, in *Phoebe* conspicuous; in *Ocotea* the tepals do not persist in the fruiting stage and a cupule is present, while in *Phoebe* tepals harden and persist in fruit, but no cupule is present. The staminodial character is relative and difficult to interpret. Because flowers of *Ocotea* and *Phoebe* are small and the staminodes almost never exceed 1 mm, one may rightly ask what makes minute staminodes conspicuous in some flowers and inconspicuous in others. Besides, the presence of staminodes is not constant for *Phoebe helicterifolia* (W. Burger, pers. comm.). The presence of persistent tepals in fruit is also a doubtful character. Of the 18 Central American species attributed to *Phoebe* for which I have data, only five have persistent tepals in fruit. However, fruits are unknown for several species. Cupule development in *Ocotea* is very variable and ranges from a widened pedicel with a minute cupule to well-developed cups. Placement of new taxa in *Ocotea* or *Phoebe* has been subjective and will remain so until *Cinnamomum, Ocotea, Phoebe,* and their satellite groups are studied critically.

I use the following characters as indicators for *Phoebe*: tepals erect in flower and persistent in fruit, flowers with relatively long pedicels, staminodes present, and a tendency toward tripliveined leaves. Because the new species has four of the five characters, I place it in *Phoebe.*

Using these indicator characters for *Phoebe,* species such as *P. helicterifolia* (of which *Nectandra corzoana* Lundell is a synonym) and its allies [*P. bourgeauviana* (of which *Ocotea tenejapensis* Lundell is a synonym), *P. obtusata, P. valeriana, Nectandra capituliforma,* and *N. longicuspis*] would be excluded from *Phoebe.* These species should all be placed in the same genus, probably in the already variable *Ocotea,* or, if future study turns up additional characters, in a new genus.

Phoebe glabra van der Werff, sp. nov. TYPE: Mexico. Oaxaca: Municipio Matías Romero, tree, 13 m, *Wendt et al. 4813* (holotype, MO). Figure 3.

Arbor, ad 13 m. Ramuli glabri, teretes. Gemma terminalis glabra. Folia glabra, alterna, chartacea, basi acuta vel rotundata, apice acuminata, reticulatione elevata, axillis nervorum basalium domatiis cavitatibus instructis. Inflorescentiae glabrae, in axillis foliorum vel bractearum deciduarum; flores glabri, ad 3 mm longi, pedicellis 2–3 mm longis; tepala 6, aequalia, ovata, antheris 4-locellatis. Ovarium glabrum, globosum, ca. 1.8 mm longum. Staminodia 3, ca. 0.9 mm longa. Fructus ellipsoideus, 2 cm longus, cupula plana margine integra pedunculo incrassato.

Tree, 8–13 m. Twigs terete, slender, glabrous. Terminal bud glabrous. Leaves chartaceous, alternate, the apex acuminate, the base acute or somewhat rounded, elliptic, 12–16 × 4–6 cm; lateral veins 3–5 pairs, the lowest pair most strongly developed and with slitlike domatia in the axils, these visible as small lumps on the upper surface; veins and reticulation prominently raised on both surfaces; petioles to 1.5 cm long, glabrous. Inflorescences paniculate, glabrous, 5–10 cm long, in the axils of persistent leaves or deciduous bracts, often appearing terminal. Pedicels glabrous, 2–3 mm long. Flowers glabrous, 2.5–3 mm long, funnel-shaped. Tepals 6, equal, ca. 1 mm long, ovate. Stamens 9, all 4-celled, the filaments narrower than the anthers, 1.3–1.4 mm long, glabrous; outer 6 anthers with cells introrse, inner 3 with cells extrorse. Staminodia 3, ca. 0.9 mm long. Ovary globose, glabrous, ca. 1.8 mm long; style short, ca. 0.5 mm long. Fruit an ellipsoid berry, 2 cm long, cupule platelike, the margin entire, 1.4 cm wide, peduncle gradually widened towards the fruit.

Additional specimens examined. MEXICO. VERACRUZ: Municipio Minatitlán, *Wendt et al. 3217* (MO); Municipio Hidalgotitlán, *Wendt et al. 3141* (MO). OAXACA: Municipio Matías Romero, *Wendt et al. 3064* (MO).

Phoebe glabra is closely related to *Ocotea euvenosa* Lundell. Both species have twigs, leaves, and flowers glabrous, raised reticulation, and slitlike domatia (these were not mentioned by Lundell (1965), but the GH isotype of *O. euvenosa* shows the domatia clearly). *Ocotea euvenosa* differs in its larger leaves, laxer reticulation (even a small leaf of *O. euvenosa,* of comparable size to a regular leaf of *Phoebe glabra,* has a laxer reticulation), and in its pinnately veined leaves, not subtripliveined as in *P. glabra.* The type of *O. euvenosa* is in young fruiting stage, which makes comparison difficult. In the fruiting stage the pedicels become much larger, to 2.5 cm long and I therefore attach little taxonomic value to the longer pedicels reported by Lundell (1965) for *O. euvenosa.* Three of the four collections of *P. glabra* come from limestone-derived soils.

PLEUROTHYRIUM NEES

The genus *Pleurothyrium* is separated from the other neotropical lauraceous genera by a set of characteristics associated with strong enlargement of the staminal glands. Each of the filaments of the inner three anthers carries two glands, which, in other genera, are roundish and rather small. There is no doubt these glands produce nectar. In the genus *Pleurothyrium* these glands become strongly enlarged and grow outward between the outer six stamens. In the related genera *Ocotea* and *Nectandra* the outer stamens usually form a tight ring, with the anthers touching each other. The anther cells of the outer stamens in these genera are all introrse; lateral cells are not possible because the anthers form such a tight ring. However, in *Pleurothyrium* the stamens are separated from each other by the outgrowing staminal glands and the stamens stand rather isolated. There are no spatial constraints against lateral cells on the anthers, and indeed one characteristic of *Pleurothyrium* is that the lower pair of cells on the six outer anthers is laterally positioned.

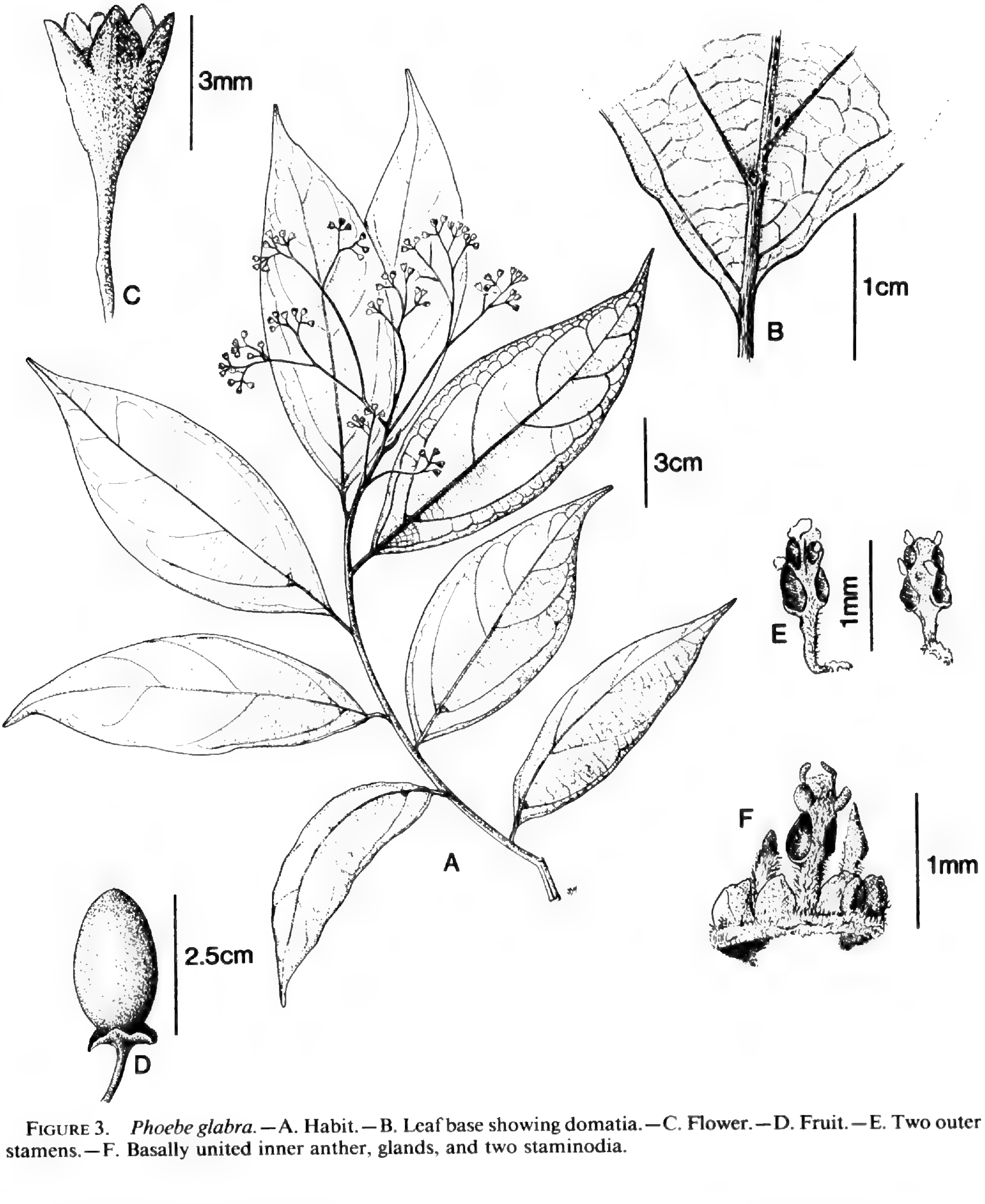

FIGURE 3. *Phoebe glabra.*—A. Habit.—B. Leaf base showing domatia.—C. Flower.—D. Fruit.—E. Two outer stamens.—F. Basally united inner anther, glands, and two staminodia.

A second characteristic of *Pleurothyrium* is that in many species the staminal glands become fused into a ring at the margin of the flower or even form a cushionlike glandular mass with only the anthers and the pistil protruding. This glandular mass has been called a disc by some authors (Hutchinson, 1964). Sometimes one can still discern that the glandular mass is the result of fusion of six glands, and reports that in *Pleurothyrium* nine stamens have two glands each are erroneous, as Rohwer & Kubitzki (1985) pointed out.

Additional characteristics for *Pleurothyrium* are the relatively large, warty cupules, distinctly larger than in most *Ocotea* and *Nectandra* species and quite like the cupules in *Aniba*. The leaves have many lateral veins for their size, a character that, in addition to the large cupules, makes identification of fruiting material possible. Several

Pleurothyrium species also have hollow twigs, which are frequently inhabited by ants.

I noticed in several species that the margins of the tepals are thinner than the centers and that in old flowers the margins of the tepals curl downward and become revolute. I have not seen this in other neotropical Lauraceae.

Pleurothyrium costanense van der Werff, sp. nov. TYPE: Venezuela. Edo. Falcón: Sierra de San Luis, above La Chapa, 1,200 m, 10 Aug. 1979, *van der Werff 3654* (holotype, U; isotype, CORO). Figure 4.

Arbor, 15–20 m. Ramuli teretes, dense ferrugineo-pubescentes. Folia alterna, chartacea, elliptica vel late elliptica, apice rotundata vel breviter acuta, basi obtusa vel acuta, 20–35 × 8–17 cm. Venatio super immersa, subtus elevata reticulatione conspicua. Inflorescentiae axillares, pubescentia ferruginea, 10–15 cm longae. Tepala 6, aequalia, patentia, elliptica. Stamina 9, 4-locellata, 3 interiora locellis extrorsis, 6 exteriora locellis inferioribus lateralibus, locellis superioribus introrsis. Stylum crassum dense pubescens. Glandulae staminium in muro humile connatae, staminibus gynoecioque in centro exposito. Cupula magna, verrucata.

Tree, 15–20 m. Twigs more or less terete, densely ferruginous pubescent, glabrescent with age. Terminal bud densely ferruginous pubescent. Leaves alternate; laminae chartaceous, elliptic or broadly elliptic, the apex rounded or shortly acute, the base obtuse or acute, 20–35 × 8–17 cm; with upper surface opaque, the venation sunken, glabrous except for some pubescence on midvein and main lateral veins; lower surface with raised midvein, lateral veins, and reticulate venation, the midvein and lateral veins with brown pubescence, otherwise with spreading hairs in flowering stage, but glabrous when fruiting; lateral veins 10–15 pairs, the veins arching upwards near the margin and becoming connected with the superior vein; petioles 2–3 cm long, ferruginous pubescent. Inflorescences in axils of deciduous or persisting leaves, 10–15 cm long, ferruginous-pubescent, rather laxly flowered. Flowers white or buff, ca. 1 cm diam. Tepals 6, equal, spreading at anthesis, the outer 3 ferruginous-pubescent outside, the inner 3 puberulous outside except for a narrow, median, pubescent strip, puberulous inside, elliptic, ca. 4 mm long. Stamens 9, all 4-celled, the inner 3 with extrorse cells, the outer 6 with the lower cells lateral, the upper ones introrse. Staminal glands fused into a low wall surrounding the stamens and gynoecium. Style short, stout, densely grey pubescent; stigma flat, about as wide as the style, glabrous; ovary glabrous. Flowering in August. Cupule large, ca. 2 cm high when pressed, conspicuously warty.

Additional specimens examined. VENEZUELA. SUCRE: Peninsula de Paria, Cerro Espejo (fl.), *Steyermark & Rabe 96072* (US, VEN). MONAGAS: Yucucual, E of Caripe (fr.), *Lao 10* (MO).

Pleurothyrium costanense is known from three collections in the Cordillera de La Costa and the Sierra de San Luis, in northern Venezuela. Diagnostic characters are the reticulate venation of the leaves, the broad leaves, and the ferruginous pubescence. The only other *Pleurothyrium* species in northern Venezuela are *P. reflexum* Lasser and *P. zulianense* Lasser (these two names represent the same species, for which I have used the name *P. zulianense* Lasser). *Pleurothyrium zulianense* differs in the lack of reticulate venation, in having narrower leaves and smaller flowers, and in the absence of dense ferruginous pubescence.

The epithet *costanense* refers to the Cordillera de La Costa, where this species is found.

Pleurothyrium grandiflorum van der Werff, sp. nov. TYPE: Colombia. Chocó: Rio Mecana, 5–10 m. Tree, 15 m, along river. Flowers yellow, with pleasant but strange fragrance (as in some euglossine bee-pollinated flowers), *A. Juncosa 1675* (holotype, MO; isotypes to be distributed). Figure 5.

Arbor, 15 m. Ramuli teretes dense breviter pubescentes. Folia elliptica, 15–25 × 4–7 cm, membranacea, glabra, apice acuta, basi argute acuta vel decurrente. Inflorescentiae ad 10 cm longae, pauciflorae, e foliorum deciduorum axillis ortae. Flores magni, 1.5–1.7 cm diametro, flavi, fragrantes. Tepala 6, patentia, 6–7 mm longa, subaequalia; tepala exteriora late elliptica, tepala interiora angustiora, dense breviter pubescentia. Stamina 9, 4-locellata, 3 interiora locellis extrorsis, 6 exteriora 2 locellis inferioribus lateralibus, 2 locellis superioribus laterali-introrsis. Glandulae staminium in muro connatae, staminibus styloque in centro expositis. Fructus ignoti.

Tree, 15 m. Twigs more or less terete, slender, with dense, short, brown pubescence, this velvety-shiny on the terminal bud. Leaves elliptic, 15–25 × 4–7 cm; laminae membranaceous, glabrous on both surfaces, but midvein with some pubescence on lower surface, the apex acute, the base sharply acute or decurrent on the petiole; lateral veins 15–20, departing from the midvein at angles of almost 90°, scarcely or not at all decurrent along the midvein, the venation sunken above, slightly raised on lower surface; petioles 1–1.5 cm long, canaliculate, with same pu-

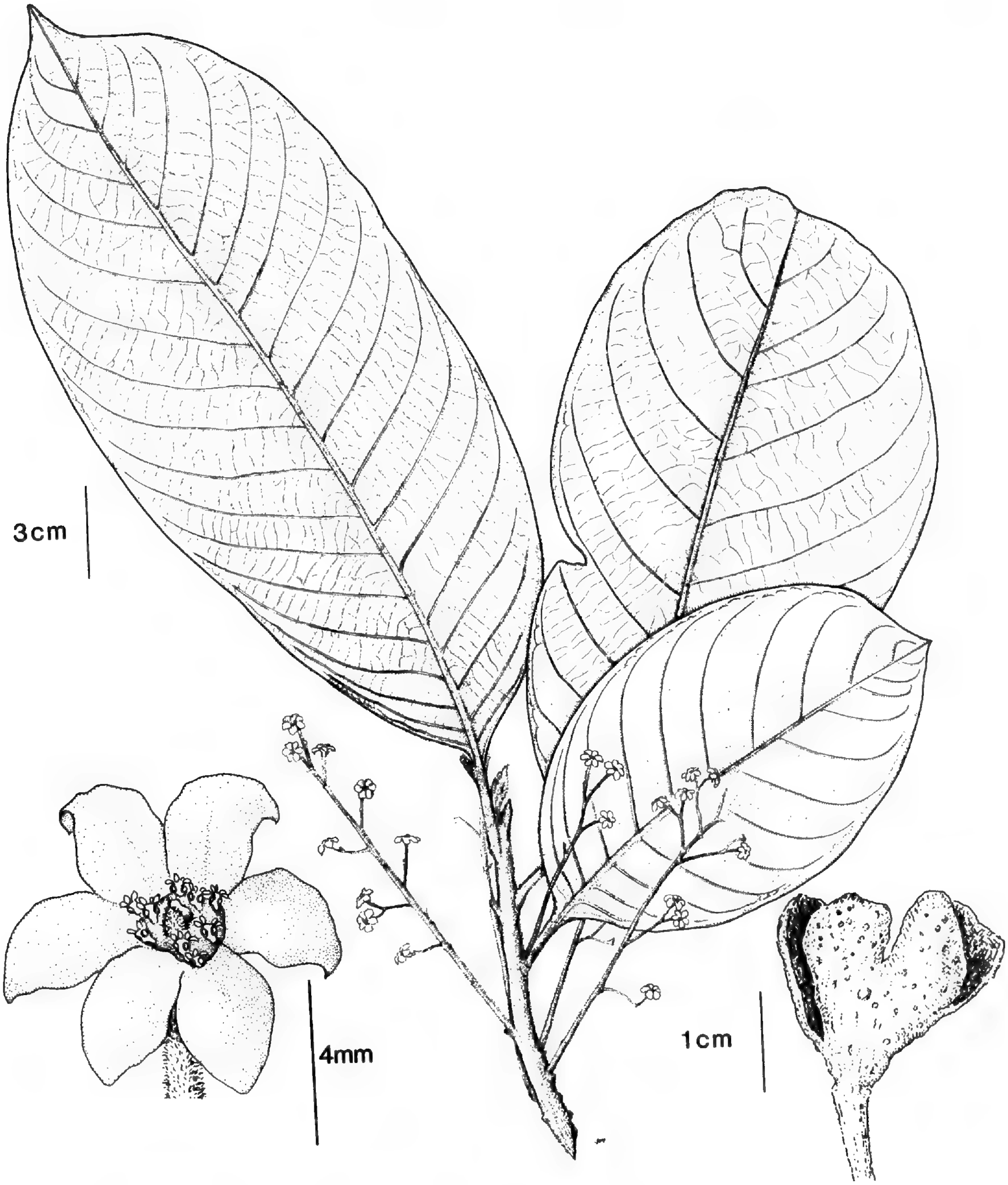

FIGURE 4. *Pleurothyrium costanense.* Habit, flower, and cupule.

bescence as twigs. Inflorescences to 10 cm long, inserted in axils of deciduous leaves below the leafy apices of the twigs, with same pubescence as twigs, few-flowered (only 2 or 3 flowers present on each inflorescence, but with scars indicating former presence of more buds); peduncles ca. 5 mm long, with same pubescence as flowers. Flowers very large for the family, 1.5–1.7 cm diam., yellow, fragrant, densely short brown pubescent, the tube 2–3 mm long. Tepals 6, spreading, 6–7 mm long, subequal; the outer 3 broadly elliptic, the inner 3 narrower, especially near the base, all with dense, short pubescence on the inner surface. Fertile stamens 9, all 4-celled, the inner 3 extrorse, the outer 6 with the lower pair of anther cells lateral, the upper pair lateral-introrse; anthers glabrous. Staminal glands forming a large wall surrounding the stamens or seem-

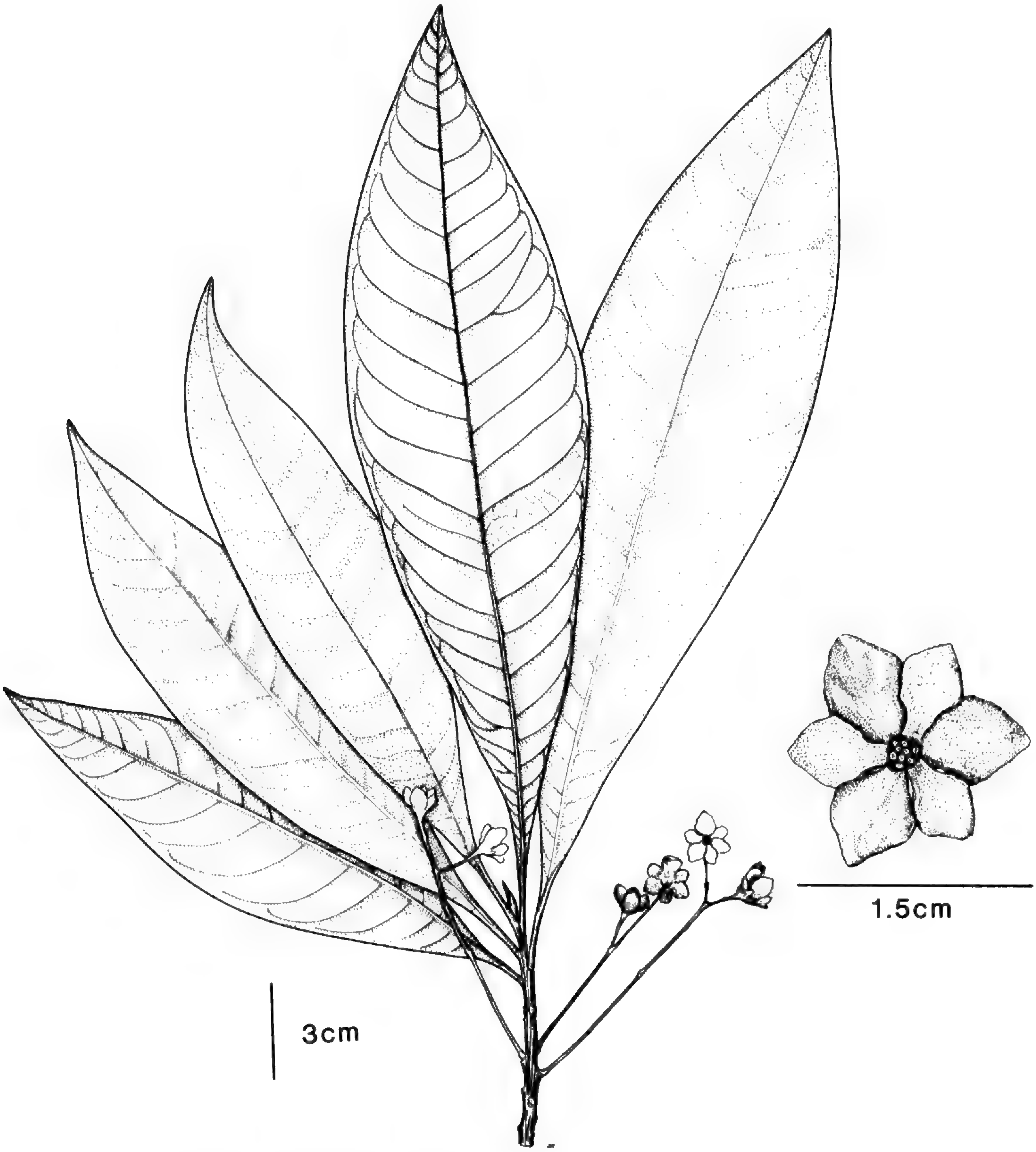

FIGURE 5. *Pleurothyrium grandiflorum.* Habit and flower.

ingly covering the stamens in very young flowers. Stigma platelike, ca. 0.3 mm diam., of almost same color and texture as the anthers. Fruit unknown.

Pleurothyrium grandiflorum is known only from the type collection made in the Chocó area, Colombia, an area rich in endemics. The species is very distinct in its large flowers and few-flowered inflorescences. In contrast to most Lauraceae, the lateral veins are hardly or not at all decurrent along the midrib.

Pleurothyrium westphalii van der Werff, sp. nov. TYPE: Guatemala. Alta Verapaz: Sacté. Tree in dense, humid forest, 20 Apr. 1976, *I. Kunkel 9* (holotype, BR). Figure 6.

Arbor, 20 m. Ramuli glabri, juvenales hinnulei pubescentes. Folia alterna, elliptica, apice acuta, basi acuta, basi acuta vel decurrenti, membranacea, glabra. Inflorescentiae ad 8 cm longae, parviflorae, pubescentia hinnulea, e foliorum vel bractearum deciduarum axillis ortae. Tepala 6, aequalia, patentia sub anthesim, pubescentia hinnulea. Stamina 9, 4-locellata, 3 interiora locellis extrorsis, 6 exteriora 2 locellis inferioribus la-

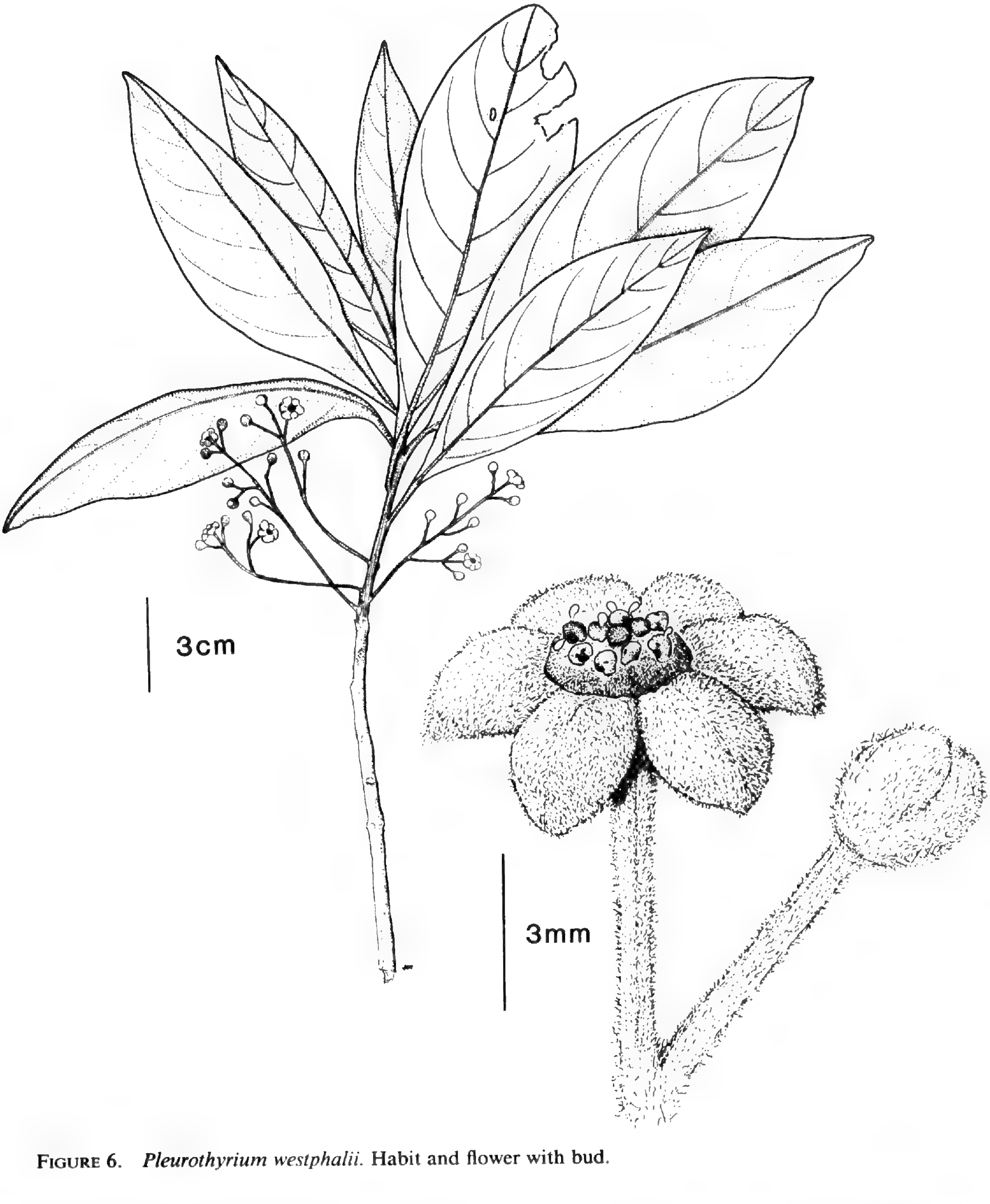

FIGURE 6. *Pleurothyrium westphalii.* Habit and flower with bud.

teralibus, 2 locellis superioribus introrsis. Glandulae staminium in muro connatae staminibus styloque in centro expositis. Fructus ignoti.

Tree, to 20 m. Older twigs glabrous, young twigs with brown, dense, short pubescence. Leaves elliptic, the apex acute, the base sharply acute or somewhat decurrent along petiole, membranaceous, 15–20 × 4–7 cm, glabrous or nearly so above, with some appressed pubescence, especially near base, but glabrescent with age below; lateral veins 5–8, fading out near the margin, not looping upward and not connected with other lateral veins; upper leaf surface dark, dull, venation sunken; midvein, secondary, and tertiary venation slightly elevated; petioles to 1 cm long, pubescent as the young twigs. Inflorescences ca. 8 cm long, densely grey-brown pubescent, few-flowered (fewer than 10 flowers per inflorescence), in the axils of deciduous leaves or bracts on the young twigs but attached below the leaves, narrowly pyramidate. Flowers with 6 equal tepals, these spreading or slightly reflexed at anthesis, densely short tomentose outside, slightly less so inside, the tepals ovate, ca. 4 mm long. Fertile stamens 9, all 4-celled, the inner 3 extrorse, the outer 6 with the lower two cells lateral, the upper two cells introrse. Anthers glabrous, staminal glands not individually visible, but fused into circular mass ca. 3 mm in diam. with the anthers and pistil protruding in the middle. Pistil platelike, gray. Fruit unknown.

Additional specimens examined. GUATEMALA. ALTA VERAPAZ: Sacté, *Kunkel 17* (fl.) (MO), *298* (sterile) (BR).

Pleurothyrium westphalii is the northernmost species of its genus and is known only from one locality in Guatemala. Two other *Pleurothyrium* species, as yet undescribed and under study by W. Burger, are known from Central America. The species represented by *Allen 5885* (GH, US) from Costa Rica differs in having leaves with acuminate apices, persistent bracts in the inflorescence, leaf bases acute but not decurrent, and the inner surfaces of the tepals papillose-puberulous, not pubescent. The leaves of *Allen 5885* also have more lateral veins which arch upward and become connected, forming almost a marginal vein, as is often seen in *Pleurothyrium* species. The second species, represented by *Bunting & Licht 872* (NY) from the Río San Juan area, Nicaragua, differs in having a many-flowered inflorescence (20–30 flowers per inflorescence), darker pubescence, and the staminal glands not fused into a large wall as in *P. westphalii.*

This species is named after the collector, Irene Kunkel, née Westphal, who collected two new and very interesting species of Lauraceae in Guatemala.

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A NEW SPECIES OF *OCOTEA* (LAURACEAE) FROM SOUTHEASTERN MEXICO[1]

TOM WENDT[2] AND HENK VAN DER WERFF[3]

ABSTRACT

The new species *Ocotea uxpanapana* is a common riparian tree of the Uxpanapa area of extreme southern Veracruz, Mexico. It appears to be most closely related to *O. eucuneata* of Guatemala and Belize. It is yet another species apparently endemic to the rain forests of the Uxpanapa area.

Ocotea uxpanapana Wendt & van der Werff, sp. nov. TYPE: Mexico. Veracruz: Municipio Minatitlán, Zona de Uxpanapa, terracería La Laguna-Uxpanapa, orilla Oeste del Río Oaxaca, un poco al Oeste de Uxpanapa, 17°13′N, 94°13′15″O, 160 m, 14 Feb. 1981 (fl), *Wendt, Villalobos & Olmstead 2869* (holotype, MEXU; isotypes, BM, CAS, CHAPA, ENCB, MO, NY, and others).

Arbor ad 30 m. Ramuli hornotini sericei cito glabrescentes. Laminae foliorum obovatae vel ellipticae, 8–25 cm longae, 2.2–8 cm latae, plerumque 3–4.3-plo longiores quam latiores, apice acuminata, basi acuta vel cuneata, supra glabratae, subtus subtiliter strigosae axillis barbatis. Paniculae pseudoterminales; flores (4–)4.5–6 mm diam.; tepala dense minute canescentia, 1.9–3 mm longa; stamina externa stipitata. Fructus ellipticus, ad 2.2 cm longus; cupula valde 6-lobata. Figure 1.

Tree, to 30 m, to 1 m d.b.h. or often with several trunks from near the base; buttresses small to medium-sized or lacking; bark medium gray-brown to dark chocolate-brown, finely to prominently warty, soft; slash of bark aromatic, light brown or yellowish-brown, oxidizing in ca. 1 minute to darker orange-brown; sapwood pale cream-brown. Shoot apices (youngest portions of stems and new leaves) and axillary buds densely and finely sericeous; twigs soon glabrate, green (drying dark or black). Leaves alternate; blade obovate to elliptic, usually narrowly so, 8–25 cm long, 2.2–8 cm wide, some leaves smaller, mostly 3–4.3 times as long as wide, firmly membranaceous, slightly and irregularly conduplicate, medium-dark green, finely and densely glandular-punctate, distally acute or rounded to a short- or long-acuminate (to 2.5 cm) apex with a minutely rounded tip, the base acute to usually cuneate; venation slightly raised above, prominently so below, laterals 7–14, diverging at 40–65°, the lowest 1–2 pairs usually more strongly ascending (20–35°), basically eucamptodromous but often more or less brochidodromous distally, the tertiary venation more or less transverse between laterals, the fine venation reticulate; adaxial surface glabrous, abaxially finely strigose on surface and sides of midvein, at length sometimes subglabrate, lowest 1–several pairs of lateral veins prominently barbate in axils; petioles 1–2.3 cm long, canaliculate adaxially, at first finely strigose, soon glabrate. Inflorescence complex formed by a group of paniculate cymes, each of these arising from the axil of a quickly deciduous bracteate leaf (or rarely a foliage leaf), the apex of each complex a small, temporarily dormant vegetative shoot, each inflorescence arising either in the axil of a mature leaf or along the apical portion of the main stem, several inflorescences occurring together to form a large pseudoterminal inflorescence complex, the vegetative apices usually elongating after flowering and producing mature leaves, the fruiting panicles thus more obviously lateral; individual inflorescences 5–20 cm long, 2–13 cm broad, cylindrical to pyramidal, with a more or less straight central axis bearing strongly diverging laterals, the latter sometimes similarly rebranched, bearing dichasial groups of flowers, the axes flattened, green to pinkish, lightly canescent to glabrate in basal parts, to densely canescent distally; flower bracts lance-ovate to deltate, 2–2.5 mm long, densely and finely canescent, very quickly deciduous; pedicels stout, 1.5–3.5 mm long, densely and finely canescent, green. Flowers (4–)4.5–6 mm diam. at anthesis;

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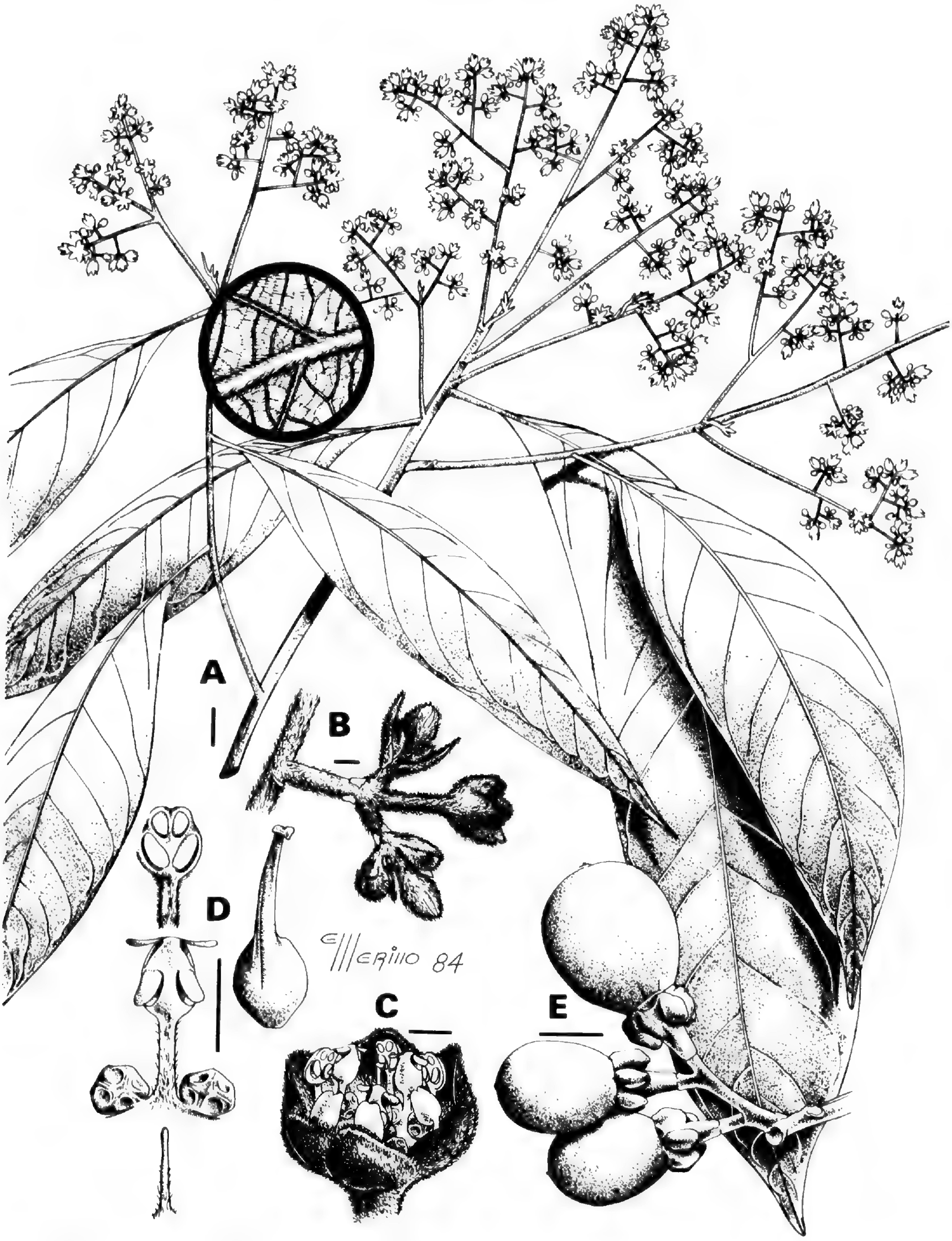

FIGURE 1. *Ocotea uxpanapana.*—A. Branchlet with inflorescences; inset, lower surface of leaf.—B. Portion of inflorescence, pre-anthesis.—C. Flower.—D. Parts of the flower: above, outer stamen, adaxial view; center, inner stamen, abaxial view; below, staminode (frequently absent); right, gynoecium.—E. Fruits with unique lobed calyx. Bar scales: A, E = 1 cm; B, C, D = 1 mm. Vouchers: A–D, *Wendt et al. 2869* (staminode in D, *2865*); E, *Wendt et al. 2777.*

tepals at anthesis ascending 25–45° or more, broadly ovate, 1.9–3 mm long, 1.5–2.4 mm wide, thick-textured, cream to creamy-green, abaxially canescent with short, thick, gray hairs mostly 0.05–0.15 mm long, adaxially less densely so, the apex broadly acute to acute; hypanthium 0.6–1 mm long. Outer 6 stamens 1.1–1.6 mm long; filaments 0.5–0.9 mm long, pubescent; anthers quadrate-ovate, with truncate to emarginate apices, and with the upper pair of thecae more or less above the lower pair; inner 3 stamens 1.5–2 mm long; filaments 0.7–1.2 mm long, pubescent, the basal pair of glands short-stipitate to subsessile; staminodes absent or, when present, less than 1 mm long, linear, pubescent. Ovary 1–1.5 mm long, glabrous; style (0.5–)1–1.4 mm long, shorter than to slightly longer than ovary. Fruit (nearly mature) broadly ellipsoid, to 2.2 cm long, to 1.9 cm thick, green, seated in a very shallow strongly 6-lobed red, fleshy cupule, the lobes 5–7 mm long, 3–5 mm high, 2–3 mm thick; flesh of fruit ca. 1 mm thick, pale green. Testa dark brown; flesh of cotyledons pink.

Paratypes. MEXICO. VERACRUZ: Zona de Uxpanapa. *Mpio. Hidalgotitlán:* Campamento La Laguna, along Río Las Cuevas, 6 Mar. 1984 (fl.), *Taylor 387* (F, MO, XAL); Campamento Hnos. Cedillo, 18 Jun. 1974 (fr), *P. E. Valdivia Q. 808* (MO, XAL); Propiamente en la Escuadra, 7 Aug. 1974 (fr), *P. E. Valdivia Q. 1312* (MO, XAL); A 600 m del Campamento Hnos. Cedillo hacia Paso Moral, 8 Aug. 1974 (fr), *P. E. Valdivia Q. 1334* (MO, XAL); Campamento Hnos. Cedillo, 17°16′N, 94°36′W, 150 m, 27 Aug. 1974 (young fr), *Brigada Vázquez 1029* (MEXU, MO); Brecha Hnos. Cedillo-Agustín Melgar, 5 Mar. 1974 (fl), *Brigada Vázquez 535* (MO, XAL); La Escuadra-Hnos. Cedillo, por el Río Soloxuchil, 3 May 1974 (fr), *Brigada Vázquez 729* (MO, XAL); Campamento La Laguna, Río Las Cuevas, 17°16′30″N, 94°30′W, 130 m, 17 Mar. 1982 (fl), *Wendt, Villalobos & Navarrete 3725* (CHAPA, MEXU, MO, and others); *Mpio. Minatitlán:* Río Uxpanapa, desde el poblado de Uxpanapa arriba, 17°12′N, 94°10′W, 130 m, 14 Jul. 1980 (young fr), *Wendt, Villalobos & Lara 2564* (CHAPA, MEXU, MO, and others); Uxpanapa, orilla del Río Uxpanapa, 17°13′10″N, 94°12′45″W, 130 m, 27 Sep. 1980 (fr), *Wendt et al. 2777* (CHAPA, MEXU, MO, and others); 32 km al E de La Laguna sobre terracería a Uxpanapa, 1.1 km al W de La Garganta, 17°13′30″N, 94°15′30″W, 180 m, 13 Feb. 1981 (fl), *Wendt, Villalobos & Olmstead 2865* (CHAPA, MEXU, MO, and others); type locality and date, *Wendt, Villalobos & Olmstead 2869A* (CHAPA, MEXU, MO, and others).

Common names. Aguacatillo, laurel.

Ocotea uxpanapana is a common riverside tree of the Uxpanapa area of southern Veracruz, a region of lowland rain forests with high endemism (see Wendt et al., 1985, and references there cited); it is interesting that this riparian tree has never been collected farther downstream in the Río Coatzacoalcos basin. In the Uxpanapa area, the new species and *Ficus insipida* Willd. are the most common large riparian trees. The root system of *O. uxpanapana* is apparently deep and well adapted to resist flooding; during the major flooding of the Río Oaxaca in October of 1980, all trees (including *Ficus insipida*) except for many individuals of *O. uxpanapana* were toppled and carried away. *Ocotea uxpanapana* also occurs scattered in nonriparian sites on deep limestone-derived soils. It flowers mostly in February and March, fruiting in September and October.

Ocotea is a large, mostly neotropical genus with a few hundred species. The last comprehensive treatment was by Mez (1889), and since that time many additional species have been described. The Central American species were treated by Allen (1945), but the genus has remained difficult and almost inaccessible to the nonspecialist. Under these circumstances, we were initially hesitant to describe yet another *Ocotea* species, but the striking, deeply six-lobed cupule is such a unique feature in the genus, even in the family, that we decided to publish a new species. It appears to be most closely related to *O. eucuneata* Lundell (type from Belize). In addition to its less strongly lobed cupule (fruiting material collected in the mountains of Guatemala, identified by C. Allen), *O. eucuneata* differs in its inflorescences borne in the axils of mature leaves (not forming a pseudoterminal inflorescence as in *O. uxpanapana*), its smaller flowers, and in having the reticulation on the upper leaf surface immersed (not raised as in *O. uxpanapana*).

Specimens collected by the Brigada Vázquez and P. E. Valdivia Q. are distributed under several names (*Nectandra loeseneri* Mez, *N. salicifolia* Kunth, *Persea americana* Miller, and *Phoebe gentlei* (Lundell) Standley & Steyerm.) and are likely filed as such in several additional herbaria.

Wood and bark samples of the new species (*Wendt et al. 3725*) were examined by H. G. Richter. He noted (pers. comm.) that the wood and bark anatomy are typical of *Ocotea* in general and are nondescript within the genus.

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FOUR NEW SPECIES OF *AXONOPUS* (POACEAE: PANICEAE) FROM TROPICAL AMERICA[1]

GERRIT DAVIDSE[2]

ABSTRACT

The following species of *Axonopus* sect. *Axonopus* are described: *A. rupestris,* from Goiás, Brazil, *A. casiquiarensis* from Guainía, Colombia, and Amazonas, Venezuela, *A. chimantensis* from Bolívar, Venezuela, and *A. jeanyae* from Coclé, Panama.

Axonopus is a predominantly tropical American grass genus with a few species extending into the American subtropics and the Old World tropics. Black (1963) monographed the genus and recognized 109 species. With continued exploration it has become apparent that new species remain to be described. On the other hand, it is also probable that some of the species recognized by Black must eventually be synonymized as intermediate populations become known.

Axonopus belongs to the tribe Paniceae and is distinguished by the absence of a lower glume, lower palea, and lower flower, and by its solitary, dorsally compressed spikelets borne inversely (i.e., with the back of the upper glume facing away from the rachis) in two rows on one or usually several to many racemes.

This paper reports on recent fieldwork in tropical America that has brought to light four undescribed species of *Axonopus* sect. *Axonopus.* These are published now so that the names will be available for two forthcoming floras, *Flora Mesoamericana* and *Flora of the Venezuelan Guayana.*

Axonopus rupestris Davidse, sp. nov. TYPE: Brazil. Goiás: Mun. Presidente Kennedy, road from highway BR-153 to Itaporá, 12 km W of village of Presidente Kennedy, Fazenda Primavera along Ribeirão Feínho, ca. 3°25′S, 40°37′W, 400–500 m, 1 Feb. 1980, *T. Plowman, G. Davidse, N. A. Rosa, C. S. Rosário & M. R. dos Santos 8216* (holotype, MG; isotypes, F, MO, NY). Figure 1.

Axonopus rupestris Davidse, sp. nov. *A. triglochinoides* (Mez) Dedecca affinis sed spiculis brevioribus, racemis paucispiculis, glumis minus valde nervis, et anthoeciis glabris differt.

Caespitose perennial; culms 10–35 cm tall, the internodes 1–2 mm wide, hollow, glabrous, the nodes 1–2, glabrous, the uppermost geniculate. Leaves erect; sheaths to 7.5 cm long, strongly distichous, conduplicate and keeled, apically winged, mostly glabrous, sparsely hirsute near the juncture with the blade; flag leaf sheath to 10 cm long; collar not differentiated, the sheath with a slight marginal constriction apically but otherwise merging imperceptibly with the blade; ligule a ciliate membrane 0.5–0.6 mm long, the membrane 0.1–0.2 mm long, the cilia 0.4–0.5 mm long; blades erect, mostly 5–10 cm long, folded, mostly 1–2 mm wide as folded, sparsely papillose-hirsute abaxially and adaxially along the midrib to glabrescent, the apex acute. Inflorescences 4.5–7 cm long; peduncles 1 or 2, the uppermost to 19 cm long; racemes usually 2, conjugate, sometimes 3 with the lowermost borne 5–10 mm below the upper pair, 4.5–6.5 cm long, widely spreading at maturity, the axil puberulent; rachis ca. 0.6 mm wide, glabrous, 14–16 spikelets per 25 mm; pedicels 0–0.1 mm long, glabrous; spikelets 2.9–3.5 mm long, 0.8–1 mm wide, elliptic-oblong, obtuse, the upper glume 0.2–0.3 mm longer than the lower lemma, 5-nerved, the lateral nerves marginal, the midnerve weakly developed, prominently pubescent marginally and between the nerves with hairs 0.5–1 mm long, the hairs longest apically, the upper ¼ glabrous; lower lemma marginally 4-nerved, the midnerve not developed, prominently pubescent marginally and between the nerves; anthoecium 0.5–0.9 mm shorter than the upper glume, stramineous,

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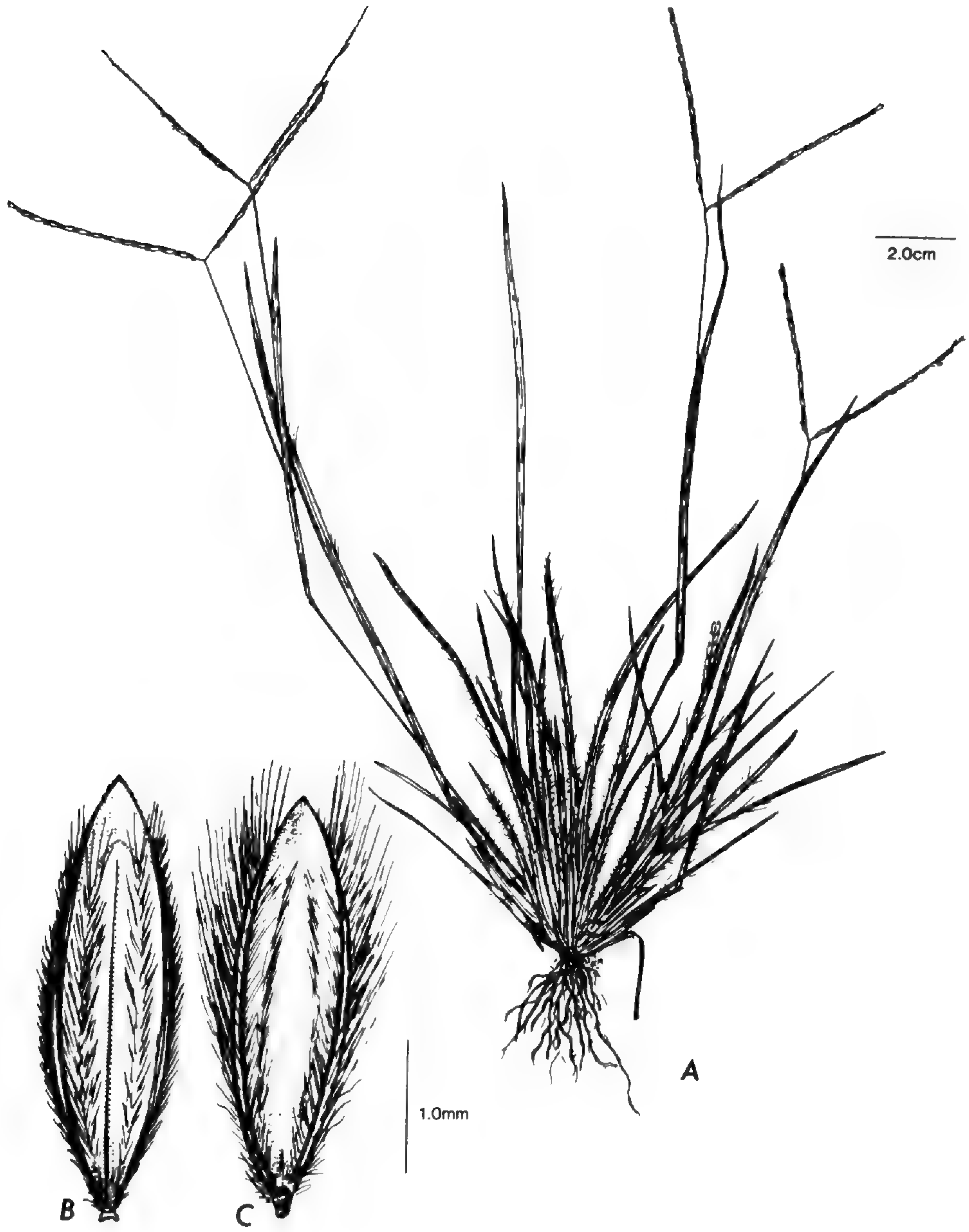

FIGURE 1. Isotype of *Axonopus rupestris.*—A. Habit.—B. Abaxial view of spikelet showing the upper glume.—C. Adaxial view of spikelet showing the lower lemma. [After *Plowman et al. 8216* (MO).]

nearly glabrous at the tip, obtuse; lodicules 2, fleshy, truncate, glabrous; stamens 3, the anthers 1–1.2 mm long, dark yellow; styles 2, separate; stigmas plumose, white; caryopsis not seen.

This species is known only from the type collection, which was encountered in cracks and shallow, gravelly soil pockets of a black, granitic rock outcrop (Fig. 2). The epithet alludes to this rocky habitat.

This species, by virtue of its glabrous rachis, stramineous anthoecia, perennial habit, few racemes, and weakly developed midnerve of the glumes, belongs to sect. *Axonopus* ser. *Axonopus* of Black (1963). However, it does not seem closely related to any of the species grouped by Black in this series. Rather, *A. rupestris* seems most closely related to *A. triglochinoides,* a species of the Río Atabapo and upper Río Negro drainages, which Black placed in sect. *Axonopus* ser. *Barbigeri* subser. *Barbigeri* because the midnerve of the glume is developed, although not as strongly as in typical members of this series.

Axonopus rupestris differs from *A. triglochinoides* in the smaller, much more conspicuously pubescent spikelets (2.9–3.5 vs. 3.9–4.8 mm), greater spikelet density on the inflorescence branches (14–16 vs. 6–7 spikelets per 25 mm), less prominently nerved glumes, and lack of a prominent tuft of hairs at the tip of the anthoecium. The two species are similar in the general facies of their inflorescences and leaves, especially in the prominently distichous, densely tufted sheaths. Both species are relatively uncommon, although local populations may consist of hundreds of individuals. *Axonopus triglochinoides* also grows in cracks of granite outcrops and shallow soil pockets.

Figure 2. *Axonopus rupestris* habit and habitat, type locality, Goiás, Brazil.

Axonopus chimantensis Davidse, sp. nov. TYPE: Venezuela. Bolívar: Distr. Piar, Macizo del Chimantá, sector centro-noreste del Chimantá-tepui, cabeceras orientales del Caño Chimantá, vegetación litófita y ribereña alrededor del comienzo E del Cañón recto del Río Chimantá superior, ca. 5°18′N, 62°09′W, ca. 2,000 m, 26–29 Jan. 1983, *O. Huber & J. A. Steyermark 6931* (holotype, MO; isotypes, K, NY, US, VEN). Figure 3.

Axonopus chimantensis Davidse, sp. nov. *A. villosus* Swallen affinis sed foliis culmis ligulis et spiculis minoribus differt.

Caespitose perennial; culms 25–60 cm tall, the internodes 1–2 mm wide, hollow, somewhat flattened, glabrous or apically with two lines of pubescence along the margins, unbranched, the nodes 1, rarely 2, densely pilose; sheaths 3–9 cm long, very strongly distichous, conduplicate and keeled, apically winged, glabrous except for the upper ⅓ of the margin and keel where ciliate, the margin membranous; flag leaf sheath 10–21 cm long; collar prominent, densely pilose; ligule a ciliate membrane 0.3–0.5 mm long, the membrane 0.1–0.2 mm long, the cilia 0.2–0.4 mm long; blades folded, 6–18 cm long, 3.5–5 mm wide as folded, divergent, usually prominently ciliate on the margins, the keel sparsely ciliate to glabrescent, the tip obtuse, scabrous, adaxially very sparsely pilose to glabrous, abaxially glabrous. Inflorescence 3–10.5 cm long; axis 5–18 mm long; peduncles 1–2, usually well-exserted; racemes 2–4, 2.5–10 cm long, spreading at acute angles, the axils pubescent, the rachis 0.5–0.8 mm wide, scaberulous or pubescent marginally, 9–13 spikelets per 25 mm; pedicels 0.2–1.1 mm long. Spikelets 3–3.4 mm long, 0.9–1.1 mm wide, oblong-elliptic, obtuse; upper glume as long as the lower lemma or to 0.4 mm longer, 5-nerved, the midnerve developed, inconspicuously and sparsely short-pubescent between the nerves; lower lemma similar to the upper glume; anthoecium 0.3–0.7 mm shorter than the upper glume, stramineous, apically with a distinct tuft of hairs, obtuse; lodicules 2, fleshy, minutely erose, glabrous; stamens 3, the anthers 1.2–1.5 mm long, purple; styles 2, separate; stigmas plumose, purple; caryopsis not seen.

Paratypes. VENEZUELA. BOLIVAR: Distr. Piar, Macizo del Chimantá, sector centro-noreste del Chimantá-tepui, cabeceras orientales del Caño Chimantá, ca. 5°18′N, 62°09′W, ca. 2,000 m, 26–29 Jan. 1983, *Steyermark et al. 128195* (MG, MO, NY, US, VEN), *128007* (MO), *Huber & Steyermark 6896* (MO, VEN); Dist. Piar, Macizo del Chimantá, altiplanicie en la base meriodional de los farrallones superiores del Apacarátepui, sector norte del Macizo, ca. 5°20′N, 62°12′W, ca. 2,200 m, 30 Jan.–1 Feb. 1983, *Steyermark et al. 128405* (K, MO, VEN), *Huber & Steyermark 7043* (MO, VEN), *7032* (MO, VEN); Chimantá Massif, central section, island in Río Tirica above Middle Falls below Summit Camp, 1,925 m, 5 Feb. 1955, *Steyermark & Wurdack 463* (US, VEN); Chimantá Massif, central section, swampy savanna along tributary valley of E branch of headwaters of Río Tirica, 2,120 m, 13 Feb. 1955, *Steyermark & Wurdack 836* (US, VEN).

Axonopus chimantensis belongs to Black's (1963) sect. *Axonopus* ser. *Barbigeri* subser. *Ancipites* because of the perennial habit, non-papillose-pilose rachis and spikelets, stramineous anthoecia, developed midnerve of the glume, and broad, folded blades with obtuse apices. This group of species is best developed in northern South America, especially in the Guayana Region.

Axonopus chimantensis seems most closely related to *A. villosus* and *A. steyermarkii* Swallen. Both of these are much larger than *A. chimantensis*. In addition *A. villosus* has slightly larger

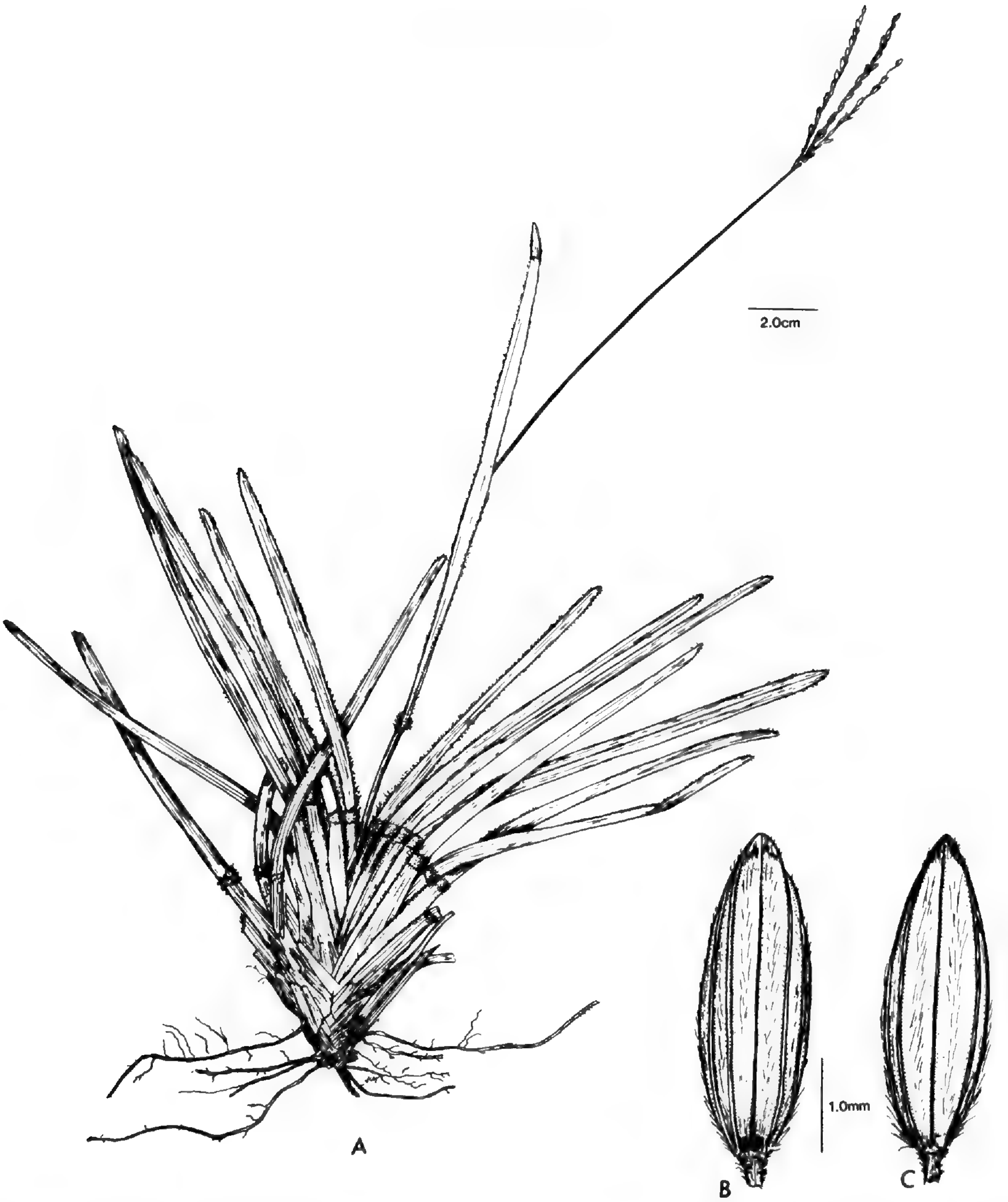

FIGURE 3. Holotype of *Axonopus chimantensis.*—A. Habit.—B. Abaxial view of spikelet showing the upper glume.—C. Adaxial view of spikelet showing the lower lemma. [After *Huber & Steyermark 6931* (MO).]

and broader spikelets with more prominent nerves, larger ligules, relatively longer anthoecia, and a tendency toward densely pubescent blades and sheaths. *Axonopus steyermarkii* differs further in its nearly glabrous foliage, blades noticeably narrowed at their bases, and usually longer pedicels.

Many of the cited specimens of *A. chimantensis* have smut-infected spikelets.

The rachis of the racemes in *A. chimantensis* varies from pubescent to scabrous, a characteristic also attributed to *A. villosus* by Black (1963). Black cited *Steyermark & Wurdack 463* and *863* as *A. villosus*, but I refer them to *A. chimantensis.* As far as presently known, *A. chimantensis* is endemic to the large Chimantá-tepui system in Bolívar and derives its epithet from this.

Axonopus steyermarkii is endemic to Cerro Marahuaca and nearby Cerro Duida in Amazonas, Venezuela. *Axonopus villosus* occurs in the same area as *A. steyermarkii* and may reach as far north as the Río Manapiare.

Axonopus casiquiarensis Davidse, sp. nov. TYPE. Venezuela. Amazonas: Dpt. Atabapo, Cucurital de Caname, S bank of the middle part

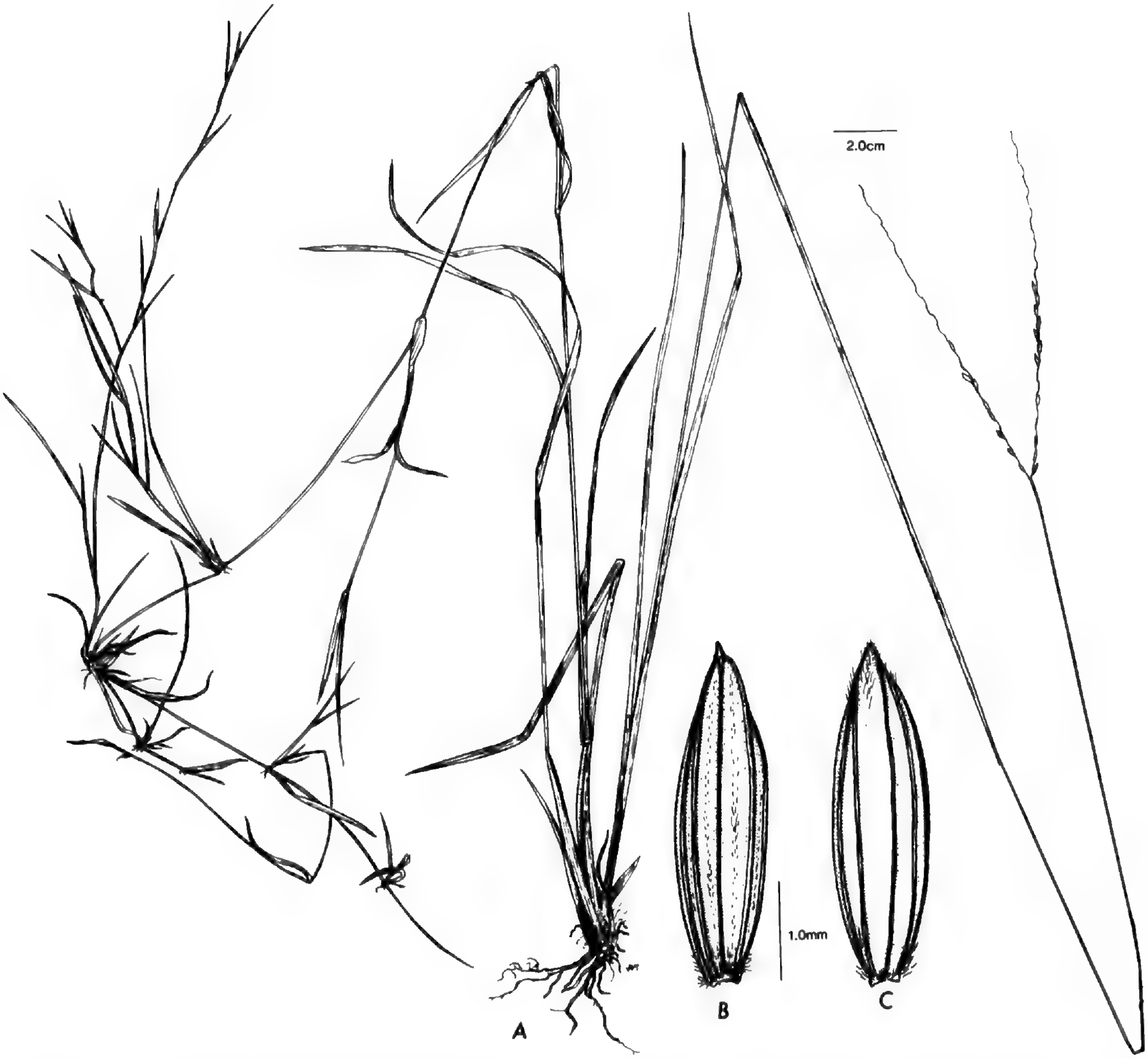

FIGURE 4. Holotype of *Axonopus casiquiarensis.*—A. Habit.—B. Abaxial view of spikelet showing the upper glume.—C. Adaxial view of spikelets showing the lower lemma. [After *Davidse et al. 16907A* (MO).]

of Caño Caname, 67°22′W, 3°40′N, ca. 100 m, 30 Apr.–1 May 1979, *G. Davidse, O. Huber & S. S. Tillett 16907A* (holotype, MO, mounted as 2 sheets; isotypes, K, US, VEN). Figure 4.

Axonopus casiquiarensis Davidse, sp. nov. *A. comans* (Trin.) Kuhlm. et *A. camargoanus* Black affinis sed stolonibus, basibus culmi gracilioribus et foliis latioribus differt.

Stoloniferous perennial; stolons infrequent, when present well-developed, to 70 cm long, leafy, frequently rebranching and producing tufts of leaves at the nodes, the internodes to 20 cm long; culms 24–90 cm tall, the internodes ca. 1 mm wide, hollow, slightly flattened, glabrous, the nodes 1–2, usually appressed-pubescent, rarely glabrous. Sheaths mostly 3–12 cm long, rounded on the back, not strongly distichous, not winged, usually glabrous, sometimes pilose at the base, auricular hairs 1–3 mm long usually present; flag leaf sheath to 29 cm long; collar not differentiated; ligule a ciliolate membrane 0.1–0.2 mm long, the membrane nearly obsolete to 0.1 mm long, the cilia ca. 0.1 mm long; blades mostly 7–60 cm long, 1–3 mm wide, flat to convolute, commonly ciliate in the lower ⅓, otherwise glabrous, the apex acute. Inflorescence 4–15 cm long; axis 2–30 mm long; peduncles 1 or 2, usually well-exserted; racemes 2–3(–5), 4–14.5 cm long, nearly appressed to spreading at acute angles, the axils puberulent; rachis 0.3–0.5 mm wide, scaberulous, 10–15 spikelets per 25 mm; pedicels 0.1–0.7 mm long. Spikelets (2.5–)2.7–3.7(–4.1) mm long, 0.8–1.3 mm wide, oblong-elliptic to lanceolate-elliptic, obtuse; lower glume as long as to 0.3 mm shorter than the lower lemma, 5–7-nerved, the midnerve developed, slightly sulcate between the nerves, usually sparsely pubescent between the nerves, sometimes nearly glabrous or strongly pubescent; lower lemma similar to the upper glume; anthoecium 0.1–0.7 mm shorter than the upper glume, stramineous, apically with a distinct tuft of hairs, obtuse; lodicules 2, fleshy, inconspicuously 3-lobed, glabrous, vasculated; stamens 3, the anthers 1.5–2.2 mm long, purple; styles 2, separate; stigmas plumose, purple; caryopsis ca. 1.5 mm long and 0.7 mm wide, elliptic-obovate, the hilum elliptic-punctate, the embryo ca. ½ the length of the caryopsis.

Paratypes. COLOMBIA. GUIANÍA: Río Atabapo, ca. 7 km S of San Fernando de Atabapo, 67°43′W, 3°55′N, 28 Apr. 1979, *Davidse 16825* (MO, VEN). VENEZUELA. AMAZONAS: DPT. ATABAPO: Caño Caname, 67°22′W, 3°40′N, 29 Apr.–4 May 1979, *Huber et al. 3643* (MO, VEN), 30 Apr. 1979, *Huber et al. 3651* (MO, VEN), 2 May 1979, *Davidse et al. 17049* (COL, K, MO, TFAV, VEN), 67°13′W, 3°40′N, 3 May 1979, *Davidse et al. 17126* (MO, VEN), 67°23′W, 3°41′N, 2 May 1979, *Davidse et al. 17084* (MO, VEN); Caño Yagua, 66°34′W, 3°36′N, *Davidse et al. 17421* (MO, VEN), 66°41′W, 3°29′N, 7 May 1979, *Davidse et al. 17314* (MO, VEN); 5 km al S de la Laguna Yagua, 66°38′W, 3°43′N, 22 Jul. 1980, *Huber & Tillett 5476* (MO, VEN); Río Atabapo, 20 km S of San Fernando de Atabapo, 67°39′W, 3°50′N, 29 Apr. 1979, *Davidse et al. 16856* (INPA, MG, MO, VEN); Caño Cotuá, cerca Cerro Yapacana, 66°50′O, 3°40′N, 14–28 Feb. 1978, *Huber 1605, 1679* (MO, VEN), 66°52′W, 3°38′N, 6 May 1979, *Davidse et al. 17262* (MO, NY, VEN), *17229, 17239* (MO, VEN). DPT. CASIQUIARE: medio Río Temi, 67°29′O, 2°57′N, 24 Feb. 1979, *Huber 3410* (K, MO, TFAV, VEN). DPT. RIO NEGRO: lower Río Baria, 66°32′–66°25′W, 1°27′–1°10′N, 22–23 Jul. 1984, *Davidse 27688* (F, MEXU, MO, NY, TFAV, VEN); Río Pasimoni, 66°35′–66°32′W, 1°53′–1°27′N, 23–25 Jul. 1984, *Davidse 27757* (MO, NY, VEN), 66°32′W, 1°38′N, 9 Feb. 1981, *Huber & Medina 5888* (MO, VEN), 66°33′W, 1°35′N, 8 Feb. 1981, *Huber & Medina 5858* (VEN); Río Siapa, 66°25′W, 2°05′N, 7 Feb. 1981, *Huber & Medina 5807* (VEN).

By virtue of its few, scaberulous racemes, stramineous anthoecia, perennial habit, well-developed midnerve of the glume, and narrow leaves *A. casiquiarensis* belongs to sect. *Axonopus* ser. *Barbigeri* subser. *Barbigeri* of Black (1963).

It is related to *A. comans* and *A. camargoanus* of central to southern Brazil both of which lack stolons, and have consistently convolute blades and thickened, usually deeply buried culm bases.

Both *A. comans* and *A. camargoanus* inhabit wet savannas, whereas *A. casiquiarensis* grows in white-sand savannas and river banks, including sandy pockets on granite rock outcrops.

This species is distributed in Colombia and Venezuela in the lowland area (elev. 80–125 m) centering around the Departamento Casiquiare from whence it derives its epithet. So far it has been collected from the Río Baria and the Río Siapa in the south to Cerro Yapacana and the Río Atabapo in the north.

Approximately one-fifth of the cited collections have some specimens with conspicuous, long stolons. Apparently in this species, as in many of its congeners capable of producing stolons, stolon production is negatively correlated with density of plants and in general is highly dependent upon local growing conditions. Those plants (e.g., *Davidse et al. 17421, Huber & Medina 5858*) from completely open exposures in herbaceous, white-sand savannas have very short, erect, stiff leaves, whereas those from more favorable sites, such as sabanetas (e.g., *Davidse et al. 16856*) and the margins of savannas (e.g., *Davidse et al. 16907A*), have a more luxurious, lax growth habit.

Axonopus jeanyae Davidse, sp. nov. TYPE: Panama. Coclé: area between Caño Blanco del Norte, Caño Sucio and Chorro del Río Tife, 80°36′30″–80°38′W, 8°42′19″–8°43′06″N, spray basin of waterfall, 3 Feb. 1983, *G. Davidse & C. W. Hamilton 23570* (holotype, MO; isotypes, ISC, PMA, US). Figure 5.

Axonopus jeanyae Davidse, sp. nov. *A. ciliatifolius* Swallen affinis sed nodis et spiculis pubescentibus et gluma et lemmate anthoecio longiore differt.

Densely tufted, caespitose perennial; culms 50–75 cm tall, the internodes 1–2 mm wide, solid or nearly so, glabrous, flattened, especially toward the base, the nodes mostly 2, blackish, often noticeably elongated, appressed pubescent with hairs to 1.5 mm long. Sheaths mostly less than 10 cm long, keeled, not strongly distichous, glabrous, the overlapping margin ciliate at least when young; flag leaf sheath to 16 cm long; collar not differentiated; ligule a ciliolate membrane 0.5 mm long, the membrane 0.2 mm long, the cilia 0.3 mm long; blades to 25 cm long, 2–3 mm wide, folded at the base, flat to folded above, papillose-ciliate towards the base, otherwise glabrous, the apex obtuse, scabrous. Inflorescence 6–12 cm long; axis 2–24 mm long; peduncles usually 2, well-exserted; racemes 2–5, 4–11 cm long, spreading at acute angles, the axils puberulent to

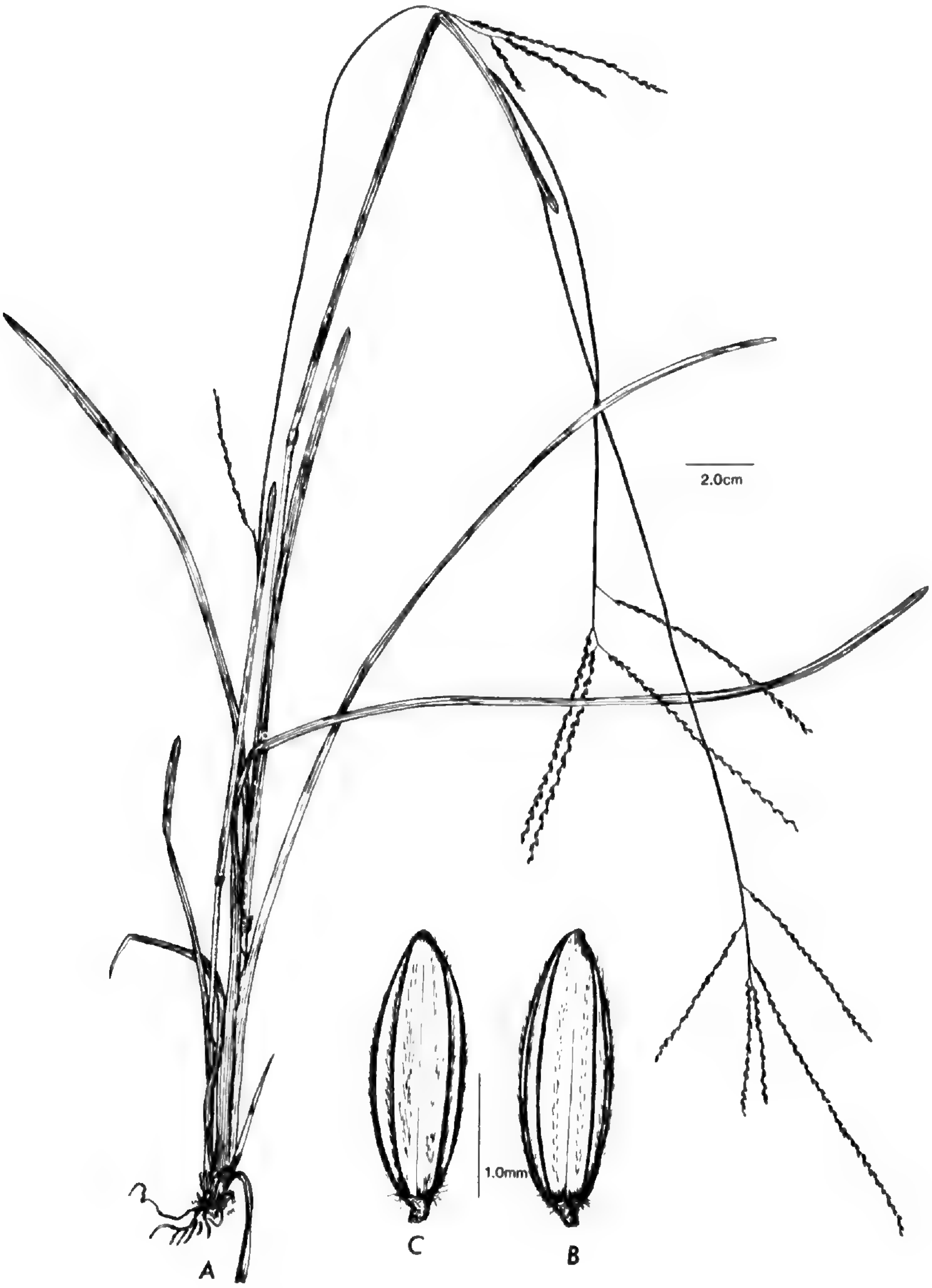

FIGURE 5. Holotype of *Axonopus jeanyae*.—A. Habit.—B. Abaxial view of spikelet showing the upper glume.—C. Adaxial view of spikelet showing the lower lemma. [After *Davidse & Hamilton 23570* (MO).]

pubescent, the rachis 0.4–0.6 mm wide, glabrous, 10–13 spikelets per 25 mm; pedicels 0.2–0.5 mm long, glabrous. Spikelets 1.9–2.5 mm long, 0.7–0.8 mm wide, elliptic-oblong, obtuse; upper glume about as long as the lower lemma, 4.5-nerved, the midnerve not or only weakly developed, with appressed lines of pubescence between the nerves; lower lemma similar to the upper glume; anthoecium 0.1–0.4 mm shorter than the upper glume, brown, apically minutely papillate, obtuse; lodicules 2, minutely 3-lobed, fleshy, vasculated, glabrous; stamens 3, the anthers 1.0–1.1 mm long, purple; styles 2, separate; stigmas plumose, purple; caryopsis 1.3 mm long, 0.7 mm wide, oblong, broadly obtuse, the hilum elliptic-punctate, the embryo ca. ½ the length of the caryopsis.

The perennial habit, glabrous racemes, and brown anthoecia place *A. jeanyae* in sect. *Axonopus* ser. *Suffulti* of Black (1963). This new species appears to be most closely related to *A. ciliatifolius* Swallen, a species so far known only from Belize. *Axonopus ciliatifolius* differs in its glabrous nodes and more fragile, glabrous, less strongly nerved glume and lower lemma, both of which are as long as the anthoecium.

The epithet recognizes the contributions of my wife, Jeany Vander Neut Davidse, to the *Flora Mesoamericana* project. She is largely responsible for processing the thousands of collections generated by Missouri Botanical Garden collectors in Mesoamerica.

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TWO NEW MESOAMERICAN SPECIES OF *CHUSQUEA* (POACEAE: BAMBUSOIDEAE)[1]

LYNN G. CLARK[2]

ABSTRACT

Two new Mesoamerican species of *Chusquea* are described and illustrated, both from complete collections of vegetative and flowering material. *Chusquea grandiflora*, a cloud-forest species from Panama and northwestern Colombia, has infravaginal branching, long, relatively narrow foliage leaves, open panicles, and rather large spikelets. It is allied to *C. longifolia* Swallen and related species. *Chusquea aperta* occurs in pine-oak cloud forests in Oaxaca, Mexico. It also has infravaginal branching and open panicles, but its foliage leaves are smaller, wider, yellowish-green, and strongly tessellate abaxially. This species is probably most closely related to *C. nelsonii* Scribn. & Smith, and *C. muelleri* Munro.

During preparation of a treatment of *Chusquea* Kunth for *Flora Mesoamericana*, examination of herbarium material revealed the existence of two more undescribed species of this diverse bamboo genus. Both are represented by complete collections of vegetative and flowering material. For explanation of terminology relating to the vegetative parts, especially buds and branching, see Clark (1985). In the specimen citations, a flowering specimen is indicated by the insertion of (fl) after the collection date.

Chusquea grandiflora L. G. Clark, sp. nov. TYPE: Panama. Panamá: along road past Cerro Jefe toward La Eneida, 6 Jan. 1971 (fl), *Croat 13070* (holotype, ISC; isotypes, COL, CR, K, MEXU, MO as two sheets, PMA, US). Figure 1A–D.

Culmi scandentes, usque ad 18 m longi. Folia culmorum 16–50 cm longa; vaginae 12–33 cm longae, 2–3-plo longiores quam laminae, abaxiales scabrae superne; laminae 4–17 cm longae, abaxiales scabrae; cingulum 2–3 mm longum. Nodi gemma centralis singularis triangularis subtenta gemmis numerosis (± 50) parvioribus subaequantibus. Ramificatio infravaginalis. Laminae foliorum 8–20 cm longae, (0.5–)0.7–1.4 cm latae, L:W = 11–27, glabrae, non tessellatae, apicibus brevi-setosis, basibus attenuatis. Inflorescentia aperta, paniculata, 6–11 cm longa; rhachis triquetra, pubescens; rami breves patentes, angulati, pubescentes. Spiculae 9.7–12.6 mm longae, scaberulae. Glumae 2; gluma I 2–2.4 mm longa, 1-nervis; gluma II 2.2–4.8 mm longa, 1–3-nervis. Lemmata sterilia 2; lemma sterile I subulatum, 5.2–6.7 mm longum, 5–7-nerve; lemma sterile II subulatum, 7–9.5 mm longum, 7-nerve. Lemma fertile subulatum, 8.4–10.9 mm longum, 7–9-nerve. Palea bicarinata, 6.9–10.2 mm longa, 6–8-nervis.

Culms clambering, viny, to 18 m long. *Internodes* terete, smooth to scabrous-hirsute just below the nodes. *Culm leaves* 16–50 cm long, the juncture of sheath and blade abaxially indistinct; sheaths 12–33 cm long, 2–3 times as long as the blade, abaxially smooth at the base, scabrous toward the apex; blades erect, usually persistent, 4–17 cm long, abaxially scabrous; girdle well-developed, 2–3 mm wide, glabrous; corky ridge present at the juncture of the sheath and girdle. *Nodes* with one triangular central bud subtended by numerous (up to 50) smaller, subequal subsidiary branches; sheath scar dipping markedly below the bud/branch complement. *Branching* infravaginal; the central bud developing tardily or sometimes not at all; leafy subsidiary branches not rebranching. *Foliage leaves* with sheaths glabrous, the margins ciliate near apex; blades 8–20 cm long, (0.5–)0.7–1.4 cm wide, L:W = 11–27, the adaxial surface glabrous, the abaxial surface glabrous, not tessellate, the apex short setose, the base attenuate; pseudopetiole more or less distinct, 2–4 mm long; outer ligule evident, to 1 mm long; inner ligule truncate, asymmetrical, 1–1.5(–2) mm long. *Inflorescence* an open panicle 6–11 cm long, usually not fully exserted from the subtending sheath; rachis triquetrous, pubescent; branches strongly spreading, angular, pubescent, the lower ones short, up to 3 cm long; pedicels 1–2 mm long, angular, pubescent. *Spikelets* 9.7–12.6 mm long, scaberulous. *Glumes* 2; glume I ca. ⅕ the spikelet length, 2–2.4 mm long, apically acute, abaxially scaberulous, 1-nerved; glume II ca. ⅓ the spikelet length, 2.2–4.8 mm long, apically pointed, abaxially scabrous, 1–3-

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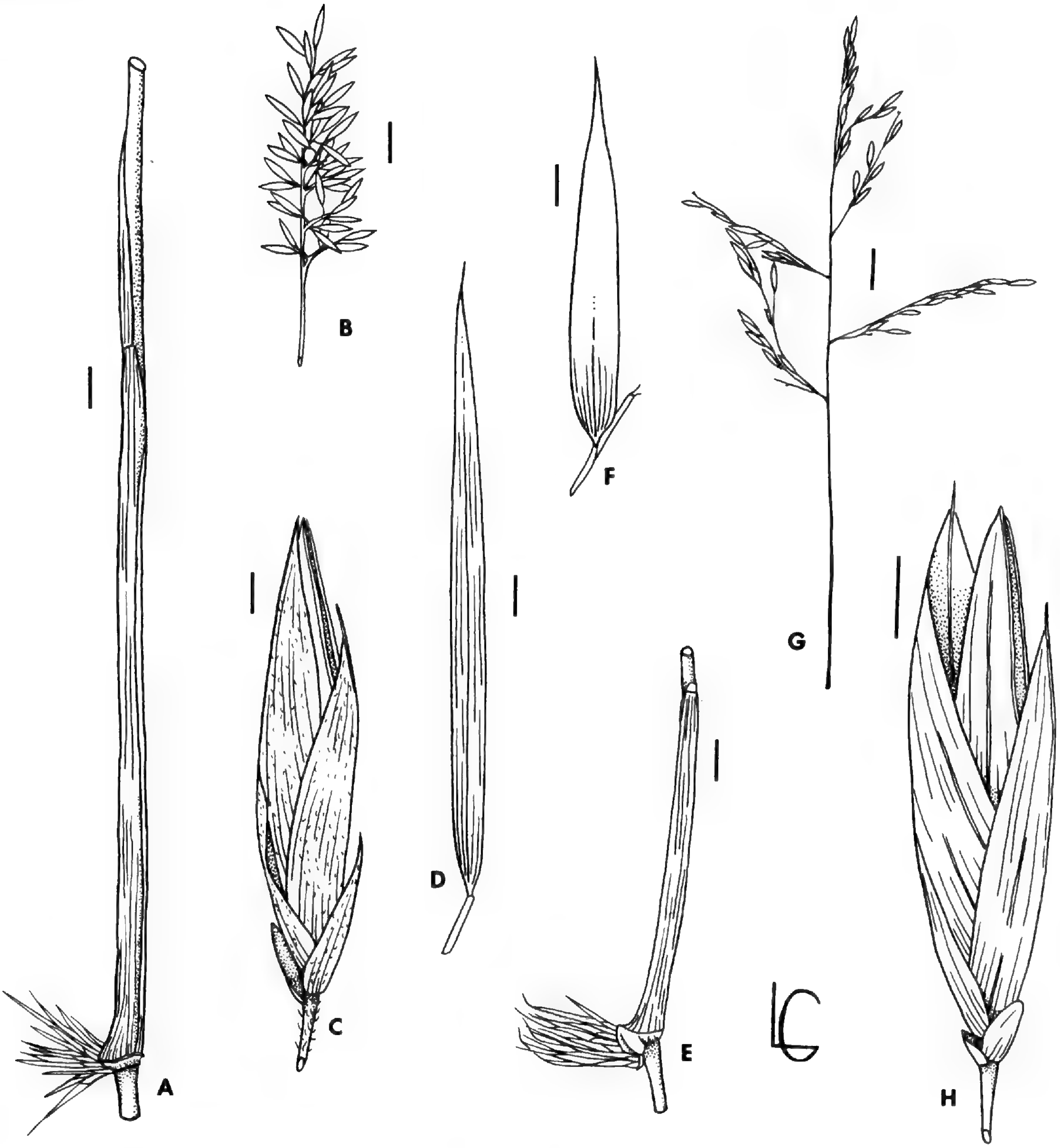

FIGURE 1. *Chusquea grandiflora* and *C. aperta*. A–D. *C. grandiflora*.—A. Culm leaf with emerging branches, scale = 1 cm.—B. Inflorescence, scale = 1 cm.—C. Spikelet, scale = 1 mm.—D. Foliage leaf blade, abaxial view, scale = 1 cm. (A, D based on *Soderstrom 2014*, B, C based on *Croat 13070*.) E–H. *C. aperta*.—E. Culm leaf with emerging branches, scale = 1 cm.—F. Foliage leaf blade, adaxial view, scale = 1 cm.—G. Inflorescence, scale = 1 cm.—H. Spikelet, scale = 1 mm. (E based on *Soderstrom 2237*, F–H based on *Soderstrom 2239*.)

nerved. *Sterile lemmas* 2; sterile lemma I ca. ½ the spikelet length, 5.2–6.7 mm long, apically subulate, abaxially scaberulous, 5–7-nerved; sterile lemma II ca. ⅞ the spikelet length, 7–9.5 mm long, apically subulate, abaxially scaberulous, 7-nerved. *Fertile lemma* 8.4–10.9 mm long, apically subulate, abaxially scaberulous, 7–9-nerved. *Palea* 2-keeled, sulcate except toward the base, 6.9–10.2 mm long, apiculate, abaxially scaberulous, 6–8-nerved, the sulcus pubescent. *Lodicules* 3; 3–3.5 mm long. *Stamens* 3; anthers 4.3–5.5 mm long. *Fruit* unknown.

Additional specimens examined. COLOMBIA. ANTIOQUIA: along camino between Alto del Tigre and El Soccoro, E of Argelia, 1 Jun. 1944 (fl), *Core 817* (US). CHOCÓ: Emisora La Sirena, 3 km W of La Mansa at top of Cord. Occidental, *Gentry & Renteria 24203* (US). PANAMA. CHIRIQUÍ: Vicinity of Gualaca ca. 7.8 mi. from Planes de Hornito, La Fortuna on road to dam site, *Antonio 5182* (MO, US); camino hacia la finca Landau, NE del campamento de Fortuna (sitio de presa), 6 Sep. 1976 (fl), *Correa et al. 2185* (F, MO, NY). COCLÉ: El Valle, *Soderstrom 2014* (US). PANAMÁ: Cerro Jefe, near tower, *Antonio 4473* (MO, US); Cerro Jefe, *Croat s.n.* (MO); top of Cerro Jefe near antenna, 17 Oct. 1977 (fl), *Folsom & Page 5944* (MO, PMA, US, VEN); La Eneida, 12 km N of Goofy Lake, *Soderstrom 2006* (US). VERAGUAS: Cerro Tute, trail past agricultural school near Santa Fe, *Antonio 1878* (MO).

Chusquea grandiflora is characterized by infravaginal branching, culm leaves abaxially scabrous (except basally), open panicles with short, spreading primary branches, pubescent rachis, and scaberulous spikelet with glume II usually twice as long as glume I. This species is known from montane forests at altitudes of 700 to 1,700 m in Panama and northwestern Colombia. *Gentry & Renteria 24203,* a vegetative specimen referred to this species, was collected at 2,300–2,400 m.

Chusquea grandiflora lacks the leafless, fibrillar branchlets so characteristic of *C. scabra,* but otherwise the two species are strikingly similar vegetatively. *Chusquea scabra* usually exhibits much more rounded leaf bases and consistently scabrous internodes. *Chusquea grandiflora* is also closely related to *C. foliosa* L. G. Clark, *C. longifolia* Swallen, and *C. patens* L. G. Clark, sharing infravaginal branching and long, relatively narrow foliage leaves with these three species. The open panicles with strongly spreading branches of *C. grandiflora* and *C. patens* are similar in some specimens, but *C. grandiflora* is distinguished by its pubescent rachis, shorter inflorescence branches, larger spikelets, and wider foliage leaf blades.

Chusquea aperta L. G. Clark, sp. nov. TYPE: Mexico. Oaxaca: 107 km SW of Tuxtepec, 2,650 m, 4 Oct. 1977 (fl), *Soderstrom 2239* (holotype, US). Figure 1E–H.

Culmi usque ad 1 cm diam., usque ad 1–2 m alti. Folia culmorum: vaginae persistentes, 6.8–8.5 cm longae, laeves; lamina triangularis, 1 cm longa, laevis; cingulum asymmetricum, ad 5 mm longum, prominens non nisi prope gemmam. Ramificatio infravaginalis. Laminae foliorum rigidae, 7–12 cm longae, 0.8–1.5 cm latae, L : W = 7–11, glabrae, valde tessellatae inferne, apicibus brevi-setosis, basibus rotundatis vel attenuatis. Inflorescentia aperta, paniculata, 7–11 cm longa, exserta; rhachis triquetra, glabra; rami patentes, usque ad 4–6 cm longi, angulati, glabri. Spiculae 6–8 mm longae, glabrae, adpressae. Glumae 2, squamiformes; gluma I 0.3–0.5 mm longa, enervis; gluma II 0.4–0.8 mm longa, enervis. Lemmata sterilia 2; lemma sterile I apiculatum, 4–4.6 mm longum, 1–3-nerve; lemma sterile II subulatum, 4.5–5.1 mm longum, 1–5-nerve. Lemma fertile subulatum, 5.7–7.1 mm, 7-nerve. Palea bicarinata, 5.5–6.8 mm longa, 4–6-nerve.

Culms to 1 cm diam., to 1–2 m tall. *Internodes* terete, solid, smooth. *Culm leaves* with the sheaths persistent, the overlapping margin fused to the sheath to 5 mm above the base, 6.8–8.5 cm long, abaxially smooth; blades evidently not persistent, in the one example seen, blade triangular, 1 cm long, abaxially smooth; girdle asymmetrically developed, prominent only near the bud complement, to 5 mm wide; inner ligule 2–3 mm long. *Nodes* swollen, the central bud subtended by up to 25–30 subsidiary branches; supranodal ridge prominent. *Branching* infravaginal, the central bud often developing; leafy subsidiary branches occasionally rebranching. *Foliage leaves* with the blades stiff, 7–12 cm long, 0.8–1.5 cm wide, L : W = 7–11, yellowish-green, the adaxial surface smooth and not tessellate, the abaxial surface smooth and strongly tessellate, the apex short-setose, the base rounded to attenuate; pseudopetiole usually distinct, 2–3 mm long; outer ligule a stiff rim to 0.5 mm long; inner ligule elongate, 2–9 mm long, rounded to acute at the tip. *Inflorescence* an open panicle 7–11 cm long, completely exserted from the subtending sheath on a peduncle up to 12 cm long; rachis triquetrous, glabrous; branches spreading, angular, glabrous, the lower branches to 4–6 cm long; pedicels variable, to 14 mm long, angular, glabrous. *Spikelets* 6–8 mm long, glabrous, appressed to branches. *Glumes* 2, scalelike, less than ⅒ the spikelet length; glume I 0.3–0.5 mm long, nerveless; glume II 0.4–0.8 mm long, nerveless. *Sterile lemmas* 2, ⅔–¾ the spikelet length; sterile lemma I 4–4.6 mm long, apiculate, glabrous, 1–3-nerved; sterile lemma II 4.5–5.1 mm long, subulate, glabrous, 1–5-nerved. *Fertile lemma* 5.7–7.1 mm long, subulate, glabrous, 7-nerved. *Palea* 2-keeled, the upper half sulcate, 5.5–6.8 mm long, acute, glabrous, 4–6-nerved. *Lodicules* 3. *Stamens* 3; anthers 4–5 mm long. *Fruit* unknown.

Additional specimens examined. MEXICO. OAXACA: ca. 0.5 mi. N of summit pass, ca. 18 mi. SW of La Esperanza, Highway 175 ca. Km 109, *Bauml & Kimnach 499* (US); 50 km después de Guelatao rumbo a Tuxtepec, *Beetle 5016* (US); 30 mi. NE of Guelatao along Hwy. 175 to Tuxtepec, 16 Aug. 1975 (fl), *Davidse & Davidse 9733* (MO, US); on road between Oaxaca and Tuxtepec, 11 Apr. 1975 (fl), *Fisher & Engleman 75-41* (MO); Distrito de Ixtlán, Sierra de Juarez, ruta

175 Tuxtepec a Oaxaca, ca. 0.5 km al S de Cerro Pelón, 13 Apr. 1982 (fl), *Lorence et al. 4004* (US); 108 km SW of Tuxtepec on road to Oaxaca, *Soderstrom 2237* (US).

According to label data, *Chusquea aperta* occurs in pine-oak cloud forests at elevations from 1,670 to 2,750 m. At present, this species is known only from a relatively restricted area of Oaxaca, Mexico, on the road between Oaxaca and Tuxtepec. *Chusquea aperta* is characterized by infravaginal branching, deciduous culm leaf blades, stiff, yellowish-green foliage leaves with blades strongly tessellate abaxially, and long-exserted, open panicles with spikelets appressed to the spreading branches. Vegetatively, *C. aperta* resembles *C. nelsonii* Scribn. & Smith, but can be distinguished by its glabrous, abaxially tessellate foliage leaf blades, in contrast to the narrower, abaxially pubescent, non-tessellate leaf blades of the latter species. The inflorescences and spikelets of *C. aperta* are similar to those of *C. muelleri* Munro (= *C. carinata* Fournier and *C. mexicana* Hackel), but the inflorescences of *C. muelleri* are smaller, less open, and not long-exserted. With regard to the spikelets, the glumes of *C. aperta* are both small and scalelike, while the glumes of *C. muelleri* are more developed, with the second glume usually about twice as long as the first.

The type specimen exhibits mostly older, spent inflorescences (but still with some spikelets), and a few younger, fresh inflorescences derived from regrowth of subsidiary branches. These newer spikelets are just at anthesis, and are slightly larger and fuller than the old spikelets produced during the primary flowering period. The newer spikelets are unusual because they all have a one- or two-keeled palea-like bract in the axil of the second sterile lemma. I observed individual spikelets with two fertile florets subtended by two sterile lemmas in some specimens of a few *Chusquea* species, but this is the first indication of a rudimentary floret in the position of a sterile lemma. No other flowering specimens of *C. aperta* show this condition. The abnormal spikelets were left out of the description.

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NOTES

NEW COMBINATIONS IN *CHUSQUEA* (POACEAE: BAMBUSOIDEAE)

The genus *Swallenochloa* McClure was segregated from *Chusquea* Kunth solely on the basis of differences in certain vegetative features (McClure, 1973). To my knowledge, McClure never collected *Swallenochloa*, and only limited, incomplete herbarium material of this group of species was available to him. Soderstrom & C. Calderón (1978) applied the terms extravaginal and intravaginal respectively to the branching patterns in *Chusquea* and *Swallenochloa*, and discussed other vegetative differences in addition to those listed by McClure. As the result of extensive field and herbarium studies, I determined that the species of *Swallenochloa* constitute a coherent, natural group that falls within the generic limits of *Chusquea*. Details of the reduction of *Swallenochloa* to a section of *Chusquea* will be presented in a later publication (Clark, in prep.). For the present, this transfer necessitates new combinations for three species.

Chusquea angustifolia (Soderstrom & C. Calderón) L. G. Clark, comb. nov. *Swallenochloa angustifolia* Soderstrom & C. Calderón, Brittonia 30: 303. 1978. TYPE: Venezuela. Tachira: subparamo y bosque enano, faldas inmediatamente debajo del Paramo de Tama, cerca de la frontera Colombo-Venezolana, *Steyermark, Dunsterville & Dunsterville 98615* (holotype, US; isotype, VEN).

Chusquea longiligulata (Soderstrom & C. Calderón) L. G. Clark, comb. nov. *Swallenochloa longiligulata* Soderstrom & C. Calderón, Brittonia 30: 305. 1978. TYPE: Costa Rica. San José: along the Carretera Interamericana, ca. 5 km SE of Empalme, near Tres de Junio, *Pohl & Selva 12842* (holotype, US; isotypes, F, ISC, MO).

Chusquea vulcanalis (Soderstrom & C. Calderón) L. G. Clark, comb. nov. *Swallenochloa vulcanalis* Soderstrom & C. Calderón, Brittonia 30: 309. 1978. TYPE: Costa Rica. Cartago: abrupte dominante La Playita, Volcán Irazu, *Pittier 14126* (holotype, US; isotypes, ISC, US).

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NOTES ON *CORNUS* (CORNACEAE) IN SOUTH AMERICA

The family Cornaceae is represented in South America by the genera *Cornus* L. and *Griselinia* Forster f. The latter, often segregated as Griseliniaceae, occurs in Brazil and Chile, and in New Zealand, while the former has been known previously from Bolivia north to Colombia in the Andes. We report here, for the first time, *Cornus* in Venezuela, this being the first record of the family in Venezuela.

Macbride (1929) was first to record the genus from South America. Based on fragmentary fruiting material collected from Peru and Bolivia, he described two species, *C. peruviana* and *C. boliviana*, the former based on the collection *Macbride 3439* from Cani, Depto. Huánuco, Peru, the latter based on *Bang 1799* from Bolivia without exact locality indicated. His decision to separate the two collections as distinct taxa was based on his observation of the "equally two-armed" trichomes on the abaxial leaf surface of the Peruvian plant as contrasted with the "unequally branched or pronged" hairs with "one of their two 'arms' being much longer than the other" in the Bolivian material. A year later, however, Macbride (1930) changed his mind and concluded that *Cornus peruviana* was identical with an unpublished species of *Viburnum* from Peru collected by Ruiz & Pavon which he examined at B, and, accordingly, he transferred it to *Viburnum peruvianum* (J. F. Macbr.) J. F. Macbr. At the same time, he decided that the Bolivian material did not belong to *Cornus*, but, being uncertain as to its proper family position, did not assign it to any genus.

Subsequently, Standley (1935) re-examined the specimens described by Macbride and concluded that they did indeed belong to *Cornus*, and that, moreover, they were conspecific. Standley chose the epithet *peruviana* for them. In the Flora of Peru Macbride (1959) accepted Standley's conclusions and placed *C. boliviana* J. F. Macbr. in synonymy.

During an expedition to the Andes of Estado Táchira, Venezuela, near the Colombian border, the authors found a fallen branch from a tree that proved, upon later examination, to belong to the genus *Cornus*. In determining that this collection pertained to *Cornus*, and not to *Viburnum*, the criterion of leaf pubescence, as indicated by Solereder (1899) and Metcalfe & Chalk (1950), proved critical. A comparison of the *Steyermark & Liesner* collection from Venezuela with other South American specimens initiated the present study of the genus.

In general, we have observed, after examination of available herbarium material, that the specimens from Venezuela and Colombia show a more appressed type of indument on the calyx, hypanthium, and lower surface of the leaf in contrast with collections from Ecuador, Peru, and Bolivia, which have a more loosely crisp, spreading, and often denser type of pubescence. However, the total number of specimens examined from South America remains inadequate for conclusions as to the variability present. The apparent differences noted between the northern and southern populations may disappear when more abundant material becomes available. For the present, therefore, we do not recognize any segregation of taxa, and conclude that the plants from Venezuela are conspecific (sensu lato) with those from the other parts of South America. In this connection, we are employing the name *C. peruviana* J. F. Macbr. as selected by Standley (1935) when he concluded that the Peruvian and Bolivian populations were conspecific.

Specimens examined (listed geographically from north to south). VENEZUELA. EDO. TÁCHIRA: wet forested slopes along Quebrada Agua Azul, over slate-shale substrata, south of El Reposo, 14 km SE of Delicias, 7°31'N, 72°24'W, 2,150–2,300 m, 22–23 Jul. 1979, *Steyermark & Liesner 118420* (MO, VEN). COLOMBIA: *Mutis 2313* (US). ECUADOR: Pastaza river, 2,000 m, Feb. 1935, *Rimbach 271* (F). PERU. DEPT. HUÁNUCO: Cani, 7 mi. NE of Mito, 2,575 m, 16–26 Apr. 1923, *Macbride 3439* (type of *C. peruviana*, F); DEPT. CAJAMARCA: Prov. Celendin, canyon of the Río Marañon above Balsas, 5 km below summit of the road to Celendin, 24 May 1964, *Hutchison & Wright 5336* (US); DEPT. AMAZONAS: Leimebambo, 2,100 m, 23 Dec. 1962, *Woytowski 7796* (MO, US); Ambay, 3,100 m, Jun. 1938, *Univ. Cuzco s.n.* (MO). BOLIVIA. DEPT. COCHABAMBA: Ayopaya, Sailapata, 2,800 m, Nov. 1935, *Cardenas 3355* (US); *Bang 1799* (type of *C. boliviana*, MO, US).

The following key indicates the main characters distinguishing *Cornus* from *Viburnum*:

1. Abaxial surface of leaves with 2-branched, unicellular, nodose trichomes incrusted with lime carbonate; flowers tetramerous; petals free, separate; ovary bilocular .... *Cornus*
1. Abaxial surface of leaves not as above, the

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pubescence, when present, of simple, stellate, peltate, tufted, or glandular hairs; flowers pentamerous; corolla sympetalous; ovary unilocular .... *Viburnum*

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A NEW COMBINATION IN *LUCILIA* (COMPOSITAE–INULEAE)

Lucilia pusilla (Kunth) Hieron. (1900) is the generally accepted name for a small, caespitose herb from the high Andes of Venezuela, Colombia, Ecuador, and Peru. While working on a nomenclator of *Conyza* (Compositae—Astereae), I found that its basionym *Conyza pusilla* Kunth (1818) is illegitimate, being a later homonym of *C. pusilla* Houtt. (1779) from South Africa. De Candolle changed the name of *Conyza pusilla* Kunth to *C. kunthiana* DC. (1836). Since under article 55.1 of the 1983 International Code of Botanical Nomenclature the specific epithet of the former correct name must be retained on generic transferences, the correct name for this species in *Lucilia* is *L. kunthiana* (DC.) Zardini, comb. nov.

Lucilia kunthiana (DC.) Zardini, comb. nov. Based on *Conyza kunthiana* DC., Prodr. 5: 379. 1836 (new name for *C. pusilla* Kunth). *Gnaphalium kunthianum* (DC.) Kuntze, Revis. Gen. Pl. 3(2): 152. 1898. *Conyza pusilla* Kunth, Nov. Gen. Sp. 4: 69. 1818, non *C. pusilla* Houtt. (1779). *Lucilia pusilla* (Kunth) Hieron., Bot. Jahrb. Syst. 29: 29. 1900; Freire, Darwiniana 27: 482. 1986. TYPE: Ecuador: in Andean region, *Humboldt & Bonpland s.n.* (P holotype; P isotype, B isotype photograph F 15128).

I thank Dr. Zijlstra (U) for confirming the necessity of this new combination.

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FIGURE 1. Holotype of *Conyza pusilla* Kunth (P, photograph Zardini n. 1036, MO).

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CHROMOSOME COUNTS OF MISSOURI ASTERACEAE AND POACEAE

Few native Missouri plants are chromosomally known from Missouri populations. The list of chromosome counts for composites and grasses in Table 1 is a small contribution in this area. The counts were made from standard anther squashes stained in propionic-carmine and dissected from buds fixed in Carnoy's or Newcomer's fixative. Except for *Paspalum laeve*, meiosis was normal in all collections, and the observed numbers agree with previously reported numbers as summarized in Federov (1969), Moore (1973, 1974, 1975), and Goldblatt (1981, 1984, 1985). Vouchers are deposited in MO and KUH.

The chromosome number for *Paspalum laeve* has previously been reported as $2n = 40$ (Brown, 1948), $2n = 60$ (Burton, 1942, as *P. longipilum* Nash), and $n = 40$ (Banks, 1964). Our count of $n = 29$ apparently represents an aneuploid reduction from the hexaploid level of $n = 30$. Meiosis and pairing were normal. The second population sampled had the heptaploid number, $n = 35$, and the chromosomes were almost completely asynaptic in early meiosis. No more than five bivalents were ever observed at diakinesis or metaphase I (Fig. 1). When chromosomes were paired, the association was very loose. Structures that we believe may be micronucleoli were present in variable numbers at diakinesis (Fig. 1A). We suspect, based on a similar pattern of asynapsis in the tetraploid apomictic cytotype of *P. conjugatum* Berg. (Fang & Li, 1966; Mehra, 1982), that the plant may have been apomictic. Since only one plant was examined, we do not know whether this condition was isolated or widespread in the population. The species is morphologically variable and further cytotaxonomic studies throughout its range may be helpful in relating some of this variation to ploidy levels.

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TABLE 1. Chromosome numbers of Missouri Asteraceae and Poaceae.

Taxon	*n*	Voucher[a]
Asteraceae		
Erigeron strigosus Muhlenb.	18	*Vahidy & Davidse 21*
Eupatorium coelestinum L. f.	10	*Vahidy & Davidse 20*
Lactuca floridana (L.) Gaertner	17	*Vahidy & Davidse 12*
Rudbeckia laciniata L.	27	*Davidse & Vahidy 30845*
Rudbeckia missouriensis Engelm.	19	*Davidse & Vahidy 30838*
Solidago nemoralis Aiton	27	*Vahidy & Davidse 15*
Solidago ulmifolia Muhlenb.	9	*Davidse & Vahidy 30835*
Poaceae		
Leersia virginica Willd.	ca. 24	*Davidse & Vahidy 30840*
Panicum capillare L.	9	*Vahidy & Davidse 17*
Paspalum fluitans (Elliott) Kunth	10	*Davidse & Vahidy 30854*
Paspalum laeve Michaux var. *laeve*	35	*Vahidy & Davidse 1*
Paspalum laeve Michaux var. *pilosum* Scribner	29	St. Louis, Tower Grove Park, *Davidse & Vahidy 30846*
Paspalum pubiflorum Rupr. var. *glabrum* Vasey	30	*Vahidy & Davidse 24*
Paspalum setaceum Michaux var. *muhlenbergii* (Nash) D. Banks	10	*Vahidy & Davidse 14*
Sorghastrum nutans (L.) Nash	20	*Vahidy & Davidse 16*

[a] Collected at Shaw Arboretum, Franklin County, Missouri, unless indicated otherwise.

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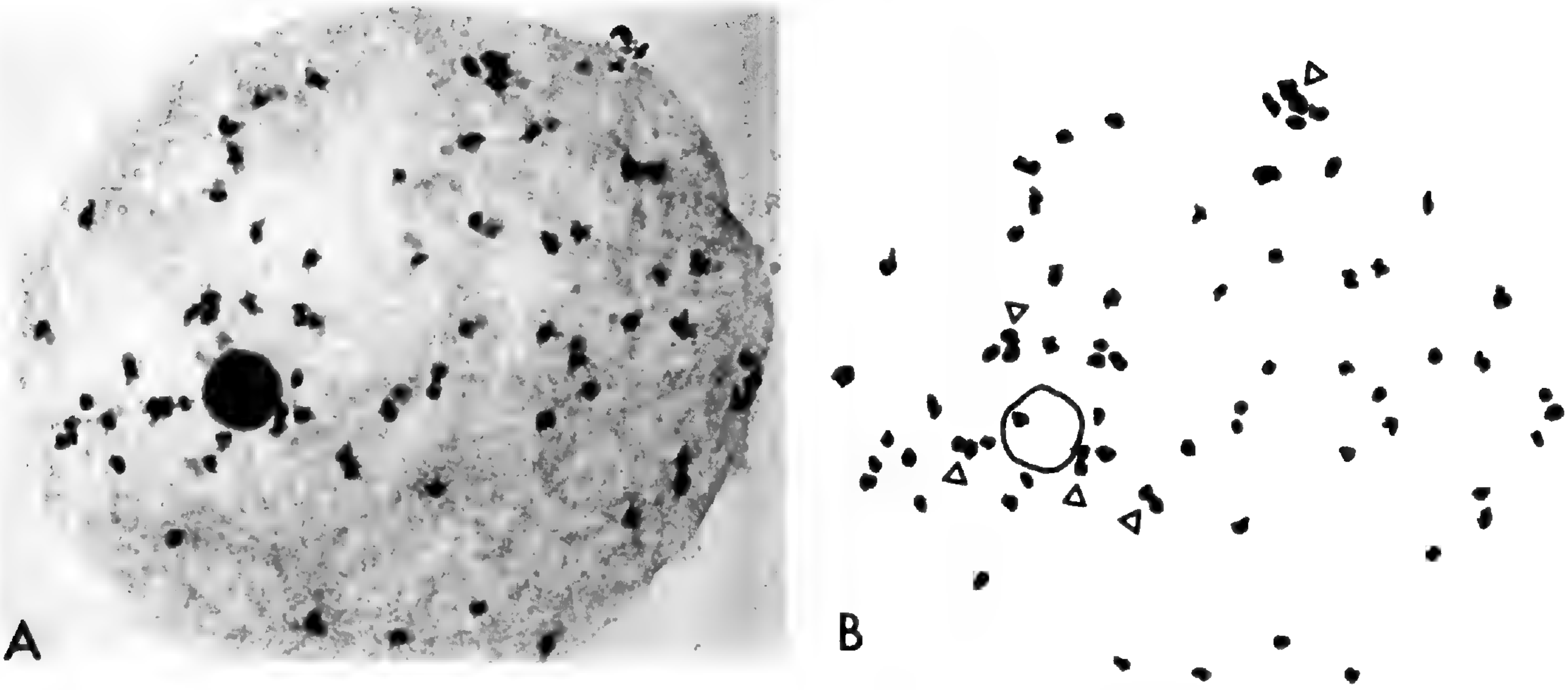

FIGURE 1. Diakinesis in *Paspalum laeve* var. *laeve*, $n = 35$.—A. Photomicrograph showing nearly complete asynapsis.—B. Camera lucida drawing of A with 5_{II} (marked) + 60_{I}.

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A NEW SPECIES OF *THRASYA* (POACEAE: PANICOIDEAE) FROM THE MOSQUITIA OF NICARAGUA AND HONDURAS

Recent work for the account of the Poaceae for the *Flora Mesoamericana* has brought to light a previously undescribed species of *Thrasya.*

Thrasya mosquitiensis Davidse & Burman, sp. nov. TYPE: Nicaragua. Zelaya: Along banks and surrounding gallery forest of Río Likas near Silima Lila, ca. 14°30'N, 83°50'W, 50 m, 5 Mar. 1979, *John J. Pipoly 4107* (holotype, MO; isotypes, HNMN, SP, US). Figure 1.

Gramen perenne; culmi 65–110 cm longi; ligula membranacea, 1.5–2.4 mm longa; laminae lineares, 16–32 cm longae, 9–16 mm latae; racemus singularis, 10–16 cm longus; rhachis alata, 2.0–2.8 mm lata; spiculae 3.4–4.0 mm longae, glabrae, binatae, in seriebus unis dorso ad dorso dispositis, pedicelli inaequales; gluma infera 0.6–2.5 mm longa; gluma supera 2.8–3.4 mm longa; lemma inferum subinduratum, sulcatum; flos inferus staminatus; lemma superum induratum, papillosum minute; flos superus perfectus.

Perennial herb; culms 65–110 cm long, erect, sometimes rooting at the lower nodes, the internodes slightly compressed, hollow, mostly glabrous, the upper portions and the nodes appressed pubescent. Sheaths glabrous or puberulent toward the apex, keeled, the collar appressed pubescent; ligule a membrane 1.5–2.4 mm long; blades 16–32 cm long, 9–16 mm wide, linear, flat, glabrous or puberulent toward the base below, acuminate, the base slightly rounded to gradually narrowed; leaf subtending the inflorescence distinctly smaller. Racemes terminal and axillary, solitary, 10–16 cm long, arcuate, usually well-exserted from the sheath; peduncles puberulent near the tip or entirely glabrous; rachis 2.0–2.8 mm wide, winged, dorsally and ventrally glabrous, the margin minutely scabrous, the base with an inconspicuous tuft of hairs. Spikelets 3.4–4.0 mm long, 1.4–1.8 mm wide, glabrous, elliptic, broadly acute, arrayed in one row, oriented back-to-back, paired, the pairs borne on alternate sides of the rachis; pedicels puberulent, unequal, the upper 1.8–2.0 mm long, its lower half adnate to the rachis, the lower 0.2–0.4 mm long; glumes with the bases clasping and slightly swollen; lower glume dimorphic between the short- and long-pedicellate spikelets, variable in the short-pedicellate spikelets, 0.6–2.5 mm long, triangular, membranous to herbaceous, 0–1-nerved, obtuse to acute or aristate, uniform in the long-pedicellate spikelets, 0.7–1.2 mm long, triangular, membranous, nerveless, acute; upper glume 2.8–3.4 mm long, ca. ¾ as long as the spikelet, herbaceous, 5(–7)-nerved; lower lemma as long as the spikelet, subindurate, deeply sulcate on the back, sometimes splitting at maturity, 6(–7)-nerved, the midnerve often absent, the inner pair of nerves well-developed, slightly keeled and crested toward the tip; lower palea as long as the lower lemma, 2-nerved and 2-keeled; lower flower staminate: lodicules 2, the stamens 3, the anthers 1.3–1.9 mm long, purple; upper lemma 3.0–3.6 mm long, 1.4–1.6 mm wide, indurate, elliptic, minutely papillose, the tip bearing a tuft of minute hairs; upper palea of the same texture as the upper lemma; upper flower perfect: lodicules 2, the stamens 3, the anthers 1.4–1.8 mm long, purple, the styles 2, separate, the stigmas plumose, purple; caryopsis (immature) ca. 1.7 mm long, 1.1 mm wide, the embryo nearly ½ as long as the caryopsis, the hilum narrowly elliptic, ca. ⅓ as long as the caryopsis.

Paratypes. NICARAGUA. ZELAYA: Comarco del Cabo, Kornuk Creek, Puente Pozo Azul, 10 Jul. 1972, *Seymour 5802A* (MO), *5803* (MO). HONDURAS. GRACIAS A DIOS: 5 km de Puerto Lempira, 28 Jan. 1984, *Nelson & Cruz 8621* (TEFH).

The generic placement of this new species must be considered since the limits of the genus *Thrasya* have always been difficult to circumscribe precisely. The core group of *Thrasya* is composed of species that have the following features: 1) winged, one-sided, solitary racemes; 2) solitary spikelets arrayed in a single row; 3) back-to-back orientation of the spikelets, i.e., the backs of the lower glume and lower lemma of the short-pedicellate spikelet face the backs of these same structures of the long-pedicellate spikelet. The problem of the outlying species that show varying intermediate characteristics between the core group of *Thrasya* and the *Decumbentes* group of *Paspalum* (sensu Chase, 1929) has been discussed in detail by Burman (1982, in press).

In the core group of *Thrasya,* which clearly consists of the most specialized species in the genus, the fundamentally paired nature of the spikelets is superficially lost through the fusion of both the long and short pedicels to the rachis so that the free portion of all the pedicels is basically the same length.

In *T. mosquitiensis* the spikelets are arranged in a single row in a back-to-back orientation along a winged, one-sided, solitary raceme. Although the spikelets are arranged in a single row, the spikelets are clearly paired and the longer pedicel is only partially fused to the rachis (Fig. 1). The spikelet pairs themselves are arranged alternately along the rachis. With respect to the distinctly paired spikelets, *T. mosquitiensis* is similar to the *Decumbentes* group of *Paspalum*. However, in *T. mosquitiensis* the basal half of the upper pedicel is adnate to the rachis, in contrast to the *Decumbentes* group where both pedicels of a spikelet pair remain completely free. In addition, in *Decumbentes* species the spikelets are arranged in several rows and the regular back-to-back position of the spikelets is never attained. Therefore, although *T. mosquitiensis* is intermediate between the core group of *Thrasya* and the *Decumbentes* group of *Paspalum*, similarities with *Thrasya* are greater, and this is the reason for its inclusion in that genus.

There is a tendency for the spikelets to be dimorphic in the development of the lower glume within single inflorescences. In the short-pedicellate spikelets the lower glume may vary from nerveless, membranous, and obtuse to 1-nerved, herbaceous, and aristate. In the long-pedicellate spikelets the lower glume is uniformly nerveless, membranous, and acute. Also, the length of the upper glume relative to the upper lemma is greater in the short-pedicellate spikelet than in the long-pedicellate spikelet. This is most easily observed as the length of the upper lemma that is not covered by the upper glume: (0.1–)0.4–0.5 mm in the short-pedicellate spikelets, 0.5–0.7 mm in the long-pedicellate spikelets. Although such dimorphism is characteristic of *Paspalum* species of the *Decumbentes* group, it also occurs in two *Thrasya* species: *T. campylostachya* (Hackel) Chase and *T. petrosa* (Trin.) Chase.

Thrasya mosquitiensis seems to be most closely related to *T. campylostachya*, the only other Mesoamerican species with glabrous spikelets. *Thrasya mosquitiensis* is distinguished from the latter by the larger size of all its parts, most noticeably the spikelets (3.4–4.0 mm vs. 2.6–3.0 mm long and 1.4–1.8 mm vs. 0.8–1.5 mm wide), racemes (10–16 cm vs. 4–10 cm long), and blades (9–16 mm vs. 3–10 mm wide and 16–32 cm vs. 6–20 cm long). Moreover, the upper glume of the long-pedicellate spikelet is proportionally longer (3/4 vs. 1/2–2/3 the length of the spikelet), broader, more clasping, and less papery in texture. Finally, the upper pedicel in *T. mosquitiensis* tends to be less adnate to the rachis than

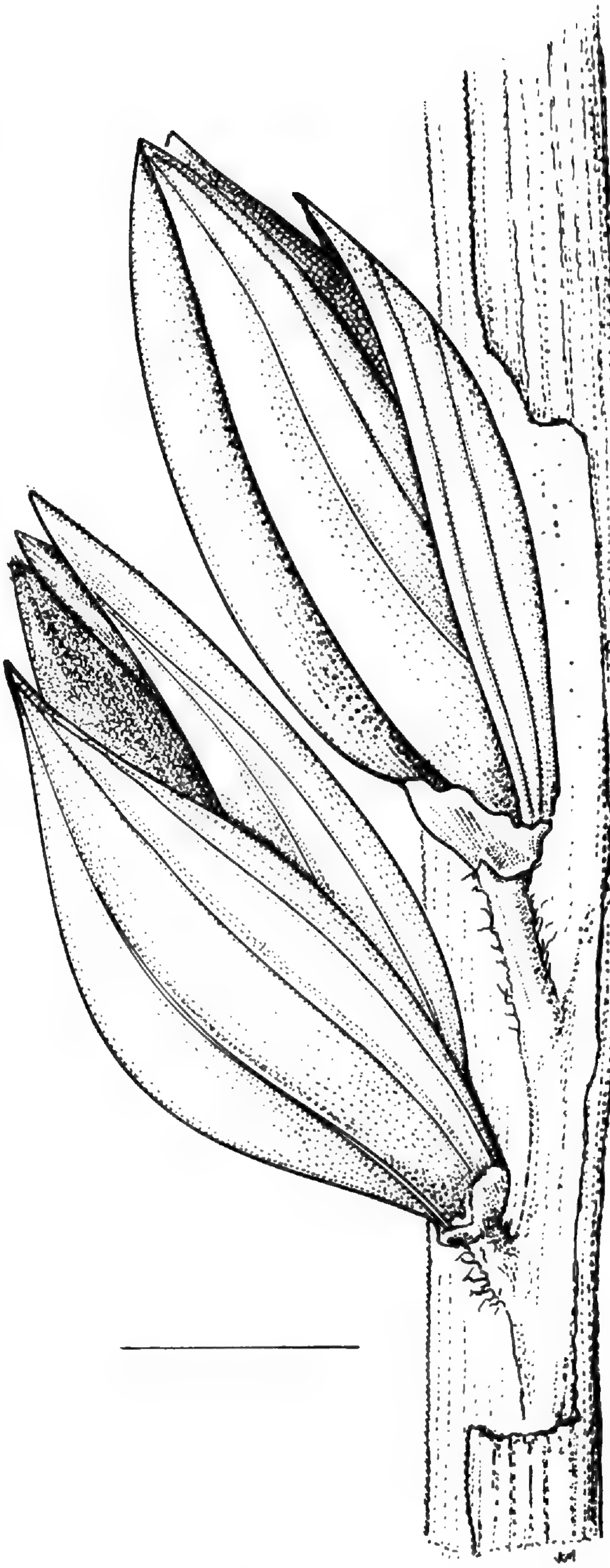

FIGURE 1. Spikelet pair of *Thrasya mosquitiensis* Davidse & Burman showing the back-to-back orientation of the spikelets, winged rachis (partially removed on one side), and partially adnate pedicel of the long-pedicellate spikelet. Scale line = 1 mm.

in *T. campylostachya*, although the latter species is somewhat variable in this regard.

The specific epithet refers to the area of Nicaragua and Honduras, dominated by pine savannas, that is commonly referred to as the Mosquitia or sometimes as the Costa de Miskitos.

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A NEW SPECIES OF *BULBOSTYLIS* (CYPERACEAE) FROM TROPICAL AMERICA

Bulbostylis, in the sense employed here, includes ca. 100 species centering in the tropics and subtropics of both hemispheres, with best representation in Africa and South America. It is usually placed in the tribe Scirpeae and is taxonomically (some state inextricably) related both to *Abildgaardia* and *Fimbristylis*. It is distinguishable from both by the sheaths which bear a sparse to dense beard of long, firm, often bristly hairs at the orifice and by the achenes which are surmounted by a persistent tubercle formed from the style base. Many species have weedy tendencies, are heliophytes, and thus grow abundantly in open areas that are artificially or naturally disturbed, in soils that are typically acid, sandy, azonal, and seasonally moist or wet. Thus they are much a part of vegetation of savanna, acid rock outcrops, natural or artificial clearings, and fluctuating, sandy-silty shores. Since such habitats are common in many areas of Amazonia, *Bulbostylis* species are an important component of the herbaceous vegetation. One species, frequently collected in the last decade along banks and bars of major streams in Amazonian Brazil, Colombia, and Venezuela, represents a new one that we describe here.

Bulbostylis fluviatilis Kral & Davidse, sp. nov. TYPE: Venezuela. Amazonas: Dpto. Río Negro, south side of hamlet of Santa Lucia, sandy recently cleared area for heliport, by Río Negro, common, 25 Nov. 1984, *R. Kral 71973* (holotype, VEN; isotypes, F, FSU, GH, ISC, MICH, MO, NY, P, U, US, VEN, VDB). Figure 1.

Bulbostylis tenuifolia (Rudge) Macbride affine a quo glumis mucronibus excurrentibus et antheris 2, 0.2–0.3 mm longis differt.

Annual, densely cespitose, 5–30 cm high. Roots capillary-fibrous. Leaves few per culm, polystichous, sub-basal, the lowest mostly bladeless or with blades shorter than the sheaths; principal leaves usually ⅓–½ as long as the scapes, sometimes as long, green; sheaths medially convex or keeled, multicostate, the costas strongly hirtellous, the broad, scarious, tan borders hirtellous, narrowing acutely to a long ciliate apex; blades 5–15 cm long, capillary, erect or spreading, proximally involute, 0.2–0.3 mm broad, pentacostate, distally triquetrous with costas scabridulous, the tips narrow but blunt. Scapes 0.2–0.3 mm thick, capillary, erect, sharply 5–7-costate, smooth or proximally sparsely scabridulous. Inflorescence a broad anthella 2–4 cm high, subumbellate, diffuse; involucral bracts 3–5, leaflike, subtending prophyllate rays, the longest bract equalling or slightly overtopping the anthella, the central spikelet sessile, 3–4 mm long, its lowest bracts also subtending primary rays; primary rays 0.5–3 cm long, erect to spreading, capillary and costate, 1–3-spicate; secondary rays 5–15 mm long. Spikelets mostly 3–6 mm long, lance-ovoid to lance-cylindric, pedicellate except for the central spikelet, acute; bracts 1.0–2.0 mm long, loosely spirally imbricate, lance-ovate, navicular, glabrous or hispidulous, 1-nerved, medially carinate, the midnerve green, the apex acute, villosulous, the margins sparsely ciliolate, the cusps and mucros 0.1–0.3 mm long, excurvate, scabridulous, the broad sides scarious, tan or red-brown, glabrous or hirtellous; lowest bract 2–3 mm long, usually sterile, strongly cuspidate, the cusp to 2 mm long; stamens mostly 2, the filaments flat, the anthers 0.2–0.3 mm long, basifixed, bilocular, laterally dehiscent, ellipsoidal, apiculate; style glabrous, branched medially to 3 slender, papillate stigmas. Achene 0.5–0.7 mm long, broadly obovoid-trigonous, the faces nearly plane, the adaxial face broadest, the surfaces finely papillose-lined longitudinally, transversely rugulose, whitish gray to brown; tubercle ca. 0.1 mm long, subglobose to oblate, apiculate, dark brown.

Paratypes. COLOMBIA. GUAINÍA: near Coitara, ca. 7 km S of San Fernando, 67°43′W, 3°55′N, *Davidse 16827* (COL, MO, VDB, VEN); Finca Buena Vista on the Río Negro, ca. 15 km S of San Felipe and San Carlos de Río Negro, 67°00′W, 1°42′N, *Liesner 8780* (COL, MO, NY, VDB, VEN). VENEZUELA. AMAZONAS: Dpto. Atabapo, Río Atacavi, 6–7 km de la desembocadura, 67°21′W, 3°14′N, *Guánchez 1372* (MO, TFAV). Dpto. Casiquiare, ca. 4 km up Casiquiare from Boca de Casiquiare on Río Negro, 67°4′W, 2°1′N, *Liesner 3927* (MO, VEN). Isla José, Alto Orinoco, *Vareschi 6768* (VEN). APURE: Dist. Pedro Camejo, 4 km NE of El Betun along the Río Capanaparo, 67°49′W, 6°58′N, *Davidse & González 13121* (MO, VEN); 27 km WSW of Paso de Cinaruco along the Río Cinaruco, 67°45′W, 6°31′N, *Davidse & González 12574* (MO, VEN); bank of Río Orinoco on Isla Poyatón, 67°05′W, 7°02′N, *Davidse & González 12216A* (MO, VEN); 9 km W of Paso

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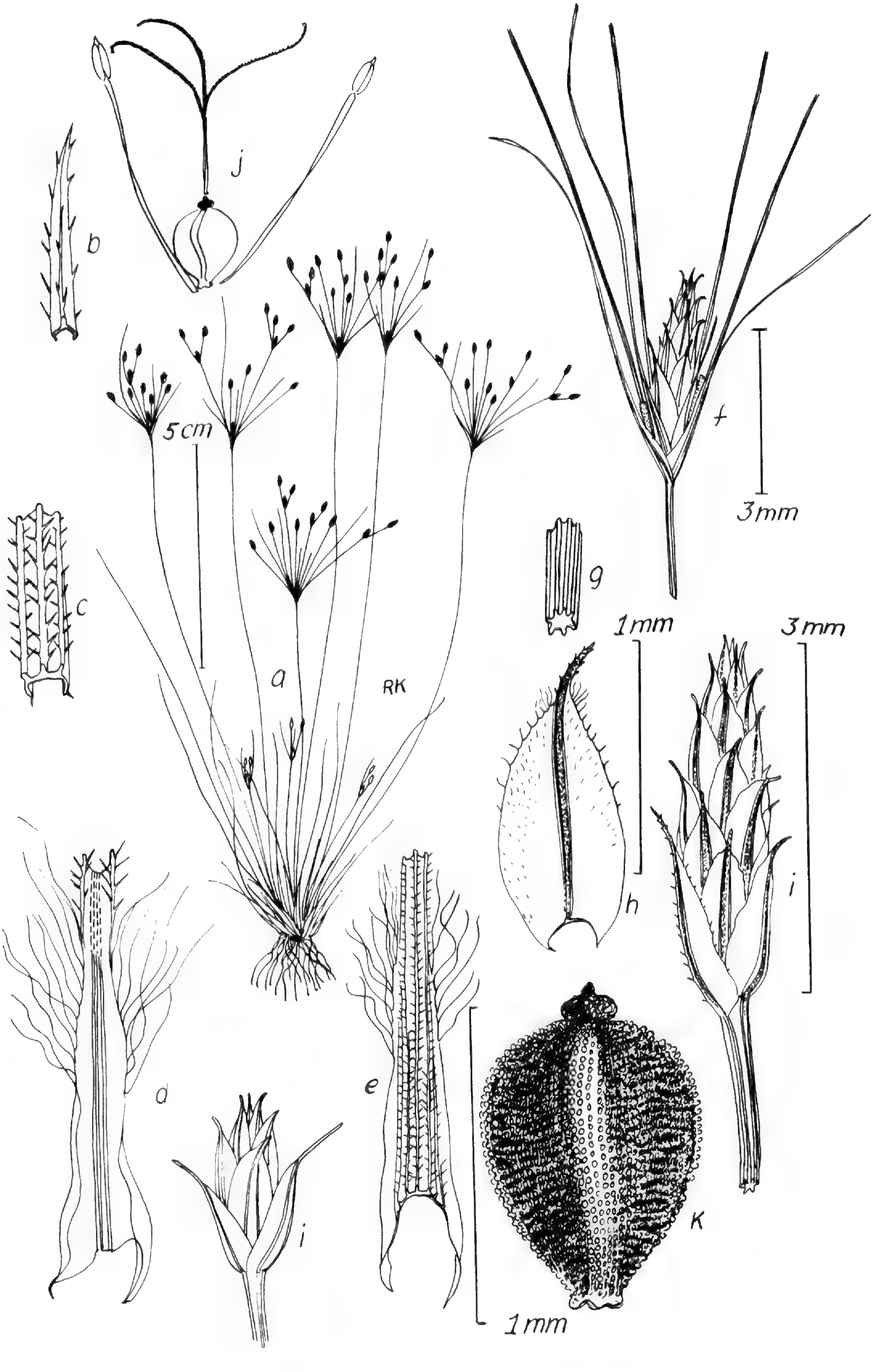
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de Cinaruco along the Río Cinaruco, 67°35′W, 6°35′N, *Davidse & González 12495* (MO, VEN). BOLIVAR: Auyan-tepui, *Vareschi s.n.* (VEN). BRAZIL. MATO GROSSO: Rio Aripuaña, N of Humboldt Campus, 59°21′N, 10°12′S, *Prance et al. 18319* (MO, NY).

Among the tropical American species of *Bulbostylis, B. fluviatilis* seems most closely related to *B. tenuifolia* (Rudge) Macbride, and some of the cited paratypes have been distributed under that name. *Bulbostylis fluviatilis* is similar to *B. tenuifolia* in its general facies and annual life cycle but differs in having one-nerved glumes with an excurrent mucro and two stamens with anthers 0.2–0.3 mm long. *Bulbostylis tenuifolia* has three-nerved glumes with the midrib slightly or not at all excurrent and one stamen with anthers 0.4–0.5 mm long.

In superficial appearance *B. fluviatilis* also resembles some species of the *Trichelostylis* group of *Fimbristylis*. However, the prominent hairs along the mouth of the sheath and the distinctly tuberculate style base clearly indicate that this species belongs in *Bulbostylis.*

Bulbostylis fluviatilis grows along large rivers (hence the epithet) at elevations of 65–120 m. It grows primarily on the sand bars that become prominently exposed in these rivers during the dry season and on accumulations of sand on exposed granite outcrops along the rivers.

We believe that the cited collection of Vareschi from Auyan-tepui is not a reliable record and that it is probable that the wrong label was mounted with the plant. It is perhaps possible that the plant originated along one of the rivers at the base of Auyan-tepui, but it is extremely unlikely that it originated from the highly different habitats atop Auyan-tepui. The Brazilian collection differs from the others in having the leaves about as long as the inflorescences.

The fieldwork that resulted in some of the cited collections was supported by the National Science Foundation, National Geographic Society, Consejo Nacional de Investigaciones Científicas y Tecnológicas (Venezuela), and Fundación para el Desarrollo de las Ciencias Físicas, Matemáticas y Naturales (Caracas). We thank Otto Huber and Charles Brewer-Carías for providing opportunities for fieldwork in southern Venezuela, and the Herbario Nacional (VEN), INPARQUES, for use of their facilities.

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FIGURE 1. *Bulbostylis fluviatilis* Kral & Davidse, drawn from the type collection, *Kral 71973.*—a. Habit sketch.—b. Leaf blade apex.—c. Mid-sector of the leaf blade, dorsal view.—d. Inner view of the leaf base.—e. Outer view of the leaf base.—f. Anthella base, showing the central sessile spikelet, involucre, and bases of primary rays.—g. Sector of the scape.—h. Fertile bract.—i. Two sorts of spikelets.—j. Floret.—k. Fruit.

A NEW *CAREX* SECT. *OLIGOCARPAE* (CYPERACEAE) FROM WESTERN ARKANSAS AND EASTERN OKLAHOMA

In late April of 1977, during fieldwork along the summit of Rich Mountain, the highest range of the Ouachita trend in western Arkansas, the senior author discovered on the dry, oak-pine slopes of the southwestern-facing side numerous clones of a *Carex* similar to *C. hitchcockiana* Dewey but distinct in habit, indument, and foliar character. On being informed of this plant, Arkansas botanists such as R. Davis and J. Rettig and caricologist C. T. Bryson conducted productive searches for it, not only in the original locality but elsewhere on Rich Mountain (including Oklahoma) and southward. We are aware now of an abundance of it, often in association with *C. hitchcockiana* and *C. oligocarpa* Schk. of sect. *Oligocarpae* over a substantial range of arenaceous oak-hickory-pine uplands in Arkansas (Howard, Polk, Scott counties) as well as in LeFlore County, Oklahoma. This habitat system is so well represented in the Interior Highlands physiographic province, particularly the Ouachitas, that a sedge thought to be rare and local may indeed be widespread and locally abundant within that physiography, as has now been shown in the case of *C. latebracteata* Waterf. (Kral, 1983). The new *Carex* is named after the mountain complex where it first was found.

Carex ouachitana Kral, Manhart & Bryson, sp. nov. TYPE: United States. Arkansas: Polk Co.: sandy rocky woods at summit of Rich Mountain, just W of Queen Wilhelmina Park Headquarters, 26 Apr. 1977, *R. Kral 59803* (holotype, MO; isotypes, BM, CTB, GA, GH, MICH, MO, US, VDB). Figure 1.

Spec. nova e sectione *Oligocarpae*. Planta perennis, 30–80 cm longa, glabra, laxe cespitosa, valde squamate rhizomatosa, foliis principalibus culmo longioribus vel paulo brevioribus. Rhizoma repens vel ascendens, plus minus lignescens, 2–4 mm crassum, in cataphyllis gradatim transiens. Cataphylla oblonga, 1–5 cm longa, acuta vel acuminata, fuscopurpurea, carinata. Culmi dimorphi, lateralibus sterilibus foliosissimis. Folia principalia 30–70 cm longa. Laminae compressae, 3–5 mm latae, scabridae, apicem versus attenuatae, scabromarginatae; pagina ad medium foliorum superna impressinervis, inferna elevatinervosa, costa media valde elevata, scabrida. Spicae 2–4, lineares; spica ultima omnino mascula, 2–4 cm longa, ca. 3 mm crassa, pedunculo 2–3-plo breviora. Spicae penultima omnino foeminae vel androgynae, peranguste lineares, pauci-vel-multiflorae, 3–6 cm longae basin versus interruptae. Bracteae spiculae masculae sine vagina, lanceolatae, 10–15 mm longae, anguste acuminatae vel cuspidatae; bracteae spiculae lateralis foliaceae, erectae, pedunculis ascendentibus vel erectis, 2–6 mm longis subtendentes, infimae laminis 10–13 cm longis et vaginis usque ad 4 cm longis. Glumae masculae oblongo-lanceolatae ca. 2.5–3.0 mm longae, acutae, carinatae, lateribus pallide brunneolis, costale virides. Glumae foeminae ovatae vel lanceolatae, naviculares, cum cuspide 5–15 mm longae, acutae vel anguste truncatae, zona media viridi, unicostali, lateribus stramineis vel brunneolis, apicibus glumarum infernarum valde cuspidatis. Perigynium obovoideum, 4–6 mm longum, obscure trigonum, superficiebus leviter concavis vel planis, impressinervis, rostro brevi-excurvato. Achaenia arcte inclusa, stipitato-obovoidea trigona, cum erecto rostro ca. 4.5–5.0 mm longa superficie concava, pallide brunneola, minute papillosa.

Perennial 30–80 cm long, smooth, loosely cespitose, strongly scaly-rhizomatous, the principal leaves slightly longer or slightly shorter than the culms. Rhizome creeping to ascending, ± ligneous, 2–4 mm thick, branching, the scales ovate, acute, spirally imbricate, multicostate, brown, gradually passing into cataphylls. Cataphylls oblong, 1–5 cm long, acute or acuminate, red-brown-purple, multicostate (costas often white), carinate. Culms dimorphic, spreading, slender, acutely trigonous, scabrid, the lateral ones sterile, more leafy. Principal foliage leaves longer toward culm base and approximate, 30–70 cm long. Leaf sheaths carinate, smooth; ligule erect, a narrow, horseshoe-shaped or acute scale. Blades spreading or recurved, flattened, linear, 3–5 mm wide, scabridulous, apically attenuate, triquetrous, the edges harsh, the surfaces at mid-blade above scabrellous, impressed-nerved, abaxially elevated-nerved, with midcosta strongly raised, scabrid. Spikes 2–4, narrow, the uppermost all male, nar-

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FIGURE 1. a–j. *Carex ouachitana*.—a. Habit.—b. Ventral (left) and lateral-oblique view of leaf sheath apex.—c. Leaf tip, abaxial side.—d. Axial (left) and abaxial (right) sides of midsector of leaf blade.—e. Scale of staminate flower.—f. Anther and upper part of filament.—g. Perigynium and accompanying scale, spike base.—h. Perigynium and accompanying scale, spike apex, showing stigmatic branches and outline of included fruit.—i. Detail, further enlarged, of perigynium.—j. Fruit. From *Kral 59803*.

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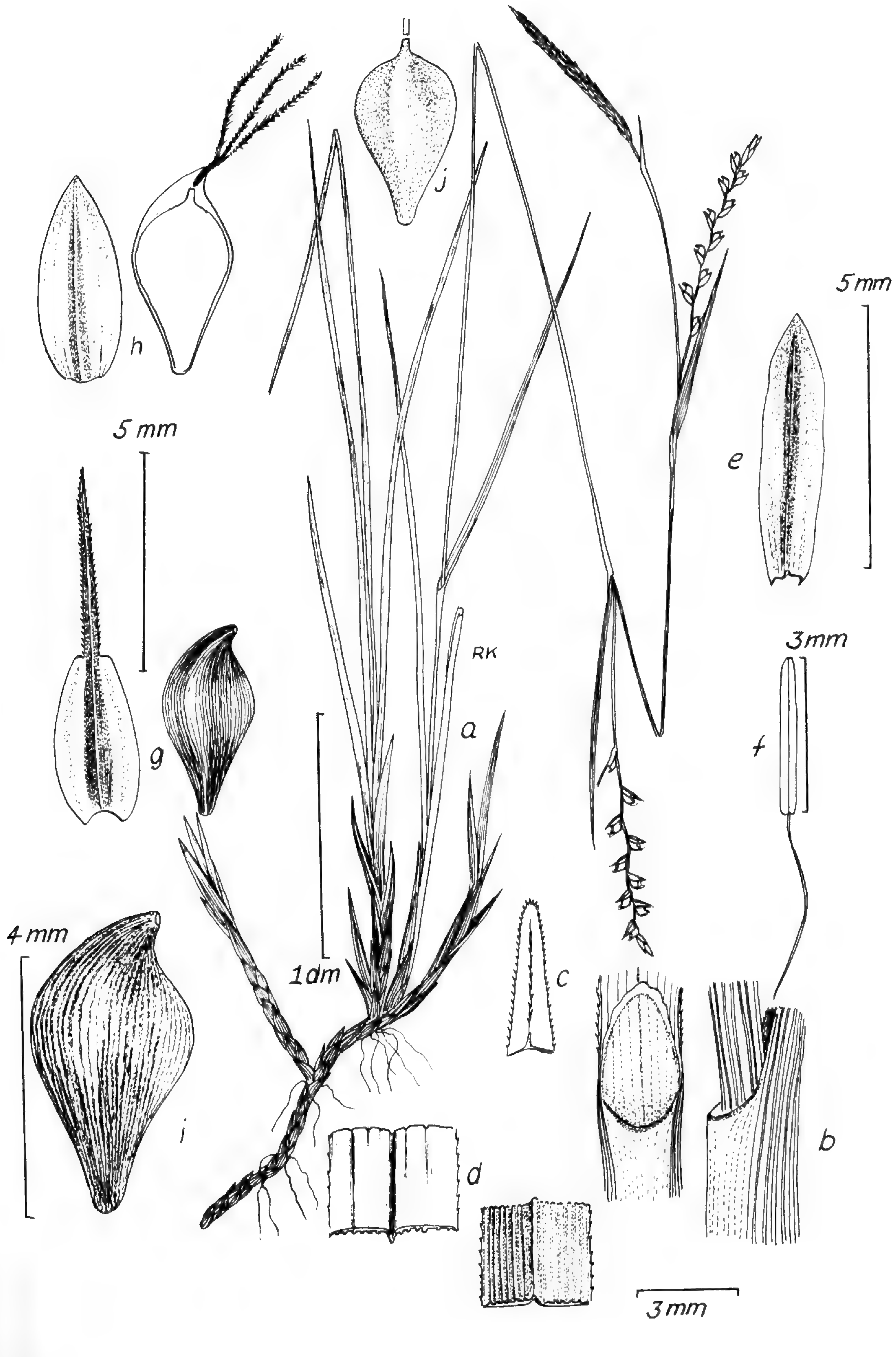
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rowly densely ellipsoid-cylindric, 2–4 cm long, ca. 3 mm thick, 2–3 times shorter than the peduncle. Spikes beneath all female, or androgynous with 1–7 male florets at the tip, narrowly linear, few-to-many-flowered, 3–6 cm long, basally interrupted, at apex with the flowers more approximate. Male spike bract without sheath, lanceolate, 10–15 mm long, narrowly acuminate or cuspidate, carinate; bracts of lateral spikes foliaceous, erect, subtending erect to ascending peduncles 2–6 cm long, the lower with blades 10–15 cm long and with closed sheaths to 4 cm long. Male scales scarious, oblong-lanceolate, ca. 2.5–3.0 mm long, acute, carinate, the sides pale brown, the costal area green. Female scales ovate to lanceolate, navicular, 5–15 mm long including the cusp, acute to narrowly truncate, the midzone green, unicostate, the sides stramineous to brown, the tips of the lower scales strongly cuspidate. Perigynia obovoid, 4–6 mm long, obscurely trigonous, the faces slightly concave to level, impressed-nerved, the beak short, excurved. Fruit tightly included, stipitate-obovoid, trigonous, 4.5–5.0 mm long including the short erect beak, the faces concave, pale brown, minutely papillate.

Additional specimens examined. UNITED STATES. ARKANSAS: Howard Co.: shaley wooded river bluffs, 9.6 mi. E of Wickes, 9 May 1979, *Kral 63507*; NW of AR Hwy. 4 and Cossatot River on slopes above river under mixed hardwoods, 10 May 1986, *Bryson 4332.* Polk Co.: Rich Mtn., along Ouachita Trail near Hwy. 88 N 0.3 mi. W of Rich Mtn. tower, 27 Apr. 1981, *Rettig & Davis 239*; Queen Wilhelmina State Park, Sect. 11, R32W, T1S, below and to N of visitor center and AR Hwy. 88 along trail on N-facing slope under mixed hardwood forest, rich rocky soil, 10 May 1986, *Bryson 4289*; NW of Rich Mtn. Lookout Tower, N of AR Hwy. 88, SW ¼ Sec. 8, R31W, T1S, along Ouachita Trail on N-facing slope under hardwood forest with dense herbaceous undergrowth, 10 May 1986, *Bryson 4290*; NE of AR Hwy. 246 and Cossatot River crossing NE ¼ Sec. 30, R30W, T4S under rich hardwood forest with few pines, on W-facing slope, rocky soil with thick leaf litter, 10 May 1986, *Bryson 4326.* Scott Co.: N slopes of Black Fork Mountain W of Mena, W of Cemetery, 4 May 1982, *Davis 3066*; Blackfork Mtn., W of Little Cemetery on long ridge road, rich humus, Jackfork Sandstone, T1N, R32W, Sec. 27, 3 May 1982, *Rettig et al. 501.* OKLAHOMA. LeFlore Co.: mesic N-facing slope of Rich Mountain ca. 150 yards W of the Oklahoma-Arkansas state line near Hwy. #1, 30 Aug. 1979, *Taylor 28122*; just W of State Line Historical Site S of OK Hwy. 1, rocky soil in soil islands on rock outcrops on top of Rich Mtn., open area, 10 May 1986, *Bryson 4300*; NW and below State Line Historical Site N of OK Hwy. 1 on N-facing slope under thick oak-hickory forest with few pines toward top, thick brushy and herbaceous understory, rich rocky soil in association with *Carex jamesii, C. oligocarpa, C. hitchcockiana, C. albursina,* 10 May 1986, *Bryson 4310.* Duplicates are to be distributed later, thus acronyms for recipients are not cited.

Staminate terminal spikes, female spike scales with harsh cusps and costae, perigynia with many impressed nerves, and short toothless beaks place this sedge squarely in sect. *Oligocarpae,* a section first designated by Carey in Gray (1848), and subsequently revised by Kukenthal (1909), Mackenzie (1931–1935) and Fernald (1950). In most modern classifications this complex comprises just *C. oligocarpa* and *C. hitchcockiana.* Both of these are densely cespitose and erhizomatous; whereas *C. ouachitana* is loosely cespitose, sometimes forming colonies up to 0.5 m across in open areas and up to 1–2 m across in shaded areas, and produces strong, ligneous, imbricate-scaly rhizomes. The staminate spike is larger, with a longer peduncle, thicker, and bears more florets. The lateral spikes are frequently androgynous, while in *C. oligocarpa* and *C. hitchcockiana* they are solely carpellate. The perigynia are much like those of *C. hitchcockiana* in size and shape but differ in that the beak is shorter, broader, and more bent outward. On the other hand, the fruit beak resembles that of *C. oligocarpa* by being erect or suberect. However the members of this triad are related morphologically, it is significant that, even though they have been observed to share habitat in the same localities, no apparent naturally occurring hybrids have thus far been seen.

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NOTES ON CHROMOSOME CYTOLOGY OF RUTACEAE—DIOSMEAE

The tribe Diosmeae R. Br. emend. Benth. & Hook. f. (1862) of the Rutaceae is strictly African in distribution and consists of the widespread tree *Calodendrum capense* (L.f.) Thunb. (southern Cape to north Kenya) and some 280 species of small to medium-sized shrubs, mostly of ericoid habit. The tribe is, with the exception of *Calodendrum,* restricted to southern Africa and largely to the Cape Region of the south and west coast of South Africa. Taxonomic revisions of the tribe have recently been published for all but the large genus *Agathosma* (Strid, 1972; Williams, 1975, 1978, 1981a, 1981b, 1982) but chromosome cytology of the group is poorly known.

Apart from several counts by Strid (1972) for *Adenandra,* there are only scattered reports for a few genera. The monotypic *Calodendrum* is a high paleopolyploid with $2n = 54$ (Honsell, 1954; Smith-White, 1954). In *Agathosma, A. crenulata* (L.) Pill. has been reported as having $2n = 45$ (as *Barosma*) (Riley & Hoff, 1961), while Guerra (1984a) found $2n = 26$ in *A. apiculata* E. Meyer (also as *Barosma*) and *A. lanceolata* (L.) Engl.

There are two counts for *Coleonema pulchellum* I. J. Williams (as *C. pulchrum* Hook.), Smith-White (1954) reporting $2n = 36$ and Guerra (1984a) $2n = 34$; Guerra also reported $2n = 34$ in the closely related *C. album* (Thunb.) Bartling & Wendl. Numbers reported in *Adenandra* are $2n = 28$ in two species, 38 in one more, 42 or ca. 42 in two species including *A. fragrans,* and $2n = 48$–50 in another three. In conjunction with continuing systematic studies of Diosmeae a preliminary investigation of the chromosomes of some genera was undertaken and this report is the result of the study.

All counts were made from mitotic metaphase in root tip squashes of germinating seeds, following a method described fully elsewhere (Goldblatt, 1979, 1980). Chromosome number and voucher information are as follows:

Diosma subulata Wendl. $2n = 30$. South Africa, Cape, ex hort. Williams, *Williams s.n.* (NBG); Wortelgat, Caledon Div., *Williams 1721* (NBG).

Diosma aristata I. J. Williams $2n = 30$. South Africa, Cape, ex hort. Williams, *Williams s.n.* (NBG).

Diosma oppositifolia L. $2n = 30$. South Africa, Cape, Vogelgat, Caledon Div., *Williams 2406* (NBG).

Euchaetes avisylvana I. J. Williams $2n = 28$. South Africa, Cape, Grootvadersbos, Heidelberg Div., *Williams 2377* (NBG).

Adenandra fragrans (Sims) Roemer & Schultes $2n = 42$. South Africa, Cape, Grootvadersbos, Heidelberg Div., *Williams 2378* (NBG).

DISCUSSION

The count of $2n = 42$ for *Adenandra fragrans* confirms the earlier report by Strid (1972) for this species. Reports here for *Euchaetes* and *Diosma* are the first records for these genera. On the basis of four counts for three species of *Diosma,* all $2n = 30$, we suggest that $x = 15$ is basic for the genus. In *Euchaetes* the single count suggests a generic base of $x = 14$; $x = 7$ seems unlikely since all other counts in Diosmeae are at paleotetraploid or paleohexaploid levels.

Basic chromosome number for Rutaceae is most likely $x = 9$ as suggested by Smith-White (1954). This hypothesis is founded on the predominance of $n = 18$ and 36 in the unspecialized Xanthoxyleae and Flindersieae, and Ehrendorfer (1981, 1987) has also pointed out the occurrence of only $n = 9$ and 18 in Aurantieae. Data for Diosmeae throw no direct light on the possible base number for the family, as they are relatively specialized. However, the number in *Calodendrum,* $n = 27$, is most likely paleohexaploid based on $x = 9$, and the same base number is by extension probable for all Diosmeae, given the basal position of *Calodendrum* in the tribe. Other genera of Diosmeae that have been counted appear fundamentally paleotetraploid, a view endorsed by Guerra (1984b) for *Coleonema* based on a comparison of genome size in Rutaceae. Thus *Coleonema,* either $n = 18$ or 17, is probably hypotetraploid based on $x = 9$. The base of $x = 15$ in *Diosma* may represent either further aneuploid decrease from an ancestral $x = 18$, or less likely, allopolyploidy from hypothetical ancestors with $x = 7$ and 8. *Euchaetes,* closely related to *Diosma,* with $n = 14$ fits with the apparent trend for decrease from an ancestral tetraploid base. *Adenandra* appears basically paleotetraploid (? $x = 14$) but some species may be octoploid and derived from the secondary hypotetraploid base. This may best explain the range from $n = 25$, 24, 21, and 19, as well as $n = 14$ in two species.

Further counts in Diosmeae are needed to resolve the several questions that this initial study has posed. The variation in chromosome number in the tribe is unexpected and is likely to be of considerable value in future studies of generic limits and of the relationships of genera and species, and ultimately of phylogeny.

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THE FRUITS OF *DECARYDENDRON* (MONIMIACEAE)

Decarydendron Danguy is a poorly known genus of Monimiaceae (subfamily Mollinedioideae, tribe Hedycareae) comprising three species endemic to Madagascar (Danguy, 1928; Cavaco, 1958a, 1958b; Lorence, 1985). Fruiting material of the genus, hitherto unknown, is described here for the first time based on a specimen of *D. perrieri* Cavaco recently collected by L. J. Dorr and L. Barnett in Madagascar. The following description is based on FAA-fixed fruits of *Dorr & Barnett 3203* (Madagascar. Province Tamatave: environs d'Andasibe-Pèrinet, 18°56'S, 48°25'E, 2–4 Nov. 1984). Voucher specimens have been deposited at MO and TAN, and the fixed collection is at PTBG.

Fruiting receptacle attached at or below ground level, terminal on a finely velutinous peduncle 2.5–3 mm diam., swollen, fleshy, obconical-turbinate, initially 3 cm diam., during development curling outwards and splitting irregularly into 3 partly everted segments, externally and internally velutinous with simple trichomes; mature carpels 12, free, interspersed with numerous aborted carpels. Mature carpels sessile to subsessile, obpyriform, 2–2.5 cm long including the constricted, curved, beak-like apex 5–7 mm long, 1.3–1.6 cm diam., externally yellowish brown, corky, bearing circular to elliptic corky lenticels over most of the surface; exocarp fleshy, to 1 mm thick (thicker at apex), the surface corky, parenchymatous, the tissue replete with densely aggregated brachysclereids, underlain by a vascularized zone, the mesocarp parenchymatous with scattered ± cuboidal idioblasts; endocarp hard, white, ± smooth, discontinuous apically at the micropyle, 0.8–1 mm thick, composed of a densely packed, radially oriented layer of narrow, thick-walled, fusiform columnar sclereids; testa 0.1–0.2 mm thick, brown, composed of 2 layers of tangentially elongated cells with slightly thickened walls, underlain by an endotesta many layers thick of short, rounded tracheids with scalariform thickenings; tegumen 3–4 layers thick, composed of elongate thin-walled cells. Endosperm about 1 cm diam., white, copious, oily, interspersed with crystals. Embryo situated apically in the endosperm below the micropyle, cylindrical-clavate, 2–3 mm long, 1 mm diam. distally, the cotyledons erect, ± appressed, about half the total embryo length. Figure 1a, b.

DISCUSSION

In a recent monographic treatment of the Malagasy Monimiaceae (Lorence, 1985), it was concluded that *Decarydendron* possessed the greatest constellation of primitive characters of

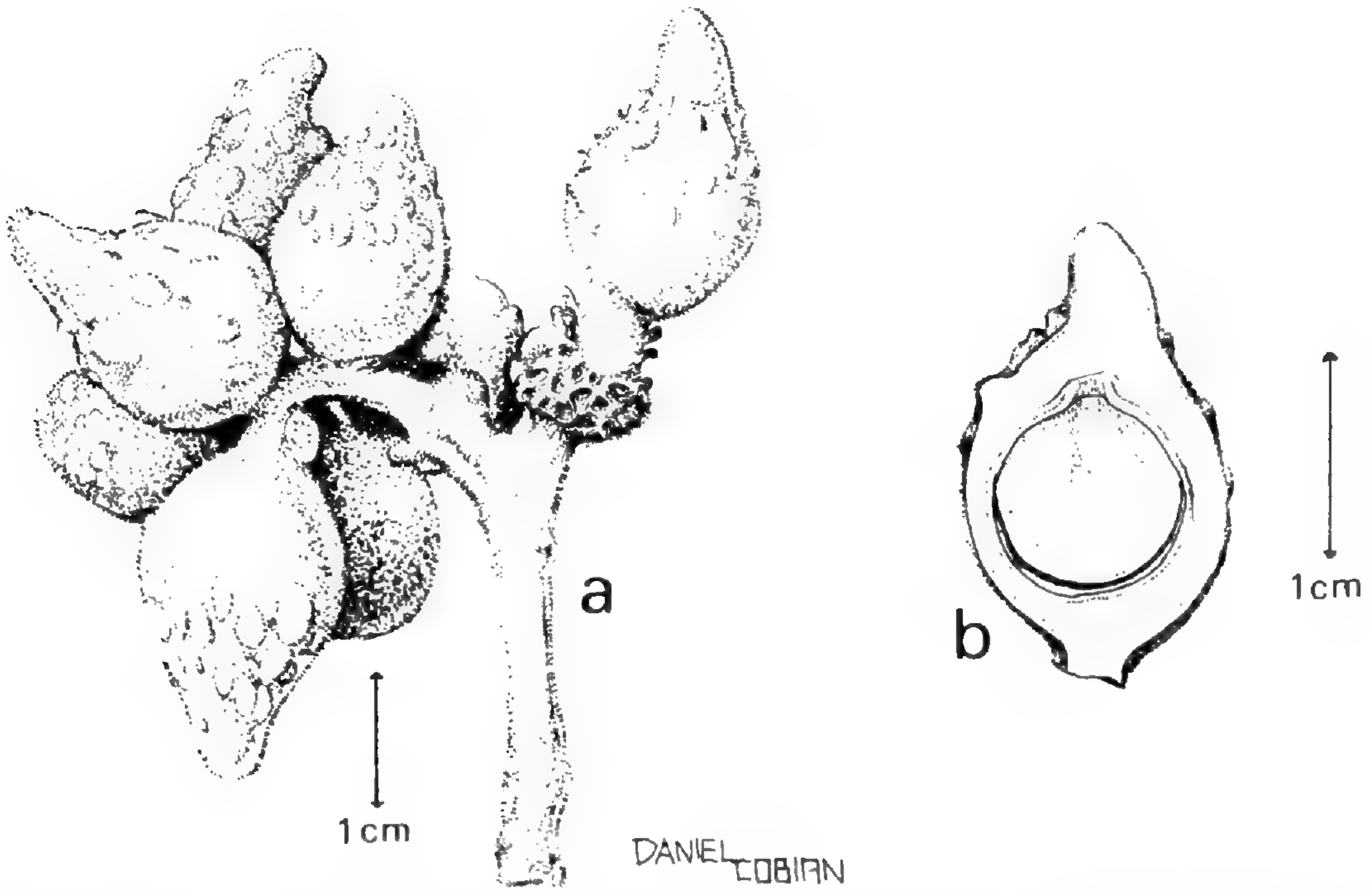

FIGURE 1. Fruiting receptacle and carpels of *Decarydendron perrieri*.—a. Mature, irregularly split receptacle with attached carpels.—b. Carpel, longitudinal section. Based on *Dorr & Barnett 3203* (PTBG).

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any of the Malagasy genera: both androecious and gynoecious flowers with shallowly concave receptacles bearing 1–2 whorls of large, imbricate tepals; flowers that unfold gradually at anthesis without splitting into segments as in the other three genera (i.e., *Ephippiandra* Decne., *Monimia* Thouars, and *Tambourissa* Sonn.); gynoecious flowers with numerous (ca. 300–1,000) free, subsessile, clavate carpels. As *Decarydendron* closely resembles *Hedycarya* Forster & Forster f. from Oceania and various Pacific islands in terms of gynoecious floral morphology, it was postulated that mature fruits of the former genus would most likely resemble those of the latter one (Lorence, 1985).

The findings reported here confirm that mature fruits of *Decarydendron perrieri* do strongly resemble those of other genera in the tribe Hedycareae (Philipson, unpublished) and support its placement there. Members of this tribe are characterized by gynoecious flowers with a noncalyptrate floral cup that encloses few to many free carpels, and fleshy discoidal or cupuliform fruiting receptacles that gradually split or become everted as the carpels mature. Among the other Malagasy genera belonging to the Hedycareae, the free, sessile to subsessile carpels of *Decarydendron* are less specialized than those of *Ephippiandra*, which are also free but partly immersed in cupules formed by the receptacle. Fruits of both these genera are in turn less specialized than the inferior, syncarpous carpels of *Tambourissa*, which are completely immersed in and united with the ovary wall (Lorence, 1985). Thus, fruit morphology also supports the suggestion that the three Malagasy genera of Mollinedioideae form part of an increasingly specialized evolutionary series.

Among the extra-Malagasy members of the tribe Hedycareae of the subfamily Mollinedioideae, *Decarydendron* is most closely allied to *Levieria* Becc. from Malesia and Australia, and particularly to *Hedycarya*, in terms of floral and fruit morphology. *Decarydendron* differs from both these genera in being monoecious, in having sexually mixed cauliflorous inflorescences, and in having gynoecious flowers with more numerous clavate carpels having the stylar canal situated in the basal half of the carpel.

I thank L. Dorr of the Missouri Botanical Garden for providing fixed material of *Decarydendron perrieri* and Danial Cobian of the Instituto de Biología for the illustration.

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RECONSIDERATION OF THE GENERIC PLACEMENT OF *PALICOUREA DOMINGENSIS* (RUBIACEAE: PSYCHOTRIEAE)

Although the Caribbean species sometimes known as "*Palicourea domingensis*" has commonly been treated in *Palicourea,* it lacks the distinguishing features of this genus and is better placed in *Psychotria.*

Palicourea Aublet (Rubiaceae: Psychotrieae) is distinguished within its tribe by comparatively long (tubes 5–40 mm long), tubular corollas that are slightly to strongly swollen at the base with a ring of trichomes borne internally, immediately above the basal swelling. Characteristically, the corollas are often also gibbous basally and brightly colored, usually red, yellow, blue, or purple. The thyrsiform inflorescences are typically open, with well-developed branches, bracts, and pedicels. This genus has been loosely circumscribed by many authors, who have used variously one or a few of these features or characters to separate it from *Psychotria* L.

The species of Psychotrieae now usually called "*Palicourea domingensis*" (Jacq.) DC. is a shrub or small tree of moist forest on soils derived from limestone. It is distributed through most of the Caribbean islands (Cuba, Jamaica, Hispaniola, Puerto Rico, St. Thomas, St. Croix, Tortola, Antigua, St. Kitts, St. Eustatius, Guadeloupe, Martinique, Dominica) and is found on the mainland in Mexico, Belize, Guatemala, and Nicaragua, although it has not been previously reported from these areas (Standley & Williams, 1975).

This species is characterized by salverform corollas with tubes 5–15 mm long. The corollas are predominantly white, although often tinged with rose or purple. Their tubes are glabrous externally and internally, and are not at all swollen or asymmetrical at the base, although the tube may be curved somewhat through its length. The inflorescences are thyrsiform, with the flowers subsessile in glomerulate groups of three. The inflorescence bracts are poorly developed or lacking.

Thus, "*Palicourea domingensis*" lacks the distinctive floral features and the common inflorescence characters of *Palicourea.* It has been placed in *Palicourea* by most authors apparently based on its relatively long, tubular, often rosy corollas, combined with an inconsistent circumscription of *Palicourea* and a respect for previous practice.

This species is better placed in *Psychotria* subg. *Heteropsychotria* Steyerm., which is closely related to *Palicourea.* The floral features of *Psychotria domingensis* are similar to those of other species of *Psychotria,* and the inflorescence characters described above that are rare or lacking in *Palicourea* are common conditions in this subgenus. This relationship was recognized previously by Standley when he described this same species from Nicaragua under the synonym *Psychotria mombachensis* Standley. Although the corollas of *Psychotria* are described in most treatments as comparatively short, and typically do have tubes 5 mm long or shorter, long corollas occur in the genus as well, as in *Psychotria chiapensis* Standley which has corollas with tubes 30–50 mm long. In fact, within subg. *Heteropsychotria, Psychotria domingensis* is similar in several characters to *Psychotria chiapensis* and to *Psychotria gardenioides* (Scheidw.) Standley: these species share glomerulate, subsessile flowers, sharply ridged pyrenes, and salverform, white or rosy corollas with internally glabrous tubes 20 mm long or longer. (The last two species differ from *Psychotria domingensis* in their longer corolla tubes and well-developed inflorescence bracts.)

Therefore, "*Palicourea domingensis*" seems better classified in *Psychotria.* In this case, the correct name of this species is *Psychotria domingensis* Jacq. A complete list of synonymy and citations of specimens from Central America are presented below.

NOMENCLATURE

Psychotria domingensis Jacq., Enum. Pl. Carib. 16. 1760. *Palicourea domingensis* (Jacq.) DC., Prodr. 4: 529. 1830. TYPE: Santo Domingo.

Psychotria pavetta Sw., Prodr. 45. 1788. *Pavetta pentandra* Sw., Fl. Ind. Occ. 1: 233. 1797. *Palicourea pavetta* (Sw.) DC., Prodr. 4: 525. 1830. *Palicourea pentandra* (Sw.) K. Schum., Nat. Pflanzenfam. 4(4): 115. 1891, nom. illeg., Art. 63. TYPE: Jamaica (photographs A, NY).

Psychotria tabernaefolia Poir., Encycl. 5: 704. 1804.

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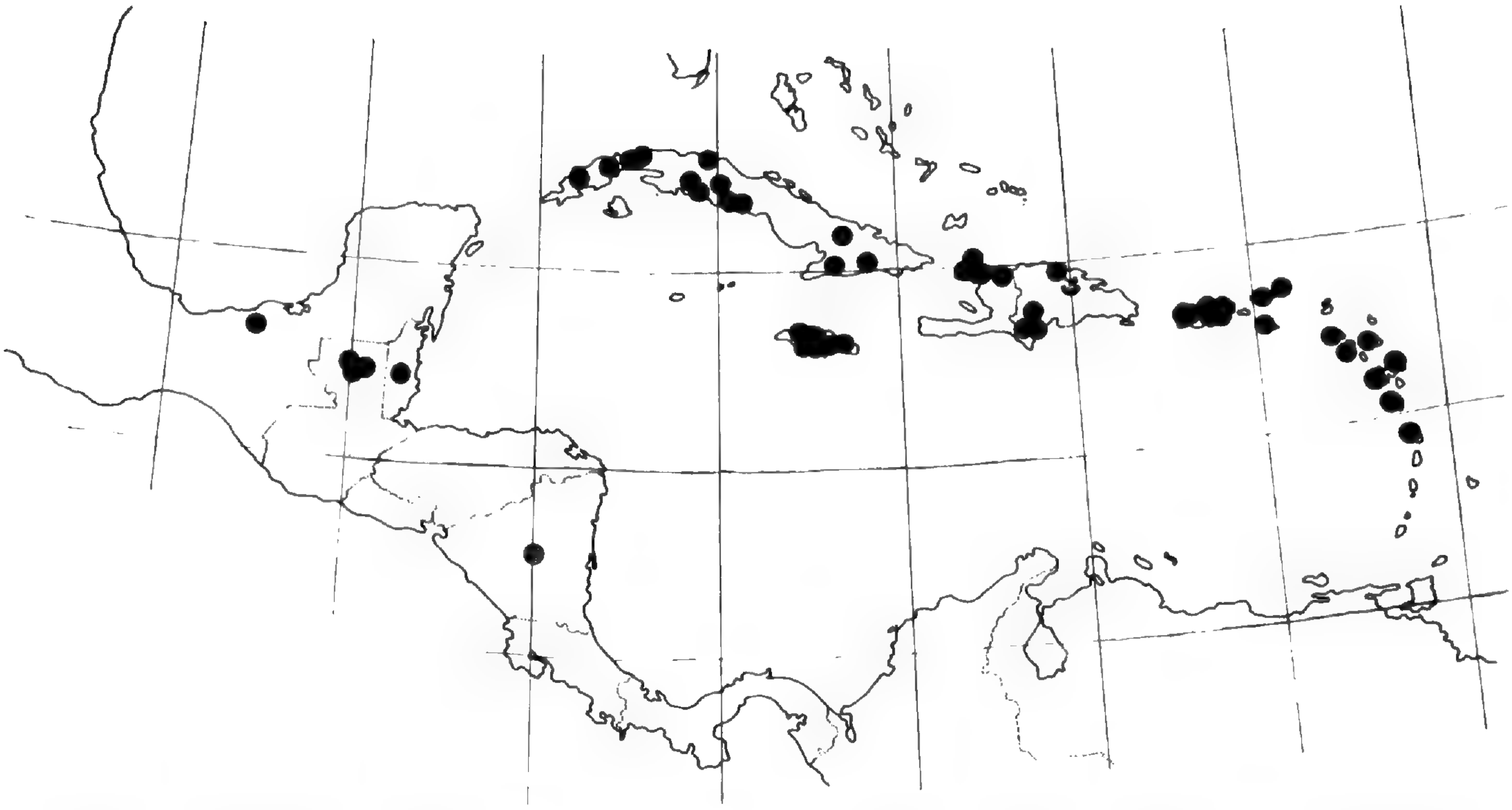

FIGURE 1. Distribution of *Psychotria domingensis* Jacq. in Mexico, Central America, and the West Indies.

Palicourea tabernaefolia (Poir.) DC., Prodr. 4: 525. 1830. TYPE: Santo Domingo.

Psychotria angustifolia Poir., Encycl. 5: 703. 1804. TYPE: Santo Domingo.

Psychotria mombachensis Standl., Publ. Field Colombian Mus., Bot. Ser. 8: 188. 1930. TYPE: Nicaragua: coffee plantation, Mombacho Volcano, 600–750 m, *Maxon, Harvey & Valentine 7818* (holotype, F).

Specimens examined from Mexico and Central America. MEXICO. TABASCO: La Palma, Balancán, *Matuda 3236* (NY).

GUATEMALA. PETÉN: Tikal, *Contreras 124* (MO), *1413* (TEFH); Dolores, *Contreras 2503* (MO); Macanche, *Contreras 5847* (DS); Chincila, *Contreras 6360* (MO); Isla del Armadillo, Laguna Macanche, *Contreras 7191* (MO); Sayaxche Road, km 59, *Contreras 7247* (MO, TEFH); Guayacuan, La Pita, *Contreras 7477* (MO); Tikal, *Contreras 7707* (MO); between Paso Caballo and Carmelita, *Cox 2835* (EAP); Tikal, *Molina 15750* (EAP).

BELIZE. CAYO: vicinity of La Flor at Río de La Flor, 6 mi. S of San Grano de Oro, 1,700–2,700 ft. [520–820 m], *Croat 23739* (MO), *Dwyer 10876* (MO); in advanced forest, *Lundell 6199* (NY); W of Hummingbird Hwy. 7 mi. S of junction with Western Hwy., N boundary of Roaring River Estate, 80 m, *Spellman & Newey 1669* (MO); 1 mi. S of Belmopan and 0.5 km E of Hummingbird Hwy., 80 m, *Spellman & Newey 1915* (MO); 1,700 yd. W of Hummingbird Hwy., 7 mi. S of junction with Western Hwy., 80 m, *Spellman & Newey 2010* (MO); TOLEDO: *Dwyer 9863* (MO).

I thank the curators of the following herbaria, who very kindly made specimens available for study: A, CAS, DUKE, EAP, F, GH, M, MO, NY, TEFH, and US; I thank in particular Dr. James Ackerman of UPRRP, who provided working space. I also thank Orlando Matos Concepción for help in preparing the distribution data.

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CLARIFICATION OF THE TAXONOMY OF *LEUCAENA SALVADORENSIS* STANDLEY EX BRITTON & ROSE

The nomen nudum *Leucaena salvadorensis* Standley was first published by him in Standley & Calderón (1925) in a list of El Salvador plants, without a complete description or designation of type. In their revision of the genus, Britton & Rose (1928) supplied a description and designated a type, giving the authority as Standley. Later, Standley & Steyermark (1946) reduced the species, cited as *L. salvadorensis* Standley ex Britton & Rose, to synonymy under *L. shannonii* J. D. Smith. Brewbaker et al. (1972) and Brewbaker in a mimeographed leaflet (1978) placed *L. salvadorensis* under the synonymy of *L. leucocephala* (Lam.) de Wit, and more recently Brewbaker & Ito (1980) treated it as a subspecies of *L. leucocephala* (also see Brewbaker's mimeographed revision, 1984). Zárate (1982, 1985) concluded that it was the same as the small-leaflet form of *L. shannonii* and returned it to synonymy with that species.

Recently, Colin Hughes, Brian Styles, and Angela Laguna have collected material in Honduras and Nicaragua (*C. Hughes 332, 334, 446* (FHO, MEXU); *C. Hughes & B. Styles 37, 102, 129* (FHO, MEXU); *A. Laguna 427* (HNMN, MEXU)) referable to this taxon. From study of these specimens it became apparent that it deserves recognition as a subspecies of *L. shannonii.*

The dome-shaped or truncate-conic, oblong petiolar glands and the corolla-to-calyx length ratio of ca. 0.7 in *L. shannonii* and *L. salvadorensis* clearly distinguish these taxa from *L. leucocephala* with suborbicular or elliptic or obovate thick-bordered and furrowed to concave glands and a corolla-to-calyx length ratio of ca. 0.5. The more numerous pairs of pinnae and leaflets, 6–11 and 23–35, respectively; consistently narrow oblong leaflets, ca. 1.5 cm long; florets 4 mm long; and pods strongly stiped, 11–21 cm long and ca. 2.5 cm wide, separate it from the typical element of *L. shannonii* with (2–)4–6(–8) pairs of pinnae, 8–22 leaflet pairs, very variable leaflets (0.8–)1–2 cm long, florets 3–3.5 mm long, and slender-stiped pods ca. 15 cm long and 1.4–2.2 cm wide. Therefore, the following combination is made.

Leucaena shannonii J. D. Smith subsp. **salvadorensis** (Standley ex Britton & Rose) S. Zárate, comb. et stat. nov. Basionym: *L. salvadorensis* Standley ex Britton & Rose, Fl. N. Amer. 23(2): 125. 1928. TYPE: El Salvador. Morazán: Jocoro, *Calderón 2031* (holotype, NY).

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AN UNUSUAL NEW SPECIES OF *HELMIOPSIS* H. PERRIER (STERCULIACEAE) FROM MADAGASCAR

Eight species of *Helmiopsis* H. Perrier (Sterculiaceae) currently are recognized in the *Flore de Madagascar et des Comores* (Arènes, 1959). All are characterized by monodelphous androecia with staminodes opposite the petals, sessile ovaries, caducous petals, capsular fruits with apically winged seeds, and overall vestitures of peltate or fimbriate (i.e., peltate with fimbriate margins) scales. All species described to date are restricted to western Madagascar. A new species of *Helmiopsis* is described here from the northern mountains of Madagascar, also part of the phytogeographical Domaine de l'Ouest of the island (Humbert, 1965). This species combines several features that are unusual for the genus. For example, its spheroid, rather than conical, capsule morphology is unique and provides the basis for the name *Helmiopsis sphaerocarpa* L. Barnett. The seed wings of *H. sphaerocarpa* are atypical for the genus in being reduced to only a thin, ventral keel; ordinarily seed wings of *Helmiopsis* species are apical and elongate, to 10 mm in length. The inflorescence is complex in structure, being multibranched and many-flowered, as opposed to the few-flowered cymose inflorescences more commonly found in the genus. The terminal nature of the inflorescence is also unusual in this species, although terminal inflorescences also have been observed in isolated collections of *H. pseudopopulus* (Baillon) Capuron (e.g., *Capuron 24661*, P). Finally, this new species is unique in bearing glandular tissue both on the calyx lobes and on the petals; in all other *Helmiopsis* species with glandular tissue, the tissue is restricted to either the calyx or the corolla, but is never found in both perianth whorls.

Helmiopsis sphaerocarpa L. Barnett, sp. nov. TYPE: Madagascar: Centre (Nord) jusqu'aux confins de l'Ouest (Nord), Massif de la Montagne d'Ambre, crête entre les bassins de la rivière des Makis et de la rivière d'Ankazobe, entre 800 et 600 m d'alt., 26–27 May 1970 (fl), *Capuron 29194 SF* (holotype, P; isotype, TEF). Figure 1.

Arbuscula vel arbor, squamarum lepidotarum deciduarum vestita. Folia late ovata vel anguste obovata, cordata, palmatim 5(–7) nervata. Inflorescentiae axillares et terminales, 15–30 floribus. Calyx 5-partita, lobis intus glandulosis. Petala 5, intus glandulosa. Tubus staminalis 1 mm altus; staminibus 10, staminodiis 5. Ovarium 5-loculare, loculis 2-ovulatis; stylo glabrato, stigmate leviter 5-lobata. Capsula sphaerica, loculicida. Semen carina ventrale membranacea.

Large shrub or tree to 8–12 m tall, branches terete, finely striate, new growth sparsely peltate-scaled, older twigs glabrate. Leaves alternate, deciduous, blades broadly ovate to narrowly obovate, 6.5–12 cm long, 4–9 cm wide, apex acute to acuminate, base shallowly cordate to cordate, palmately 5(–7) nerved, midvein and secondary veins conspicuous, raised below and slightly depressed above, discolorous, margins irregularly crenulate, lower surface with scattered peltate and fimbriate scales, becoming glabrate; petioles 1–6 cm long, with scattered peltate and fimbriate scales. Inflorescences terminal and in the axils of uppermost 3–5 leaves, determinate, branching 3–5 times, bearing 15–30 flowers. Floral buds ovoid, 4–5 mm long, 4–4.5 mm wide. Calyx 5-lobed, lobes connate only at the bases, lanceolate, ca. 7 mm long, 3 mm wide, outer surfaces densely covered with peltate scales, inner surfaces glabrate and with an arc of glandular tissue at the base. Petals 5, white (according to label data of *Capuron 29194 SF*), obovate, asymmetrical, 7–8 mm long and 7 mm wide, inner surface gland-dotted toward the base. Androecium coroniform, staminal column ca. 1 mm tall; stamens 10, ca. 3 mm long from the base of the column, each of the 5 antisepalous pairs alternating with a staminode; filaments 1–1.5 mm long; anthers ca. 2 mm long; staminodes 5, oblanceolate, 4–5 mm long, ca. 1 mm wide. Ovary 5-locular, densely peltate-scaled; ovules 2 per locule, collateral; style 5–6 mm tall, glabrate; stigma obscurely 5-lobed. Fruit capsular, woody, spheroid, dorsally loculicidal, 6–8 mm long, 8–10 mm wide, subtended by a woody, persistent calyx. Seeds 2 per carpel, asymmetrically ovate and laterally flattened, 5–6 mm long, 3–4 mm wide, each with a narrow, membranous, ventral keel.

Additional specimens examined. MADAGASCAR. NORTHERN SECTOR. DISTRICT DIÉGO-SUAREZ: Versant Est du massif de l'Ankerana, 17 Dec. 1966 (fr), *Capuron 27349 SF* (P, TEF); Montagne des Français, 11 Sept. 1952 (fr), *Service Forestier 5673 SF* (P, TEF); Ambalafary, Ambodipo-Antsahalalina, 7 June 1956 (fl), *Service Forestier 15962 SF* (P, TEF).

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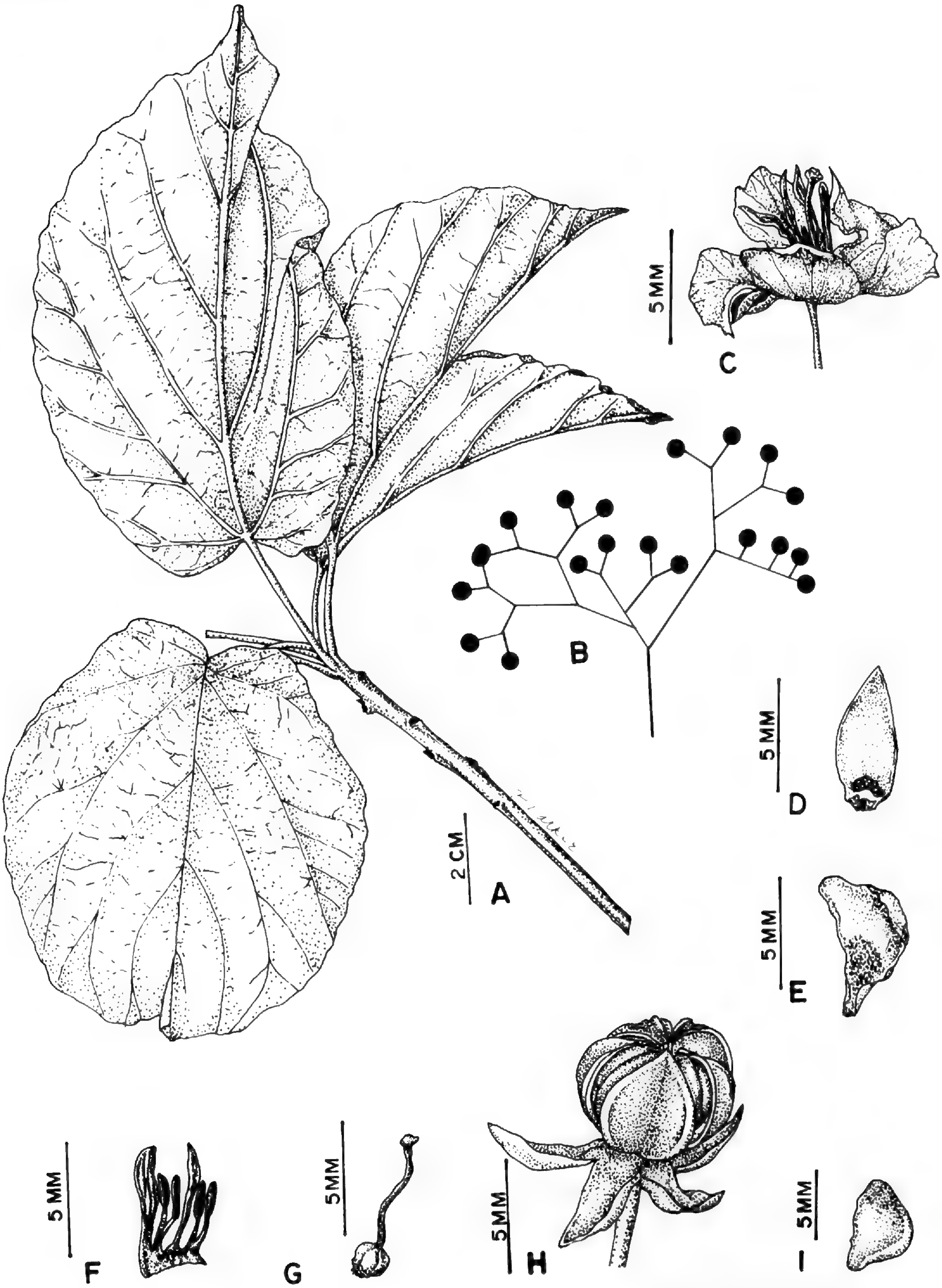

FIGURE 1. A–I. *Helmiopsis sphaerocarpa.*—A. Twig.—B. Schematic diagram of an inflorescence axis.—C. Flower.—D. Inner surface of calyx lobe showing glandular tissue.—E. Inner surface of petal showing glandular tissue.—F. Detail of the androecium.—G. Gynoecium.—H. Fruit.—I. Seed. (A, B. *Capuron 27349 SF*; C–G. *Capuron 29194 SF*; H, I. *Service Forestier 5673 SF.*)

Helmiopsis sphaerocarpa occurs on mountain slopes between 50 and 800 m altitude. It has been reported on black volcanic soils, but its presence on the Montagne des Français suggests that it also may occur on limestone (Lemoine, 1906).

The 5-carpellate gynoecium and reduced stigmata of *Helmiopsis sphaerocarpa* place this species in *Helmiopsis* subg. *Helmiopsis*. Its broadly ovate leaves, glandular petals, and ten stamens ally it with sect. *Glandulipetalae* Arènes in subg. *Helmiopsis*. *Helmiopsis pseudopopulus* (Baillon) Capuron, a member of the same section, may be the most closely related species; it also has a many-flowered inflorescence, occasionally with a terminal axis. Glandular tissue at the base of the calyx, however, has been observed in only one other *Helmiopsis* species, *H. inversa* H. Perrier (sect. *Helmiopsis*).

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WITHERINGIA FOLLICULOIDES (SOLANACEAE): A NEW SPECIES FROM COSTA RICA

The genus *Witheringia* L'Hér. embraces about a dozen species. One species, *W. solanacea* L'Hér., is weedy in nature and ranges from northern Mexico to Bolivia. The other species tend to be more localized, and the genus seems to be best developed in mature wet forests of Costa Rica, Panama, and northern South America. *Witheringia* is a member of subfamily Solanoideae. The species of *Witheringia* are mostly shrubs or small trees with few- to many-flowered inflorescences of yellow or green flowers held under the leaves, and berries held erect above the foliage. The calyces range from minute and nonaccrescent to large and, as in the present species, completely enveloping the fruit.

Witheringia folliculoides D'Arcy & J. L. Gentry, sp. nov. TYPE: Costa Rica. Puntarenas: moist forest in valley bottom, tropical wet forest with open understory on steep slopes and ridges and areas of secondary vegetation north and west of the air field 5 km W of Rincón de Osa, 50–200 m, *J. L. Gentry & Burger 2844* (holotype, MO-2825976; isotype, F).

Frutex 3–5 m altus, ramis hornotinis gracilibus, glabratis. Folia integra, elliptica lanceolatave, saepe obliqua, 9.5–23 cm longa, 2.3–7 cm lata, venis supra planis subtus elevatis, venis lateralibus 6–14 utrinque, petiolis gracilibus. Pedicelli pauci, 3–4 mm longi. Flores 5-meri, calyce parvo, 2.5–4 mm longo, glabrato, campanulato, apice truncato, in statu fructificanti magnopere accrescenti, corolla lutea, extus glabra, e tubo 2.5–3 mm longo ampliata, limbo campanulato, fauce pubescenti, lobis obtusis, 3–4 mm longis, filamentis base pubescentibus, antheris oblongis, haud apiculatis, longitudinaliter dehiscentibus. Acinus subglobosus, 12 mm longus, ab folliculo tectus, calyce in folliculum magnum maturescenti.

Small tree 3–5 m tall; young branches slender, glabrate, drying smooth. Leaves entire, drying concolorous, mostly elliptic or lanceolate, sometimes oblanceolate, often oblique, 9.5–23 cm long, 2.3–7 cm wide, apically short acuminate, basally mostly cuneate, the veins plane or slightly impressed above, sometimes drying somewhat rugose, the costs and major lateral veins elevated beneath, the lateral veins arching, 6–14 on each side; minor leaves lanceolate to broadly elliptic or rotund, 2.3–7.8 cm long, 1.4–4.2 cm wide, acute to acuminate or sometimes rounded apically, cuneate to rounded basally; petioles slender, 4–9 mm long, those of the minor leaves 2–3 mm long. Inflorescence with the peduncle mostly subobsolete but sometimes 2–4 mm long and the flowers appearing fasciculate but only one or two appearing at a time; pedicels few, 1–7 (evidenced by scars), 3–4 mm long, becoming 4–7 mm long, perhaps all but one flower aborting. Flowers 5-merous; calyx campanulate, apically truncate, 2.5–4 mm long, accrescent in fruit, drying dark, minutely and sparsely pubescent with short curved simple hairs mostly on the apical portion, glabrescent, inconspicuously ribbed; corolla yellowish, apparently unmarked, glabrous outside, tubular campanulate, the tube 2.5–3 mm long, the throat pubescent with reduced hairs, the limb lobed less than halfway down, the lobes ovate, 3–4 mm long, marginally puberulent; stamens with the filaments pubescent at the base, apically glabrous, 1.5 mm long, the anthers yellow, oblong, 2 mm long, not apiculate; ovary glabrous, the style equalling the stamens, glabrous, the stigma minute. Fruit a subglobose ?juicy berry 10–12 mm across, loosely and completely enveloped by the strongly accrescent calyx; fruiting calyx rotund, much enlarged and inflated around the berry but open at the apex, apparently unribbed, glabrous, 15–20 mm across, approximately twice the length of the fruit; seeds numerous (?ca. 40), dark brown, flattened, reniform, 2–3 mm across, the testa wavy reticulate on the face, scalariform on the rim; embryo broadly horseshoe-shaped, terete throughout (lacking any notching along its length).

Paratypes. COSTA RICA. PUNTARENAS: Osa Peninsula, tropical wet forest along dry stream bed paralleling airport at Rincón, *Duke 16107* (MO); moist forest in valley bottom, tropical wet forest with open understory on steep slopes and ridges and areas of secondary vegetation north and west of the air field 5 km W of Rincón de Osa, 50–200 m, *Gentry & Burger 2842* (F, MO). Slopes adjacent to airport, disturbed primary forest, Rincón de Osa, 20–300 m, *Liesner 1887* (MO).

This species is distinct from most other species of *Witheringia* in its bladdery fruiting calyx, which loosely and completely envelops the fruit. It occurs in southern Costa Rica where a number of other species of the genus occur. It is perhaps most similar to *W. exiguiflora* D'Arcy and *W. morii* D'Arcy, which also occur in western Pan-

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ama and southern Costa Rica, and which both have accrescent calyces, but their calyces do not form the large bladderlike enclosures of *W. folliculoides. Witheringia folliculoides* differs further from *W. exiguiflora* in its tubular campanulate corolla, in its smaller and much less coriaceous leaves, and in its larger fruiting calyx. From *W. morii* it differs in its broadly open corolla and its few-flowered inflorescences. In habitat *W. folliculoides* also differs from these two species: it occurs near sea level in the seasonally dry Osa Peninsula of Costa Rica, whereas *W. exiguiflora* and *W. morii* occur in perennially rainy forests. Both *W. exiguiflora* and *W. morii* occur in the uplands of 1,100–1,800 m in Costa Rica and Panama, but *W. exiguiflora* also ranges down to near sea level on the Atlantic slopes of Panama.

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ESCHWEILERA COSTARICENSIS (LECYTHIDACEAE): A NEW SPECIES FOR THE FLORAS OF COSTA RICA AND NICARAGUA

Eschweilera C. Martius ex DC. is the largest (ca. 90 species) and most poorly known genus of neotropical Lecythidaceae. The genus is characterized by zygomorphic flowers with coiled androecial hoods, absence of anthers and production of nectar in the androecial hoods, bilocular ovaries with basal placentation, seeds often with lateral arils, and lack of differentiated cotyledons (for illustrations of these features see figs. 9, 10G, 13, and 18 in Prance & Mori, 1979). The Central American species of *Eschweilera* provide examples of how poorly collected the species of *Eschweilera* are. Woodson (1958) included only four species of *Eschweilera* from Panama, whereas today we know of at least 14 from that country. Further north, species diversity of *Eschweilera* is markedly reduced. There are only three species in Costa Rica, two or possibly three in Nicaragua, one in Honduras, and one in Mexico. Most of these are known only from one or very few collections. The recently described *E. mexicana* (Wendt et al., 1985) is the first species of Lecythidaceae recorded from Mexico. It escaped collection until 1983 despite being common locally.

Although it might seem more appropriate to describe *E. costaricensis* in our forthcoming monograph of the zygomorphic-flowered genera of Lecythidaceae (Mori & Prance, manuscript), the need to have a name available for a treatment of the family for the Flora of Nicaragua (Prance & Mori, in press) mandates separate publication.

Eschweilera costaricensis Mori, sp. nov. TYPE: Costa Rica. Heredia: Tropical wet forest along Guacimo ridge trail, La Selva Protection Zone, 275 m, 18 Jan. 1983 (fl), *Hartshorn 2555* (holotype, NY; isotypes, BM, CR, F, K, MO, PMA, US).

Ab *E. pittieri* venis impressis in pagina adaxiali foliorum et sine lobis calycis amplificatis in fructibus differt.

Understory tree, 5–10 m tall. Leaf-bearing branches 3–5 mm thick. Leaf blades elliptic to widely elliptic, 15–26 × 7–15 cm, glabrous, chartaceous, with 10–11 pairs of adaxially impressed lateral veins; apex long acuminate; base obtuse to rounded; margins entire; petiole 7–8 mm long. Inflorescences simple racemes or weakly once-branched, terminal, in axils of uppermost leaves, or from branches, the principal rachis 1.5–3 cm long, pubescent, the pedicels ca. 7 mm long, pubescent. Flowers 3–4 cm in diam., calyx with 6, very widely ovate, obliquely oriented lobes, 6–7 × 5–7 mm, flat adaxially, convex abaxially, imbricate for ½ length; petals 6, widely elliptic to orbiculate, cream colored or light yellow. Hood of androecium 17 × 17 mm, forming double coil with slight beginning of triple coil; staminal ring with 169–181 stamens; filaments ca. 1 mm long, expanded towards apex; anthers 0.5 mm long. Hypanthium sulcate, pubescent; ovary 2-locular, with 6–9 ovules in each locule, ovules attached to a hemispherically shaped placenta arising from floor of locule; style obconical, oblique, 2 mm long, arising from umbonate ovary summit 1 mm high. Fruits cup-shaped, 2.5 × 4 cm (excluding operculum), the calycine ring inserted near apex of fruit base, supracalycine zone 0.5 cm wide, bearing persistent calyx lobes and pedicel when mature, pericarp 2–3 mm thick, with rough, lenticellate exterior surface; operculum umbonate, 2 cm high, umbo 5 mm high. Seeds triangular in cross section, ca. 20 × 15 mm, laterally arillate.

Distribution. Known only from wet forests in the Caribbean foothills of Costa Rica and Nicaragua where it is an occasional (0.1–1.0/ha) understory tree (Hartshorn, pers. comm.). Flowers have been collected in January and August and mature fruits have been gathered in January.

Additional specimens examined. NICARAGUA. RÍO SAN JUÁN: Río Indio, Caño Negro, 4 Dec. 1982 (immature fr), *Araquistain 3424* (MO).

COSTA RICA. HEREDIA: La Selva Protection Zone, along Guacimo Ridge Trail, 300 m, 18 Jan. 1983 (fr, seed), *Hartshorn s.n.* (NY). LIMÓN: Hacienda Topeyco-Hacienda La Suerte, 29 km W of Tortuguero, 10°30′N, 83°47′W, 40 m, 22 Aug. 1979 (buds), *Davidson & Donahue 8632* (NY), 25 Aug. 1979 (fl), *Davidson & Donahue 8777* (NY).

Eschweilera costaricensis is most closely related to *E. pittieri* R. Knuth, which is relatively common and distributed from the Pacific coast of western Panama to the Magdalena Valley in the east and to the coastal forest of northern Ecuador in the west. *Eschweilera pittieri* does not

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co-occur in the Caribbean forests of Costa Rica and Nicaragua with *E. costaricensis.*

Eschweilera costaricensis differs from *E. pittieri* by having impressed lateral veins on the adaxial leaf surface and fruits without knobby calycine protuberances.

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—*Scott A. Mori, The New York Botanical Garden, Bronx, New York, 10458-5126, U.S.A.*

A NEW VARIETY OF *HEDYOSMUM* (CHLORANTHACEAE) FROM NICARAGUA

Hedyosmum Swartz is a genus of ca. 40 species of primarily montane neotropical trees and shrubs with one herbaceous species in the Far East. In the New World species are found from southern Mexico to Panama, Venezuela, Colombia, Ecuador, Peru, Bolivia, Brazil, and Paraguay, as well as in the West Indies. The greatest density of species occurs in the northern wet Andes. In the field the genus is distinguished by its opposite leaves with connate sheathing petiole bases, stipular appendages along the distal margin of the sheath, staminate inflorescences composed of many ebracteate flowers of single stamens, and pistillate inflorescences composed of solitary or clustered, bracteate flowers.

Until a recent monograph (Todzia, 1986), the genus has been in a state of taxonomic confusion, in part because in the last hundred years *Hedyosmum* had never been studied over its entire geographic range. Several species proposed from Central American material had, in fact, already been described from South America. Such is the case of *Hedyosmum goudotianum* Solms, a species originally described from Colombia but now recognized to range from Nicaragua to Peru (Todzia, 1986). This species is distinguished from all other *Hedyosmum* species by its elongate racemose or paniculate pistillate inflorescences with many-flowered cymules on short peduncles, notably coriaceous leaves with impressed secondary venation and sharp, closely spaced teeth, long leaf sheaths with striate triangular patches of appressed hairs below the stipules, and trichomes (when present) restricted to the abaxial sides of the primary, secondary, and sometimes tertiary veins.

Although populations throughout its range are variable with respect to trichome density, leaf size, and inflorescence length, the northernmost population of *H. goudotianum* is morphologically quite distinct and, given its isolated geographic position, is thought worthy of taxonomic recognition. These collections from Nicaragua already have been recognized as morphologically different from conspecific populations in Costa Rica (Burger, 1973, 1977). They are unusual in being glabrous and in having shorter internodes with often overlapping leaf bases, shorter leaf sheaths that lack the striate patch beneath the stipular processes, and leaves with more widely spaced teeth.

A key to the varieties is provided below with a full description for *Hedyosmum goudotianum* var. *mombachanum*.

Hedyosmum goudotianum Solms *in* A. P. de Candolle, Prodr. 16: 482. 1869. TYPE: Colombia: "Quindiu, El Inciendial, La pallmilla." Nov.–May 1844 (pist.), *Goudot s.n.* [lectotype (here designated), P.]. This is the only specimen of Goudot seen from this locality. It is clearly designated as type material in Solms's handwriting.

KEY TO VARIETIES OF *HEDYOSMUM GOUDOTIANUM*

1\. Internodes (3–)4–9 cm long; leaves with teeth 1–2(–3) mm distant and with impressed secondary veins, these strigose beneath; leaf sheaths well-spaced and not overlapping, (1–) 1.8–3 cm long, with a triangular patch of appressed hairs below stipular processes; Costa Rica, Panama, Venezuela, Colombia, Ecuador, and Peru .... *H. goudotianum* var. *goudotianum*

1\. Internodes 1–4(–5) cm long; leaves with teeth 2.5–4 mm distant and with secondary veins flush with surface, these glabrous beneath; leaf sheaths often overlapping, (0.7–)1–1.6 cm long without a striate patch below stipular processes; Nicaragua .... *H. goudotianum* var. *mombachum*

Hedyosmum goudotianum Solms var. **goudotianum**

Tafallaea goudotiana (Solms) O. Kuntze, Revis. Gen. Pl. 2: 566. 1891.

Hedyosmum montanum W. Burger, Phytologia 26: 133. 1973. TYPE: Costa Rica. Heredia: Río Vueltas (upper Río Patria), eastern slope of Volcán Barba near the continental divide, 2,000 m, 22 & 24 Nov. 1969 (pist.), *Burger & Liesner 6336* (holotype, F; isotypes, BM, COL, CR, GH, MO).

Distribution. Costa Rica, Panama, Venezuela, Colombia, Ecuador, and Peru in montane cloud forest. In Peru this variety has been recorded in association with *Chusquea*, while in Costa Rica it is known to occur with *Podocarpus*, *Weinmannia*, and *Clethra*. In Central America flowering is most common May through August,

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while in South America flowering occurs sporadically throughout the year.

Hedyosmum goudotianum Solms var. **mombachanum** Todzia, var. nov. TYPE: Nicaragua. Granada: "En las últimas antenas del Volcán Mombacho, 1,200–1,220 m, 23 Feb. 1981 (pist.), *Moreno & Lôpez 7134* (holotype, MO; isotypes, F, HNMN not seen).

Differt a var. *goudotianum* internodiis 1–4(–5) cm longis, laminis foliorum subtus glabris dentibus 2.5–4 mm distantibus, venis lateralibus subtus non elevatis, vaginae glabrae superpositae.

Dioecious, aromatic shrubs or small trees, 2–4 m tall, with prop roots; bark whitish-gray to gray, smooth; young stems quadrate, brittle, usually rugose, sometimes glabrous; large stems terete, with tubular leaf bases persisting and becoming fibrous with age; internodes 1–4(–5) cm long, the nodes slightly swollen. Leaf blades narrowly elliptic, elliptic, ovate to obovate, 3.3–13.6 cm long, (1–)2.7–5.3(–7) cm broad, with acuminate tips 0.2–0.7 cm long, cuneate to obliquely cuneate at base, at margins sharply serrulate with teeth 2.5–4 mm distant continuing to apex, sometimes revolute, smooth, dull, light green above and beneath when fresh, drying chartaceous to subcoriaceous, slightly scabrous, gray to brown above and beneath; midveins impressed above, raised beneath, glabrous; lateral veins 6–8, 7–13 mm distant, arcuate, flush with surface and glabrous beneath; intersecondary veins extending ⅓ to ½ distance to margin; free portions of petioles smooth to asperous, 0.5–0.8 cm long, narrowly winged; petiolar sheaths smooth to asperous, glabrous, (0.7–)1–1.6 cm long, 0.6–0.8 cm broad at apex, slightly inflated, terete or quadrangular, with or without 2 raised longitudinal ciliate lines extending down length of sheath from stipular appendages, overlapping, persistent, becoming gray and fibrous with age, not extending beyond free portions of petioles, at distal margin with 2 caducous, linear to slightly fimbriate stipular appendages ca. 1 mm long. Staminate inflorescences terminal or axillary, 1.5–4 cm long, composed of 1–2 opposing pairs of spikes on a short rachis terminated by a single spike; bracts subtending terminal inflorescence linear to obovate, 0.7–2 cm long, 0.1–0.5 cm broad; mature spikes 1.5–4.5 cm long, 0.3–0.6 cm broad, with ca. 100 stamens, sessile or borne on short peduncles 1–2 mm long, each subtended by a small, dentate or entire, spatulate to obovate bract 0.2–1 cm long, 1–2 mm broad; stamens congested on axis but becoming 0.5–1.5 mm distant; rachis 1–2.5 mm thick with a thick, irregularly margined, basal annulus; anthers yellowish-green, 1.3–1.8 mm long, 0.6–1 mm thick; connectives extended ca. 0.2 mm beyond thecae, acute. Pistillate inflorescences axillary or terminal, racemes or panicles (1.3–)2.5–4.4 cm long bearing 8–13 cymules; subtending inflorescence bracts 15–20 mm long, 3–5 mm broad; cymules with (2–)3–4 clustered flowers, 3–4 mm long and broad, borne on short peduncles 1–3(–5) mm long, alternate or opposite on inflorescence axis, 2–6 mm distant; subtending floral bracts green, connate in lower ¼ to ¾, 2–3 mm long including acuminate tips 1–2 mm long, 2–4 mm broad, ciliate or entire along free margins, enclosing ½ to ¾ of flower. Pistillate flowers trigonous, 2–3 mm long, 1.5–2 mm thick with a minute to large pore on each face of the ovary; perianth lobes deltate, acute, 0.2–0.5 mm long, basally connate; stigmas white, 2–3 mm long, irregular in shape, linear to irregularly lobulate, 2- or 3-angled, with long papillae. Fruiting cymules white, irregularly globose, 5–8 mm diam.; seeds ca. 3 mm long, brown, trigonous, minutely papillate.

Distribution. Elfin and cloud forest on Volcán Mombacho and Volcán Maderas in Nicaragua in association with *Cavendishia, Clusia,* and *Freziera* at elevations of 740–1,220 m. Flowering and fruiting occur sporadically throughout the year.

Additional specimens examined. NICARAGUA. GRANADA: Volcán Mombacho, *Atwood 7771* (MO, US); upper slopes of Volcán Mombacho along W shore of Lake Nicaragua, ca. 15 km S of Granada, 1,100–1,200 m, *Croat 39092* (F, MO); Volcán Mombacho, Plan de Flores, 740 m, *Grijalva 2506* (HNMN, TEX); N slope of Volcán Mombacho, above Finca El Progreso, *Neill 878* (MO, MSC); W slope of Volcán Mombacho, rd. and trail above Finca Santa Ana, from reservoir to somewhat above Plan del Flores, 950–1,150 m, *Stevens 4332* (F, HNMN, MO, TEX). RIVAS: near summit and upper slopes of Volcán Maderas above Balgüe, Isla Ometepe, 1,000–1,200 m, *Nee & Robleto Téllez 28086* (HNMN, TEX).

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—*Carol A. Todzia, Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 61366, U.S.A.*

BOOK REVIEW

Tomlinson, P. B. 1986. The Botany of Mangroves. Cambridge University Press. ISBN 0-521-25567-8. Price: $69.50. (Initiating a new series: the Cambridge Tropical Biology Series.)

Almost any botanist who has visited the tropics or subtropics will have encountered mangroves, and this refreshingly written book is the perfect introduction to both their taxonomy and biology. Overall, the book is a pleasing potpourri of selected data from many different fields about many different aspects of mangroves. The bulk of the book (211 pages) is a family-by-family summary of mangrove taxa, including original and very useful keys to the different species and genera of most of the mangrove families. Also included are discussions of various aspects of morphology, architecture, reproductive biology, and biogeography, as well as miscellaneous taxonomic notes and elegant illustrations of important species and genera. Although a key to "strict mangrove" genera is provided in the floristic section, no attempt is made to key out the different back-mangrove families. Thus the reader must first know the genus or family of the plant in which he is interested in order to take full advantage of Tomlinson's taxonomic section. Nevertheless, from the viewpoint of the systematic botanist, the gathering together in one place of the available nomenclatural and taxonomic data for mangrove species and genera is a high point of the book, as are the author's personal observations on identification and biology of the individual species.

Throughout, but especially in the photo captions, the author's puckish sense of humor often comes to the fore. A *Nypa* stem is aptly described as "resembling nothing so much as a series of overlapping cowplats." The fruits of *Avicennia alba* are said "to resemble a gorged leech." An "obliging butterfly visitor" in a photo of *Lumnitzera racemosa* is contrasted with lack of an obliging bird visitor in *L. littorea.*

Another strong point of the book, as might be expected considering the author's research predilection, is the series of chapters devoted to the fascinating morphological and anatomical specializations of mangroves. No fewer than four chapters and 71 pages treat shoot systems, root systems, water relations and salt balance, and seedlings and seeds. In contrast, the five chapters devoted to ecology, floristics, biogeography, flowering, and utilization and exploitation amount to only 68 pages.

I found the treatment of mangrove ecology disappointing. The author acknowledges this deficiency and justifies it by noting that ecology is generally outside his area of expertise. However, a tremendous amount of effort has been devoted to this field, and a few extra pages devoted to mangrove zonation and summarizing some of the abundant and often conflicting literature that implicates different toleration of salt concentrations vs. soil texture and edaphic conditions vs. rainfall would have been a welcome addition, especially if accompanied by the author's own trenchant evaluations.

A minor but bothersome ecological problem is Dr. Tomlinson's adoption of the word "mangal" to refer to the mangrove community while "mangrove" is reserved for the constituent plants. I find this to serve no useful purpose and to be distinctly cumbersome in the same way as the plethora of Braun-Blanquet classificatory endings. Luckily, after emphasizing "mangal" in the first chapter, the author himself largely abandons it in later chapters where traditional terms like "mangroves," "mangrove associates," and "mangrove communities" are often used instead. In this review I will use exclusively the traditional terms in hopes that "mangal" (as well as Rhizophoretum, etc.) will soon pass into well-deserved oblivion.

Another, more significant, ecological problem is the author's attempt to separate mangrove species into "strict mangroves" (subdivided as to major and minor components) and "mangrove associates." While this should be quite a natural way to divide mangrove taxa, in my opinion many taxa are wrongly placed in the tables on pages 27–30, and others, even those treated elsewhere in the book, are outright omitted. This is especially obvious for the Pacific-American mangrove taxa, and inclusion of some of the omitted full-mangrove species would give rise to very different conclusions. For example, the taxonomic distinctiveness of strict mangrove species is far more often at the level of species than Tomlinson implies. Glaring outright omissions from these lists include *Tabebuia palustris* and *Phryganocydia phellosperma,* which are strict mangroves, not even "back-mangroves"; indeed in the case of Bignoniaceae the back mangroves are correctly listed but the full mangroves are completely ignored! *Crenea patentinervis,* mentioned as a potential herbaceous mangrove in the text, is not included in any of the tables of mangroves or mangrove associates on the grounds that as an herb it cannot be a true mangrove. Actually *Crenea* is a subshrub and is at least as woody as such included genera as *Acrostichum, Tuberostylis, Acanthus,* or *Batis.* Even were it an herb, that would be no reason to exclude it, especially as it is a full-mangrove species, not a back-mangrove. Both species of *Tuberostylis* are mangroves and they are mostly epiphytic on the roots and lower trunks of full-mangroves rather than on back-mangroves. Some major mangrove components are relegated to the "minor" list, e.g., *Pelliciera* which forms pure mangrove forests many km^2 in extent in the delta of the Río San Juan in Colombia. Gymnosperms are specifically mentioned as playing no role in mangroves even though *Zamia roezli* is typically found in mangroves and is restricted to them and to the adjacent coastal fringe. *Muellera* (p. 263) is stated to be most commonly recorded well away from the sea, but I have seen it only in the back-mangrove regions with a distinct tidal influence and strongly suspect that the entire genus is restricted to this habitat.

There are also serious problems with the numbers of species given for mangrove genera, especially since the data in these tables are used as evidence of the taxonomic distinctiveness of mangrove plants. Thus the single back-mangrove species of *Amphitecna* is not the only species of this 18-species genus, and *Hippomane* has four noncoastal species as well as the well-known coastal one. Mangrove epiphytes are implied to be basically plants from nearby terrestrial communities that transgress into the mangroves. Yet many epiphytes seem unique to mangroves (such as the entire genus *Tuberostylis*) and others are certainly more characteristic of mangroves than other habitats. Similarly, Tomlinson states that there are no climbers in mangroves, presumably because climbers have wide vessels subject to extreme water tension, yet there is at least one clear exception. *Phryganocydia phellosperma* is not a species that roots behind the mangroves and scrambles into them (although its unlisted confamilial *Cydista aequinoctialis* is and should probably be added to the list of mangrove associates); it is a strict mangrove and roots in (and only in) the mangroves themselves.

The biogeographic discussion focuses so much on the dichotomy between the relatively depauperate western mangroves vs. the more diverse eastern ones that the almost equally striking difference between the richer mangrove flora of the Pacific Coast of South America as compared with the Atlantic one (possibly related to the relatively recent opening of the Atlantic Ocean?) is overlooked. Only eight true mangroves are said to occur in the western hemisphere, although a local concentration of "incipient mangroves" in western Colombia is acknowledged. While these species are said to be mere mangrove associates that "lack complete fidelity to mangal" (p. 55), several of them are true and obligate mangroves in the strictest sense (although there are also endemic back-mangrove species in this region). It may well be that the western Colombian mangroves are fundamentally different from other mangroves in their greater habit diversity and in being mostly individual mangrove species of otherwise nonmangrove genera, but they are not less true mangroves for that. Knowledge of mangroves would be better served by focusing on the unusual aspects of these species rather than by trying to sweep them under the rug.

There are a number of inconsistencies, especially in the biogeographic discussions. *Rhizophora racemosa* is on both Atlantic and Pacific sides of tropical America as reported on p. 334, but in the key (p. 329) it is characterized as being only on the Atlantic coast of South America. There are five Pacific coast collections in the MO herbarium, as well as collections from Honduras, Costa Rica, and Panama, all outside the Venezuela and Guianas to West Africa range indicated by Tomlinson (p. 335). *Rhizophora harrisonii* is rather precisely mapped as having a disjunct population in the middle of the Peruvian coastal desert outside the range of any mangrove, but the numerous records from coastal Ecuador and Colombia were apparently overlooked. On the other hand, the range of *R. samoensis* is hypothetically extended to include the Pacific coast of South America, where it may occur but has not yet been documented; that species does reach the Galapagos, according to R. Horna (pers. comm.).

Inevitably a few insignificant errors in spelling of Latin binomials, taxonomic authorities, etc. are unavoidable in a book of this scope. Examples include "*Anaemopegma*" (p. 32), "*Mouriria*" and "*Pachyra*" (p. 56) and the authors of both species of *Phryganocydia* (p. 214). More problematic is *Lysianthus* (presumably = *Lysiana*?) supposed to be a mangrove mistletoe (p. 33). *Dalbergia amerimnion* Benth. (p. 261) has long been regarded as a synonym of *D. brownei*. *Phryganocydia phellosperma* is not distinguished from *P. corymbosa* by a simple tendril, a trait shared with the entire genus. *Tabebuia palustris* is not deciduous as stated (p. 214), which would have been quite remarkable in a mangrove, but evergreen like all other mangroves known to me.

Similar minor errors in biogeographic distributions include *Tuberostylis rhizophorae*, whose claimed "wider distribution in Central America" consists of a single collection from southernmost Darién, and *Pavonia rhizophorae*, supposed to be recorded only for Colombia but reported in the *Flora of Panama* to cross the Panama border in the same part of southern Darién.

Obviously, it is difficult to eliminate such miscellaneous errors. Whether they are as frequent in other taxa and regions as among the mangroves I happen to know personally (i.e., mostly Bignoniaceae and Pacific American), I do not know. But it seems likely that it would have been useful for the author to run a draft of his manuscript past a few taxonomic specialists or field botanists as well as checking a few more herbaria for distributional data. Such minor imperfections detract very little from the message of the book, except that inasmuch as this is the closest thing to a monograph of many mangrove taxa that we are likely to have in the foreseeable future, it is a bit of a shame that some of the work that would have gone into an actual monograph was neglected. Overall *The Botany of Mangroves* succeeds admirably in its purpose of providing a concise and highly readable introduction to the world's mangroves.—*Alwyn Gentry, Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166, U.S.A.*

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A REVISION OF *PANICUM* SUBGENUS *PANICUM* SECTION *RUDGEANA* (POACEAE: PANICEAE)[1]

FERNANDO O. ZULOAGA[2]

ABSTRACT

Panicum subg. *Panicum* sect. *Rudgeana,* herein revised, includes six species: *P. cayennense, P. campestre, P. cervicatum, P. ligulare, P. rudgei* and *P. vinaceum.* It is characterized mainly by a stipitate upper anthecium. The stipe consists of two portions: a membranous portion towards the ventral face of the spikelet and an indurate portion towards its dorsal face. The position of the section within subg. *Panicum* is discussed, as is the relationship of *Rudgeana* with other sections containing species having a stipitate upper anthecium.

Hitchcock & Chase (1910) included *P. rudgei* Roemer & Schultes and *P. rotundum* A. Hitchc. & Chase within the ungrouped species of the genus and noted their close relationship. In 1915 they repeated this treatment, indicating also that the species they had described was the same as *P. campestre* Nees ex Trinius. The same year, Hitchcock also placed *P. rudgei* in an informal group he named Rudgeana. Chase, in unpublished manuscripts, later placed both species in the Rudgeana group, which she characterized as "Rather stout much branched perennials with usually harshly pilose or papillose sheaths. Spikelets abruptly pointed, the first glume pointed, more than half the length of the spikelet, the midnerve scabrous."

The two species mentioned above plus *P. cayennense* Lam., *P. ligulare* Nees ex Trin., *P. vinaceum* Sw., and *P. cervicatum* Chase share characters that allow them to be included in sect. *Rudgeana* (A. Hitchc.) Zuloaga.

Section *Rudgeana* falls within subg. *Panicum,* having the following characters in common with the rest of the sections in the subgenus [which are sects. *Panicum, Repentia* Stapf, *Urvilleana* (A. Hitchc. & Chase) Pilger, and *Dichotomiflora* (A. Hitchc. & Chase) Honda].

Species of subg. *Panicum* are characterized by the presence of the C_4 photosynthetic pathway of the NAD-me subtype (Brown, 1977) and are distinguished anatomically by having a double sheath around the vascular bundles. The inner

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one is a mestome sheath with thick-walled cells. It is surrounded by a Kranz outer sheath containing specialized chloroplasts that are usually disposed centripetally. Between each vascular bundle there are two or three tabular cells arranged radially. The number of secondary vascular bundles present between each primary bundle varies from two to six.

In sect. *Rudgeana,* as in most sections of subg. *Panicum,* the plants are cespitose and short rhizomatous with erect, few- to many-noded culms. The ligule is membranous at the base and short- to long-ciliate at the upper portion. The leaf blades are lanceolate to linear-lanceolate, with or without involute borders. The species are usually found in dry and open places, but some species in sect. *Dichotomiflora* and in sect. *Repentia* grow in wet places and have decumbent culms that root at the lower nodes.

The inflorescences are pyramidal, lax and diffuse, and have ellipsoid to lanceolate spikelets dispersed on the branches.

The nervation of the glumes and lemmas and ornamentation of the upper anthecium are distinctive characters that hold together the sections of the subgenus. The upper glume and lower lemma are 7- to 9-nerved (11- to 15-nerved in species of sects. *Rudgeana, Panicum* and *Urvilleana*), with a few exceptions in species of sects. *Dichotomiflora* and *Repentia,* in which these bracts are 5-nerved. The upper anthecium is smooth and shiny over the entire surface, and compound or both compound and simple papillae are present near the apex of the upper palea.

Panicum sect. *Rudgeana* differs from sect. *Dichotomiflora* by the length of the lower glume (¼ to ⅓ the length of the spikelet in sect. *Dichotomiflora*) and by the absence of papillae on both surfaces of the leaf epidermis; also, as noted before, species of sect. *Dichotomiflora* grow in humid places with the culms decumbent and rooting at the lower nodes. Section *Rudgeana* is separated from sect. *Repentia* by the absence of stout rootstocks at the base of the plant. Section *Urvilleana* is distinguished from sect. *Rudgeana* by having long macrohairs at the base of the upper lemma and numerous, whitish hairs covering both glumes and the lower lemma.

Section *Rudgeana* can be distinguished clearly from sect. *Panicum* and the sections mentioned above by the occurrence of a well-developed stipe at the base of the upper anthecium. Two segments of the stipe can be distinguished: a) a portion of membranous tissue towards the palea of the upper anthecium (Figs. 1a, e, 2d, e, 3b) and b) a portion of indurate, smooth, and shiny tissue towards the lemma of the upper anthecium (Figs. 1b, f, 2a, 3c–e). The texture of the indurate portion is similar to that of the main portion of the upper anthecium. The membranous portion of the stipe is reduced in *P. cayennense* and *P. campestre* (Figs. 1e, 4g, h) or is larger and more expanded in *P. rudgei* (Fig. 3b) or remarkably noticeable in the rest of the species of the section. In *P. ligulare* and *P. vinaceum* the membranous portion of the stipe is prominent and may be prolonged into one (Fig. 5h, i) or two wings (Fig. 2e) that cover the base of the upper anthecium. In all cases the membranous portion appears turgid when the spikelet is rehydrated, and it is free from the base of the upper anthecium.

The indurate portion of the stipe is found below the upper anthecium and is appressed to the membranous portion, at least when the spikelet is immature (Figs. 1a, b, 2a, 3d, e). At maturity, it extends behind the upper anthecium as a mucro (Fig. 1f). Size and length of this mucro vary among species of the section, but it usually remains on the rachilla when the upper anthecium falls (Fig. 3c).

In Australia there exists a group of *Panicum* species with a structure similar to the stipe found in sect. *Rudgeana.* These species were transferred from *Ichnanthus* Beauv. to *Panicum* by Lazarides (1959), who noted that the appendages found at the base of the upper anthecium are not adnate to the upper lemma (as in *Ichnanthus*) but rather originate from the apex of a noticeable stipe. Shaw & Webster (1983) supported this concept, emphasizing distinctness of the appendages in *Ichnanthus* from Australian species of *Panicum.*

More recently, Lazarides & Webster (1984) removed these "ichnanthoid" species from *Panicum,* erecting for them the new genus *Yakirra.* Included in it were four species previously treated in *Panicum*: *Y. muelleri* (Hughes) Lazarides & Webster, *Y. majuscula* (F. Muell. ex Benth.) Lazarides & Webster, *Y. australiensis* (Domin) Lazarides & Webster, and *Y. pauciflora* (R. Br.) Lazarides & Webster; also included was a new species, *Y. nulla.*

They provided a table of features separating *Yakirra* from *Ichnanthus* and *Panicum* and stated that there were no conclusive characters to differentiate *Yakirra* from *Panicum* besides the presence of a stipe at the base of the upper anthecium. I regard this as correct, since the other

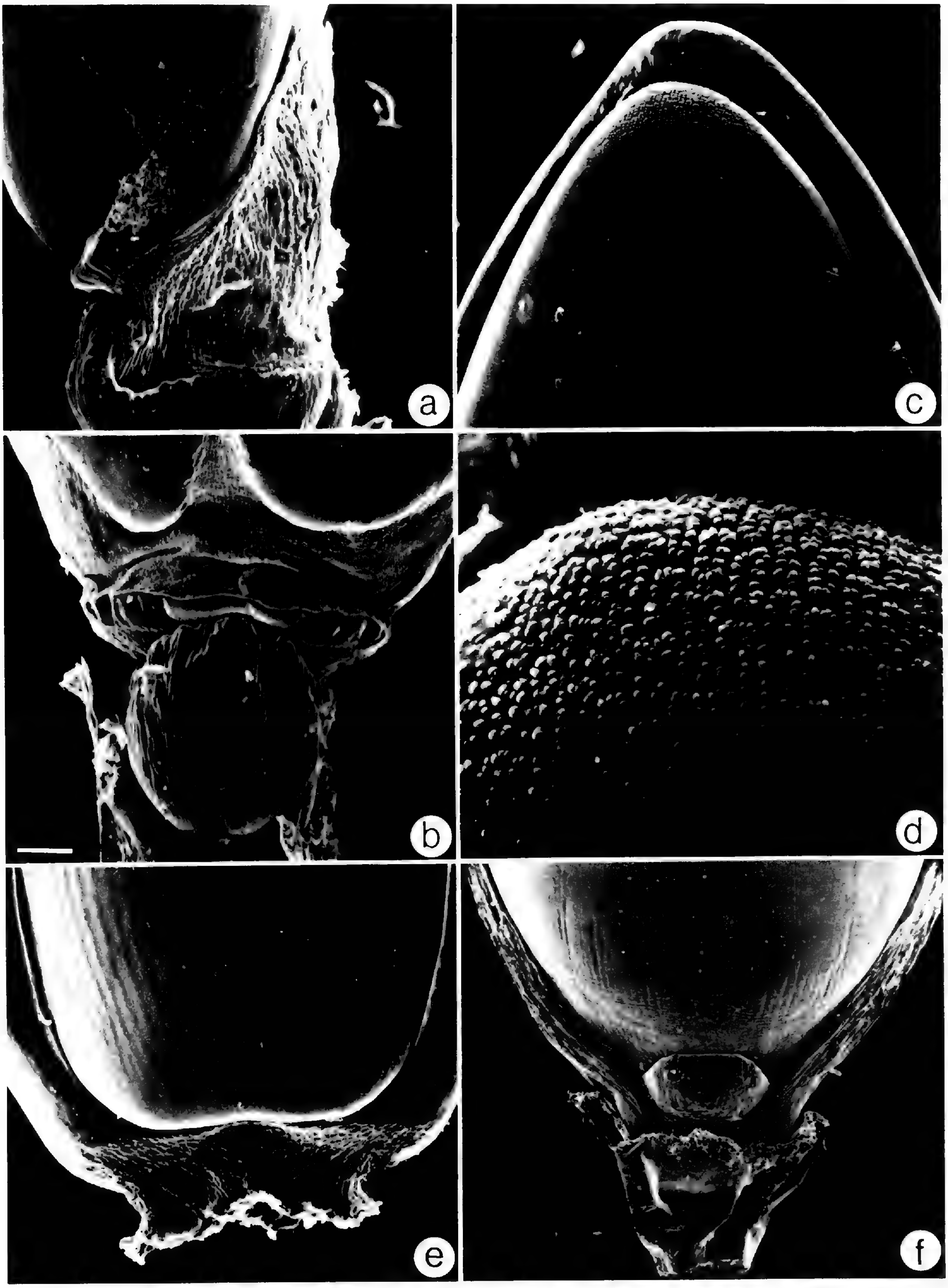

FIGURE 1. Scanning electron micrographs of the upper anthecium of *Panicum* species. a–d. *P. ligulare.*—a. Lateral view of the base showing the stipe.—b. Dorsal view of the base showing the indurate portion of the stipe.—c. Apex of the upper anthecium showing papillae at the tip of the palea.—d. Detail of the papillae. e, f. *P. campestre.*—e. Ventral view of the base of the upper anthecium showing the membranous portion of the stipe.—f. Dorsal view showing indurate portion of stipe. a–d, based on *Irwin 14904*; e, f, based on *Chase 8645.* Scale bars: a–c, f, ×100; d, ×500; e, ×150.

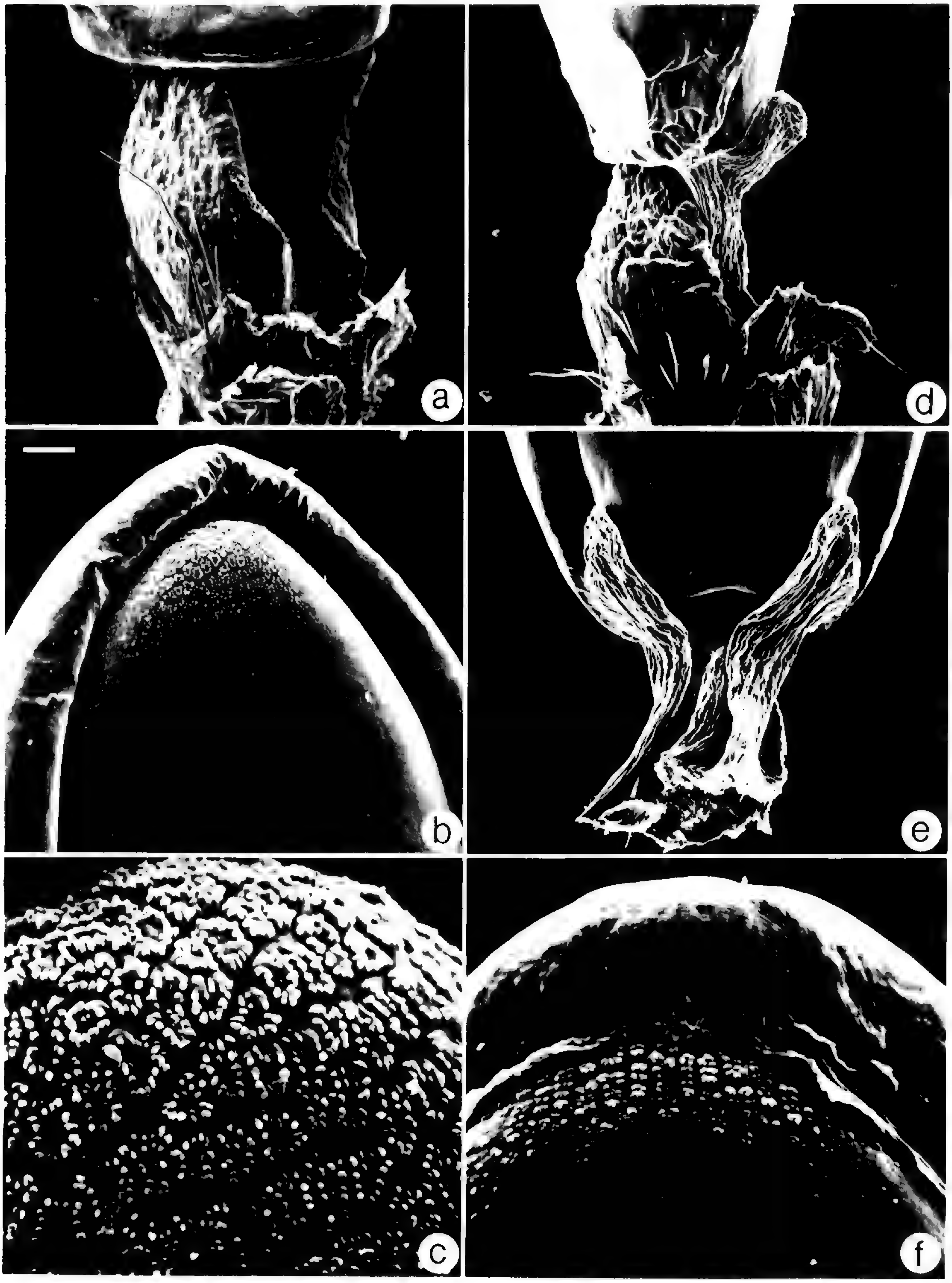

FIGURE 2. Scanning electron micrographs of the upper anthecium of *Panicum* species. a–c. *P. cervicatum*.—a. Lateral view showing the membranous and indurate portion of the stipe.—b. Apex showing compound papillae at the tip of the palea.—c. Detail of the papillae. d–f. *P. vinaceum*.—d. Lateral view of the base showing the stipe.—e. Ventral view showing the membranous appendages.—f. Apex of the upper anthecium showing compound papillae at the tip of the palea. a–c, based on *Chase 10737*; d–f, based on *Steyermark 59173*. Scale bars: a, d, ×50; b, ×100; c, ×500; e, ×70; f, ×300.

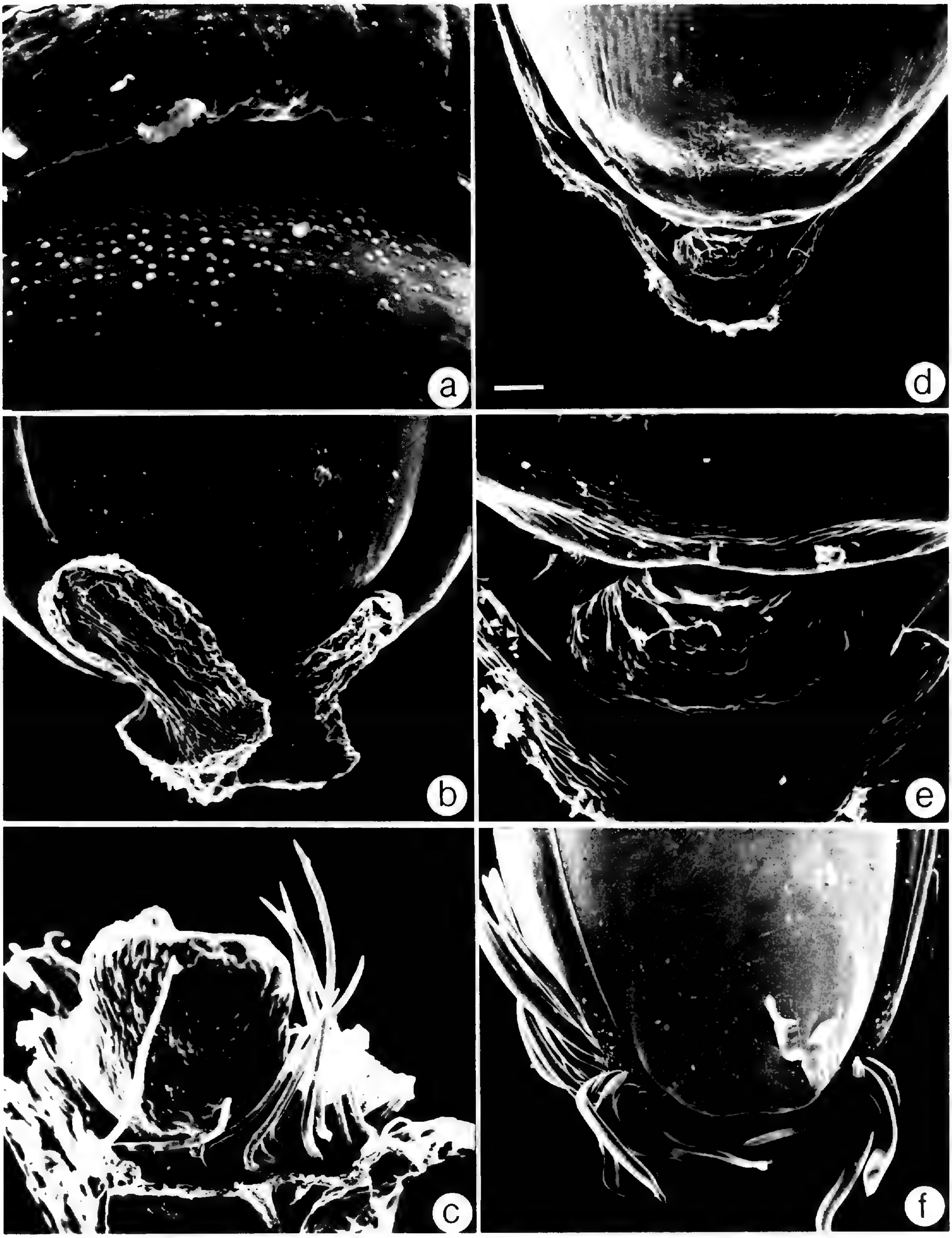

FIGURE 3. Scanning electron micrographs of the upper anthecium of *Panicum* species. a–c. *P. rudgei.*—a. Apex of the palea.—b. Ventral view of the upper anthecium showing membranous portion of stipe.—c. Indurate portion of stipe. d, e. *P. cayennense.*—d. Dorsal view of the upper anthecium showing indurate portion of stipe.—e. Indurate portion of stipe.—f. *P. olyroides*, details of hairs in the base of the upper anthecium. a–c, based on *Mexia 5975*; d, e, based on *Bommer 54*; f, based on *Chase 10820*. Scale bars: a, ×500; b, ×130; c, ×150; d, f, ×100; e, ×300.

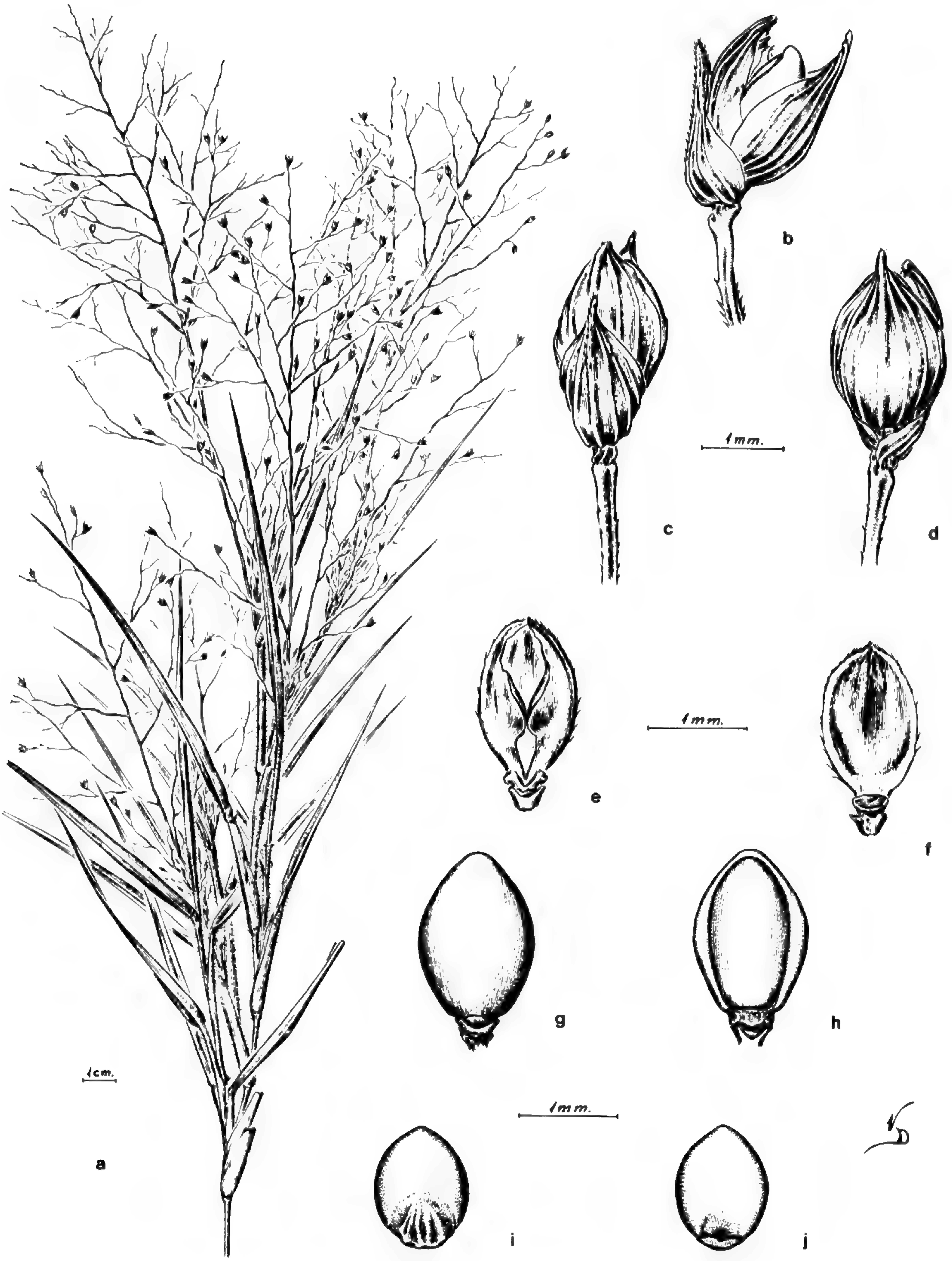

FIGURE 4. *Panicum campestre.*—a. Habit.—b. Spikelet, lateral view.—c. Spikelet, ventral view.—d. Spikelet, dorsal view.—e. Lower palea, dorsal view.—f. Lower palea, ventral view.—g. Upper anthecium, dorsal view.—h. Upper anthecium, ventral view.—i. Caryopsis, embryo side.—j. Caryopsis, hilum side. Based on *Sendulsky 637.*

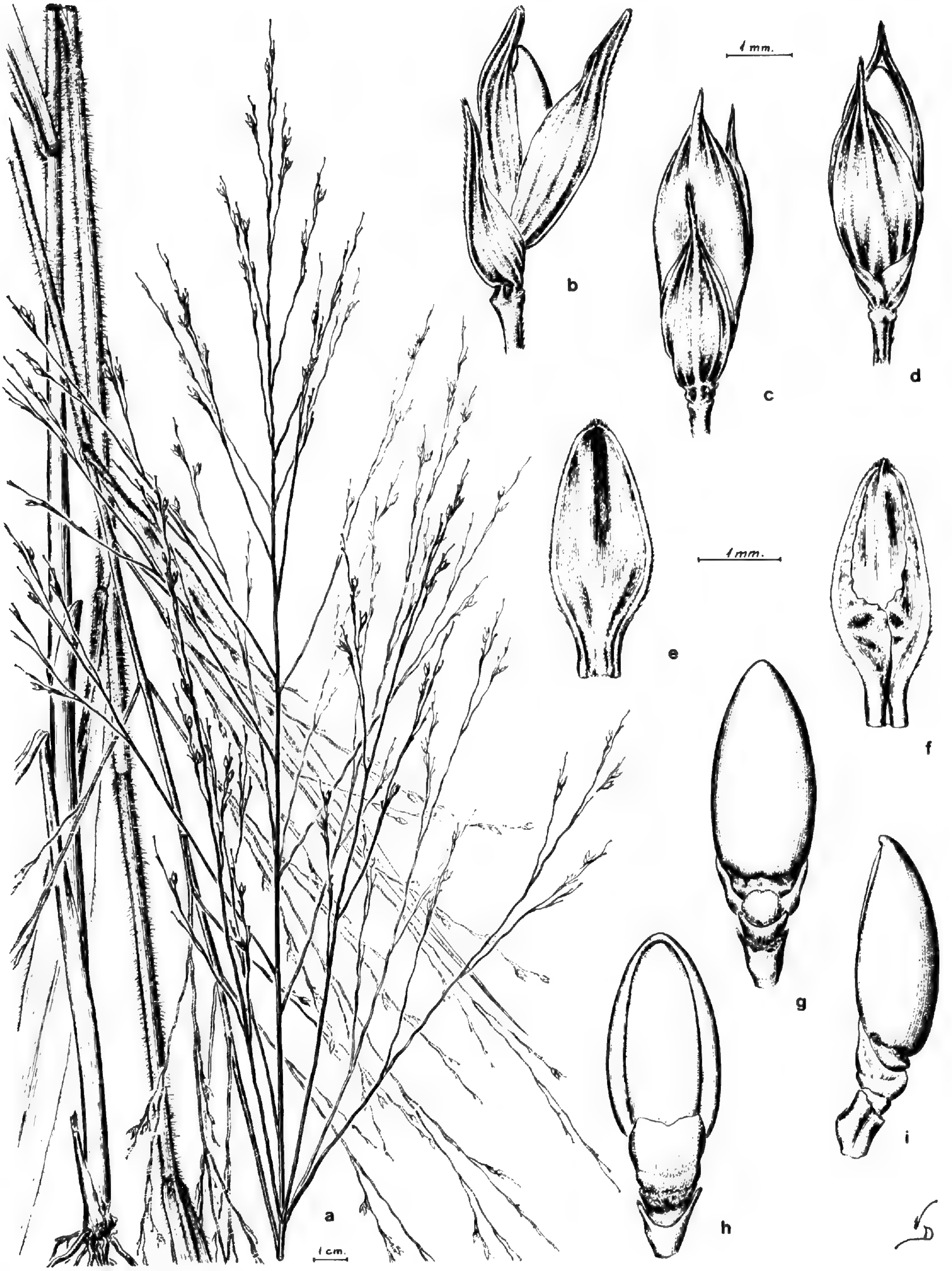

FIGURE 5. *Panicum ligulare.*—a. Habit.—b. Spikelet, lateral view.—c. Spikelet, ventral view.—d. Spikelet, dorsal view.—e. Lower palea, ventral view.—f. Lower palea, dorsal view.—g. Upper anthecium, dorsal view.—h. Upper anthecium, ventral view.—i. Upper anthecium, lateral view. Based on *Irwin 14904*.

TABLE 1. Comparison of sections of *Panicum* with stipitate upper anthecia.

	Subg. *Phanopyrum*		
Characters	Sect. *Stolonifera*	Sect. *Parvifolia*	Sect. *Phanopyrum*
Stipe morphology	Homogeneous	Homogeneous	Homogeneous
Stipe presence	In all species	In a few species	In the only species
Photosynthetic pathway	C_3	C_3	C_3
Compound papillae at tip of palea	Absent	Absent	Absent
Inflorescence type	Racemose branches	Paniculate branches	Racemose branches
Upper glume and lower lemma nervation	3- to 5-nerved	3- to 5-nerved	3- to 5-nerved
Panicle dimorphism	Absent	Absent	Absent

characters listed for *Yakirra* (habit, life form, spikelet compression, type of glumes and lower lemma, lower floret, and photosynthetic pathway) are common features of different sections of subg. *Panicum.*

Lazarides & Webster (1984) noted the presence of a stipitate flower in the American *P. gymnocarpon* Ell. On this basis they accepted this species as correctly placed by some authors in the monotypic genus *Phanopyrum* (Raf.) Nash and asserted that "The acceptance of *Phanopyrum* as a valid genus makes *Yakirra* morphologically distinct from *Panicum,* based on the presence or absence of a stipitate flower."

However, stipitate upper florets are also present in species of sects. *Lorea* Zuloaga, *Agrostoidea* (A. Hitchc. & Chase) Hsu, *Stolonifera* (A. Hitchc. & Chase) Pilger, *Dichanthelium,* and *Parvifolia* (A. Hitchc. & Chase) Pilger. Characters distinguishing these taxa are summarized in Table 1.

Section *Rudgeana* is similar to *Yakirra* in details of habit, leaf blades, ligules, inflorescences, spikelet compression and length, form and nervation of glumes and lower lemma. It differs from the Australian genus mainly by having a heterogeneous stipe below the upper anthecium, a lower palea (almost absent in *Yakirra*) well-developed, and the upper anthecium with compound papillae at the tip of the palea only. In species of *Yakirra* the anthecium has simple papillae in longitudinal rows all over the lemma and palea.

Therefore, the presence of a heterogeneous stipe in sect. *Rudgeana* is a good character for its delimitation within subg. *Panicum,* but I judge it to be an insufficient one for removing species from *Panicum.*

The elongation of the rachilla could help in opening the spikelet and posterior dispersal of the caryopsis. Davidse (in press) has pointed out that the stipe below the upper anthecium in *P. cervicatum* is an elaiosome involved in ant dispersal of the diaspore and noted that a similar elaiosome might be present in *P. vinaceum* and *P. trinii.* Berg (1985) reported a similar elaiosome in the stipe of *Panicum australiense* Domin.

METHODS AND MATERIALS

Classical taxonomic studies have been carried out in this paper, utilizing a Wild M5 dissecting microscope and a Wild M20 microscope. For higher magnification, specimens were viewed in a Cambridge S4-10 or Cambridge Stereoscan 250 Mk 2 scanning electron microscope operating at 10–20 kV. Specimens from the following herbaria were examined: B, BAA, CEPEC, F, GH, LE, M, MO, NY, P, R, RB, S, SI, SP, and US.

SYSTEMATIC TREATMENT

Panicum subg. **Panicum** sect. **Rudgeana** (Hitchcock) Zuloaga, stat. nov. Group Rudgeana A. Hitchc., North American Flora 17(3): 201. 1915. TYPE: *Panicum rudgei* Roemer & Schultes.

Cespitose perennials or occasionally annuals, with erect, more or less branched culms and usually pilose leaves. *Ligule* membranous, short- to long-ciliate. *Leaf blades* lanceolate to linear-lan-

TABLE 1. Continued.

Subg. *Phanopyrum*	*Subg. Dichanthelium*	Subg. *Agrostoides*	Subg. *Panicum*	Genus *Yakirra*
Lorea	*Dichanthelium*	*Agrostoidea*	*Rudgeana*	
Homogeneous	Homogeneous	Homogeneous	Heterogeneous	Homogeneous
In a few species	In a few species	In a few species	In all species	In all species
C_3	C_3	C_4 NADP-me	C_4 NAD-me	C_4 NAD-me
Absent	Absent	Absent	Present	Present
Paniculate branches	Paniculate branches	Paniculate branches	Paniculate branches	Paniculate branches
3- to 5-nerved	7- to 9-nerved	3- to 5-nerved	7- to 11-nerved	7- to 9-nerved
Absent	Present	Absent	Absent	Absent

ceolate, flat. *Inflorescence* a single, terminal and lax panicle or a terminal and several axillary panicles forming an elongated, compound arrangement; pedicels long, flexuous. *Spikelets* obovoid to ellipsoid, falling from the pedicels, pilose with long, rigid hairs to glabrous, pale to nearly purplish; glumes and lower lemma with 5–9(–11) prominent nerves, gaping and exposing the fertile floret at maturity. *Glumes* unequal, the lower glume ½ to ¾ as long as the spikelet; upper glume and lower lemma a little longer than the anthecium, pointed at the apex. *Lower palea* conspicuous, membranous, with or without a male flower. *Upper anthecium* stipitate, ovoid, glabrous, smooth and shiny, indurate; stipe membranous ventrally, indurate dorsally; *palea* with compound papillae at the apex (papillae occasionally absent in *P. cayennense*). *Stamens* 3; *stigmas* 2, plumose and purple; *lodicules* 2, membranous, glabrous. *Caryopsis* with the hilum punctiform. Embryo less than half the length of the caryopsis.

Species of sect. *Rudgeana* grow in open and sunny places, and are common in savannas of Central and South America and in the cerrado of Brazil; they are frequently found in sandy soils from sea level to ca. 1,500 m.

KEY TO THE SPECIES OF SECTION *RUDGEANA*

1a. Panicles terminal, lax; axillary panicles usually absent; spikelets 4.4–9 mm long, 1.2–2.5 mm wide; stipe prominent, 1 mm or longer.
  2a. Stipe glabrous basally; leaf sheaths papillose-pilose, with glassy hairs; ligule 1.8–3.2 mm long; spikelets 4.4–5.7 mm long .... 4. *P. ligulare*
  2b. Stipe pilose basally; leaf sheaths glabrous to pilose, but without glassy hairs; ligule 0.6–2 mm long; spikelets 5.9–9 mm long.
    3a. Spikelets 7–9 mm long, 2.1–2.5 mm wide; upper anthecium 4–4.5 mm long .... 3. *P. cervicatum*
    3b. Spikelets 5.9–6.7 mm long, 1.5–2 mm wide; upper anthecium 3–3.5 mm long .... 6. *P. vinaceum*
1b. Panicles terminal and axillary, forming an oblong compound inflorescence; spikelets 2.1–3.5 mm long, 1–1.3 mm wide; stipe 0.5 mm or shorter.
  4a. Spikelets 3–3.5 mm long; leaf sheaths usually with glassy hairs .... 5. *P. rudgei*
  4b. Spikelets 2.1–2.8 mm long; leaf sheaths without glassy hairs.
    5a. Plants perennial; spikelets ovoid, sparsely pilose, 2.6–2.8 mm long .... 1. *P. campestre*
    5b. Plants annual; spikelets obovoid, glabrous, 2.1–2.6 mm long .... 2. *P. cayennense*

1. **Panicum campestre** Nees ex Trin., Gram. Pan. 197. 1826. TYPE: "V. sp. Brasil (N. ab Esenb.)." Not seen.

P. rotundum A. Hitchc. & Chase, Contr. U.S. Natl. Herb. 15: 139. 1910. TYPE: Brazil. Minas Gerais: 1845, *Widgren s.n.* (holotype, US; fragment of holotype, BAA).

Perennial, 30–74 cm tall, usually with thick adventitious roots. *Culms* erect or geniculate at the base, rooting or not at the lower nodes, many-branched; internodes cylindrical or compressed, 3–10 cm long, hirsute with appressed, rigid hairs to glabrescent; nodes densely pilose, with long and whitish hairs. *Leaf sheaths* 3–7 cm long, usually shorter than the internodes, the lower ones longer, hirsute with long, tuberculate hairs; margins ciliate. *Ligule* 1.5–2.5 mm long, with hairs on the back towards the base of the blade; collar pilose, stramineous to brownish. *Leaf blades* linear-lanceolate, 7–25 cm long, 0.5–0.7 cm wide, flat or with involute borders, acuminate apically, rounded or subcordate basally, densely hirsute on both surfaces, with scabrous and ciliate margins, the midnerve manifest. *Panicles* terminal and axillary, forming an oblong, compound inflorescence, sometimes the terminal panicle distant from the other ones, lax and diffuse; *axis* sparsely hirsute, at least in the lower portion, longitudinally ridged, flexuous, scabrous, the branches alternate, divaricate, flexuous and scabrous, the axils of the branches pilose; pedicels long, scabrous. *Spikelets* ovoid, 2.6–2.8 mm long, 1–1.2 mm wide, sparsely pilose, pale to purple toward the apex to completely purplish. *Lower glume* 1.8–2.2 mm long, ½–¾ as long as the spikelet, acuminate to subulate, with rigid hairs toward the apex, 5–9-nerved, the midnerve scabrous. *Upper glume* and *lower lemma* subequal, acuminate, 2.6–2.7 mm long, 7–9-nerved, sparsely pilose on the inner surface and with or without long and sparse hairs on the outer surface. *Lower palea* elliptic, 1.8–2 mm long, present or absent. *Upper anthecium* broadly ellipsoid, 1.8–2 mm long, 1 mm wide, pale; lemma 7-nerved; palea with compound papillae at the apex; stipe with the membranous and indurate portion ca. 0.2 mm long. *Caryopsis* 1.2–1.3 mm long, 1 mm wide. In flower December–May. Figure 4.

Distribution. Brazil, from Pará and Bahia to Paraná; 0–1,500 m; growing in sandy or red clay soils in campos or cerrados.

Selected specimens examined. BRAZIL. BAHIA: Serra Geral de Caitité, 9.5 km S of Caitité on road to Brejinhos da Ametistas, *Harley 21319* (CEPEC). DISTRITO FEDERAL: Universidad de Brasilia, *Clayton 4795* (NY, US), *4842* (MO, NY, US); E of Lagoa Paranoa, *Irwin et al. 11181* (F, GH, NY, US); 15 km S of Brasilia, *Irwin & Soderstrom 5700* (US); Sobradinho, *Clayton 4875* (NY). GOIAS: 6–7 km E of Alto Paraíso, *Anderson 6515* (MO, NY); 26 km NE of Catalão, *Irwin et al. 25210* (F, MO, NY, US); 75 km N of Corumbá de Goiás, *Irwin et al. 19000* (F, GH, MO, NY, US); 14 km S of Niquelandia, *Irwin et al. 34386, 34387* (F, NY, US); 16 km N of São Joao da Aliança, *Dawson 14442* (US); between Viannápolis and Ponta Funda, *Chase 11315* (US); Serra do Rio Preto, 14 km E of Cabeceiras, *Irwin et al. 10354* (US); Corumbá, *Macedo 4482* (BAA, US). MATO GROSSO: 1 km NE of Garapé, 1 Oct. 1964, *Irwin & Soderstrom s.n.* (US-2642542). MATO GROSSO DO SUL: Campo Grande, *Chase 10790* (GH, RB, US), *Swallen 9598* (US). MINAS GERAIS: Barbacena, Serra Mantiqueira, *Chase 8645* (F, GH, NY, RB, US); Corinto, Fazenda Diamante, *Mexia 5567* (F, GH, NY, R, US); 11 km N of Gouveia, *Anderson et al. 35584* (MO, NY); Faría, Serra da Bocaina, *Chase 10533* (F, NY); 10 km W of Barao de Coçais, *Irwin et al. 28827* (F, MO, NY, US); 7 km W of Campanha, *Davidse et al. 10651* (MO, NY); 33 km NE of Francisco Sá, *Irwin et al. 23071* (F, MO, NY, SP); 35 km SW of Gouveia, *Anderson et al. 35148* (F, MO, NY); 9 km NE of Estiva, *Davidse et al. 10544* (MO); Ouro Preto, *Chase 9354* (F, NY, US); 2 km S of Itacolumy, *Irwin et al. 29364* (F, MO); Poços de Caldas, *Chase 10637* (US); Piloes, *Macedo 4876* (NY, US); lower slopes of Sierra da Piedade, *Irwin et al. 28730* (NY); between Sucupira and Omega, *Chase 11198* (US); Oliveira, *Chase 8856* (US); Lavras, *Chase 8815* (US), *Maia 18* (RB); Jardim, *Widgren 908* (US); Lagoa Santa, *Chase 8995* (US); Hermilo Alves, *Duarte 6352* (US). PARA: Marajó ate Natal, *Schwacke 62* (R); Fazenda Conceiçao, Rio Aurá, *Black 54-16109* (R). PARANA: Jaguariahyva, *Dusén 16393* (F, GH, NY, US), *10074* (US), *Swallen 8678* (US); 2 km W of Rio Itararé and road PR-11, *Davidse et al. 11375* (MO, NY). RIO DE JANEIRO: Monte Serrat, Serra da Itatiaia, *Chase 8358* (F, GH, MO, NY, US); Resende, *Hoehne & Gert 17583* (GH, US). SAO PAULO: 8 km N of Avare, *Clayton 4526* (BAA, GH, NY, SP, US); Campinas, *Novaes 1269* (US); Ytú, *Russell 186* (US); Mandaquí, *Usteri 9820* (SP, US); 10 km S de São Paulo, Parque do Estado, *Sendulsky 208, 311* (SP, US), *637, 716, 725* (SP), *Fonseca 13* (MO, NY, SP, US); 3 km from Cajurú, *Sendulsky 126* (SP, US); 16 km NNE of Padua Sales, *Eiten 1669* (NY).

Although it was not possible to examine the type specimen of this species, *P. campestre* is clearly differentiated by the diagnosis given by Trinius and by the illustration of this same author (1829).

Nees (1829) published another species with the same name, the type specimen being completely different from the species described by Trinius. *Panicum campestre* Nees of 1829 was validly renamed as *P. peladoense* by Henrard (1940).

2. **Panicum cayennense** Lamarck, Tabl. Encycl. 1: 173. 1791. TYPE: "Cayenne, *D. Stoupy*" (holotype, P, not seen; fragment of holotype, BAA, US-81397).

P. sessilicaule Desv., Opusc. 95. 1831. TYPE: "Habitat in Carolina" (holotype, P; fragment of the holotype, BAA).

P. floribundum Rich. ex Lam., Encycl. 4: 742. 1798, pro syn. *P. cayennense*.

P. pedunculare Willd. ex Steudel, Syn. Pl. Glum. 1: 77. 1854. TYPE: "*P. cayennense* Nees. Agr. Bras. 195. Brasil" (fragment of the syntype: "America meridionale, from Humboldt," US-2907507).

P. cayennense var. *curtatum* Doell, in C. Martius, Fl. Bras. 2(2): 220. 1877. TYPE: "extra fines in via inter Cayenne et Baduel (Yelski, inter plantas a cl. Rostafinski benigne mecum communicatas)" (fragment, US-80517).

Annual, to 110 cm tall. *Culms* erect or spreading, usually branching at the lower and middle nodes, often zigzag, few-noded; internodes hollow, compressed, hispid to glabrous; nodes dark, covered with whitish hairs. *Leaf sheaths* 2–8 cm long, shorter or longer than the internodes, pilose, with thick, tuberculate hairs; margins ciliate. *Ligule* 0.8–1.6 mm long; collar pilose, pale. *Leaf blades* linear-lanceolate, 5–28 cm long, 0.4–1 cm wide, flat, acuminate apically, rounded at the narrowed base, hispid on both surfaces to glabrescent, the margins scabrous and ciliate, the midnerve manifest. *Panicles* several, terminal and from the upper leaf axils, forming an elongated compound inflorescence 5–32 cm long, 3–12 cm wide, reaching ⅔ to almost the entire height of the plant, each panicle included at the base; *axis* longitudinally ridged, flexuous, scabrous and hispid towards the base, the branches divaricate, alternate to opposite, sometimes pseudoverticillate, scabrous and flexuous, the axils of the branches pilose to glabrous; pedicels long, flexuous and scabrous. *Spikelets* obovoid, 2.1–2.6 mm long, 1.1–1.3 mm wide, glabrous, globose, pale to purplish. *Lower glume* 1.2–1.8 mm long, more than half the length of the spikelet, acuminate apically, pilose on the inner surface, 5-nerved, the midnerve scabrous toward the apex. *Upper glume* 2.2–2.5 mm long, acute apically, 7-nerved, pilose to glabrous on the inner surface. *Lower lemma* 2–2.4 mm long, 7-nerved. *Lower palea* elliptic, 1.6–1.9 mm long, 0.6–1.1 mm wide, membranous, glabrous; male flower absent. *Upper anthecium* broadly ovoid, 1.5–1.8 mm long, 0.9–1.2 mm wide, pale; stipe less than 0.3 mm long, the indurate portion prolonged beyond the upper anthecium as a mucro. *Caryopsis* broadly ovoid, 0.9 mm long, 0.7 mm wide, pale. In flower all year.

Distribution. Mesoamerica, West Indies (Cuba, Jamaica and Dominican Republic), and South America, from Venezuela to Bolivia; 0–1,500 m; occurring in savannas, in sandy or clay soils.

Chromosome number. $n = 27$ (Davidse & Pohl, 1974).

Selected specimens examined. MEXICO. CHIAPAS: Escuintla, *Matuda 1799* (F, NY, US). OAXACA: Tuxtepec, *Martínez 1676* (MO, NY); Santiago de Jocotepec, *Vera Santos 3372* (MO, US). TABASCO: 21 km W of Cárdenas, *Conrad & Conrad 2959* (MO). VERACRUZ: Vicinity of Río Tonto, 6 km W of Campo Experimental de Hule, *Vera Santos 2275* (NY, US). GUATEMALA. IZABAL: S of Río Dulce, at Shell Station, *LeDoux et al. 106* (NY). PETEN: Santa Rita, 20 km al S de Santa Elena, *Molina 15533* (US). BELIZE. EL CAYO: Mountain Pine Ridge, San Agustín, *Lundell 6585* (F, NY, US). HONDURAS. ATLANTIDA: Vicinity of Tela, *Standley 54701* (US). COSTA RICA. PUNTARENAS: 0.5 km S of Buenos Aires, *Pohl & Davidse 10761* (F); between San Antonio and Boruca, *Pohl & Davidse 10979* (F). SAN JOSE: Buenos Aires, *Tonduz 3685* (US), *Valerio 1062* (F). ALAJUELA: Grecia, Hacienda La Argentina, *Valerio 601* (F, US), *605* (F). PANAMA. CHIRIQUI: 5 miles S of Boquete, *McDaniel 6807* (MO); vicinity of David, *Hitchcock 8372* (F, MO, NY, US). PANAMA: Near Arraiján, *Woodson, Jr. 1402* (MO, NY, US). CUBA. ISLA DE PINOS: Near Nueva Gerona, *Curtiss 267* (MO, US); vicinity of San Pedro, *Britton et al. 14455* (MO, US); Isla de Pinos, *Taylor 34* (MO, US). ORIENTE: Cayo del Rey, *Ekman 10028* (US). PINAR DEL RIO: Herradura, *Tracy 9073* (US), *9093* (MO), *Britton et al. 6520* (US); Sierra de Cabra on Guane road, *Britton et al. 7275* (US); Laguna Jovero and vicinity, *Shafer 10510* (US). JAMAICA. Halliss Savanna, Upper Clarendon, *Harris 12226* (MO). DOMINICAN REPUBLIC. DISTRITO NACIONAL: Sierra Prieta, Villa Mella, *Liogier 17408* (US). LA VEGA: Vicinity of Pedra Blanca, *Allard 16060, 16067* (US); Cordillera Central, Sabana de la Mar, El Valle, *Ekman 15694* (US). MONTE CRISTI: Lagunas de Canobi, *Valeur 7* (US). COLOMBIA. CAUCA: Buenos Aires, *Lehmann 5268, 5269* (US). CORDOBA: Ayapel, Hacienda Simba, *Fernández 11* (MO). Without department and locality, *Mutis 5359, 5378, 5498, 6110* (US). VENEZUELA. AMAZONAS: Puerto Ayacucho, *Williams 13085* (F, US); near Capuana, *Davidse & Huber 16811* (MO); 23 km NE of Puerto Ayacucho, *Davidse & Huber 15340* (MO). ANZOATEGUI: Pariaguán, 1 Oct. 1939, *Muller s.n.* (US). GUARICO: 28 km N of Santa Rita, *Davidse 4319* (MO). MONAGAS: 3 km E of Jusepín, *Davidse et al. 4548* (MO). FRENCH GUIANA. Cayenne, *Leprieur s.n.* (MO-1640162, US-2305642), *54* (R); route de Rachombeau, *Hoock s.n.* (NY). SURINAME. In distr. Pará, *Kappler 1495* (MO). BOLIVIA. SANTA CRUZ: Buena Vista, *Steinbach 6935* (BAA, F, GH, LIL, MO, NY, US). BRAZIL. AMAPA: Rio Pedreira, *Fróes & Black 17322* (US); Macapá, Fazendinha, *Black & Lobato 50-9659* (US). AMAZONAS: 2 km S of Labrea, *Prance et al. 8177* (F, GH, MO, NY); km 27 of road Humaitá-Porto Velho, *Prance et al. 3517* (MO). BAHIA: Col. Valença, *Pinto 1021* (US). GOIAS: 2 km SW of Araguiana, *Eiten 10154* (US). MATO GROSSO: 20 km S of Garapú, *Irwin & Soderstrom 6485* (US). MATO GROSSO DO SUL: 100 km W of Coxim, *Bommer 54* (NY, US); Paiaguás, Fazenda Alvorada, *Allem & Vieira 1001* (MO); Xavantina-Cachimbo road, W of km 229, *Philcox et al. 3631* (NY, RB). MARANHAO: Barra do Corda to Grajahú, *Swallen 3674* (RB, SP, US). PARA: Ilha de Marajó, Fazenda Gavinho, *Goeldi 245* (F, US); Oriximina, Cachoeira Porteira, *Davidson et al. 10692* (MO); Belém, *Archer 7587* (US); Cuminá, *Kuhlmann 1701* (US). RONDONIA: 2–4 km E of Abuna, *Prance et al. 8600* (MO, NY, R); 2–4 km E of Mutumparaná, *Prance et al. 8831* (F, MO).

Panicum cayennense differs from *P. campestre* mainly by its smaller, glabrous, and obovoid spikelets. It also differs in its annual habit; in *P. cayennense* the culms are generally short, branched, and bear numerous panicles nearly from the base, the axillary ones aggregating with the apical ones. Nevertheless, there are some specimens with elongated culms in which the terminal panicles are somewhat separated from the axillary ones.

This species was included by A. Hitchcock & Chase (1915) in the *Capillaria* group, along with *P. miliaceum, P. capillare,* and others, but the presence of the characteristic stipe of sect. *Rudgeana* clearly separates it from these species.

3. **Panicum cervicatum** Chase, J. Wash. Acad. Sci. 32: 164, f. 10, 1942. TYPE: Brazil. Mato Grosso do Sul: Tres Lagoas, 4 Feb. 1930, *A. Chase 10737* (holotype, US-1500814; isotypes, RB, US-1816795).

Perennial, 40–100 cm tall. *Culms* erect, simple or occasionally branched; internodes 7–23 cm long, terete, glabrous to sparsely pubescent just below the nodes; nodes densely pilose to glabrous. *Leaf sheaths* 7–13 cm long, the lower ones overlapping, pale, densely hirsute to glabrous; margins ciliate. *Ligule* 1.5–2 mm long; collar dark brown, short- to long-pilose. *Leaf blades* lanceolate, stiff, 16–36 cm long, 0.8–1.6 cm wide, long-acuminate apically, subcordate basally, flat or the margins involute in drying, hispid or strigose to glabrous on both surfaces, the margins scabrous and largely ciliate with papillose-pilose hairs (these hairs caducous), the midnerve prominent. *Panicles* lax, diffuse, many-flowered, 25–60 cm long, 12–35 cm wide, the spikelets in pairs; *axis* longitudinally ridged and scabrous, the branches alternate or opposite, scabrous, the axils of the branches pilose and pale; axillary panicles usually absent, when present similar in shape and smaller than the terminal one; pedicels scabrous, 2–20 mm long, the spikelets set obliquely on the pedicels. *Spikelets* ellipsoid, 7–9 mm long, 2.1–2.5 mm wide, glabrous, pale to purplish. *Lower glume* 3.5–3.8 mm long, acuminate, 7–11-nerved, the midnerve scabrous towards the apex. *Upper glume* 6.7–8.4 mm long, sparsely pilose to glabrous, long pilose at the base, the inner surface pilose towards the apex, 7–11-nerved, the midnerve scabrous. *Lower lemma* glumiform, 6.2–7.3 mm long, long pilose at the base, the inner surface pilose, purplish, 7–9-nerved. *Lower palea* elliptic to obovate, 4–5.8 mm long, 1.3–2.2 mm wide, membranous, the borders pilose; male flower absent. *Upper anthecium* ovoid to ellipsoid, 4–4.5 mm long, 1.8–2.1 mm wide, at maturity 2.5 mm wide and dark brown; stipe ca. 1 mm long, somewhat fleshy with an expanded summit and a thick, indurate process on the back, prolonged beyond the base of upper anthecium at maturity; rachilla pilose below the stipe. *Caryopsis* 2.8–3.2 mm long, 1.5–2.2 mm wide. In flower December–September.

Distribution. Bolivia and Brazil; sandy or sandy-clay savannas, campos or open cerrados; 400–1,300 m.

Additional specimens examined. BOLIVIA. SANTA CRUZ: Santiago de Chiquitos, San Micerato, *Cárdenas 4506* (US); Chiquitos, cerca de El Carmen, *Cárdenas 4503* (US). BRAZIL. BAHIA: Road to Posse, 225 km SW of Barreiras, *Irwin et al. 14657* (MO, NY, SP, US); Espigão Mestre, 100 km WSW of Barreiras, *Anderson et al. 36654* (F, MO, NY, US); Rio Roda Velha and highway BR-020, *Davidse et al. 12084* (MO, NY). DISTRITO FEDERAL: Universidade de Brasilia, *Clayton 4809* (SP), *4839* (NY, SP); 20 km E of Brasilia, *Irwin et al. 9213* (F, MO, NY, US); Brasilia, *Belém 1970* (CEPEC); 15 km E of Brasilia, *Irwin & Soderstrom 5711* (F, MO, NY, US); 1 km W of Sobradinho, *Irwin et al. 11077* (MO, NY, US); Brasilia, entre UNB y Parque Flor, *Pires et al. 9176* (F, SP, US). GOIAS: 1 km W of Veadeiros, *Irwin et al. 12754* (F, MO, NY, US); 3 km N of Cristalina, *Irwin et al. 13268* (F, MO, NY, US); 16 km SW of Goiás-Bahia border, *Davidse et al. 12193* (NY); between Jatahy and Rio Araguaya, *Chase 11736* (US); vicinity of Annápolis, *Chase 11519* (US); 38 km N of São Jose da Aliança, *Dawson 14354* (US); 40 km W of Rio Verde, *Chase 11713* (US); W of Santa Rita do Araguaya, *Chase 11863* (US); between Viannápolis and Ponta Funda, *Chase 11281* (US). MATO GROSSO: Rodovía Cuiabá-Santarem, *Lemes 4125* (RB); Rondonópolis, Rio Paguba, *Rondon 2566* (RB, US); Diamantina, *Weddell 3081* (US). MATO GROSSO DO SUL: Xavantina-Cachimbo road, 85 km from Xavantina, *Hunt & Ferreira 5739* (NY, SP, US); NW of São Lourenço, *Chase 11959* (US). MINAS GERAIS: Lagoa Santa, 14 Feb. 1864, *Warming s.n.* (US); 26 km NE of Patrocinio, *Irwin et al. 25582* (F, NY, SP); Serra do Cipó, 110 km NE of Belo Horizonte, *Chase 9138* (F, GH, MO, NY, US); between Sucupira and Omega, S of Uberlandia, *Chase 11167* (US); 3–4 km de Prata, *Sendulsky 18* (SP), *37* (SP, US); Frutal, *Valls 649* (US); Caldas, *Regnell III 1369* (US); Pratinha, *Dorsett 189b* (US). RONDONIA: Vilhena, *Silva & Pinheiro 4101* (MO, NY). SAO PAULO: Moji-Guaçu, *Mattos 12255* (SP); Cajurú, *Sendulsky 169* (SP); Botucatu, *Gottsberger 950-95B* (SP); Casa Branca, *Chase 10951* (US); Cabaceiras, *Pickel 5887* (US); de Santa Rita a São Simão, *Sendulsky 148* (US); 4 km SW de Paraguaçu Paulista, *Clayton 4596* (SP, US); campo de Itirapina, *Black 51-11072* (BAA, US). MARANHAO: Barra do Corda to Grajahú, *Swallen 3648* (RB, SP, US).

When publishing this species, Chase described and illustrated the fragment of rachilla below the upper anthecium, showing the two constituent parts. Although she indicated that she had not observed this character in any other species of the genus, she related *P. cervicatum* to *P. olyroides* Kunth, and in unpublished manuscripts placed both species in the "Olyroides" group; recently, Renvoize (1984) also related *P. cervicatum* and *P. ligulare* to *P. olyroides.*

However, in *P. olyroides* the characteristic stipe of sect. *Rudgeana* is absent, and there are long, acintate hairs at the base of the upper anthecium on its ventral face (Fig. 4d).

The spikelet is frequently obliquely disposed on its pedicel in *P. cervicatum,* a character present also in other species of *Panicum* (e.g., *P. hirtum*).

I consider one of the paratypes, *Williams 13221* of Venezuela, to belong to *P. vinaceum* Swallen. Consequently *P. cervicatum* remains known only from Brazil and northern Bolivia.

4. **Panicum ligulare** Nees ex Trinius, Gram. Pan. 206. 1826. TYPE: "V. sp. imperfectum Brasil (N. ab Esenb.)" (lectotype here designated: floriferous part, LE), non Nees, Agrost. Bras.: 196. 1829. TYPE: "Hab. in campis prope Almeirim provinciae Paraensis" (lectotype here designated: floriferous part of number *3800,* M).

Perennial, 1.30–2 m tall, with thick adventitious roots and lanose cataphylls. *Culms* erect, many-noded; internodes 8–24 cm long, solid or hollow, pilose to glabrous; nodes dark, pilose to glabrous. *Leaf sheaths* 8–23 cm long, greenish to purplish, papillose-pilose, the hairs urticant and caducous; margins ciliate. *Ligule* 1.8–3.2 mm long, with long hairs on the back towards the base of the blade; collar pale, densely villous. *Leaf blades* linear-lanceolate, 30–55 cm long, 0.9–1.9 cm wide, flat, acuminate apically, subcordate basally, densely pilose on both surfaces to glabrescent, the margins ciliate and scabrous, involute or not, the midnerve prominent. *Panicles* lax, diffuse, many-flowered, 47–65 cm long, 15–30 cm wide, the branches spreading; *axis* longitudinally ridged, pilose towards its base, otherwise scabrous, the branches alternate or opposite, sometimes verticillate at the base of the panicle, scabrous, the axils of the branches pilose, pale to brown; axillary panicles usually absent, when present similar to the upper one but smaller; pedicels claviform, 2–20 mm long, scabrous. *Spikelets* ellipsoid, 4.4–5.7 mm long, 1.2–1.6 mm wide, glabrous, greenish to purplish. *Lower glume* 2.9–3.8 mm long, ½–¾ the length of the spikelet, subulate apically, shortly pilose towards the apex on the inner surface, 7–9-nerved, the midnerve scabrous. *Lower lemma* glumiform, 4.1–4.9 mm long, acuminate apically, pilose towards the apex in the inner surface, 5–7-nerved. *Lower palea* elliptic, 3–3.3 mm long, 0.9–1.5 mm wide, glabrous, whitish, membranous, the margins with or without short hairs; male flower absent. *Upper anthecium* ovoid, 2.5–3.2 mm long, 1.1–1.5 mm wide, pale; palea with compound papillae at the apex; stipe conspicuous, glabrous, with 1 or 2 wings nearly 0.8–1.1 mm long, the indurate portion 0.4–0.7 mm long. *Caryopsis* 2.4 mm long, 1.3 mm wide. In flower March–October. Figure 5.

Distribution. Brazil, from Maranhão and Bahia to Mato Grosso; cerrado; 500–1,100 m.

Common name. Capim elefante.

Additional specimens examined. BRAZIL. BAHIA: 150 km SW of Barreiras, *Irwin 14904* (F, MO, US). DISTRITO FEDERAL: Chapada de Contagem, ca. 20 km NE of Brasilia, *Irwin & Soderstrom 5166* (US), *Irwin et al. 9653* (F, MO, NY, US). GOIAS: 20 km N of Cristalina, Serra dos Cristais, *Irwin et al. 13699* (F, GH, MO, NY, US), *13700* (F, MO, NY, US); 35 km NE of Catalao, *Irwin et al. 21525* (F, US); Serra Dourada, *Glaziou 22525* (US); vicinity of Goiás, *Chase 11460* (F, GH, NY); 26–31 km S of Goiania, *Davidse et al. 12278* (MO). MARANHAO: Carolina to San Antonio de Balsas, *Swallen 4094* (US); Serra do Penitente, *Miranda 128* (RB). MATO GROSSO: between Rondonópolis and São Lourenço, *Chase 11987* (US); Rio Turvo, 210 km N of Xavantina, *Irwin et al. 16122* (F, MO, NY, US); Serra Azul, 77 km from Barra do Garças, *Hunt 6075* (NY, US); Serra do Roncador, 86 km N of Xavantina, *Irwin et al. 16386* (F, NY, US); Xavantina-Cachimbo road, 215 km from Xavantina, *Hunt & Ferreira Ramos 5606* (NY, US); 8 km NE of Base Camp, 12°54′S, 51°52′W, *Ratter et al. 2090* (NY, RB); Campos Novos, *Kuhlmann 1745* (RB).

Trinius (1826), in attributing *P. ligulare* to Nees, described the species as possessing a lanceolate, membranous ligule 6–10 mm long, and used the epithet *ligulare* in reference to this character. After examining abundant material of *P. ligulare* and studying the type of *P. ligulare* in Leningrad, I discovered that the type sheet contains a mixture of material. The panicle of this specimen does correspond to what I consider *P. ligulare* (which agrees with the description given by Trinius for the floriferous part), but the vegetative portion (which is separated from the floriferous part) is markedly different from the vegetative parts of the species. The leaf sheaths and leaf blades are completely glabrous, and the membranous ligule is exceptional because of its size. This type of ligule has never been found in any species of *Panicum* up to now.

In 1829, Nees described *P. ligulare* as Trinius did, mentioning that the type of ligule he observed was unique in *Panicum.* In his description, Nees reported the type locality as "Hab. in campis prope Almeirim provinciae Paraensis." On studying the type material in Munich, I found two specimens collected by Martius in that locality, one with the number *3798* (attached to the plant) and the other identified as *3800.* In *3800* there is a mixture of material similar to the specimen from Leningrad. Specimen *3800* is undoubtedly the one Nees used in his diagnosis. In specimen *3798* there is no mixture, and it fits perfectly with what I have described as *Panicum ligulare.* In this specimen there is a note on which Trinius stated that this material is different in its vegetative parts to the one examined at Leningrad.

Trinius (1835) and Steudel (1855) treated the species in the same way as Nees and Trinius did before.

Doell (1877), in *Flora Brasiliensis,* noted the difference between specimens *3798* and *3800* of Munich. He considered *3800* to be *P. ligulare* "in sensu strictiore," but erroneously judged *3798* to be *P. virgatum* (a completely different North American species).

I select the floriferous portion of the Leningrad material as the lectotype of *Panicum ligulare* Nees ex Trin., and the floriferous portion of the Munich specimen *3800* as a lectotype of *P. ligulare* Nees.

5. **Panicum rudgei** Roemer & Schultes, Syst. Veg. 2: 444. 1817. Based on *P. scoparium* Rudge, Pl. Guian. 1: 21, pl. 29. 1805, non Lam., 1798. TYPE: "*Panicum scoparium* Rudge, ex herb. Rudge" (fragment, US-2830540).

P. pilosissimum Roth ex Roemer & Schultes, Syst. Veg. 2: 458. 1817. TYPE: "Roth nov. plant Spec. Ms. . . . In Essequebo, *Mertens*" (fragment, US-2830939).

P. rudgei var. *brasiliense* Raddi, Agrost. Bras. 48. 1823. TYPE: ". . . in viciniis fluminis inhumirim, in locis silvosis et herbosis" (fragment, US-80665).

P. dasytrichum Sprengel, Syst. Veg. 1: 317. 1825. TYPE: "*Panicum dasytrichum* Spr. hirsutum Willd. herb. Hoffmansegg" (fragment, US-80665).

P. rhigiophyllum Steudel, Syn. Pl. Glum. 1: 76. 1855. TYPE: "*P. rigens* Salzm. Hrbr. Bahia" (isotype, US-81104).

P. cayennense var. *divaricatum* Doell, in C. Martius, Fl. Bras. 2(2): 220. 1877. TYPE: same as the species.

Perennial, 30–130 cm tall, with short rhizomes and pilose, scaly cataphylls. *Culms* decumbent or geniculate to erect, often zigzag, rigid, hollow, branching from the lower and upper nodes, many-noded; internodes 5–15 cm long, cylindrical, densely to sparsely pilose; nodes covered with whitish, appressed hairs to completely glabrous. *Leaf sheaths* 4–13 cm long, densely papillose with thick, glassy hairs; margins ciliate. *Ligule* 1.5–2 mm long, with long hairs on the back towards the base of the blade; collar pale, densely to sparsely pilose. *Leaf blades* linear-lanceolate, 20–40 cm long, 0.6–1.1 cm wide, acuminate apically, narrowed basally, flat or with involute borders, densely hispid to sericeous on both surfaces to glabrescent, the margins scabrous, ciliate or not in the lower portion, the midnerve manifest. *Panicles* terminal and axillary from the upper nodes, forming an elongated, compound inflorescence ⅓ or more the length of the plant, 25–50 cm long, 10–20 cm wide; *axis* and branches longitudinally ridged, scabrous to pilose, the axils of the branches long-pilose to glabrous, brownish to pale, the branches alternate and divaricate, somewhat flexuous; pedicels scabrous, long-pilose, flexuous. *Spikelets* ovoid, acuminate, 3–3.5 mm long, 1–1.2 mm wide, pale to nearly purplish, sparsely hirsute, with stiff hairs irregularly distributed. *Lower glume* 2–2.7 mm long, ⅔ as long as the spikelet, acuminate apically, with stiff, whitish hairs on the upper part to completely pilose, the inner surface pilose, 3–5-nerved, the midnerve scabrous. *Upper glume* 2.7–3 mm long, acuminate apically, pilose on the inner surface, 7–9-nerved, the midnerve scabrous. *Lower lemma* 2.5–2.9 mm long, acute apically, long-pilose to glabrous, 7–9-nerved, the midnerve scabrous. *Lower palea* elliptic, 1.8–2.3 mm long, 0.5–1.1 mm wide, membranous, the margins shortly pilose; male flower present, the anthers purplish; rachilla with or without whitish hairs. *Upper anthecium* ellipsoid, 1.8–2.2 mm long, 0.8–1.1 mm wide; palea with compound papillae towards the apex; stipe with the membranous portion ca. 0.4 mm long, the indurate portion 0.5 mm long, prolonged beyond the back of the lemma as a mucro. *Caryopsis* pale, 1.5 mm long, 1 mm wide. In flower all year.

Distribution. Mesoamerica, West Indies (Jamaica, Trinidad) and South America from Colombia to Bolivia and Brazil; 0–1,000 m; in open savannas, campos or cerrados, usually in sandy soils.

Common names. makuna-ta (Colombia); carricillo (Venezuela).

Chromosome number. $n = 9$ (Davidse & Pohl, 1974, 1978); $2n = 18$ (Pohl & Davidse, 1971).

Selected specimens examined. MEXICO. TABASCO: Achotal, *Matuda 3087* (F, GH, US). GUATEMALA. IZABAL: Montaña del Mico, 6 mi. S of Izabal, *Steyermark 38581* (F); Santa Cruz, N of Lago Izabal, *Steyermark 39673* (F). BELIZE. Cabbage Hall, *Dwyer et al. 454* (F, MO); Swasey Branch, Monkey River, *Gentle 3862* (F, GH, MO, NY, US); Machaca, *Gentle 6893, 6923* (F, NY, US). COSTA RICA. ALAJUELA: Buenos Aires, *León 1184* (US), *Tonduz 3679, 4875* (US); Los Palmares, *Pittier 10588* (US). PUNTARENAS: Buenos Aires, *Molina 27395* (F, MO, US); east of CIA, road to Buenos Aires, *Pohl et al. 13116* (F, MO). SAN JOSE: Vicinity of El General, *Skutch 3065* (GH, MO, NY, US), *Pittier 12064* (US). NICARAGUA. ZELAYA: Entre Siuna y Limbaikán, *Seymour 4977* (F, NY). PANAMA. Jaboga, *Killip 4163* (US); Canal Zone, near Fort Randolph, *Standley 28598* (MO, US); Perlas Archipelago, San José Island, *Johnston 324* (GH, US). JAMAICA: James Hill, Upper Clarendon, *Harriss 12845* (NY, US); Halliss Savanna, Upper Clarendon, *Harriss 12235* (MO, NY, US); Bunkers Hill Savanna, *Harriss 11170* (NY, US); Mason River Savanna, 275 miles NW of Kellits, *Proctor 26301* (NY, US). TRINIDAD. O'Mearey Savanna, *Soderstrom 1010* (US), *Britton & Hazen 1563* (NY, US); Pitch Lake, *Hitchcock 10083* (MO, NY, US); St. Joseph, *Hitchcock 10181* (US); Piarco Savanna, S of Dabadie, *Britton 688* (NY). COLOMBIA. AMAZONAS: Corregimiento de Araracuara, *Aguirre Galviz 877* (COL). ANTIOQUIA: Morro Pan de Azúcar, *Orozco et al. 767* (COL). GUAINIA: Río Guainía, Puerto Colombia, *Schultes et al. 17936* (US). META: 73 km W of Las Gaviotas, *Davidse 5390* (MO); 43 km NE of Puerto López, *Davidse 5106* (MO); 15 km al E de San Martín, *Blydenstein 1658* (MO). NORTE DE SANTANDER: La Motilona, hoya del Río de Oro, *García Barriga 18723* (NY, US). SANTANDER: Entre Puerto Wilches y Puerto Santos, km 16, *Killip & Smith 14859* (F, GH, MO, NY, US). TOLIMA: El Convento, W of San Lorenzo, *Pennell 3509* (F, GH, MO, NY, US). VAUPES: Cerro de Circasia, *Cuatrecasas 7201* (US). VICHADA: 25 km E of Cumaribo, *Davidse 5325* (MO); 10 km W of Las Gaviotas, *Davidse 5367* (COL, MO, NY). VENEZUELA. AMAZONAS: Cerro Duida, *Maguire 29424, 29060* (NY); Serrania Parú, *Cowan 31486* (NY, US); 20 km S of Puerto Ayacucho, *Davidse 2841* (MO); 5 km NE of San Carlos de Río Negro, *Liesner 3703* (MO); 25 km S of Samariapo, *Gentry & Berry 14600* (MO); Yavita, *Williams 13879* (F, US); pie del Cerro Huachacamari, *Huber 4990* (MO); El Manguito, 1 km N of Caño Caname, *Davidse et al. 17482* (MO); alrededores de Canaripo, *Huber 1981* (MO); 8 km S de Puerto Ayacucho, *Davidse & Huber 14916* (MO). ANZOATEGUI: Vicinity of Santo Tomé, *Chase 12841* (GH, US). APURE: end of the Galerías de Cinaruco, *Davidse & González 14667* (MO); near the Río Meta at Fundo El Algarrobo, *Davidse & González 14217* (MO). BARINAS: 16 km SW of the Merida intersection just outside of Barinas, *Davidse 3182* (MO, NY). BOLIVAR: Sabanas de Santa Teresa, *Tamayo 2808* (MO); Gran Sabana, S of Mt. Roraima, *Steyermark 59429* (F, US); 0.5 km NE of Urimán, *Steyermark & Wurdack 22* (F, NY, US). MONAGAS: E de Maturín, ca. caserío La Pica, *Aristeguieta 4048* (F, MO, NY); Laguna Mosú, 12 km N de Capirito, *Trujillo 14194* (F). ZULIA: 60 km NW of Santa Bárbara-San Carlos del Zulia, near Campamento El Rosario, *de Bruijn 1473* (MO, NY, US). GUYANA. Tumatumari, *Gleason 40* (GH); Waini River, *de la Cruz 3634* (F, GH, MO, US); Waramuri Mission, Horuka River, *de la Cruz 2576* (F, GH, MO, NY, US); Bartica, Hills Estate, *Hitchcock 17191* (F, MO, NY, US); Kaieteur Falls, Potaro River, *de la Cruz 4478* (F, GH, MO, NY, US). SURINAME. Zandery, *Samuels 233* (GH, NY, US); Kwatta, *Maguire 23912* (F, GH, MO, NY, US); Sanderijl, *Archer 2745* (US). FRENCH GUIANA. Vicinity of Cayenne, *Broadway 348* (GH, NY, US); 10 km from St. Laurent, on road to Cayenne, *Cowan 38943* (US). PERU. LORETO: Nauta, Río Marañón, *Gentry et al. 29965* (MO); vía Nauta-Iquitos, *Díaz & Jaramillo 1270* (MO). BOLIVIA. BENI: 15 km W de Guayamerín, camino a Riberalta, *Krapovickas & Schinini 35068* (US). LA PAZ: San Carlos, *Buchtien 32* (GH, MO, NY, US); Apolo, *Williams 1020* (NY); San Antonio, *Buchtien 1159* (US). BRAZIL. AMAPA: Araguarí River, 20 minutes downriver from Porto Platón, *Pires et al. 50973* (F, GH, NY, US); Porto Platón, *Silva 2782* (NY, RB). AMAZONAS: Cucuí, Rio Negro, *Nascimento et al. 194* (MO); km 20 on road from Humaitá to Labrea, *Prance et al. 3386* (F, MO, NY, US); Fortaleza Savanna, Rio Puciari, *Prance 13791* (F, GH, NY). BAHIA: Salvador, *Chase 7883* (F, GH, MO, NY); 35 km E of Eunápolis, *Harley 17285* (CEPEC, MO, NY); Maraú, *Belém & Pinheiro 2121* (CEPEC), *Zuloaga et al. 2464* (RB, SI, US); road BR-418, 16 km del cruce con BA-001, *Mori et al. 9674* (CEPEC, NY). MATO GROSSO: Serra Azul, 75 km S of Xavantina, *Irwin et al. 17302* (F, MO, NY, US); 270 km N of Xavantina, *Ratter 2069* (NY); Serra do Roncador, 60 km N of Xavantina, *Irwin et al. 15961* (F, MO, NY, US). MATO GROSSO DO SUL: Tres Lagoas, *Chase 10745* (US). PARA: Santarém, *Swallen 3721* (US); Soure, Ilha do Marajó, *Swallen 4974* (US); Acará, Thomé Assú, *Mexia 5921, 5975* (F, GH, MO, NY, US); 73 km NE of Castanhal, *Davidse et al. 17939* (MO, NY); 17 km SE of Vigía, along road Pa-140, *Davidse et al. 17610* (MO, NY). PERNAMBUCO: Vicinity of Recife, *Chase 7675* (F, US); Poazeves, *Pickel 3137* (US). RIO DE JANEIRO: Silvestre, *Holway et al. 1116* (US); Merity, 20 km N of Rio de Janeiro, *Chase 8465* (US). RONDONIA: Porto Velho, *Black & Cordeiro 52-15348* (US). RORAIMA: Igarapé Agua Boa, Rio Mucajaí, *Prance et al. 4035* (MO); Sierra de Sururucu, *Prance et al. 9899* (F, MO); Boca da Mata, base de Serra Tepequem, *Prance et al. 4274* (MO). SAO PAULO: São Simão, *Kuhlmann 4110* (US); 7 km de São José dos Campos, *Eiten & Mimura 3351* (MO, US).

6. **Panicum vinaceum** Swallen, Fieldiana. Bot. 28(1): 27. 1951. TYPE: Venezuela. Bolívar: Gran Sabana, between Kun and waterfall at Rue-Meru, south of Mount Roraima, elev. 1,065 m, 2 Oct. 1944, *J. A. Steyermark 59173* (holotype, US-1911661; isotype, F).

Perennial, 40–100 cm tall. *Culms* erect, few-noded; internodes 6–11 cm long, pilose; nodes pilose. *Leaf sheaths* 4–14 cm long, covered by long dense hairs or glabrescent; margins ciliate to glabrous. *Ligule* 0.6–2 mm long; collar pale, pilose. *Leaf blades* linear-lanceolate, 15–42 cm long, 0.5–1.2 cm wide, flat, acuminate apically, subcordate basally, with appressed hairs on both surfaces to glabrescent, the margins scabrous, ciliate or not. *Panicles* lax and diffuse, 12–50 cm long, 6–20 cm wide, the branches spreading; *axis* longitudinally ridged, scabrous, the branches alternate to opposite, scabrous, the axils of the branches pilose, pale; axillary panicles usually absent, when present similar to the terminal one but smaller; pedicels scabrous. *Spikelets* ellipsoid, 5.9–6.7 mm long, 1.5–2 mm wide, globose and glabrous, pale to purplish, the inner surface of the glumes and lower lemma densely to sparsely pilose. *Lower glume* 2.9–3.8 mm long, subulate apically, 5–9-nerved, the midnerve scabrous. *Upper glume* 5.3–6.4 mm long, acuminate apically, 7–11-nerved, glabrous. *Lower lemma* 5.1–5.5 mm long, acute apically, 7–9-nerved. *Lower palea* obovate, 3.1–4 mm long, 1–1.5 mm wide, whitish, membranous, the margins pilose; male flower absent. *Upper anthecium* ovoid, 3–3.5 mm long, 1.4–1.8 mm wide, pale; stipe with the membranous portion 0.7–1.2 mm long, with or without wings, the indurate portion ca. 0.9 mm long, obtuse; rachilla pilose below the upper anthecium. *Caryopsis* 2.4 mm long, 1.5 mm wide. In flower September–April.

Distribution. Brazil and Venezuela; 100–1,000 m; savannas.

Additional specimens examined. BRAZIL. GOIAS: Rio da Prata, 6 km S of Posse, *Irwin et al. 14509* (US). PARA: Serra do Cachimbo, BR-163 Cuiabá-Santarém, km 823, *Prance et al. 24993* (MO, NY); Serra do Cachimbo, *Pires et al. 6302* (BAA, US). VENEZUELA. AMAZONAS: El Ratón, *Williams 13221* (F, US); alrededores de Puerto Ayacucho, 15 km al norte, *Huber 862, 1351, 2131* (MO). BOLIVAR: El Dorado, S of La Gran Sabana, *Davidse 4929* (F, MO, NY, US); Estación Bolívar, en sabanas de Santa Elena, *Tamayo 2964* (MO, NY, US).

This species is closely related to *P. cervicatum*, from which it can be separated only by the sizes of the spikelet, lower palea, and upper anthecium. The rest of the differential characters noted by Swallen (size and pilosity of the plants and size of the panicles) have no value in separating the two species. *Irwin 14509* is exceptionally large and differs from Swallen's description. Nevertheless, spikelet size (a constant character in the scant material available for this species), shows that *Irwin 14509* must be included in *P. vinaceum*, thereby partially modifying Swallen's concept of this species.

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ARUNDOCLAYTONIA, A NEW GENUS OF THE STEYERMARKOCHLOEAE (POACEAE: ARUNDINOIDEAE) FROM BRAZIL[1]

GERRIT DAVIDSE[2] AND R. P. ELLIS[3]

ABSTRACT

Arundoclaytonia dissimilis Davidse & Ellis, gen. et sp. nov. is described from Amazonian campinas in Amazonas and Pará, Brazil. It represents the second genus of the tribe Steyermarkochloeae (Poaceae: Arundinoideae). Morphologically it is characterized by a caespitose growth habit, proliferation and lignification of the numerous basal culm internodes, normally developed leaves with spiral phyllotaxy, unisexual hemispherical inflorescences aggregated into a false panicle, 3–9-flowered male spikelets with 2 anthers per flower, 3-flowered female spikelets with only the middle floret fertile and its palea convolute and many-nerved, lack of lodicules, terminal exsertion of the stigmas and stamens, and fusiform caryopsis with an elliptic-punctate hilum. Anatomically this species is characterized by C_3 anatomy, including nonradiate, compact isodiametric chlorenchyma, and 2 bundle sheaths; abaxially by the absence of stomata and microhairs, reduction of silica bodies, thick epidermis, and hypodermal sclerenchyma; and adaxially by prominent ribs and furrows. Its classification in Steyermarkochloeae is based primarily on the morphology of the spikelets.

During 1974 an unusual grass was collected by William R. Anderson and associates in Pará, Brazil. Although it was recognized as an undescribed taxon, the inflorescences were too immature to show the exact morphology of the spikelets. In 1979 Cleofé E. Calderón and coworkers collected abundant mature material of the same taxon in Amazonas, Brazil. Our study of both these collections indicates that they represent the second genus of the recently described tribe Steyermarkochloeae (Davidse & Ellis, 1984). We are naming the genus in honor of Dr. W. D. Clayton, eminent agrostologist at the Royal Botanic Gardens, Kew, who has made and continues to make outstanding contributions to agrostology. The compound generic name at the same time refers to the arundinoid affinity of the genus. The specific epithet alludes to the strongly dissimilar male and female inflorescences and spikelets.

DESCRIPTION

Arundoclaytonia dissimilis Davidse & Ellis, gen. et sp. nov. TYPE: Brazil. Amazonas: Transamazon Highway, ca. 53 km W of the Aripuaña River, abundant dominant plant of the vegetation. Growing in a white sand soil "campina." This plant grows in large, open areas mixed with shrubs and alternating with narrow strips of islands of low tree forest. Most of the population reduced to burnt bases. These trunks look like big candelabra, some ca. 70 cm or less. From them come up solid stems with thickened bases formed by aerial roots. In many cases from the top of burnt trunks, bunches of leaves start coming again. Few plants still blooming. Plants ca. 2–3 m tall when flowering. 28 June 1979, *C. E. Calderón, O. P. Monteiro & J. Guedes 2706* [holotype, INPA; isotypes, CANB, K, LE, MO (mounted as 8 sheets), PRE, RB, SP, US (mounted as 11 sheets)]. Figures 1–7.

Gramen perenne; culmi internodiis numerosis inferioribus solidis lignosis superioribus cavis arundaceis; phyllotaxis spiralis; vagina cava marginibus liberis; ligula membranacea ciliata; lamina plana vel involuta; inflorescentiae unisexuali constans ex fasciculis hemisphaericis aggregatis in inflorescentiam falsam; spiculae unisexualis rotundatae dorsales infra glumis disarticulates; glumae 2; spiculae masculinae 3–

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9-florae palea 2-carinata; stamina 2; spiculae femineae 3-florae flosculo inferissimo sterili flosculo supererissimo rudimentali, palea flosculi mediani convoluta, 9–13-nervis lemmatibus longiorior; lodiculae 0; stylus 1, stigmate 2; caryopsis fusiformis-teres hilo punctato.

Perennial 2–3 m tall, erect. *Vegetative culms* usually densely covered for 2–70 cm to a thickness of 1.5–6 cm by aerial roots tightly appressed to the culm and by remnants of leaf sheath bases; internodes numerous, 2–15 mm long, 1–1.5 cm diam., solid, lignified; nodes bearing one prominent prophyllate bud; phyllotaxy 2/5; branching intravaginal near the basal cluster of leaves. *Flowering culms* to 1 cm diam., consisting of many, often elongated internodes; internodes 1–16 cm long, glabrous, densely waxy when young, green in the exposed portions when older, hollow, gradually becoming solid toward the base of the plant; nodes glabrous; branching primarily intravaginal, profuse in the upper ⅓ of the culm to form a false inflorescence. *Leaves* primarily clustered toward the base, those of the flowering culms fewer and gradually reduced in size toward the tip of the culm. *Basal leaves* with the sheaths densely overlapping, much longer than the internodes, stramineous, long persistent, turning brown and eventually reduced to fibers in age, rounded and glabrous abaxially, without a differentiated midrib, the margins glabrous, free to the base, the base pilose at the point of insertion and between the veins or glabrescent, the apex ciliate with hairs 2–4 mm long, wider than the base of the blade, rounded, a collar not clearly differentiated; ligule a ciliate membrane 0.9–2.1 mm long, the membrane 0.3–0.9 mm long, the cilia 0.5–1.2 mm long; blades 45–80 cm long, 8–16 mm wide, flat with involute margins or entirely involute, the upper portion always involute and the apex pungent, the abaxial surface green, glabrous and smooth, the adaxial surface grayish green, densely and minutely scabrous, grooved between the veins, the veins approximately the same size, a midrib not differentiated, the margins ciliate with hairs 2–3 mm long in the lower ⅓, scaberulous in the upper ⅔. *Cauline leaves* similar to the basal leaves but smaller, the uppermost much reduced with the blade shorter than the sheath and entirely involute. *Inflorescences* numerous, borne on axillary, exserted peduncles, aggregated into a false panicle, unisexual, consisting of hemispherical clusters of 7–20 spikelets, each cluster surrounded by 1 or 2 series of bracts and/or rudimentary spikelets; male inflorescences produced before the female, 9–13 mm wide, 6–11 mm high; female inflorescences 20–36 mm wide, 15–23 mm high; peduncles geniculate and pilose at the base with hairs 0.5–1.5 mm long, sometimes with a line of pubescence or with a scarious bract 1–3 mm below the cluster of spikelets, always subtended by a sheath, the sheath terminating in a sharp point; peduncles of the male inflorescences usually longer than those of the female inflorescences. *Female spikelets* 7–19 mm long at anthesis, sessile or short-pedicellate with pedicels to 0.5 mm long, lanceoloid, rounded on the back, disarticulating below the glumes, falling as a unit, slightly curved, 3-flowered; glumes 2, unequal, herbaceous, shorter than the lemmas, ovate, broadly acute, pilose at the base, otherwise scaberulous, the nerves free or connected by cross-veinlets, the lower 1.5–2.0 mm long, 1–3-nerved, the upper 2.2–3.5 mm long, 3–5-nerved; lower floret without a flower, the lemma 3.0–5.1 mm long, 7–9-nerved, ovate, broadly acute, pilose at the base, otherwise scaberulous, cross-veinlets few, the palea absent or rudimentary, 0.7–1.5 mm long and hyaline when present; middle floret unisexual, the lemma 5.7–8 mm long, 9–11-nerved with conspicuous cross-veinlets, ovate, acute, pilose at the base and between the nerves just above the base with hairs 1–1.5 mm long, otherwise scaberulous, the palea conspicuously longer than the lemma, 7.5–17 mm long, 9–13-nerved, slightly curved in the upper half, convolute, shallowly grooved on the back, spongy-thickened, smooth and shiny in the lower ½–⅔, herbaceous and scaberulous in the upper ⅓–½, ciliate on the overlapping margin at the base with hairs 1–1.5 mm long; upper floret rudimentary or consisting of a single 3-nerved bract, 0.1–4 mm long, ciliate at the base, borne on a prominent rachilla 3.5–10.5 mm long, the floret and rachilla fitting into the palea groove of the middle floret; lodicules absent; staminodia absent or present as an anterior pair of rudiments to 0.2 mm long; gynoecium cylindrical, the ovary wall free from the ovule, the style one, dividing into 2 inconspicuously plumose stigmas slightly below the tip of the middle palea, the stigmas 2.5–4 mm long, terminally exserted through an apical, tubular orifice formed by the convolute palea; caryopsis fusiform-terete, narrowing apically, 6–7 mm long, 0.8–1.2 mm diam., glabrous, the embryo $^{3}/_{10}$–$^{4}/_{10}$ as long as the caryopsis, the hilum elliptic-punctate. *Male spikelets* 3.5–7.5 mm long, sessile or short-pedicellate with pedicels to 0.5 mm long, rounded on the back, disarticulating below the glumes, 3–9-flowered, the florets (except the uppermost) bearing flowers, the middle florets slightly larger than those above or below, the uppermost usually rudimentary; glumes 2, unequal, shorter than the lemmas, membranous, ovate, erose, truncate or obtuse, pilose at the base, usually with cross-veinlets, the lower 1.3–2.1 mm long, 1–3-nerved, the upper 1.8–2.5 mm long, 3-nerved; lemmas similar to the glumes in pubescence, shape and texture, 2.6–4.1 mm long, shorter than the paleas, 3–9-nerved; paleas 3.2–5.8 mm long, broadly obtriangular, truncate, sometimes erose, 2-keeled (each keel with a nerve), the base with hairs 1–1.5 mm long, the back sulcate, the keels ciliolate, the margins overlapping; lodicules absent; stamens 2, one situated on each side of the sulcate palea, terminally exserted through an opening formed by the overlapping palea margins, the filaments separate, basifixed, the anthers 2.2–2.9 mm long.

Paratypes. BRAZIL. PARA: Alto Tapajós, Rio Cururú, northwest edge of Serra do Cachimbo, 25 km by foot NE of Missão Velha on Rio Cururú, elev. ca. 400 m?, 7° ca. 30′S, 57° ca. 15′W, outcrop of blocky sandstone, with shrubs on rocks and smaller cover on wet sand between rocks, 2 m tall, among rocks, 14 Feb. 1974, *W. R. Anderson, S. G. da Fonsêca, R. Reis dos Santos & R. Souza 10950* (MO, NY, UB).

MORPHOLOGICAL OBSERVATIONS

Arundoclaytonia dissimilis when fully mature and undisturbed by fire has an unusual appearance caused by the thick accumulation of leaf sheath bases and adventitious aerial roots (Figs. 1, 3). Such plants in the aspect of their basal parts are more reminiscent of certain species of *Vellozia.* This unusual appearance is accentuated after the plants have been moderately or severely burned (Figs. 2, 4, 5).

Although the plant is fundamentally a tussock plant, the dense cluster of leaves, which is normally basal in a tussock grass, is raised up to 70 cm above ground level in older plants of *Arundoclaytonia* (Figs. 2–5). These small "trunks" result from the proliferation of numerous, short internodes in the basal portion of the culms. Short basal internodes are typical of grass culms. What is unusual in *Arundoclaytonia* is their large number, thickness, woodiness, and perennial duration. Annual culms characterize most grasses.

In typical caespitose perennial grasses the short basal internodes perennate and bear the buds from which new tillers are produced for the new growing season. It is this region of the culm that is much elongated by the proliferation of internodes and gives *Arundoclaytonia* its trunklike appearance. The internodes of this region are solid in most grasses, and this is also true in *Arundoclaytonia.* In contrast, the elongated internodes of the flowering culm produced above the cluster of basal leaves gradually become hollow, as is common among grasses.

When the sheath bases and mass of aerial roots have been removed from the lower portion of the culm (as may happen after severe burning and the subsequent wearing off of the root and sheath remains), it becomes apparent from the position of the axillary buds that the leaf arrangement is not distichous. Every sixth node bears a solitary, prophyllate, dormant bud (Fig. 7A) that occurs in the same relative position as the buds five nodes above and below it. Since two complete turns around the culms must be made to attain the same position, phyllotaxy is 2/5. The arrangement of the spikelet bracts appears to be nearly distichous; however, the relative position of the bracts is much more difficult to observe because the very short internodes of the spikelet and the broad bases of the glumes and lemmas obscure the exact point of insertion of these spikelet parts. Distichous phyllotaxy is characteristic of the Poaceae (Arber, 1934: 282; Barnard, 1964: 47). Only one other exception has been reported: spiral phyllotaxis in *Micraira subulifolia* F. Muell., a mosslike plant from Queensland (Watson & Dallwitz, 1980: 89).

Branching occurs near the base of the plant to form the main culms that constitute the bulk of the tussock (Figs. 4, 5). These branches originate from the buds illustrated in Figure 7A. Branching is very infrequent in the middle portion of the culms but profuse in the upper portion. At each upper node, a smaller axillary branch is produced which itself is rebranched several times (Fig. 8) into branchlets terminating in inflorescences. The branching pattern is the relatively simple one that characterizes most nonbambusoid grass genera. A prophyllum is the first foliar organ produced at the lowest node of each branch (Fig. 8). Each prophyllum is many-nerved and prominently two-keeled with narrow wings on the keels. Buds at subsequent nodes on the branch are subtended by leaves with blades reduced and generally smaller than the sheaths. These leaves are gradually reduced upward along the branches. Just below the inflorescences they are reduced to scarious bracts, presumably representing reduced sheaths only.

FIGURES 1–6. Habitat and habit photographs of *Arundoclaytonia dissimilis*; 53 km W of the Aripuaña River, Amazonas, Brazil.—1. Unburned campina.—2. Burned campina.—3. Mature unburned flowering plant.—4. Contrast between a severely burned, killed plant and a moderately burned, regenerating plant.—5. Detail of the base of a burned, regenerating plant.—6. Detail of a section of the compound inflorescence showing the small, long-peduncled male inflorescences below and above and the large, sharply pointed, short-peduncled female inflorescences in the center. Photographs by Dr. Cleofé E. Calderón.

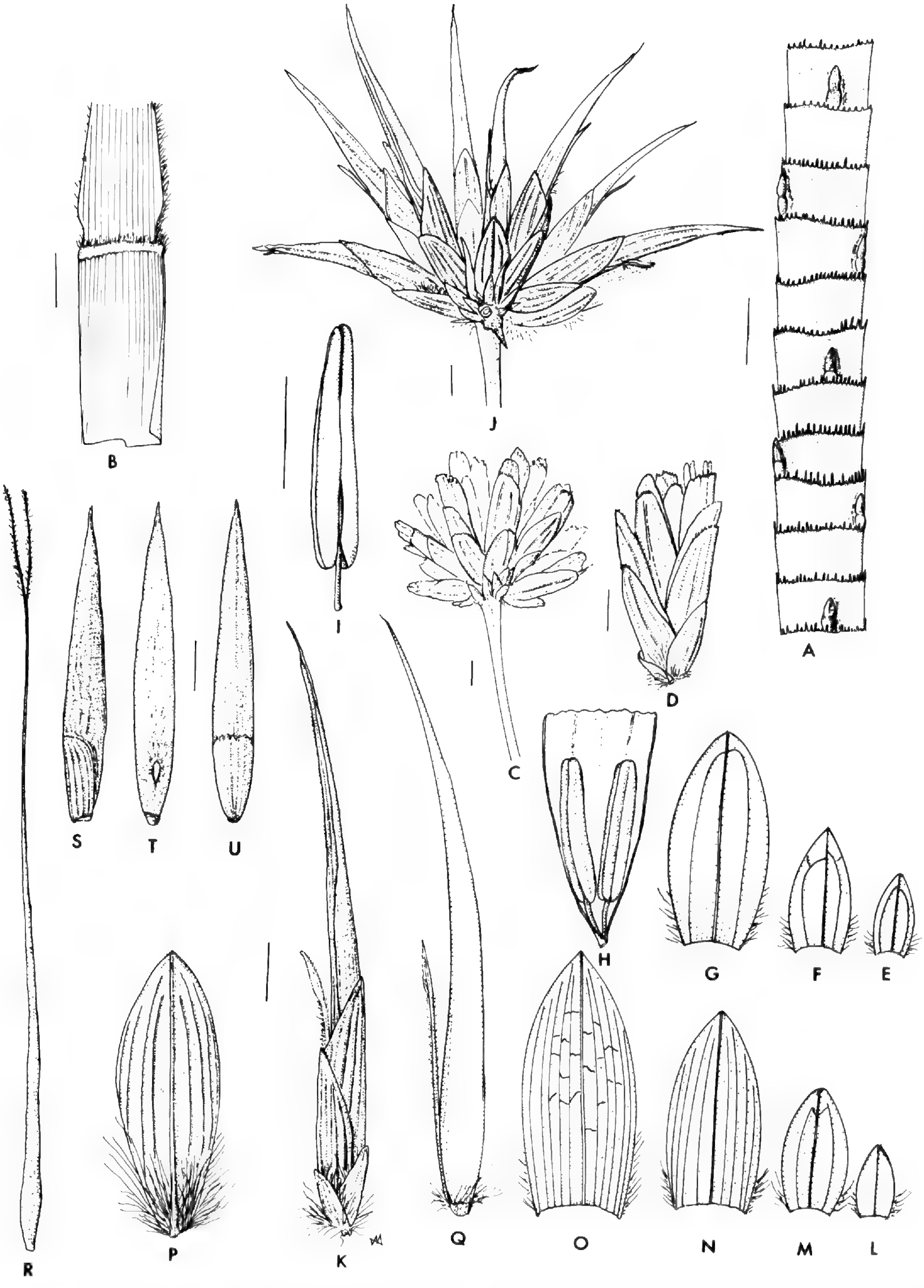


FIGURE 7. Morphology of *Arundoclaytonia dissimilis.*—A. Basal portion of culm with the sheath bases worn off and showing the approximately identical position of the buds every sixth node.—B. Portion of a leaf with ligule.—C. Male inflorescence.—D. Male spikelet. E–I. Components of male spikelet.—E. Lower glume.—F. Upper glume.—G. Lemma.—H. Inner view of palea with the two stamens composing the male flower.—I. Stamen.—J. Female inflorescence.—K. Female spikelets. L–R. Components of female spikelet.—L. Lower glume.—M. Upper glume.—N. Lower lemma.—O. Middle lemma, ventral view.—P. Middle lemma, dorsal view.—Q. Middle palea and rachilla extension with the rudimentary upper floret.—R. Gynoecium, probably pollinated and slightly expanded. S–U. Caryopsis in three different views.—S. Lateral view.—T. Hilum view.—U. Embryo view. Scales: A, B = 1 cm; C, D, I–K, U = 1 mm; magnification for E–H, K–R, and S–U the same.

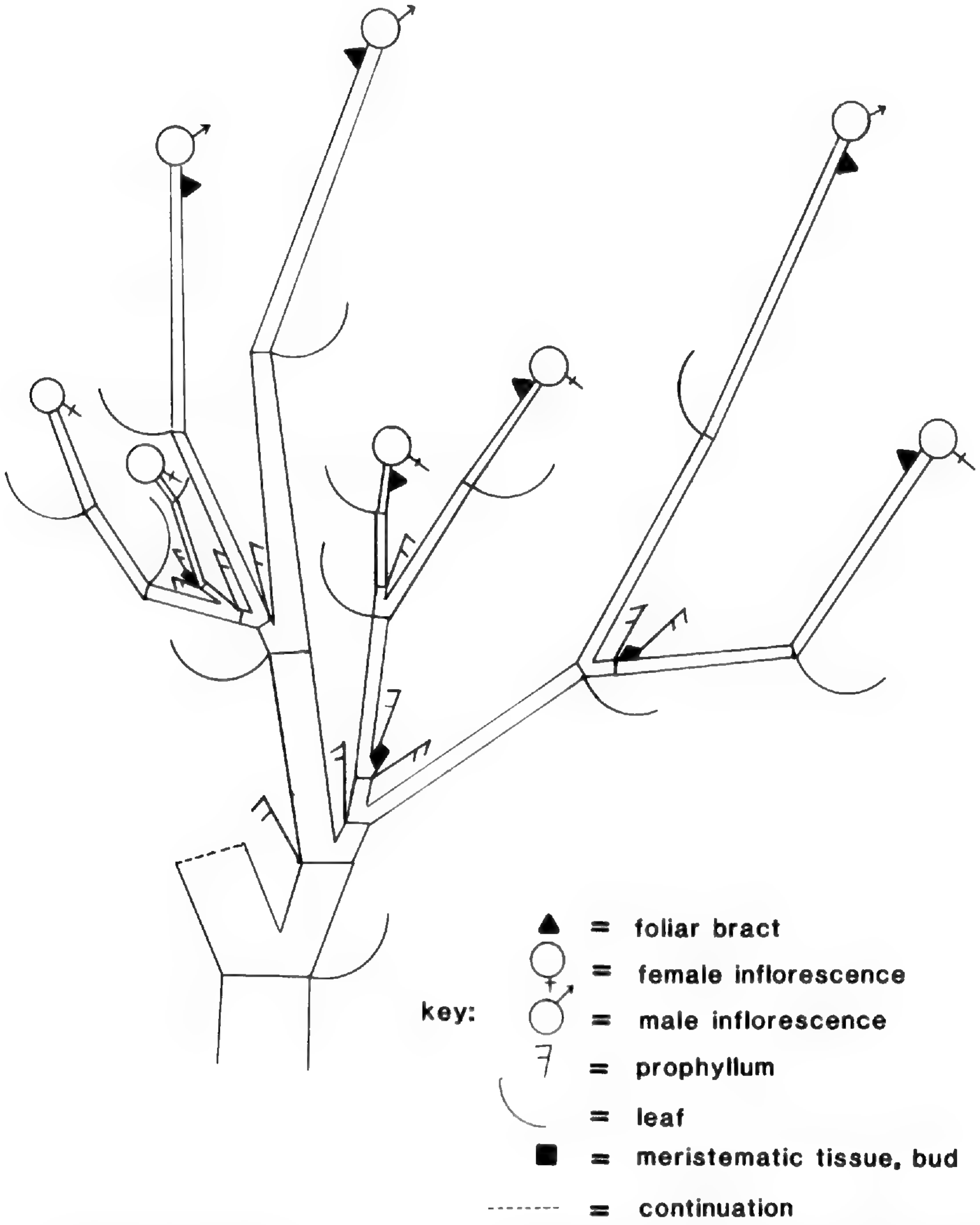


FIGURE 8. Diagrammatic illustration of a portion of the inflorescence of *Arundoclaytonia dissimilis* showing the relationship of the internodes, leaves, prophylla, and inflorescences. The proportions of the structures have been altered for clarity and are shown in two dimensions.

At any node along the flowering portion of a main culm, male inflorescences are produced before the female inflorescences, and the male inflorescences are borne on longer branches than those of the female inflorescences. Each branch complement along the main culm ultimately terminates in a male inflorescence. The proportion of male to female inflorescences varies from 2 male : 1 female in the lowest portion, gradually changing to 1 male : 3 female in the uppermost portion. However, since the male spikelets are functionally 2–8-flowered compared with the functionally one-flowered female spikelets, the total number of male flowers is greater than female flowers. Although the plant is fundamentally protandrous, the large number of inflorescences produced by any mature plant ensures a significant overlap between the flowering of male and female spikelets. No information is available about self-incompatibility or frequency of flowering.

The male and female spikelets are strongly dimorphic and, besides the difference in flowers and number of anthoecia, differ significantly in the anthoecial morphology. Both the lemma and especially the palea of the functional floret of the female spikelets are convolute and thicker in texture, and the palea is greatly elongated and 9–13-nerved (Fig. 7K, O–Q). In contrast, the lemmas and paleas of the male spikelets are membranous, the lemmas are 3–9-nerved and rounded on the back, and the paleas are 2-keeled and

2-nerved (Fig. 7D, G, H). The relative lengths of lemmas and paleas in the two kinds of spikelets are similar, the paleas being longer in both kinds, although those of the female spikelets tend to be somewhat longer than those of the male spikelets.

In both kinds of inflorescences the outer whorl of spikelets is surrounded by a ring of small sterile bracts that we interpret to represent rudimentary spikelets (Fig. 7C, J). In some cases these rudimentary spikelets may reach 4 mm in length in the female inflorescence and consist of four or five bracts in the same positions as the normal female spikelet parts. From such rudimentary spikelets there is a gradual diminution and simplification to small solitary bracts. Occasionally one of the normally sized female spikelets on the outside of the inflorescence has an extra bract. However, those on the inside of the inflorescence uniformly have the two glumes and three florets. In the several cases where a small extra bract was observed in the inner part of the inflorescence, it clearly originated below the very short pedicel and presumably also represented a rudimentary spikelet.

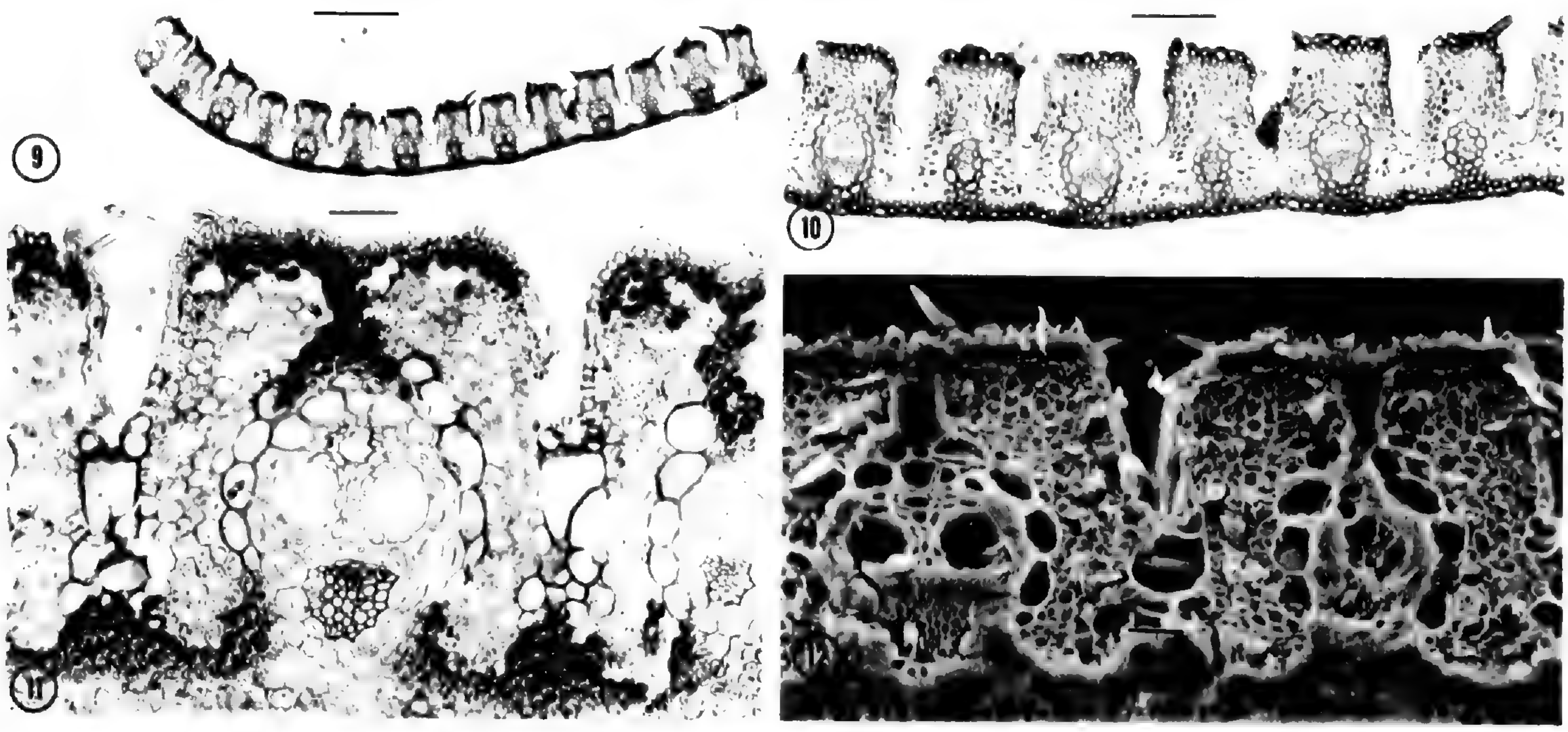
Leaf Blade Anatomy

ANATOMICAL TECHNIQUES

Anatomical studies were carried out on leaves from herbarium specimens and those fixed in the field in FAA. Preparation of the sections followed the methods outlined by Ellis (1984). The very fibrous nature of the leaf blades frequently caused the sections to tear as they were cut, making it difficult to obtain completely undamaged sections.

LEAF IN TRANSVERSE SECTION

Outline: open, expanded with the margins slightly recurved (Fig. 9). Leaf thickness 30 μm laterally to 40 μm centrally. *Ribs and furrows:* prominent, flat-topped adaxial ribs with straight, vertical sides present over all the vascular bundles (Fig. 10); ribs associated with first-order and third-order vascular bundles of identical size and shape; furrows narrow, cleftlike, penetrating at least half the leaf thickness. Abaxial ribs or furrows absent. *Median vascular bundle:* no midrib or keel developed; median vascular bundle structurally indistinguishable from lateral first-order bundles. *Vascular bundle arrangement:* more than 25 first-order bundles with metaxylem vessels per leaf section; one third-order bundle without metaxylem vessels between consecutive first-order bundles, this alternating pattern occurring across the full width of the blade (Figs. 9, 10). All vascular bundles located slightly closer to the abaxial surface. *Vascular bundle structure:* first-order bundles round to elliptical in outline (Figs. 9–12); phloem tissue adjoining the inner bundle sheath; protoxylem lacunae present; metaxylem vessel elements wide (±5 μm) with a diameter double that of the parenchyma sheath cells, thin-walled and slightly angular (Fig. 12). Third-order bundles elliptical with xylem and phloem tissue distinguishable. *Vascular bundle sheaths:* first- and third-order bundles completely surrounded by an inner bundle sheath (Fig. 11); mestome sheath cells relatively large, of the same diameter as the parenchyma sheath cells; secondary walls heavily but uniformly thickened, almost excluding the lumen (Figs. 11, 12). Outer bundle sheath round, adaxially and abaxially interrupted by sclerenchyma girders (Figs. 11, 12); bundle sheath extensions absent; cells elliptic, variable in size, thin-walled and lacking chloroplasts. *Sclerenchyma:* adaxial girders inversely anchor-shaped, following the shape of the adaxial ribs (Figs. 11, 12); abaxial sclerenchyma forming a continuous hypodermal band with projections toward the vascular bundles as well as the bulliform cell groups (Fig. 11). Fibers very thick-walled with lumens almost completely filled; lignified, except those projecting toward the bulliform cells which may have cellulose secondary walls (Fig. 10). *Mesophyll:* chlorenchyma not radiately arranged; cells small, isodiametric and tightly packed without visible intercellular air spaces (Fig. 11); occupying the sides of the ribs but divided abaxially by the bulliform cells, colorless cells, and abaxial hypodermal sclerenchyma; arm or fusoid cells absent. Colorless, inflated, thin-walled parenchyma cells linking the bulliform cells to the hypodermal sclerenchyma. *Adaxial epidermal cells:* bulliform cells at the base of all furrows and occurring in restricted, fan-shaped groups with an inflated central cell. Epidermal cells with a very thick cuticle, even on the sides of the furrows; papillae or macrohairs absent; interlocking prickles common on the sides of the furrows (Figs. 11, 12). *Abaxial epidermal cells:* bulliform cells absent; epidermal cells small, with an extremely thick, continuous cuticle equal in thickness to the diameter of the epidermal cells; hairs, papillae, and stomata absent; costal and intercostal zones not differentiated.



FIGURES 9–12. Leaf blade anatomy of *Arundoclaytonia dissimilis* in transverse section.—9. Outline showing the absence of a keel.—10. Alternating first- and third-order vascular bundles and prominent adaxial ribs and cleftlike furrows.—11. Anatomical detail showing double bundle sheath, compact mesophyll, inversely anchor-shaped adaxial sclerenchyma girder, abaxial hypodermal band and bulliform cells with associated colorless cells.—12. Scanning electron photomicrograph showing interlocking prickles in the adaxial furrows and structure of the metaxylem vessel elements. Scales: 9 = 50 μm; 10 = 20 μm; 11, 12 = 10 μm. Based on *Anderson et al. 10950* (Figs. 9, 10) and *Calderón et al. 2706* (Figs. 11, 12).

ABAXIAL EPIDERMIS

Zonation: costal and intercostal zones indistinguishable; entire epidermis composed of uniform long and short cells (Figs. 13–15). *Long cells:* elongate rectangular, length 3× the width, anticlinal walls parallel, end walls vertical (Fig. 14); horizontal and vertical anticlinal walls heavily thickened, pitted and deeply sinuous. Long cells usually adjoining one anther but infrequently separated by cork-silica cell pairs. *Stomata:* lacking on the abaxial surface (Fig. 13). *Short cells:* tall, with irregular outline; associated with silica cell of similar shape (Fig. 14); occurrence irregular. *Papillae:* absent. *Microhairs:* absent. *Silica bodies:* tall and narrow, irregular in outline; scattered throughout the epidermis.

ADAXIAL EPIDERMIS

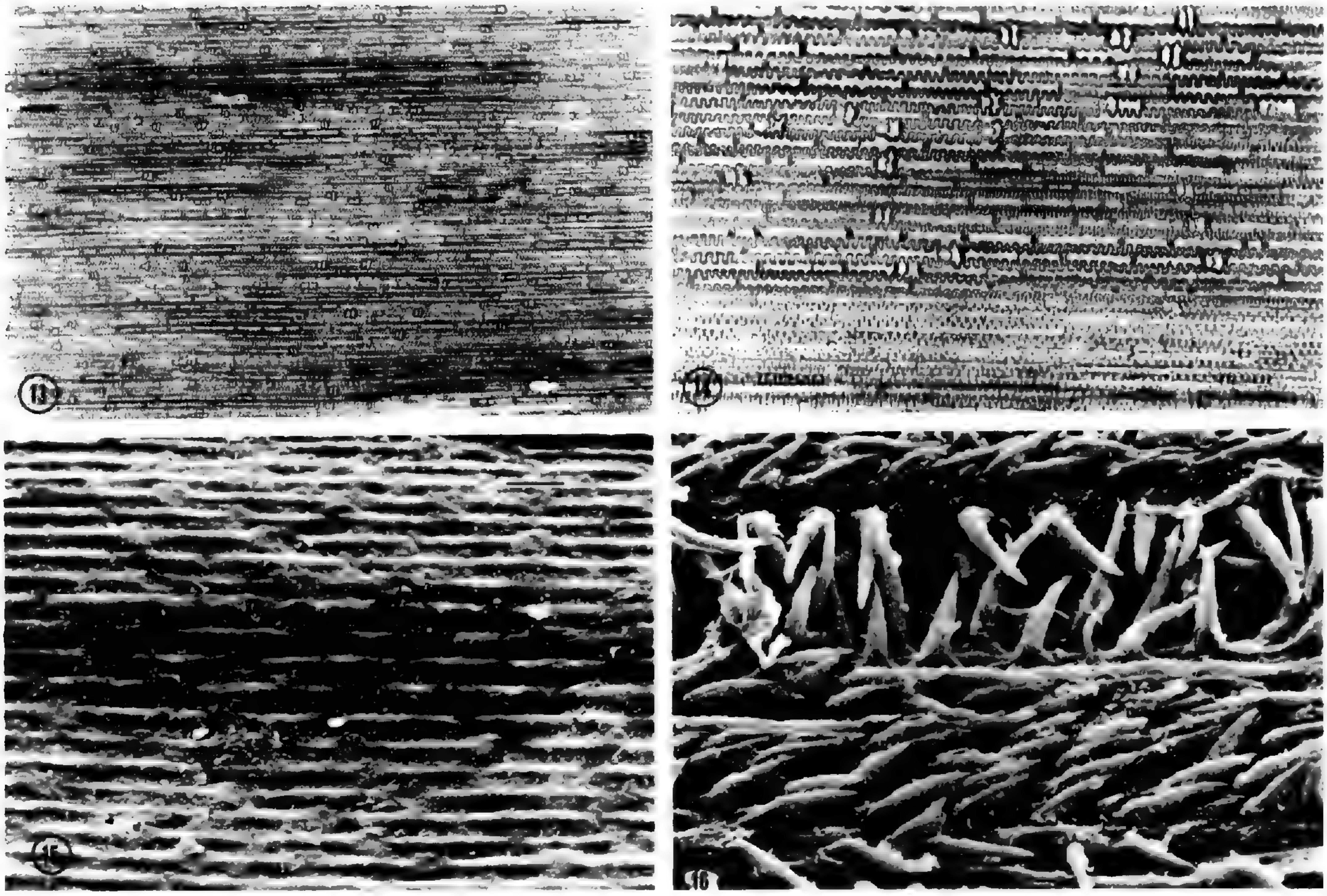
Sides and tops of the ribs covered with prickle hairs interlocking with hairs from the adjacent rib; barbs elongated, stiff and sharply pointed; prickles obscuring all other epidermal details of this surface (Fig. 16).

ANATOMICAL OBSERVATIONS

The anatomy of the leaf blade of *Arundoclaytonia* is highly modified and exhibits many xerophytic adaptations. This is demonstrated most clearly by the well-developed abaxial hypodermal sclerenchyma, extremely thickened abaxial epidermis, and strongly ribbed and furrowed adaxial surface. These xerophytic modifications appear to have led to the consequent loss or reduction of many epidermal features commonly well developed in most other grasses. The most important reductions are the lack of distinction between the abaxial costal and intercostal zones, the absence of abaxial stomata and microhairs, and the reduction of silica bodies. These xerophytic features undoubtedly allow a rapid inrolling of the leaves and may be responsible for the involute margins or completely involute leaves observed on the herbarium specimens.

Classification and Discussion

As mentioned in the introduction, we consider *Arundoclaytonia* to belong in the now bigeneric Steyermarkochloeae despite the fact that *Arundoclaytonia* differs markedly from *Steyermarkochloa* in growth habit, leaf morphology, and inflorescence morphology. When the morphology of the spikelets is compared, however, a remarkable resemblance between the genera becomes evident. Ignoring for the moment a low percentage of bisexual spikelets in *Steyermarko-*



FIGURES 13–16. Epidermal structure of the leaf of *Arundoclaytonia dissimilis.*—13. Abaxial epidermis showing uniform structure and absence of costal and intercostal zones.—14. Detail of the abaxial epidermis with heavily thickened, sinuous-walled long cells and infrequent cork-silica cell pairs.—15. Scanning electron photomicrograph of the abaxial epidermis illustrating the absence of both stomata and hairs.—16. Scanning electron photomicrograph of the adaxial epidermis showing interlocking prickles with long barbs. Scales: 13 = 30 μm; 15 = 10 μm; magnification for 14–16 = 10 μm. Based on *Anderson et al. 10950* (Figs. 13, 14) and *Calderón et al. 2706* (Figs. 15, 16).

chloa, the fundamental structure of the unisexual spikelets is identical in the two genera. The male spikelets have two stamens, are multiflowered, and lack lodicules in both genera. The major difference in the male spikelets is that those of *Arundoclaytonia* have more florets. This kind of variation is analogous to that between species of *Eragrostis, Bromus,* and *Bambusa,* to name just three of the many genera in which this kind of variation is well known. The female spikelets are identical in the number, arrangement, and shape of the florets. The only important differences are in the size and pubescence of the spikelets. These striking and fundamental spikelet similarities are almost certainly not due to convergent evolution but indicate a fundamental phylogenetic relationship which is reflected in our classification of *Arundoclaytonia* in the Steyermarkochloeae.

The generic status of *Arundoclaytonia* is justified by the following major differences from *Steyermarkochloa:* monomorphic vs. dimorphic culms; typical vegetative leaves with open sheath, many-ribbed blade, and ligule vs. highly modified vegetative leaves with stemlike, solid sheath, two-ribbed blade, and ligule absent; many small, hemispherical male and female inflorescences aggregated into a false panicle vs. single, large, terminal, spicate inflorescences bearing male, female, and bisexual spikelets; and in leaf anatomy—vascular bundles at one level vs. different levels; absence vs. presence of lacunae; absence vs. presence of abaxial stomata; and adaxial furrows and ribs associated with all vascular bundles vs. associated only with the median vascular bundle.

Our decision to place *Arundoclaytonia* in the Steyermarkochloeae necessitates a modification of the description of the tribe (Davidse & Ellis, 1984). Because the leaves of *Steyermarkochloa* are unique in the family, leaf characters were believed very important in characterizing the tribe and in differentiating it from others. This is now shown to be true only when *Steyermarkochloa* was known. In fact, at the macroscopic level, the tribe now encompasses both "normal" and highly modified leaves. In this light the unusual features of the leaves of *Steyermarkochloa,* both at the macro- and microscopic levels, must be seen as adaptations to its seasonally inundated habitat, just as the strongly xerophytic features of *Arundoclaytonia* are presumably adaptations that allow it to cope with the nutrient deficiencies, frequent moisture stress, and intense solar radiation of the white-sand soils of its campina habitat (Ab'Sáber, 1982; Anderson, 1981). Such white-sand soils are considered to be the most nutrient-deficient soils in South America (Eiten, 1978). Although the campinas are located in high rainfall regions, they dry out rapidly near the surface during periods of low rainfall and never experience the long-sustained inundation of the sabaneta or morichal habitats of *Steyermarkochloa* (Ab'Sáber, 1982; Eiten, 1978; Anderson, 1981).

The formal, emended tribal description is the following:

Steyermarkochloeae Davidse & Ellis, Ann. Missouri Bot. Gard. 71: 994. 1985.

Perennial grasses with mono- or dimorphic culms and leaves; leaves solitary or numerous per culm, consisting of a flattened sheath, blade, and ligule, or a solid, cylindrical sheath and flattened blade without a ligule, or reduced to bladeless flattened sheaths. Inflorescence spicate, elongate and cylindrical or a hemispherical cluster of spikelets, bearing male or female spikelets only, or bearing female spikelets above male and bisexual spikelets. Spikelets solitary, usually unisexual, dorsally compressed, disarticulation below the glumes; glumes 2; lodicules 0; uppermost floret rudimentary or reduced; stamens 2; stigmas 2, the style 1; caryopsis fusiform; male spikelets 2–9-flowered, the paleas 2-keeled; female spikelets 3-flowered, the lowest floret sterile, the middle floret fertile, the upper floret rudimentary and borne on a prominent rachilla segment; palea of the functional female floret spongy, curved, (5–)7–13-nerved, longer than the lemma.

When describing the Steyermarkochloeae and including it in the admittedly heterogenous Arundinoideae, Davidse & Ellis (1984) relied primarily on anatomical characters. At the same time, they recognized its uniqueness in the subfamily on the basis of the gross morphology of the leaves, inflorescence, spikelets, and flowers. Much of that detailed discussion is applicable to *Arundoclaytonia* as well.

The discovery of "normal" leaves in the Steyermarkochloeae lessens the importance of the unique leaves of *Steyermarkochloa* vis-à-vis the other genera of the Arundinoideae. In leaf morphology we now consider such leaves to be basic in the Steyermarkochloeae and thus well within the norm of the Arundinoideae, and we consider the leaves of *Steyermarkochloa* to be a later specialization that evolved in its own lineage.

In contrast, the inflorescences and flowers of *Arundoclaytonia* are derived and more specialized than those of *Steyermarkochloa.* Bisexual flowers are universally considered more primitive than unisexual flowers among grasses. Their occurrence, along with the more specialized unisexual flowers, in *Steyermarkochloa* and their absence in *Arundoclaytonia* indicates that the latter is more specialized in this respect. Similarly, we consider the occurrence of bisexual and unisexual spikelets in one inflorescence in *Steyermarkochloa* to be less specialized than the segregation of the spikelets into strictly male and female inflorescences in *Arundoclaytonia.* This strict separation of male and female flowers may be considered the ultimate step in the Charlesworth & Charlesworth (1978) model of the evolution of monoecism through a gynomonoecious pathway discussed by Davidse & Ellis (1984) for *Steyermarkochloa.*

Only in one respect of spikelet morphology might *Arundoclaytonia* be considered less specialized than *Steyermarkochloa,* and this is in the number of florets of the male spikelets. The occurrence of two sterile florets in the female spikelets of both genera suggests a reduction in number of fertile florets. This interpretation is supported by the occurrence of bisexual spikelets in *Steyermarkochloa* with two bisexual florets and others with a male floret below the bisexual floret. Against this background, the larger number of florets in the male spikelets of *Arundoclaytonia* might be less specialized. This interpretation must be tempered with the fact that floret number may easily change up or down, as is evident in the Arundinoideae, Pooideae, Chloridoideae, and Bambusoideae in general, although reduction seems to be prevalent in the family.

The number of florets in the Arundinoideae varies from one to many, but the predominant trend and probably the primitive condition in the subfamily is spikelets with many florets and with apical reduction. *Arundoclaytonia* displays this trend well in the male spikelets. In the female spikelets both apical and basal reduction are evident. In reduction of the lowest floret to a sterile lemma, *Steyermarkochloa* and *Arundoclaytonia* resemble the Panicoideae. However, the terminal rudimentary floret plus the numerous florets of the male spikelets of *Arundoclaytonia* suggest that this similarity is convergent. The rather rounded female spikelets of *Arundoclaytonia* and *Steyermarkochloa* are presumably due to reduction of the number of fertile florets to one.

One interesting aspect of the inflorescence morphology of these two genera is the reduction of the number of spikelets per inflorescence in *Arundoclaytonia*, but, at the same time, the aggregation of the many small unisexual inflorescences into a large false panicle. This exactly parallels a trend in other tribes in the family, for example, *Saccharum* vs. *Hyparrhenia* in the Andropogoneae (Clayton, 1969) and *Panicum ligulare* Nees vs. *P. rudgei* Roem. & Schult. in the Paniceae.

Anatomically, the absence of abaxial stomata and microhairs and the reduction of silica bodies in *Arundoclaytonia* complicates the phylogenetic interpretation of the anatomical structure of the leaf blade as many of these features are generally recognized as being diagnostic of the five subfamilies of the Poaceae (Renvoize, 1981). *Arundoclaytonia*, therefore, does not exhibit the complete set of diagnostic anatomical characters used to assign grasses to a given subfamily, thus limiting our ability to use these characters for determining the affinities of this unusual grass. However, by a process of elimination certain possibilities can be discarded.

Arundoclaytonia does not possess arm or fusoid cells and, therefore, cannot be accommodated in the Bambusoideae. The Chloridoideae is entirely Kranz with only one possible exception (Ellis, 1984), and the Panicoideae is predominantly C_4. Non-Kranz members of the panicoid group all have a semiradiate type of mesophyll and do not have the compact, isodiametric chlorenchyma of *Arundoclaytonia*. *Arundoclaytonia* is undoubtedly also C_3 but shows no anatomical resemblance with the panicoid grasses, and phylogenetic relationships with this subfamily appear most unlikely. The type of chlorenchyma found in *Arundoclaytonia* does, however, occur in many arundinoid grasses. Some members of the Pooideae also have this type of chlorenchyma, but the pooid grasses typically do not have sinuous long cells or tall, vertical silica bodies as does *Arundoclaytonia*. The leaf anatomical evidence, although somewhat limited, does suggest arundinoid affinities for *Arundoclaytonia*, and its systematic position does appear to lie with the Arundinoideae.

The tribes of the Arundinoideae cannot be separated on anatomical criteria and the decision to classify *Arundoclaytonia* in the Steyermarkochloeae is based on morphological evidence, mainly that of the spikelets. This decision is neither confirmed nor refuted by the anatomical evidence. The leaf anatomy of *Steyermarkochloa* and *Arundoclaytonia* differs substantially and both appear to have highly advanced and derived leaf anatomy. Because of these great anatomical differences, they undoubtedly cannot be accommodated in the same genus.

Clayton & Renvoize (1986) considered the Steyermarkochloeae to be a tribe in the Panicoideae, noting "an obvious resemblance to *Hymenachne*" in features that are not unique. They furthermore believe *Steyermarkochloa* to fundamentally differ from C_3 panicoids only in the lack of microhairs (Renvoize, in litt.). We believe that the additional evidence presented by us for *Arundoclaytonia* gives further support for our classification of the tribe, although we certainly recognize the isolated position of the Steyermarkochloeae in the Arundinoideae, and recognize that we are adding one more relatively discordant element to the traditional "dumping ground" of the family. Except for the lacunae and stellate cells in the leaves and the gross form of the inflorescence, but not its branching pattern, we find it difficult to observe any obvious resemblances between *Steyermarkochloa* and *Hymenachne*.

We do agree with Clayton & Renvoize (1986) that embryo characters would provide important new information for clarifying the taxonomic position of the tribe. Chromosome information could also be potentially useful. Unfortunately, we were unable to satisfactorily section caryopses obtained from an herbarium specimen of *Arundoclaytonia*. In the case of *Steyermarkochloa* all our meiotic cytological samples were too young. Unlike the typical situation in grasses, inflorescences of *Steyermarkochloa* must apparently be well exserted from the sheath before meiosis takes place.

The distribution of *Steyermarkochloa* in the northern Amazon basin and *Arundoclaytonia* in southcentral Amazonia suggests that other taxa of this alliance may eventually be discovered, since large areas of this region are botanically very poorly known. Obviously, the area between the ranges of these two genera would seem to be the most promising in this respect. Any relatively open vegetation on white-sand soils (campinas or Amazonian caatingas) might harbor further taxa of this tribe. These vegetation types are found in greatest abundance in the drainages of the Rio Negro and the Rio Branco (Eiten, 1978; Anderson, 1981).

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SIPHOCAMPYLUS OSCITANS (CAMPANULACEAE: LOBELIOIDEAE), A NEW NAME FOR *BURMEISTERA WEBERBAUERI* FROM PERU[1]

Bruce A. Stein[2]

Abstract

Burmeistera weberbaueri is transferred to the genus *Siphocampylus* under the new name *Siphocampylus oscitans.* The species is noteworthy in being one of only three species of *Siphocampylus* known to have a dilated anther-tube orifice.

As part of a reassessment of the Peruvian members of *Burmeistera* (Stein, 1987), it has become apparent that *B. weberbaueri* Zahlbr. actually belongs to the large Andean genus *Siphocampylus.* This paper makes the appropriate generic transfer and proposes a new name to accommodate this unusual species.

Generic delimitations in Campanulaceae subfamily Lobelioideae have long been recognized as problematic (Gleason, 1925; McVaugh, 1940). Traditional systems, such as those of Presl (1836) and Wimmer (1943), rely heavily on fruit morphology for classification at the tribal level. In particular, capsular versus baccate fruit is a fundamental character used to define and align genera. Strict reliance on this dichotomy in the classification of the subfamily has separated close relatives, for example, capsular-fruited *Siphocampylus* and baccate-fruited *Centropogon.* Although fruit type in conjunction with other features can be reliable for clustering related groups of species, probable convergence in fruit characters suggests caution in its application.

Among neotropical Lobelioideae the emphasis on fruit type, and to a lesser degree on the presence or extent of a dorsal slit in the corolla (another seemingly labile character), has yielded genera of convenience. One of the most natural groupings, however, appears to be the genus *Burmeistera,* which is characterized by baccate fruits, oblong or linear seeds, mostly nonbracteolate pedicels, entire corolla tubes, and distally open and oblique anther tubes often with little or no apical pubescence.

The distally open anther tube of *Burmeistera* is one of its most distinctive features. In most genera of Lobelioideae the three dorsal anthers are longer than the two ventral ones and curve downward at the apex, effectively closing the mouth of the anther tube. This allows the internally released pollen to build up pressure as the style and stigma elongate, pushing pistonlike through the anther tube. The characteristic tuft of stiff hairs at the tip of the ventral anthers functions as a lever that opens the orifice slightly and allows the pressurized pollen to discharge. Presumably tripped by flower visitors, this action has been elegantly documented in *Isotoma petraea* by Brantjes (1983) and has been observed in the neotropical genera *Centropogon* and *Siphocampylus* (Stein, in prep.). Since the dorsal anthers in *Burmeistera* do not curve downward closing the anther tube, this type of regulated pollen discharge does not occur. This difference in pollen presentation probably explains the correlated feature of glabrous or only sparsely pilose anther apices in *Burmeistera* sect. *Imberbes* F. Wimmer: apical hairs there have no function as trip mechanisms. Whether the densely villous tuft at the tip of the ventral anthers in *Burmeistera* sect. *Barbatae* F. Wimmer has a functional role in pollen discharge is not clear.

Burmeistera weberbaueri was included in this genus by Zahlbruckner (1906) on the basis of floral features alone, as he had no mature fruit. This decision was probably based upon his observation of a naked and dilated anther-tube orifice, the absence of bracteoles, and the somewhat

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[1] I am grateful to Carlos Reynal for locating the type specimen at MOL and to B. E. Leuenberger for searching for type material at B. Dan H. Nicolson kindly provided advice regarding lectotypification, and Porter P. Lowry II and Peter Goldblatt made useful suggestions on an earlier draft. Fieldwork in Peru was supported by National Science Foundation Doctoral Dissertation Improvement Grant BSR84-13912 and by a Garden Club of America Award in Tropical Botany.

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"burmeisteroid" corolla morphology (a short, straight tube with an abruptly ampliate throat and falcate lobes). The strongly turbinate hypanthium visible in the Field Museum type photograph suggests the mature fruit of this species to be capsular rather than baccate. Furthermore, the coriaceous and rugose texture of the leaves characterizes many members of *Siphocampylus* but is unknown in *Burmeistera*. An open anther-tube orifice of the kind described by Zahlbruckner is, however, extremely rare in *Siphocampylus*.

OBSERVATIONS

In order to investigate further the generic placement of this species, I visited the type locality in January 1987 to collect fresh material and to ascertain the fruit type and anther-tube morphology. This represents the first collection since the type was collected by August Weberbauer 85 years before. The fruits turned out to be capsular with half-superior ovaries. Careful examination of fresh pedicels occasionally revealed bracteoles, a feature often difficult to observe in dried material. The presence or absence of these bracteoles was consistent within individual inflorescences. The most interesting confirmation is of the dilated anther-tube orifice. Zahlbruckner's description of this feature is true for the species and not based on an artifact of preservation as I had previously assumed.

TAXONOMIC TREATMENT

Siphocampylus oscitans B. A. Stein, nom. nov. *Burmeistera weberbaueri* A. Zahlbr., Bot. Jahrb. Syst. 37: 451. 1906. Non *Siphocampylus weberbaueri* A. Zahlbr., Bot. Jahrb. Syst. 37: 456. 1906. TYPE: Peru. Junín: Prov. Tarma, mountains east of Huacapistana, 3,200 m, Jan. 1902, *Weberbauer 2203* (lectotype here designated, W; isolectotype, G). SYNTYPE: Peru. Junín: Prov. Tarma, mountains east of Palca, 3,200–3,600 m, Feb. 1902, *Weberbauer 2473* (MOL, photograph of lost B syntype, F neg. 9074).

Erect many-branched *shrubs* to 1.5 m tall, glabrous throughout; stems green or more commonly maroon, terete when fresh, drying compressed; white latex present in all parts. *Leaves* clustered toward branch tips, alternate and spirally arranged, rarely appearing subopposite or pseudoverticillate, sessile; blades narrowly ovate to lanceolate, (3–)5–9 cm long, (0.7–)1.5–4 cm wide, apex attenuate, base rounded to obtuse; margins densely and sharply callose-serrulate, 9–13 teeth per cm; when fresh the lamina fleshy and coriaceous with the tips recurving, the adaxial surface smooth and dark green, the abaxial surface pale or occasionally tinged purple, drying coriaceous with the adaxial surface nitid and rugose, prominently impressed by the 6–8 acutely ascending, almost straight secondary veins. *Inflorescence* subcorymbose and auxotelic, the flowers solitary in congested upper leaf axils, the rachis later elongating and producing normal foliage leaves beyond the maturing flowers and fruits; pedicels ascending to spreading, 4–8 cm long, generally exceeding length of subtending leaves, occasionally with sub-basal, subulate bracteoles to 2 mm long. *Flowers* 35–40 mm long; hypanthium widely obconic, the sides strongly divergent, 3–4 mm long, 7–9 mm wide at summit, often suffused with maroon; sepals erect or slightly spreading, triangular, 8–11 mm long, 3–4 mm wide at base, about twice the length of hypanthium, the margins entire or minutely denticulate; corolla green and maroon, yellowish within, corolla tube straight, 15–18 mm long dorsally and 10–15 mm long ventrally, ca. 6–8 mm wide at base, narrowing and re-expanding slightly above, the lobes lance-oblong with acuminate slightly revolute tips, mostly abruptly decurved, the dorsal lobes falcate, 14–17 mm long, ca. 4 mm wide at base, the lateral and ventral lobes 11–14 mm long; filament tube 27–30 mm long, adnate to corolla ca. 4 mm above base, glabrous and greenish, well exserted from corolla; anthers connate, the upper 7–8.5 mm long, the lower 6.5–7 mm long, glabrous except for sparse, wispy hairs surrounding anther-tube orifice, this open, ca. 3 mm wide; style slightly exserted from anther tube; stigma ca. 3 mm wide. *Fruit* a half-superior capsule dehiscing by two terminal valves, 15 mm long (including valves), 10 mm wide; seeds ellipsoid, minutely foveate, ca. 0.6 mm long.

Distribution. Known only from shrubland at ca. 3,200 m on the eastern slope of the Andes near Palca and Huacapistana in Junín Department of central Peru.

Additional specimens examined. PERU. JUNIN: Vitoc, 3,600 m, Feb. 1984, *Pearce s.n.* (BM); Prov. Tarma, mountains E of Palca, rd. to Illic, 10–12 km above Culebreo, 11°19′S, 75°33′W, 3,250 m, 13 Jan. 1987, *Stein, Kallunki & Diaz 3831* (AAU, B, CAS, F, G, K, MO, NY, P, US, USM).

DISCUSSION

The presence of capsular fruit in this species excludes it from *Burmeistera* as currently circumscribed. Among the capsular-fruited genera it is best placed in *Siphocampylus* based on the entire corolla tube. Since the name *Siphocampylus weberbaueri* has already been used by Zahlbruckner (1906), I propose the new name *Siphocampylus oscitans* for this species. The epithet *oscitans* derives from the Latin for yawning, in reference to the dilated anther-tube orifice, an unusual feature in *Siphocampylus*. *Siphocampylus oscitans* is easily recognized among Peruvian members of this genus by its completely glabrous, stiff, coriaceous, lanceolate leaves, relatively short and stout corolla with strongly deflexed lobes, and erect to spreading sepals that are about twice as long as the strongly obconic hypanthium.

An open anther tube of the kind found in *Siphocampylus oscitans* is known in only two other members of the genus: *S. sceptrum* Decne. of Venezuela and *S. rusbyanus* Britton of Bolivia and southern Peru. While *S. oscitans* occurs nearer geographically to *S. rusbyanus*, morphologically it more closely resembles certain phases of the highly variable *S. sceptrum*. In addition to the open and thinly pubescent anther-tube orifice, certain collections of *S. sceptrum* share the following features with *S. oscitans*: a half-superior ovary and shallow hypanthium; thick, sessile, and often lanceolate or narrowly ovate leaves with acutely ascending venation; a similar subcorymbose inflorescence; variably bracteolate pedicels; adnation of the filaments to the corolla tube near its base; and a stout, straight corolla tube. The two species differ most obviously in the length of the corolla and in the extent of fusion of the four upper lobes (the feature that best characterizes *S. sceptrum*). On the basis of these similarities, *S. oscitans* seems best placed near *S. sceptrum* in sect. *Brachysiphon* F. Wimmer.

Zahlbruckner (1906) cited two Weberbauer collections (*2203* and *2473*) in the protologue of *Burmeistera weberbaueri*. Gleason (1925) designated *Weberbauer 2203* as the "type," but it is unclear whether this constitutes valid lectotypification. He gave no indication that the type specimen was actually examined and may well have been following the then common practice of designating the first collection listed in the original description. The type specimens studied by Zahlbruckner at Berlin were both apparently destroyed during World War II (B. E. Leuenberger, pers. comm.), and my search of that herbarium confirms their absence. Because Zahlbruckner worked at Vienna and annotated the W sheet of *Weberbauer 2203*, I have designated that specimen as the lectotype.

Note added in proof: Recent examination of the type of *Burmeistera splendens* at BM shows this to be a fourth species of *Siphocampylus* with a dilated anther tube. This Colombian species appears closely related to *S. oscitans* based on anther tube, hypanthium, sepal, and foliage features, and provides support for the above discussion linking *S. oscitans* of Peru with *S. sceptrum* of Venezuela. I here make the transfer of *B. splendens* to *Siphocampylus*, as has already been suggested by Jeppesen's annotation on the type specimen.

Siphocampylus splendens (F. Wimmer) Jeppesen ex B. A. Stein, comb. nov. *Burmeistera splendens* F. Wimmer, Pflanzenreich IV. 276c: 836, fig. 15a. 1968. TYPE: Colombia. Andes del Norte, July 1857, *Triana 3059/23* (holotype, BM).

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SYNOPSIS OF THE GENUS *BURMEISTERA* (CAMPANULACEAE: LOBELIOIDEAE) IN PERU[1]

BRUCE A. STEIN[2]

ABSTRACT

The southern distributional limit of *Burmeistera* has long been obscured by the inclusion in that genus of several disharmonious elements from central and southern Peru. Of the six Peruvian species that have previously been assigned to *Burmeistera*, only *B. ramosa* is retained in that genus. The recent collection of *B. microphylla* brings the number of Peruvian species of *Burmeistera* to two. The southernmost stations known for these two species, and thus the genus as a whole, are at approximately 5°50'S in San Martín Department of northern Peru.

Burmeistera Triana is a well-delimited neotropical genus of Lobelioideae distinguished from other baccate-fruited genera by the combination of oblong or linear seeds, oblique and distally open anther tubes, and mostly nonbracteolate pedicels. The typically distorted, greenish to maroon corollas make the genus easily recognizable in the field. However, complex morphological patterns, in particular extreme local differentiation, render it taxonomically challenging at the species level.

Burmeistera is found primarily in montane wet forests from Chiapas, Mexico south to Venezuela and Peru, with its center of diversity in the Andes of Colombia and Ecuador. The southern distributional limits of the genus have been problematic, owing to the questionable inclusion of several central and southern Peruvian taxa. This paper clarifies the status of *Burmeistera* in Peru and establishes its currently known southern limit.

Six Peruvian species of *Burmeistera* were included in the *Flora of Peru* (Wimmer, 1937) and in Wimmer's (1943) revision of the genus, the most recent treatment available. These are: *Burmeistera asteriscus* F. Wimmer, *B. macrocarpa* (A. Zahlbr.) F. Wimmer, *B. peruviana* F. Wimmer, *B. ramosa* F. Wimmer, *B. tricolorata* F. Wimmer, and *B. weberbaueri* A. Zahlbr. Of these, only *B. ramosa* is retained in *Burmeistera* as the genus is presently circumscribed. McVaugh (1949) correctly noted the position of *B. macrocarpa, B. peruviana,* and *B. asteriscus* in *Centropogon* and made the necessary transfers for the last two. The two remaining species clearly belong in *Siphocampylus* and are discussed below.

An additional species, *Burmeistera microphylla* J. D. Smith, was recently collected in northern Peru, bringing the number of Peruvian species to two. This collection at approximately 5°50'S in San Martín Department, along with a recent collection of *B. ramosa* from the same general vicinity, represents the southernmost stations known for the genus.

The erroneous inclusion of several southern and central Peruvian taxa in *Burmeistera* has obscured an interesting phytogeographic pattern. The Huancabamba deflection of northern Peru marks the distributional limit for a number of plant and animal groups and appears to have been a significant barrier to north–south migration (Simpson, 1975, 1979; Berry, 1982; Vuilleumier, 1984). The geographical range of *Burmeistera* as defined here provides another example of the Huancabamba deflection comprising the boundary for a group. Although approximately 30 species are present in Ecuador (Jeppesen, 1981), diversity in the genus falls abruptly in northern Peru, where only two species are known to occur. In Peru, these species have been found only in the area along or near the Río Marañon gap, the lowest elevation depression along the eastern slope of the Central Andes and a major component of the Huancabamba deflection.

Why *Burmeistera* is absent from apparently suitable habitats further south along the eastern slope of the Peruvian Andes remains a mystery. The relatively low elevation of the Río Marañon gap (ca. 500 m) does not alone explain the pattern, since *B. ramosa* and other species occur at such elevations. Furthermore, members of the

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genus are capable of dispersal past such barriers, as evidenced by their successful establishment in areas across far more formidable low-elevation gaps, in one instance reaching the isolated Cerro de la Neblina massif of the Guayana Highland. The complex patterns of local differentiation and endemism in *Burmeistera* suggest that dispersal may often be quite limited, even though the variously spongy, juicy, or inflated fruits often appear well suited for bird-dispersal. In this regard it may be significant that *B. microphylla* is one of the widest-ranging members of the genus, extending from Costa Rica to northern Peru. An additional factor may be our insufficient knowledge of the middle and upper-elevation forests along the eastern Andean slopes of northern Peru. These inaccessible areas are among the most poorly collected in the Andes.

KEY TO THE SPECIES OF *BURMEISTERA* IN PERU

1a. Leaves thick and coriaceous when dry; sepals 5–8 mm long, divaricate; fruit spongy, less than 10 mm in diameter .... *B. microphylla*

1b. Leaves chartaceous to membranaceous when dry; sepals 2–5 mm long, erect or spreading; fruit inflated, to 25 mm in diameter ... *B. ramosa*

1. **Burmeistera microphylla** J. D. Smith, Bot. Gaz. (London) 25: 146. 1898.

The single Peruvian collection, as well as collections from southern Ecuador treated by Jeppesen (1981) under the synonym *B. aurobarbata* F. Wimmer, differ from typical Central American *B. microphylla* in their more uniformly lanceolate to narrowly lanceolate leaves and in lacking golden external anther trichomes. Further investigation of geographically intermediate populations of this wide-ranging and variable species complex (including *B. crassifolia* F. Wimmer and *B. maculata* F. Wimmer) may indicate that these southernmost populations warrant treatment as a distinct taxon.

Specimen examined. PERU. SAN MARTIN: Prov. Rioja, 100 km W of Rioja on road to Pedro Ruíz, 2 km E of Puente Río Nieva (border with Amazonas Dept.), 2,000 m, 16 Feb. 1985, *Stein & Todzia 2198* (MO).

2. **Burmeistera ramosa** F. Wimmer, Repert. Spec. Nov. Regni Veg. 30: 16. 1932.

This species is now known from two collections in Peru. The type, *Tessmann 4725*, was collected at a relatively low elevation at the mouth of the Río Santiago along the Río Marañon, not "near Iquitos" as indicated by Wimmer (1937). The second, a fruiting collection, was made in 1983 in the Venceremos region from mid-elevation cloud forest. *Burmeistera ramosa* is apparently more common in Ecuador (Jeppesen, 1981) and shows a similar wide range in elevational preference. Since the early botanical explorers Ruiz and Pavón never ventured into northeastern Peru (Steele, 1964) where this species would be expected, one of their collections, formerly thought to originate from Peru (Wimmer, 1943), was probably among the Ecuadorean collections made by their apprentice J. Tafalla.

Specimens examined. PERU. AMAZONAS: Río Marañon, Pongo de Manseriche, 160 m, *Tessmann 4725* (NY; photographs, MO, NY). SAN MARTIN: Rioja Prov., Pedro Ruíz–Moyobamba rd., km 390, Venceremos, 1,770–2,150 m, 5–7 Aug. 1983, *Smith & Vasquez 4608* (MO).

EXCLUDED SPECIES

1. *Burmeistera asteriscus* F. Wimmer, Repert. Spec. Nov. Regni Veg. 38: 5. 1935. = *Centropogon peruvianus* (F. Wimmer) McVaugh, Brittonia 6: 462. 1949. See discussion under *Burmeistera peruviana.*

2. *Burmeistera macrocarpa* (A. Zahlbr.) F. Wimmer, Repert. Spec. Nov. Regni Veg. 30: 41. 1935. = *Centropogon macrocarpus* A. Zahlbr., Bot. Jahrb. Syst. 37: 452. 1906.

3. *Burmeistera peruviana* F. Wimmer, Repert. Spec. Nov. Regni Veg. 38: 5. 1935. = *Centropogon peruvianus* (F. Wimmer) McVaugh, Brittonia 6: 462. 1949.

Field studies conducted at the type locality of *Centropogon peruvianus* and *C. asteriscus* around Pillahuata, Cuzco Department, show that the differences noted by Wimmer (1935) in describing these two species, primarily leaf width and shape and sepal length, are variable within populations. The type specimens of these two species were collected in the same general vicinity and merely represent upper and lower elevation collections (3,000–3,300 m and 2,200–2,400 m) of a single species. The names were published simultaneously; however, since McVaugh (1949) selected *C. peruvianus* as the type species for his *Centropogon* sect. *Peruviani, C. peruvianus* is the preferred name.

4. *Burmeistera tricolorata* F. Wimmer, Repert. Spec. Nov. Regni Veg. 30: 22. 1932. = *Siphocampylus rusbyanus* Britton, Bull. Torrey Bot. Club 19: 372. 1892.

A fruiting collection of this species (*Stein 2505*) made recently at the type locality of *B. tricolorata* has capsular fruits and firmly establishes its position in the genus *Siphocampylus*. The Peruvian collections closely match *Siphocampylus rusbyanus*, a species recognized previously only from northern Bolivia.

5. *Burmeistera weberbaueri* A. Zahlbr., Bot. Jahrb. Syst. 37: 451. 1906. = *Siphocampylus oscitans* B. A. Stein.

A new collection of this species (*Stein 3831*) has shown the fruit to be capsular, excluding it from *Burmeistera*. For a discussion of this species, its transfer to *Siphocampylus*, and the necessary proposal of a new name (the epithet *weberbaueri* has been used previously in *Siphocampylus*), see the accompanying paper (Stein, 1987).

The above two species, *Burmeistera weberbaueri* and *B. tricolorata*, comprise Wimmer's (1943) subsect. *aequilatae* of *Burmeistera* sect. *imberbes* F. Wimmer. Since both of these species are here excluded from *Burmeistera*, that strictly Peruvian subsection is no longer recognized.

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NEW SPECIES OF *PASSIFLORA* SUBGENUS *PASSIFLORA* FROM ECUADOR

L. B. HOLM-NIELSEN[2] AND J. E. LAWESSON[3]

ABSTRACT

Four new species of *Passiflora* from Ecuador are described, viz. *P. montana, P. palenquensis, P. deltoifolia,* and *P. pergrandis.*

A revision of Ecuadorean *Passiflora* subg. *Passiflora* (subg. *Granadilla* sensu Killip) for the *Flora of Ecuador* (Holm-Nielsen et al., in press) has revealed four new species: *P. montana, P. palenquensis, P. deltoifolia,* and *P. pergrandis,* belonging to "series" *Lobatae, Tiliaefoliae, Menispermifoliae,* and *Laurifoliae,* respectively. The total number of Ecuadorean subg. *Passiflora* species is 19. Killip (1938) divided the subgenus into 15 series; although these are not validly published, we are following Killip for convenience. The "series" occurring in Ecuador are *Digitatae, Incarnatae, Kermesianae, Simplicifoliae, Quadrangulares,* and those mentioned above.

Passiflora palenquensis Holm-Nielsen & Lawesson, sp. nov. TYPE: Ecuador. Los Rios: Quevedo—Sto. Domingo road, km 56, Río Palenque Science Center, 150–200 m, 6 Oct. 1979, *C. H. Dodson, A. Gentry & G. Shupp 8854* (holotype, MO). Figure 1.

Liana ubique glabra. Caule striato et tereto. Stipulis oblongo-lanceolatis, acutis, 1 × 0.4 cm, interdum decideosis. Petiolis angulo-alatis, 6.5–9 cm longis cum 3–4 nigris, sessilibus urceolatiaque glandibus, par apice extremo, aliae glandes infra 2–3 cm; laminibus basifixis, late ovatis, ovatis, 14–19 × 11–20 cm, profunda cordatis, manifeste pinnatinervibus, nitentibus coriaceis, margine integra. Inflorescentia saltem 2 floribus; pedicellis teretis striatisque, 3–4 cm longis; bracteae circa 5 mm infra florem portatae, verticillatae, connatae dimidium, oblongo-ovatae, mucronatae, 5 × 2 cm. Floribus 5–6 cm latis; hypanthium infundibulare, longo 3 cm, ad basin 1 cm lato, ad apicem 2 cm, lavandulo; lobi calycis oblongi, acuti, 2.5 × 1.3 cm, desinentes in minutam mucronem; petalis oblongis, obtusis, 3 × 0.6–1 cm. Corona simplice, filamentis composita in 2 seriebus ordinatis quae ad apicem extremam tubi calycis locatae sunt; series externa minute liguliformis, apex filiformis, 4 mm longa; serie interna crassisima, 4-angulata, 2 cm longa, apex filiformis, fasciata purpurea et alba; tubus calycis glaber infra coronam. Operculum positum circa 1 cm supra pavimentum tubi calycis, membranaceum, in superiore parte filiforme, 0.5 cm longum. Inferioris partis 0.5 cm gynophori limini circumcinctae. Ovario glabro.

Liana, glabrous throughout. Stem terete, striate. Stipules oblong-lanceolate, acute, 1 × 0.4 cm, sometimes deciduous. Petioles angular-winged, 6.5–9 cm long, with 3–4 black, sessile urceolate glands, 1 mm long, one pair at extreme apex, other glands 2–3 cm below; blades basifixed, broad-ovate to ovate, 14–19 × 11–20 cm, deeply cordate, prominently pinnate-veined, lustrous, coriaceous, the margin entire. Inflorescence sessile, with at least 2 flowers collateral with the tendril in the axil of the leaf, 5–6 cm diam.; pedicels terete, striate, 3–4 cm long; bracts verticillate, united halfway, inserted about 5 mm below flower, oblong-ovate, mucronate, 5 × 2 cm. Hypanthium tube funnel-shaped, 3 cm long, 1 cm wide at base, 2 cm at apex, outside lavender; calyx lobes oblong, acute, 2.5 × 1.3 cm, ending in a minute mucro; petals oblong, obtuse, 3 × 0.6–1 cm. Corona composed of 2 series situated at the edge of the hypanthium; outer series of short ligulate filaments, 4 mm long, with filiform apices; inner series of very stout, 4-angled, 2 cm long filaments with filiform apices, the inner filaments with shifting purple and white, 4 mm broad stripes; hypanthium smooth below corona. Operculum situated 1 cm above hypanthium floor, membranaceous, 0.5 cm long, split into filiform segments. Trochlea present at the androgynophore opposite the apex of the operculum. Limen surrounding lower 5 mm of androgynophore. Gynophore 1 cm longer than the androgynophore present. Ovary glabrous. Fruit

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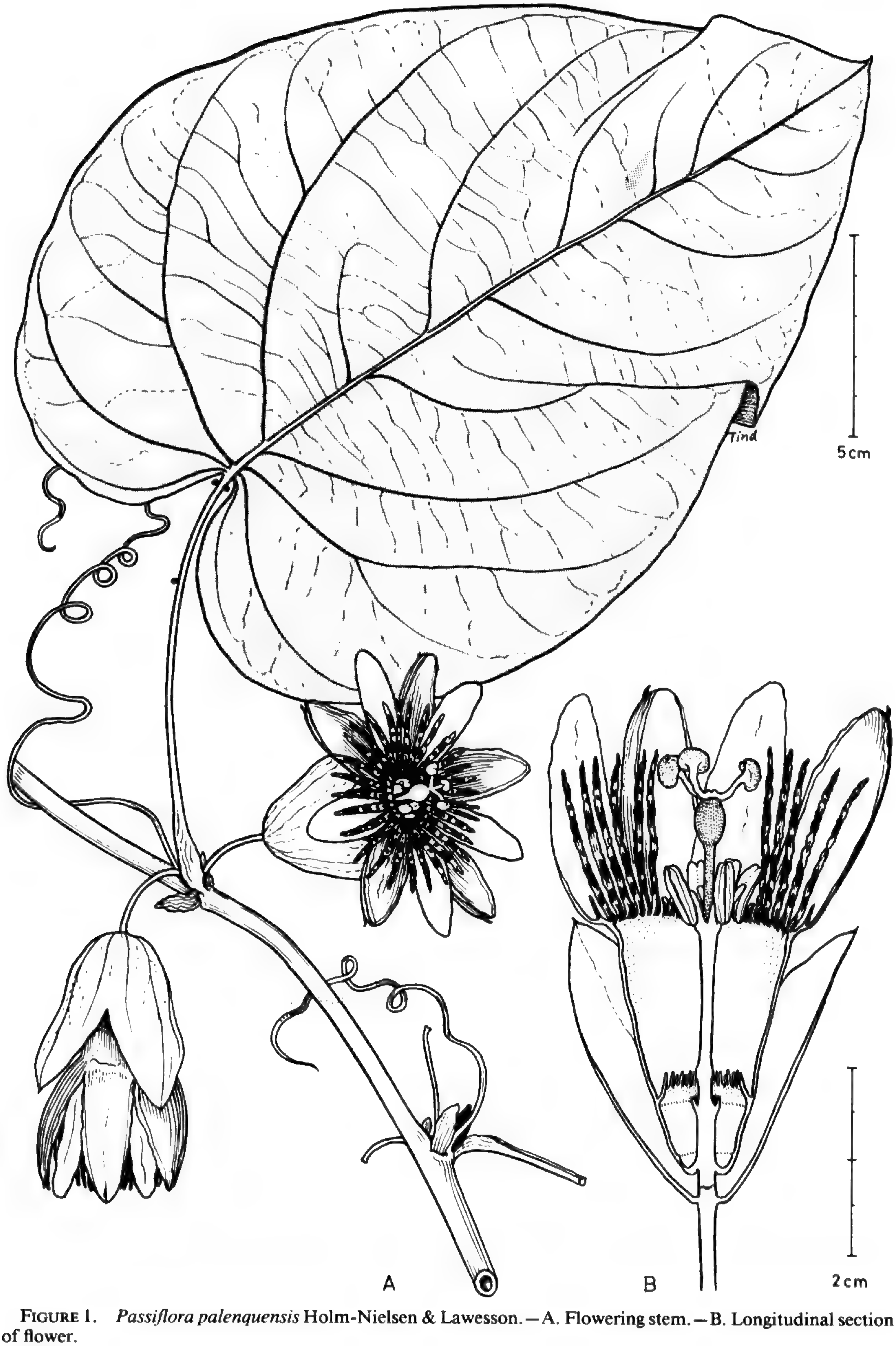

FIGURE 1. *Passiflora palenquensis* Holm-Nielsen & Lawesson. — A. Flowering stem. — B. Longitudinal section of flower.

ovoid, 7 × 4 cm, green. Seeds ovate, 5 × 3 mm, finely reticulate.

Passiflora palenquensis is a member of "series" *Tiliaefoliae,* which is characterized by united bracts and entire leaves. *Passiflora palenquensis* has a distinct gynophore 1 cm longer than the androgynophore and differs from all other members of *Tiliaefoliae* by the corona having only two series of filaments. Other species of *Tiliaefoliae* have at least three series. It is closely related to *P. seemannii* Griseb. which superficially appears to have two series. However, the two series of filaments are 1–1.2 cm and 2–2.5 cm long and have several rows of tubercles inside. *Passiflora palenquensis,* on the other hand, has only two series, these being 4 mm and 2 cm, respectively. The tubercles are absent. The new species is also related to *P. tiliaefolia* L., which has more numerous series of filaments and is confined to high altitudes (2,000–3,000 m). *Passiflora palenquensis* is restricted to low elevations.

Additional specimens examined. COLOMBIA. NARINO: railroad Tumaco-Diviso km 86, 27 July 1952, *Castaneda 3326* (AAU). ECUADOR. LOS RIOS/PICHINCHA: Sto. Domingo–Quevedo rd., km 45, Patricio Pilar-24 de Mayo rd., km 12, 600 m, Apr. 1980, *Dodson & Gentry 10337* (MO).

Passiflora montana Holm-Nielsen & Lawesson, sp. nov. TYPE: Ecuador. Carchi: Tulcan-Maldonado rd., km 67, 2,600 m, 78°04′W, 0°53′N, 21 May 1973, *L. Holm-Nielsen, S. Jeppesen, B. Løjtnant & B. Øllgaard 6200* (holotype, AAU). Figure 2.

Liana, ubique glabra. Caule striato atque tereto. Stipulis valde magnis, 4–4.5 × 2 cm, latioribus quam longioribus, reniformibus mucronatis, ad basin obtusis, margine glandulare-serrata. Petiolis 3.5–4 cm longis, teretis striatisque, cum duabus glandibus alternis supra medium. Laminibus basifixis, 3-lobatis, interdum 4-lobatis, 9–11 × 11.5–13 cm, dimidium lobatum, lobi 3 cm lati, lanceolati, acuti; pedato-venatis, integris cum glandibus in sinubus. Bracteae verticillatae, liberae, portatae 5 cm infra florem, ovatae, acuminatae, ad basin cordatae, integrae, 2.5–3.0 × 1.5 cm viridibus. Flores solitarii; pedicellis 4.5–6 cm longis, teretis. Flores 5–6 cm lati; tubo calycis breve campanulato, 5–6 × 7–8 mm; lobis calycis oblongo-lanceolatis, viridibus, 1.5 × 0.5 cm, obtusis, manifeste carinatis, carina cum arista 6 mm longa quae apicem excedit; petalis oblongis, subacutis, pallido-viridibus, 1–1.5 × 0.3–0.5 cm. Filamenta coronae in pluribus seriebus; externae 3 series ex 12 mm longis elementis consistunt, quae numero irregularium serium succeduntur, ex tenuibus et filiformibus elementis consistentium, lilacinis, extensis versus operculum. Operculum membranaceum, recurvatum, modice plicatum, 4 mm longum, pars dimidii superioris filiformiter fissum. Limen laxe in base gynophori affixum, margine lobata. Ovario glabro. Styli pallido-virides cum maculis lilacinis. Fructus non visi.

Liana, glabrous throughout. Stem striate, terete. Stipules very large, 4–4.5 × 2 cm, reniform, mucronate, obtuse at base, margin glandular-serrate. Petioles 3.5–4 cm long, terete, striate, with two alternate, stipitate glands above middle, 4 mm long; blades basifixed, 3-lobed, occasionally 4-lobed, 9–11 × 11.5–13 cm, lobed halfway; lobes 3 cm wide, lanceolate, acute; pedate-veined, entire except minutely glandular serrate in the sinuses with 2–6 glands per sinus. Bracts verticillate, free, inserted 5 mm below flower, ovate, acuminate, cordate at base, entire, 2.5–3 × 1.5 cm. Flowers 5–6 cm wide, solitary, lateral; pedicels 4.5–6.0 cm long, terete; hypanthium short campanulate, 5–6 × 7–8 mm; calyx lobes oblong-lanceolate, green, 1.5 × 0.5 cm, obtuse, prominently carinate, with a 6 mm long awn exceeding apex; petals oblong, acutish, light green, 1–1.5 × 0.3–0.5 cm. Coronal filaments of several series; outer three series of filiform elements 12 mm long succeeded by about 5 irregular series, of slender filiform elements, 6 mm long, lilac, extending towards operculum. Operculum membranaceous, recurved, slightly plicate, 4 mm long, upper half split into filiform segments. Limen attached to base of androgynophore, the margin lobulate. Nectar ring present, conspicuous. Trochlea absent. Ovary glabrous; styles light green with lilac spots. Fruits not seen.

Passiflora montana as member of "series" *Lobatae* is most clearly related to *P. sprucei* Mast., from which it differs by not having the leaves divided below the middle, by having the stipules twice as large and having two (vs. three or four) petiolar glands 4 mm long and not sessile, and, especially, by the floral composition. In *P. montana* the operculum is recurved and has a filiform upper half and the filaments are 3–4 mm long, whereas the operculum in *P. sprucei* is erect with the lower quarter membraneous and the upper two-thirds comprising a row of filaments 1 cm long. The corona in *P. montana* has three (vs. two) outer series of long filiform filaments succeeded by four or five inner series of 4–5 mm (vs. 2–3 mm) long filaments. *Passiflora montana* is the highest growing member of "series" *Lobatae* found in Ecuador at altitudes of 2,000–3,000 m; the related *P. sprucei* and *P. resticulata* Mast. & André usually do not occur above 2,000 m.

FIGURE 2. *Passiflora montana* Holm-Nielsen & Lawesson.—A. Flowering stem.—B. Longitudinal section of flower.

Additional specimens examined. ECUADOR. PICHINCHA: Niebly, Pululagua, *Sodiro s.n.* (S).

Passiflora deltoifolia Holm-Nielsen & Lawesson, sp. nov. TYPE: Ecuador. Napo: Baeza-Tena rd., Cosanga, 1,800–1,900 m, 4 Nov. 1980, *G. Harling & L. Andersson 16216* (holotype, GB; isotype, AAU). Figure 3.

Liana admodum glabra superficie foliarum. Caule striato, tereto. Stipules reniformibus, 1 × 2 cm, lobus inferior obtusus, superior lobus cuspidatus, mucrone 2 mm longa, margine glandulare serataque. Petiolae teretae, 3 cm longae, 4-glandibus, 1–2 mm longis, alternis; lamina basifixa, cordata, integra, circumscriptione deltoidea, 8 × 9–10 cm, 5–7-nervata, coriacea. Flores solitarii lateralesque; pedicellis teretis 5–6 cm longis; bracteae 1 cm infra florem feruntur, verticillatae, liberae, ovatae, acuminateae, 0.7 × 0.3 cm, cum margine glandulare serrata. Flores 7–8 cm lati, tubo calycis breve campanulato, 1 × 2 cm; lobi calycis atque petali ovate, violacei, 3–4 × 1–2 cm, lobi calycis carinati sine arista. Filamenta coronalia in 5–8 seriebus; externae duae series ex filamentis ligulatis, 2.5–3 cm longis, consistentes, apex filiformis, secunda series longissima; intimae 3–6 series irregulares quae ex filamentis spathulato-ligulatis vel tuberculatis, 1–5 mm longis, consistunt, tubum ex serie secunda usque ad operculum obtegentibus. Operculum membranaceum, erectum, dense plicatum, 8–9 mm longum, superior spathulato-ligulata. Nectarii annulus sicut crista librata 3 mm infra operculum. Limen arcte circumdans basin gynophori, margine lobata. Ovario glabro. Fructu ovoideo. Semina non matura.

Liana, stems sparsely puberulent, leaves pubescent at lower and glabrous at upper surface. Stem terete, striate. Stipules reniform, 1 × 2 cm, the lower lobe obtuse, the upper lobe cuspidate with a mucro 2 mm long, the margin glandular and serrate. Petioles terete, 3 cm long, with 4 stipitate, alternate glands 1–2 mm long; blades basifixed, cordate, entire, deltoid, 8 × 9–10 cm, 5–7-nerved, coriaceous. Flowers solitary, lateral, 7–8 cm wide; pedicels terete, 5–6 cm long; bracts verticillate, free, inserted 1 cm below flower, ovate, acuminate, 0.7 × 0.3 cm, margin glandular-serrate; hypanthium short-campanulate, 1 × 2 cm; calyx lobes and petals ovate to oblong, violet, 3–4 × 1–2 cm; calyx lobes carinate without an awn. Coronal filaments, violet, in 5–8 series; outer 2 series of ligulate, 2.5–3 cm long filaments with filiform apices, the second series longest; innermost 3–6 series irregular, of spatulate to ligulate or tuberculate filaments 1–5 mm long, covering the interior of the hypanthium from the second series to the operculum. Operculum membranaceous, erect, densely plicate, 8–9 mm long, the upper part split into spatulate or ligulate segments. Nectar ring a horizontal ridge 3 mm below operculum. Limen tightly surrounding base of gynophore, margin lobulate. Ovary glabrous. Fruit ovoid, 5.5 × 2 cm.

Passiflora deltoifolia is related to *P. menispermifolia* Kunth and *P. crassifolia* Killip in "series" *Menispermifoliae.* The new species differs from these two species by having leaves as broad as long and not longer than broad. *Passiflora menispermifolia* has three-lobed leaves, whereas *P. deltoifolia* and *P. crassifolia* have unlobed or inconspicuously lobed leaves. The operculum is plicate and there are no awns at the calyx lobes of *P. deltoifolia.* The bracts of *P. deltoifolia* are smaller, 7 mm long and 4 mm broad (vs. 1–2 cm long and 5–8 mm broad) and not cuspidate or long acuminate, as in *P. menispermifolia* and *P. crassifolia.* In addition, the new species lacks the dense indumentum characteristic for *P. menispermifolia* and *P. crassifolia.*

Passiflora pergrandis Holm-Nielsen & Lawesson, sp. nov. TYPE: Ecuador. Zamora-Chinchipe: Zamora-Gualaquiza rd., 5 km North of Cumbaraza, 900 m, 20 Apr. 1974, *G. Harling & L. Andersson 13771* (holotype, GB; isotype, AAU). Figure 4.

Liana, ubique glabra praeter inflorescentiam atque ovarium. Caule terete, striato, partes vetiores 2 cm in diametro. Stipulis non adsunt. Petiolis 2–3 cm longis cum pare glandium ovalium, sessilium, nigrarum, 3 × 1 mm, 1 cm ab base; laminibus basifixis, anguste-ovatis, acuminatis, 15–20 × 9–10 cm, obtuso-truncatis, crasso-coriaceis. Inflorescentia lateralis, pergrandis, non-terminalis, usque ad 30 cm longa, cum pluribus 15–16 cm latis floribus plerumque bracteis foliaceis 4–11 × 1–4.5 cm. Inflorescentia interdum reductus modo paucis floribus; pedicellis teretis, 3–9 cm longis, puberulis; bracteae 5 mm infra florem portatae, verticillatae, liberae, ovato-oblanceolatae 5 × 4 cm, obscure lacinato-lobatae in parte distale, obtusae in base, margo ingra cum pluribus crassis nigrisque glandibus, puberulis. Tubo calycis campanulato 1 × 2 cm; lobi calycis oblongo-ovati, 6 × 3.5–4 cm, obtusi, carinati cum arista foliacea, 4 mm longa, quae apicem non excedit. Petalis lanceolatis-ovatis, 5.5–6 × 2 cm, alba. Filamenta coronalia in 3 seriebus, filamenta primae seriei minute setaceae 2 mm longa, secundae seriei filamenta crassa, ligulata, 5 × 0.3 cm, cruciatim fasciata colore albo atque atro-violaceo; tertia serie prope operculum minute tuberculata. Operculum membranaceum, recurvatum, margine filamentis brevibus fimbriateis. Limen arcte adhaerens basin gynophori. Gynophorus trochlaean crassam supra limen ferens. Ovarium dense albidocanum tomentosum. Fructus non visi.

Liana, glabrous throughout except inflorescence and ovary. Stem terete, striate, older parts

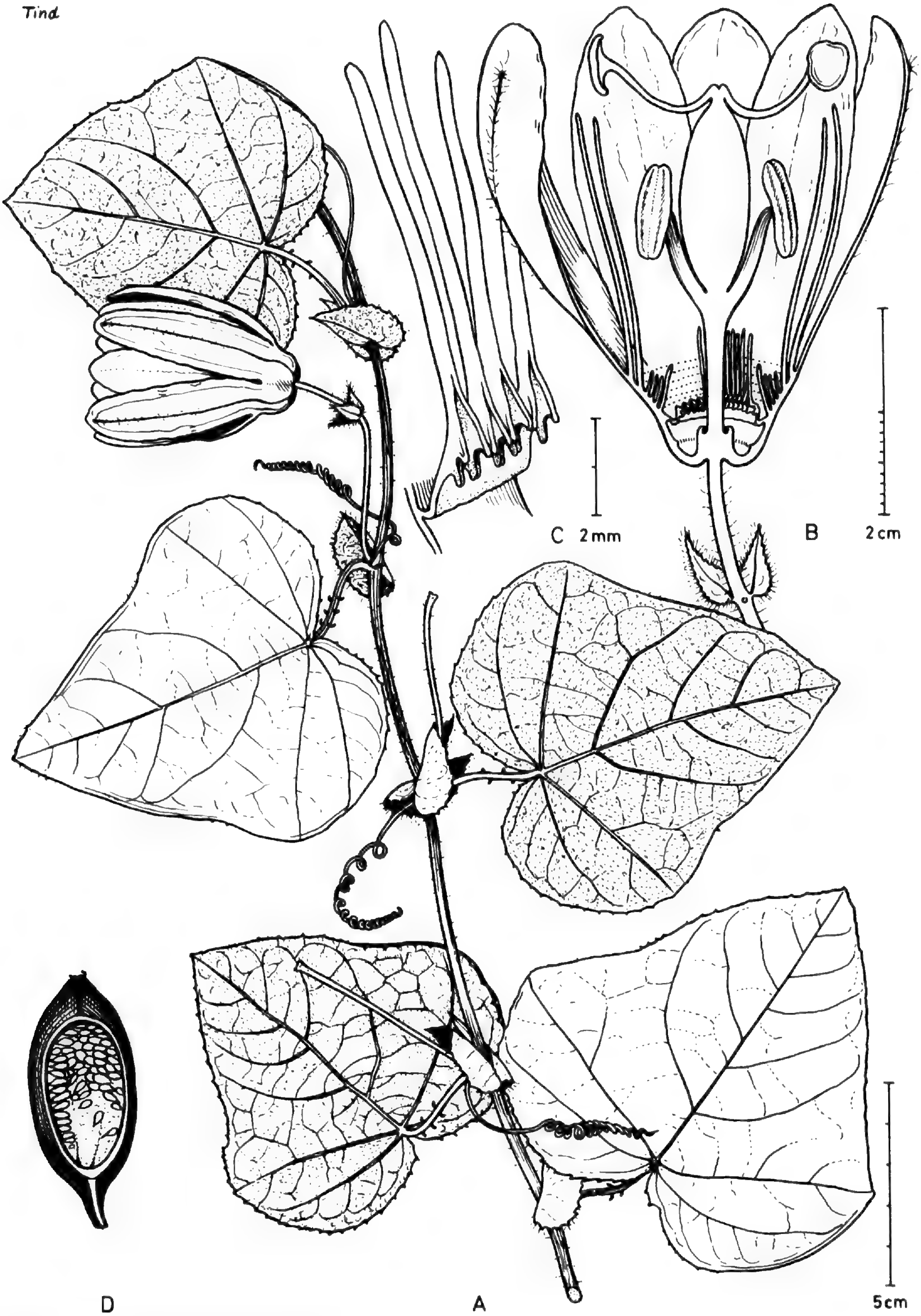

FIGURE 3. *Passiflora deltoifolia* Holm-Nielsen & Lawesson.—A. Flowering stem.—B. Longitudinal section of flower.—C. Operculum, densely plicate.—D. Fruit.

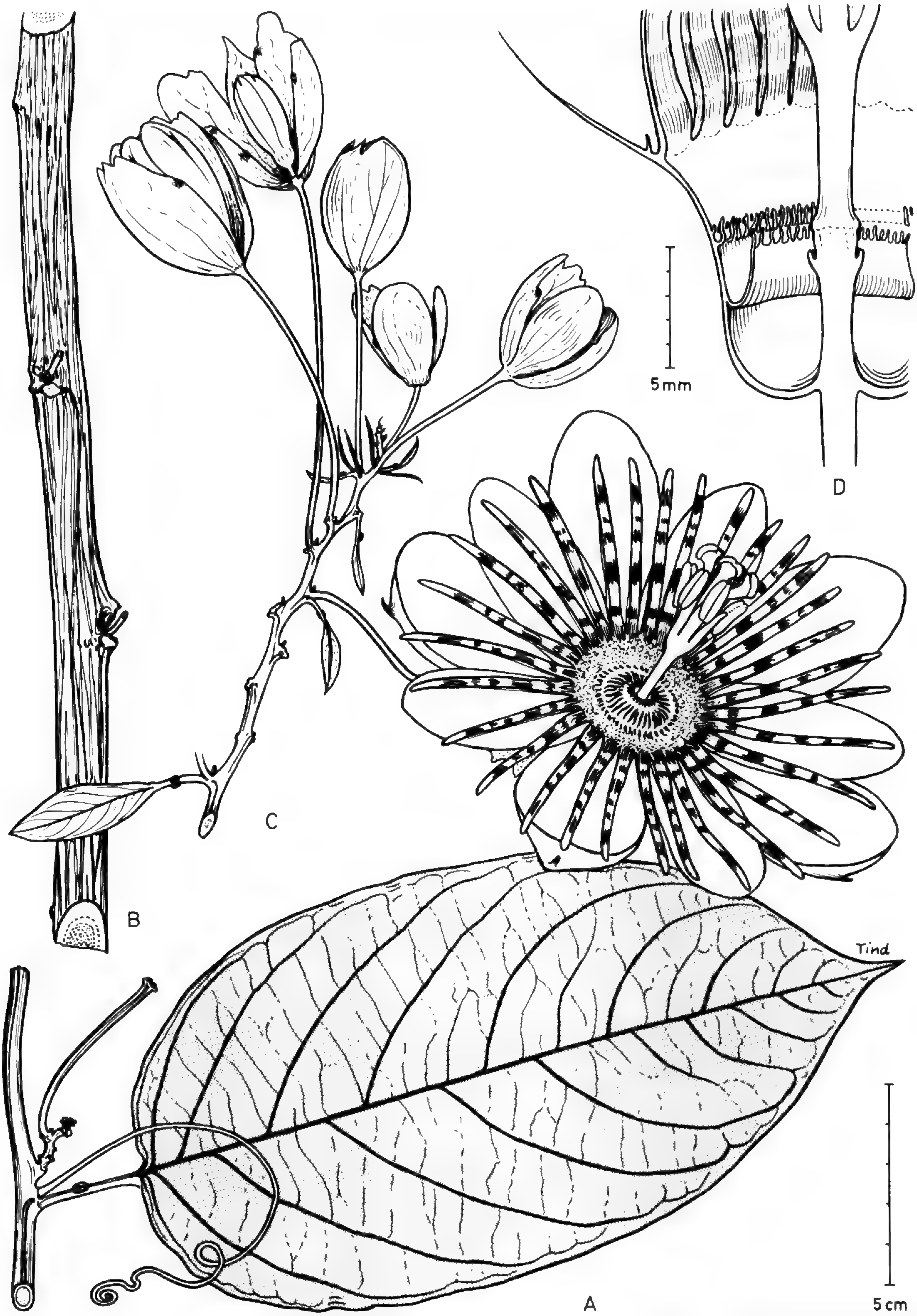

FIGURE 4. *Passiflora pergrandis* Holm-Nielsen & Lawesson.—A. Leaf and reduced inflorescence.—B. Old stem.—C. Inflorescence with several flowers and bracts.—D. Longitudinal section of flower with recurved operculum.

2 cm diam. Stipules reduced. Petioles 2–3 cm, with one pair of ovate, sessile, black glands 3 × 1 mm, 1 cm from base; blades basifixed, narrow-ovate, acuminate, 15–20 × 9–10 cm, obtuse to truncate at base, prominently pinnate-veined, entire, thick-coriaceous. Laminar nectaries absent. A distal bud developing to a short shoot, this forming a conspicuous indeterminate inflorescence to 30 × 15–16 cm with several flowers (or sometimes reduced with few flowers), the lowermost flowers developed first, the flowers subtended by 4–11 × 1–4.5 cm reduced leaves; pedicels terete, 3–9 cm long; bracteoles verticillate, free, inserted 5 mm below flower, ovate to oblanceolate, 5 × 4 cm, obscurely laciniate-lobed at distal part, obtuse at base, margin entire with several stout black glands. Hypanthium campanulate, 1 × 2 cm; calyx lobes oblong-ovate, 6 × 3.5–4 cm, obtuse, carinate with a foliaceous awn 4 mm long, not exceeding apex; petals narrow-ovate, 5.5–6 × 2 cm, white. Corona filaments of 3 series; filaments of outer series minutely setaceous, 2 mm long; filaments of second series stout, ligulate, 5 × 0.3 cm, cross-banded with white and dark violet; third series close to operculum, minutely tuberculate 1–2 mm. Operculum membranaceous, recurved, the margin with short fimbriate filaments. Limen tightly adherent to androgynophore between the prominent nectar ring and trochlea. Ovary densely whitish-gray tomentose. Mature fruits not seen.

Passiflora pergrandis is a member of "series" *Laurifoliae* and is related to *P. ambigua* Hemsley, which is also present in Ecuador. *Passiflora pergrandis* differs in several aspects from *P. ambigua,* these being much larger inflorescence and longer pedicels, larger leaflike bracts, calyx lobes and petals only twice as long as broad (vs. three or four times longer), and much shorter outer coronal filaments. The awn in *P. pergrandis* does not exceed the apex of the calyx lobe as it does in *P. ambigua. Passiflora ambigua* is known from Central America.

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THE GENUS *ATTALEA* (PALMAE) IN PANAMA[1]

GREGORY C. DE NEVERS[2]

ABSTRACT

The two Panamanian species of *Attalea* (Palmae) are described and illustrated, *A. iguadummat* for the first time.

Attalea (Palmae) is a poorly collected neotropical genus of about 25 species centered in Amazonian South America and reaching its northwestern limit in Panama. When Bailey (1943) treated the palms of Panama the genus was not known from the isthmus. *Attalea* was last revised by Glassman (1977), at which time one species was recorded in Panama. Recent fieldwork has revealed an undescribed species of *Attalea* there. A circumscription of the genus in Panama is provided, and the new plant is described and named *A. iguadummat*.

Attalea Kunth, Nov. Gen. et Sp. 1: 309. 1816. TYPE: *A. amygdalina* Kunth, Nov. Gen. et Sp. 1: 310. 1816.

Arborescent or acaulescent, monoecious. Leaves pinnate, the pinnae inequilateral at the tip, clustered in groups or evenly distributed along the rachis. Inflorescences either androgynous or staminate, bearing a pair of bracts, the peduncular bract large, woody, sulcate, terminating in a long or short rostrum, enclosing the inflorescence in bud; staminate inflorescence branched to one order, the rachillae with many flowers, these disposed in 1 or 2 rows, or spirally arranged in dyads. Staminate flowers with 3 short, triangular sepals, and 3 valvate, lanceolate-apiculate, flat petals; stamens 6–10 (in Panama), shorter than the petals, the anthers straight, dehiscing longitudinally. Androgynous inflorescence with sessile or short pedicelled pistillate flowers. Pistillate flowers 2–4 cm long, with 3 sepals and 3 petals, the sepals and petals imbricate; stamens reduced to a prominent staminodial ring; ovary ovate; stigmas 3, apical. Fruit with exocarp thin, fibrous; mesocarp pulpy and fibrous; endocarp thick, hard, without fibers. Seeds 1–3, irregularly shaped.

Attalea is characterized by its large size, separate staminate and androgynous inflorescences, stamens shorter than the flattened petals, and large, oblong, woody fruits. Within the Cocoeae, *Attalea* is closely related to *Scheelea, Orbignya,* and *Maximiliana,* together comprising the subtribe Attaleinae, the genera of which are distinguished from each other by characters of the androecium.

Attalea allenii is abundant throughout San Blas and many plants produce fruits annually, yet inflorescences at anthesis are rarely seen. During two years of collecting in San Blas, the androgynous inflorescence was seen only once and the staminate inflorescence only three times. When Glassman (1977) prepared his preliminary treatment of *Attalea,* the androgynous inflorescence was unknown. Androgynous inflorescences of *A. iguadummat* (described below) are equally rare, while the staminate inflorescences, in contrast, are abundantly produced. *Attalea iguadummat* is andromonoecious, old staminate inflorescences having been observed on fruiting plants. Whether both types of inflorescence are produced on individuals of *A. allenii* is unknown. The pollination syndrome of the genus is unknown (Henderson, 1986). The staminate inflorescences of both Panamanian species produce a strong musky odor at anthesis.

KEY TO THE SPECIES OF *ATTALEA* IN PANAMA

1a. Pinnae evenly spaced along the rachis; middle pinnae 6.5–7 cm wide; staminate inflorescence 125–155 cm long; rachillae 12.5–

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18.2 cm long; flowers spirally arranged in dyads; stamens 8–10 .... *A. iguadummat*

1b. Pinnae in groups of 3 to 5 along the rachis; middle pinnae 2–4 cm wide; staminate inflorescence 15–25 cm long; rachillae 1–4.5 cm long; flowers two-ranked; stamens 6 ...... *A. allenii*

Attalea allenii H. Moore, Gentes Herb. 8: 191. 1949. TYPE: Panama. Colón: Puerto Pilón, 10 m, *Allen 4103* (holotype, MO; isotype, BH). Figure 1.

Stem solitary, short or subterranean. Leaves 12–15, about 5 m long; petiole 60–80 cm long, 2.5 cm diam. at base, 2 cm diam. at apex; rachis 3.3–3.7 m long; pinnae 85–87 per side, arranged in groups of 3–5, linear, glabrous, inequilateral at tip, the margins ferruginous-lepidote; middle pinnae 75–95 cm long, 2–4 cm wide; apical 9–10 pinnae regularly spaced, separated basally, coherent at the apex, forming 2 broad lobes about 10 cm wide at the terminus of the rachis. Inflorescences interfoliar, produced at ground level, erect, either staminate or androgynous; bracts 2; prophyll 30 cm long, 4 cm wide, the apex short and rounded; peduncular bract 35 cm long with a rostrum 7 cm long. Staminate inflorescence 15–25 cm long; peduncle 8 cm long, 8–10 mm wide, brown furfuraceous at anthesis; rachis 23–26 cm long; rachillae about 16–28(–50), 1–4.5 cm long, bearing 6–8 staminate flowers in 2 ranks. Staminate flowers with sepals 3, deltoid, 1 mm long; petals 3, valvate, lanceolate-apiculate, glandular, 9–13 mm long, 2–3 mm wide; stamens 6, filaments 2–3 mm long, the anthers straight, 4–6 mm long; pistillode minute. Androgynous inflorescence unbranched; peduncle 10–24 cm long, 1–1.4 cm wide; rachis 10 cm long; pistillate flowers disposed in triads with 2 staminate flowers. Staminate flowers of triads 6–7 mm long, with 3 sepals, these connate for less than 0.5 mm at base, triangular, 2 mm long; petals (5–)6, 4–5 mm long; stamens 6, erect, dorsifixed, the anthers 1–1.5 mm long; pistillode minute. Pistillate flowers sessile, crowded on the rachis, 3.2 cm long, enveloped at the base by 3 triangular bracts 2 cm long and 1.6 cm wide; sepals 3, broadly imbricate, 2.7–2.9 cm long, 1.5–2 cm wide, irregularly lobed at apex; petals 3, imbricate, 2.5–2.7 cm long, 1.8–2 cm wide, irregularly lobed at apex; staminodial ring 6–7 mm deep, minutely 6-lobed; ovary conical, 2.3–2.5 cm long, 1.2–1.4 cm wide at base, densely brown tomentose; stigmas 3, arching, 8–11 mm long; ovules 3, basal. Infructescence with 7–24 fruits, these obovoid, 6–7.5 cm long, 3.5–4 cm wide, the exocarp thin, fibrous, densely ferruginous-lepidote, appearing smooth; mesocarp 1.5–2 mm thick, fibrous; endocarp 3–5 mm thick, bony. Seeds 1–3, irregularly shaped, conforming to the shape of the cavity in which they develop.

Additional specimens examined. PANAMA. BOCAS DEL TORO: Río San Pedro, *Gordon 15c* (MO). CANAL AREA: Coco Solo, *Gentry 6298* (MO). COLÓN: Nombre de Diós, July 1911, *Pittier 4237* (US); Santa Rita Ridge, *Croat 15308* (MO); Santa Rita Ridge, 300–500 m, *Gentry 6556* (MO). PANAMÁ: El Llano–Cartí Rd., 12 Jan. 1981, *Read et al. 81-57* (US). COMARCA DE SAN BLAS: El Llano–Cartí Road km 16.7, 350 m, 9°19′N, 78°55′W, "igua" (Kuna), "mange" (Spanish), 4 Nov. 1984, *de Nevers et al. 4152* (MO, NY); El Llano–Cartí Road km 19, 10 Aug. 1984, *de Nevers 3639* (MO, PMA); same locality, 18 June 1986, *de Nevers & Herrera 7954* (CAS, MO); same locality, 11 Mar. 1986, *de Nevers et al. 7301* (MO); Cangandi, 30–150 m, 9°24′N, 79°8′W, 29 Jan. 1985, *de Nevers et al. 4735* (MO); same locality, "igua kaa" or "igua sai la let" (Kuna), 10 Feb. 1986, *de Nevers & Herrera 7191* (MO); Río Tiwar (R. Acla), 8°48′N, 77°40′W, 25–100 m, *Sugden 624* (MO); Playón Chico, 0–200 m, *Gentry 6419* (MO); same locality, "ikwa e sana" (Kuna), *Stier 109* (MO). COLOMBIA. CHOCÓ: Río Salaqui, 6 days upstream of Río Sucio, Hydro Camp 14, 200 m, *Duke 11377* (BH); 2 km from Las Animas on rd. to Quibdó, 5°4′N, 76°47′W, *King et al. 664* (BH, NY). VALLE: Buenaventura Bay, Aguadulce Island, *Moore et al. 9468* (BH); Buenaventura, *Moore et al. 9460* (BH); km 14 marker between Buenaventura and Bajo Calima, below 50 m, 3°56′N, 76°59′W, *Croat 57552* (MO); Dindo area, Bajo Calima, 100 m, 3°59′N, 76°58′W, *Gentry & Monslave 48429* (MO); Bajo Calima, *Gentry et al. 40395* (MO); Río Calima, La Trojita, 5–50 m, 19 Feb. 1944, *Cuatrecasas 16397* (US); Bahía de Buenaventura, Quebrada de San Joaquin, 0–10 m, 20 Feb. 1946, *Cuatrecasas 19948* (US). BOLÍVAR: Mun. Morales, cgfo. Norosi, camino a Tiquisionuevo, 130–200 m, *Cuadros 2194* (MO).

Attalea allenii is well known from the original description and many collections. It ranges from Panama to Colombia. In Panama it occurs in tropical wet forest (sensu Holdridge et al., 1971) on the Atlantic slope. The Kuna name is "igua," the leaves are used medicinally, and the immature fruits are eaten.

Attalea iguadummat de Nevers, sp. nov. TYPE: Panama. Colón: Santa Rita Ridge 13.8 km from Transisthmica Hwy., 350 m, 9°20′N, 79°45′W, 24 Feb. 1986, *de Nevers 7197* (holotype, CAS; isotypes, K, MO, PMA). Figure 2.

Species nova *A. victoriana* Dugand similis sed floribus masculis spiratim depositis, staminibus 8–10, filamentis 4–5 mm longis, antherisque 2–3 mm longis differt.

FIGURE 1. Infructescence of *Attalea allenii, de Nevers 4152.*

Stem solitary, short or subterranean. Juvenile leaves 1.5–2 m long, 20–26 cm wide, undivided, obovate, the margins dentate with triangular teeth 1.5–2 cm long. Mature leaves 9–17, arching; petiole 55–82 cm long, 5.7–7.2 cm wide at base, broadly channeled adaxially; rachis 6.75–7.23 m long; pinnae 104–109 per side, evenly spaced, linear, glabrous, inequilateral at tip, the margins ferrugineous-lepidote; middle pinnae 144–148 cm long, 6.5–7 cm wide, with midvein raised adaxially and abaxially; apical pinnae 1.6–1.9 cm wide, 55–59 cm long, free. Inflorescences interfoliar, produced at ground level, erect, either staminate or androgynous, both inflorescence types produced on the same plant; bracts 2; prophyll 20–25 cm long, encircling base of peduncular bracts; peduncular bract woody, prominently vertically sulcate, enclosing inflorescence in bud, splitting and opening flat at anthesis, erect, 115–203 cm long, 30 cm wide, with prominent nonsplitting rostrum 12–15 cm long. Staminate inflorescence 125–155 cm long; peduncle 90–110 cm long, 1.5 cm wide, covered in a layer of furfuraceous brown tomentum, this soon eroded away; rachis 35–45 cm long; rachillae 40–50, subtended by an acute, triangular bract 1–1.5 cm long, this striate when dry; rachillae with basal sterile portion 2.5–4.2 cm long, fertile portion 10–14 cm long, with scattered groups of minute scales, these bright white in dried specimens. Staminate flowers spirally arranged in dyads, each subtended by a minute bract 0.5–1 mm long. Sepals 3, 1–1.5 mm long, striate when dry; petals 3, valvate, 1.3–1.7 cm long, 1 mm wide, flattened, curved to recurved at the tip, sometimes straight or "S" curved, striate when dry, but not when fresh; stamens 8–10, about ½ the length of the petals; filaments 2–3 mm long, separate and free; adjacent stamens occasionally with the filaments connate at the base for 1 mm or the filaments connate completely, divergent just below the anthers; tip of filament attached ⅓–½ way up the anther, the thecae united above the point of attachment, separate or occasionally united slightly below it; anthers 2–3 mm long, straight, dehiscing longitudinally; pistillode 1–2 mm long, 3-lobed. Androgynous inflorescence at anthesis not known; peduncular bract as in staminate inflorescence; peduncle 60–70 cm long, the rachis 35–45 cm long. Pistillate flowers short-pedicellate or sessile; sepals 3, 22–35 mm long, 15–18 mm wide at base, broadly triangular; petals 3, 40–45 mm long, acute; styles 3, apical, exserted from the petals; perianth persistent in fruit, the sepals chartaceous; petals chartaceous, margin thin, undulate; the staminodial ring enlarged, 1.1–1.8 cm deep, with 15–20 lobes, these 2–3 mm deep, 2–4 mm wide, commonly bifid. Infructescence with (3–)45–65 fruits, these 7–10 × 4.5–6.3 cm, obovate, brown tomentose, with the styles and stigmas persistent; exocarp 1–2 mm thick, tough, fibrous; mesocarp 3–5 mm thick, fibrous; endocarp 2–8 mm thick, bony, smooth, without fibers; seeds 1–3, irregularly shaped; endosperm homogeneous.

The specific epithet is derived from the Kuna name for the plant, "igua dummat." It honors the Kuna Indians of San Blas, Panama, who have initiated a self-managed forest reserve and wildlife sanctuary on their tribal lands.

Additional specimens examined. PANAMA. COLÓN: Santa Rita Ridge, 8 miles from Transisthmica Hwy., in primary forest along small stream, 420 m, 9°25'N, 79°40'W, 2 Feb. 1986, *Hammel, McPherson & Merello 14387* (MO); same locality, km 22, in forest on ridges, slopes and in draws, 17 Feb. 1986, *Hammel, McPherson & Roubik 14507* (MO); same locality, 9 Mar. 1968, *Dressler 3405* (US); same locality, km 13.8, 13 May 1986, *de Nevers 7734* (BH, MO, PMA). COMARCA DE SAN BLAS: Río Taindi, 9°25'N, 79°11'W, 5 Apr. 1986, *de Nevers & Herrera 7656* (F, MO, PMA).

Attalea iguadummat is distinctive in its acaulescent habit, broad leaflets evenly spaced along the rachis, large inflorescence, and dyads of spirally arranged staminate flowers with 8–10 stamens. Among acaulescent species of *Attalea* with pinnae evenly distributed along the rachis, *A. iguadummat* is similar to *A. victoriana* Dugand and *A. nucifera* Karsten. It differs from *A. victoriana* in its spirally arranged staminate flowers (vs. the staminate flowers disposed in 2 rows on one side of the rachilla), shorter staminate rachillae (12.5–18.2 cm vs. 25 cm), fewer stamens (8–10 vs. 12–15), and sessile (vs. pedicellate) pistillate flowers. *Attalea iguadummat* is distinct from *A. nucifera* in its longer middle pinnae (144–148 vs. 93–131 cm) and its glabrous staminate petals (vs. staminate petals reddish glandular). *Attalea iguadummat* may be most closely related to *A. tessmannii* Burret, the only other species with staminate flowers spirally arranged in dyads. *Attalea tessmannii* is an arborescent species from Amazonian Peru which differs from *A. iguadummat* in its branched androgynous inflorescence with pedicellate pistillate flowers. *Attalea piassabossu* Bondar has the staminate flowers paired, but they are disposed in a single row, not spirally arranged, and it is arborescent.

Attalea iguadummat is known only from the extremely wet Atlantic slope of the mountains between Colón and the western border of San Blas, Panama. This may be the wettest area in Panama (Myers, 1969; Anonymous, 1975). Further collecting may reveal additional localities in the Atlantic lowlands to the west in the Provinces of Coclé, Veraguas, or Bocas del Toro, or the palm may be truly endemic to the wet ocean slopes between Colón and the Mandinga River.

The Taindi River locality of *A. iguadummat*

FIGURE 2. Inflorescence of *Attalea iguadummat* at anthesis, *Hammel 14387*, photo B. Hammel.

was discovered via a clue from a Kuna Indian. During an ethnobotanical survey in San Blas informants were asked to name wild edible plants that they harvest. One man mentioned "igua dummat." "Igua" is the Kuna name for *A. allenii,* "dummat" means big. When asked where the "big *Attalea*" could be found the informant mentioned the Iguagandi River, a Taindi tributary. In Kuna "-gandi" signifies place of, implying the Iguagandi River is the "river of *Attalea.*"

Kuna botanists state that the Mandinga River is the eastern limit of *A. iguadummat*, which has not been found further east in San Blas during two years of intensive palm collecting there. Immature fruits of *A. iguadummat* are eaten occasionally by the Kuna.

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NOVELTIES IN MESOAMERICAN MISTLETOES (LORANTHACEAE AND VISCACEAE)[1]

Job Kuijt[2]

Abstract

Five new species of Loranthaceae (*Cladocolea primaria, Psittacanthus angustifolius, P. minor, P. pinicola,* and *Struthanthus subtilis*) and seven new species of Viscaceae (*Dendrophthora davidsei, D. talamancana, Phoradendron fasciculatum, P. molinae, P. nitens, P. tardispicum,* and *P. zelayanum*) are described from Mesoamerica. The new combination *Psittacanthus rhynchanthus* (Bentham) Kuijt (including the var. *wurdackii* (Rizzini) Kuijt) is proposed for what has usually been called *P. calyculatus* (DC.) G. Don in Mesoamerica. The latter name is now restricted to a different species endemic to Mexico.

The following novelties result from recent studies in connection with the Flora de Nicaragua and Flora Mesoamericana.

1. **Cladocolea primaria** Kuijt, sp. nov. TYPE: Panama. Panamá: Cerro Jefe, 2 km along road to Altos de Pacora from junction with road to peak, low cloud forest, 800 m, *Sytsma & Knapp 4797* (holotype, MO; isotype, LEA). Figures 1, 2.

Plantae glabrae, pauce ramosae; rami quasi teretes, saepe lenticellis insignibus ornati, recti sat rigidique. Folia bina, aliquantum coriacea, laminae late lanceolatae vel ovatae, obtusae vel leviter apiculatae; costa insignis, petioli ad 15 mm longi. Flores pallide flavi, bisexuales. Inflorescentia solitaria, determinata, subtus triadis 3- vel 4-paribus, supra pari singulo, tunc pari uno monadarum ebracteolatarum et denique flore terminali sequentibus; triadae basales ad axillas aggregatae; inflorescentiae paribus nonnullis foliorum squamiformium, crassorum, fuscorum suffultae. Flores 4-partiti; petala dimorpha, 2–2.5 mm longa; antherae perparvae, sessiles ad petala breviora, filamentis brevissimis insertae ad longiora; ovarium 1.5 × 1 mm; stylus rectus, stigma capitatum. Fructus 6 × 4 mm, ruber, obscure violascens, ellipsoideus.

Plants sparsely branched, twining, glabrous. Stems terete or slightly 4-ridged, often with conspicuous lenticels when older, straight and rather rigid, with occasional epicortical roots. Leaves paired, somewhat leathery, the blades broadly lanceolate to ovate, venation inconspicuous, the apex mostly blunt or slightly apiculate; midrib conspicuous and running into apex; petioles stout, to 15 mm long. Inflorescences subtended by several pairs of thick, brown scale leaves, solitary in leaf axils, determinate, with 3 or 4 pairs of triads below and a pair above, followed by a pair of ebracteolate monads and a terminal flower, the 4 basal triads crowded in the leaf axil. Flowers bisexual, pale yellow, 4-partite; petals dimorphic, 2–2.5 mm long; anthers very small, sessile on the shorter petals and with very short filaments on the longer ones; ovary 1.5 × 1 mm; style more or less straight, the capitate stigma reaching the petal tips. Fruit 6 × 4 mm, red, becoming dark purple, elliptic in outline; calyculus inconspicuous; embryo dicotylous, slender, the haustorial pole scarcely expanded.

Additional specimens examined. PANAMA. PANAMÁ: Cerro Jefe, *Clusia* forest near radio tower, 900 m, *D'Arcy & Hamilton 14817* (LEA, MO); in forest near road to Cerro Jefe near junction with road to Altos de Pacora, *Mori & Kallunki 72763* (LEA, MO); Cerro Jefe, 6.6 mi. above Goofy Lake, disturbed cloud forest, 850–900 m, *Sytsma et al. 2839* (LEA, MO).

Cladocolea primaria presents considerable difficulties in generic assignment. When I monographed *Cladocolea* (Kuijt, 1975), I proposed the notion that *Struthanthus* is polyphyletic, at least many species being derived from a number of independent sources within *Cladocolea.* Thus I spoke of connecting bridges, these in some cases characterized by species pairs, one member of which was placed in *Cladocolea,* the other in *Struthanthus.* With some very minor exceptions, this left *Cladocolea* as a genus with determinate spikes of monads, the flowers 4-, 5-, or 6-partite, and either bisexual or the species dioecious. *Struthanthus* remained a strictly dioecious genus (with the solitary exception of the highly aberrant *S. panamensis,* which has bisexual flowers and

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FIGURE 1. *Cladocolea primaria* Kuijt (*Sytsma & Knapp 4797*). Pendent branch.

bracteolate monads), its inflorescence made up of mostly triads. The inflorescence of *Struthanthus* is generally indeterminate, but in a few species it also bears two or four monads at the tip, followed by a truly terminal flower.

Cladocolea primaria presents a predicament from which there is no completely satisfactory escape, for placement in either genus leads to the need of significant modification of that generic concept. As a species of *Struthanthus* it would be the first four-partite species, and the second one with bisexual flowers. If placed in *Cladocolea,* however, it is the first species which is truly triadic. I feel that placement in *Cladocolea* is more acceptable, although I cannot deny an element of arbitrariness in this regard. I continue to hold the view that union of the two genera would tend to obscure the complex relationships between them, and that these difficulties concern very few species. In fact, if the evolutionary relationships are as I have proposed, such difficult intermediate species would be expected.

Viewed in the above context, *C. primaria* is closely related to *C. lenticellata* (Diels) Kuijt

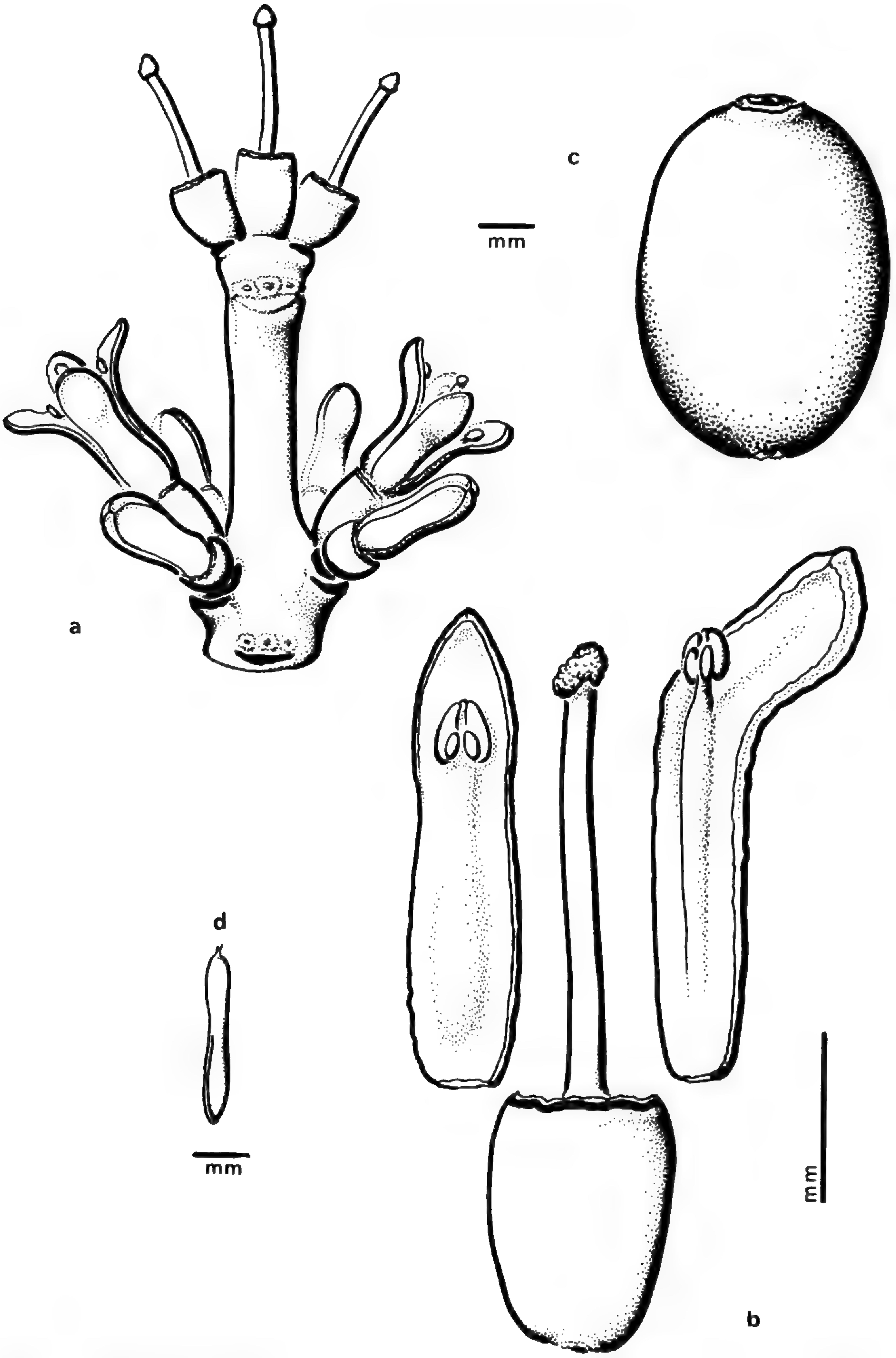

FIGURE 2. *Cladocolea primaria* Kuijt (*Sytsma & Knapp 4797*).—a. Inflorescence, the upper triads removed.—b. Flower dissection.—c. Mature fruit. —d. Embryo.

(which it greatly resembles superficially) and *C. roraimensis* (Steyerm.) Kuijt, while in *Struthanthus* it is especially *S. leptostachyus* (Kunth) G. Don and *S. polystachyus* (Ruiz & Pavon) Blume that are related. Our species represents the second *Cladocolea* reported for Panama and seems to be limited to the Cerro Jefe area.

2. **Dendrophthora davidsei** Kuijt, sp. nov. TYPE: Costa Rica. Limón: Cordillera de Talamanca, Atlantic slope, unnamed cordillera between the Río Terbi and the Río Siní, 2,400–2,750 m, elfin forest edge, *Davidse et al. 28990* (holotype, MO). Figure 3.

Planta ad circ. 15 cm alta, monoeca, erecta, olivacea, parvifoliata; cataphylla basalia nulla vel irregularia, appendices basales in plano medio. Folia (ob)lanceolata, succulenta, ad 9 × 2 mm, acuta. Flores feminei ad partes superiores internodium fertilium, plerumque quam masculi subtus inserti haud plures. Spicae solitariae, axillares terminalisque, pedunculo circ. 7 mm longo incluso ad 5 cm longae; internodia fertilia 2 vel 3, raro 4; flores uniseriati, ad 20 pro bractea fertili. Fructus albus, ellipsoideus ad globosus, 1.5 mm diam., petalis patentibus.

Plants monoecious, to ca. 15 cm high, erect, olive green, small-leaved; basal cataphylls absent throughout in some individuals, irregularly present in others; basal appendages oriented in median plane; young parts often with sparse, stiff, white bristlelike hairs. Leaves (ob)lanceolate, succulent, to 9 × 2 mm, acute. Spikes solitary and axillary as well as terminal, to 5 cm long including the peduncle ca. 7 mm long; fertile internodes 2 or 3, rarely 4. Flowers uniseriate, to 20 per fertile bract; female flowers in the upper part of the fertile internodes, not generally outnumbering the male flowers below. Fruit white, ellipsoid to globose, 1.5 mm diam.; petals spreading.

Additional specimens examined. COSTA RICA. LIMÓN: Cordillera de Talamanca, Atlantic slope, Valle de Silencio, along the Río Terbi, 0.5–1.5 airline km W of the Costa Rican-Panamanian border, 2,300—2,400 m, *Davidse et al. 28755a* (MO). HEREDIA: open road side, 1 km N of San Rafael de Vara Blanca, 1,900 m, *Lent 3826* (F).

Dendrophthora davidsei is the sixth known Mesoamerican species of subgenus *Dendrophthora,* counting *D. talamancana* described concurrently in this paper. The others are *D. guatemalensis* Standley, *D. mexicana* Kuijt, *D. squamigera* (Benth.) Kuntze, and *D. terminalis* Kuijt. No serious confusion is possible with those species. The closest relative of *D. davidsei,* however, is *D. paucifolia* (Rusby) Kuijt, which ranges from Bolivia to Venezuela. The major difference between *D. davidsei* and *D. paucifolia* is that the vegetative branches of the latter invariably have a prominent pair of basal cataphylls placed high above the leaf axil (see Fig. 39 in Kuijt, 1986a). This is not seen in any of the ten individuals present in the two Davidse collections, but basal cataphylls are present on some (not all) vegetative laterals of the Lent specimen. The latter looks extremely slender but appears to belong to the present species. A second and apparently consistent difference is that leaf size in *D. paucifolia* dwindles upwardly until the uppermost lateral spikes are subtended by leaf scales; even though perhaps a slight diminution takes place in *D. davidsei,* none of the leaves on the main stem ever reach scale size. The relationship of the two species is certainly very close, but separation appears justified.

Terminal inflorescences were not seen in the type but are represented in the otherwise identical collection *Davidse et al. 28755a.* In the type, as shown in Figure 3a, the tips of the larger branches have remained static, giving the impression of buds with crowded small leaves. Such shoot tips undoubtedly will expand into new systems of inflorescences, and perhaps mark a seasonal change. In fact, in the third collection, *Lent 3826,* there are some branches where such a new expansion seems to have taken place, demarcated from the older portion by several pairs of very small leaves.

3. **Dendrophthora talamancana** Kuijt, sp. nov. TYPE: Costa Rica. Limón: Cordillera de Talamanca, Atlantic slope, Valle de Silencio, along the Río Terbi, 0.5–1.5 airline km W of the Costa Rican–Panamanian border, 2,300–2,400 m, *Davidse et al. 28755b* (holotype, MO). Figure 4.

Planta tenuis, monoeca, erecta, ramosissima, circ. 30 cm alta, ad basem squamata; caules inflorescentias gerentes haud ultra 1 mm crassi. Cataphylla basalia omnino carentia, appendices basales positione media. Spicae solitariae, axillares, ad 15 mm longae, internodio fertili uno. Flores uniseriati, floribus usque ad 6 supra quamque bracteam fertilem, masculi irregulariter dispersi et femineis multo pauciores; bacca alba, 2 mm diam., ovoidea, sepalis clausis.

Plants monoecious, ca. 30 cm high, profusely branched, slender, erect, squamate to the base. Inflorescence-bearing stems 1 mm or less in

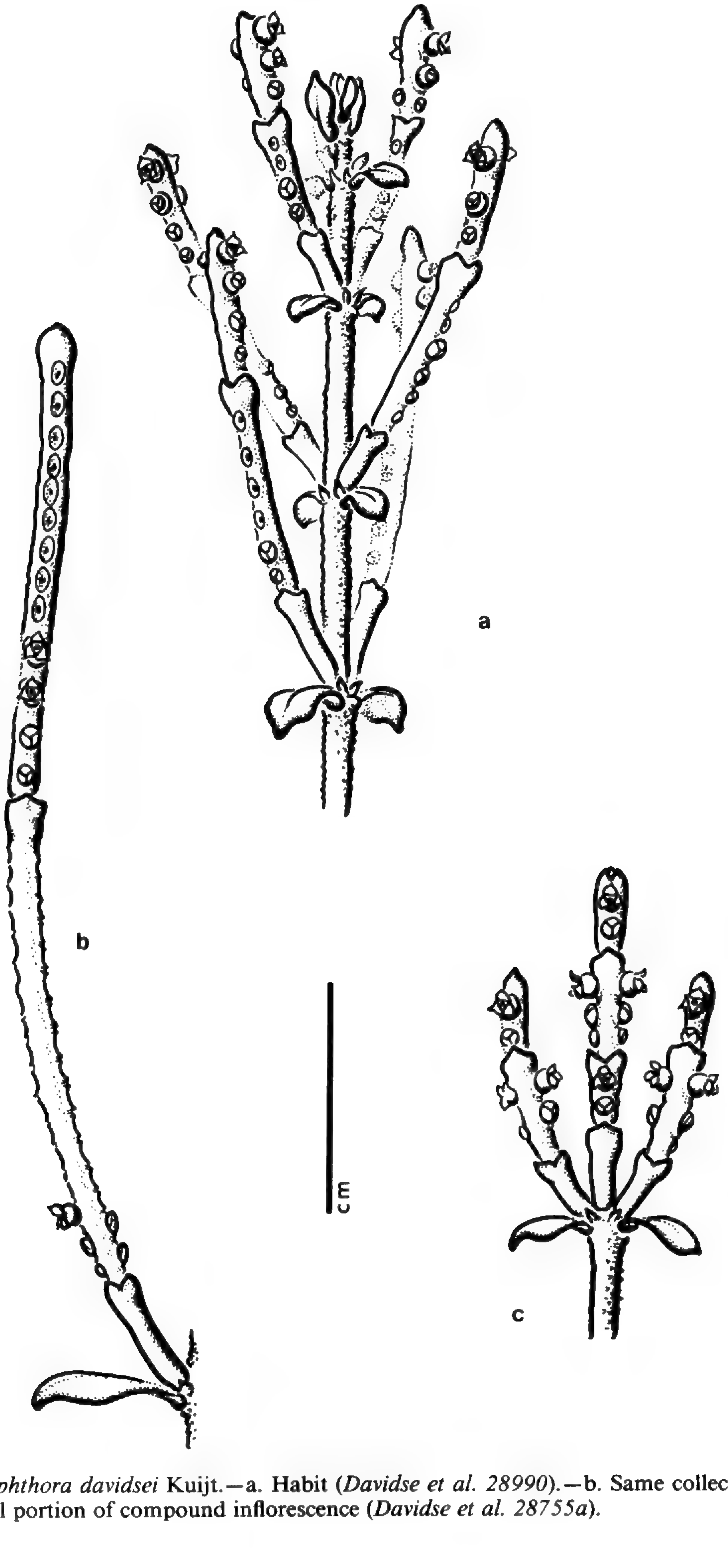

FIGURE 3. *Dendrophthora davidsei* Kuijt.—a. Habit (*Davidse et al. 28990*).—b. Same collection, old inflorescence.—c. Terminal portion of compound inflorescence (*Davidse et al. 28755a*).

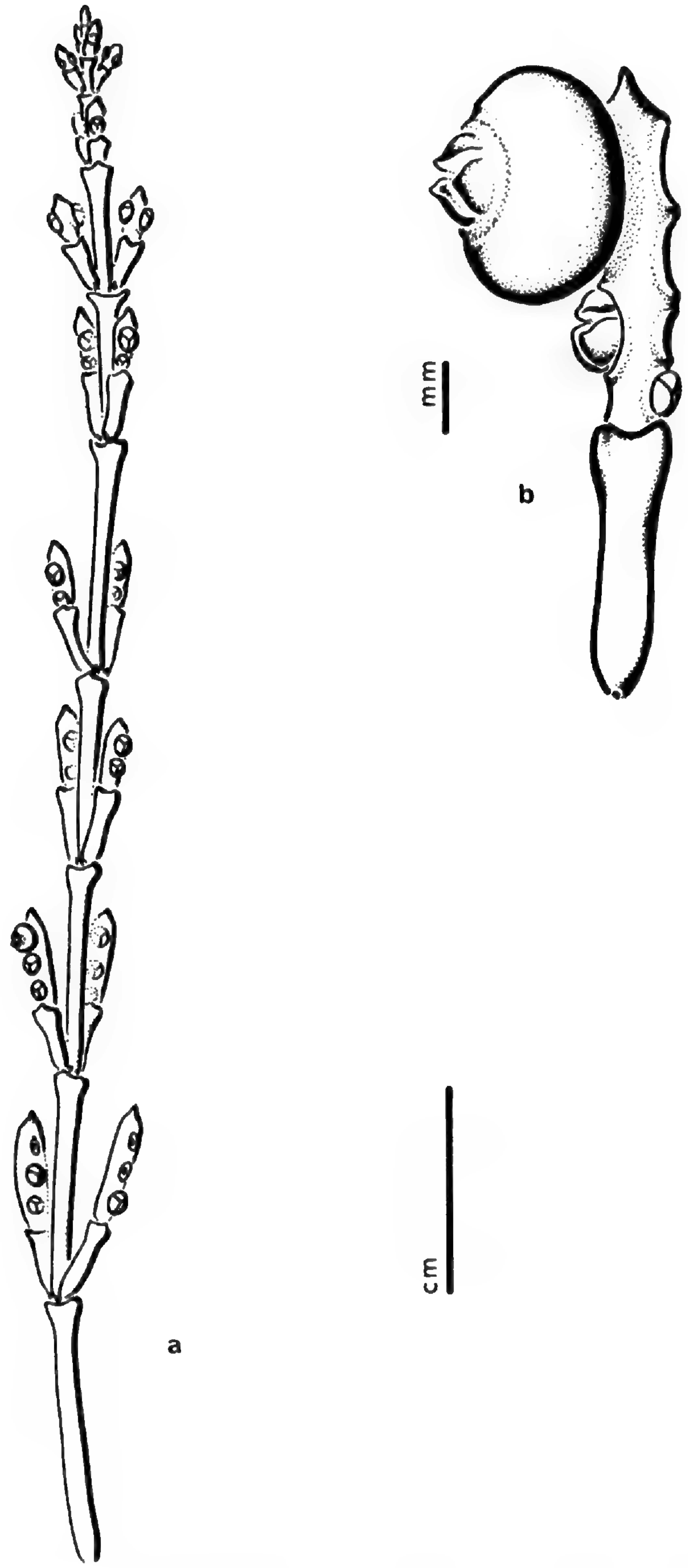

FIGURE 4. *Dendrophthora talamancana* Kuijt (*Davidse et al. 28755b*).—a. Habit.—b. Fruiting inflorescence.

thickness; basal cataphylls absent throughout, the basal appendages in a median orientation. Spikes solitary, axillary only, to 15 mm long, the single fertile internode slightly longer than the peduncle, the apex acute. Flowers uniseriate, to 6 flowers above each fertile bract; male flowers irregularly distributed and much outnumbered by the female flowers. Berry white, 2 mm diam., ovoid; sepals closed.

This distinctive plant represents the third completely squamate Mesoamerican species of *Dendrophthora*, the others being *D. squamigera*

(Benth.) Kuntze and *D. terminalis* Kuijt. It differs from the former in its extremely fine, much-branched stems and short fertile internodes, and from the latter in its size, blunt scale leaves, and lack of terminal spikes. It is conceivable that the unusually slender *Friedrichsthal s.n.* specimen from Guatemala, as cited in Kuijt (1961), will turn out to be this species. I know of no similar South American plants.

4. **Phoradendron fasciculatum** Kuijt, sp. nov. TYPE: Panama. Chiriquí: Jaramillo Arriba, near Boquete, trail to Río Palo Alto, 1,100 m, near paved road, hyperparasitic on *Phoradendron undulatum* Eichl., in turn parasitic on *Psidium guajava, Churchill & Kuijt 5106* (holotype, MO; isotypes, BM, CR, EAP, MEXU, NY, LEA, PMA). Figure 5.

Plantae erectae, glabrae, basi rami 4–6 e pulvino communi orientes; internodia vetustiora bicarinata, novella praecipue statu sicco leviter quadrangularia, ad 10 cm longa; rami laterales paribus cataphyllarum singulis. Rami solum novelli foliosi. Folia carnosa, 8 × 5 mm, apice rotundata, mox decidua. Monoeca; spicae paribus cataphyllorum sterilium vel nullis; internodia fertilia 5 vel 6. Flores masculi 1–3 ad apicem areae floriferae supra bracteam fertilem, feminei usque ad 12 pro bractea et iis suppositae, bi- vel triseriati. Fructus late ovoideus, 3 mm diam.; petalis inconspicuis, clausis.

Plants monoecious, erect, glabrous, fascicled from the base with 4–6 stems from a common cushion. Stems usually lacking basal cataphylls; internodes 2-keeled when older, somewhat quadrangular when young, especially when dry, to 10 cm long, stout; lateral branches with 1 pair of basal cataphylls ca. 4 mm above base, spreading when dry. Leaves fleshy, soon deciduous, 8 × 5 mm, the apex rounded, sides parallel, the base clasping. Spikes with 1 pair of sterile cataphylls or without, 5–6 fertile internodes sometimes proliferating terminally into a second series of younger fertile internodes. Male flowers 1–3 at the tip of the flower area above each fertile bract, the female flowers to 12 per bract below them, bi- or triseriate. Fruit broadly ovoid, 3 mm diam., the petals very small, inconspicuous, more or less closed.

This distinctive species undoubtedly belongs to the *P. dipterum* group of species, in which hyperparasitism is the rule. *Phoradendron fasciculatum* is no exception, in that all plants seen of the type collection were growing on *P. undulatum* Eichler. It is impossible to tell at this time whether this cluster of species is obligately hyperparasitic; plants growing near the base of a primary host may easily be mistaken for being parasitic directly on the host tree. Another feature apparently held in common by these various species is that several stems originate from a basal cushion, as illustrated in Figure 5a (arrow). I add a comparable illustration of a small plant of *Phoradendron dipterum* Eichler from Nicaragua (Fig. 6), which happens to be parasitic on a leaf, the host again being a *Phoradendron.* A clear basal cushion is visible (arrow). A third example is *Phoradendron aequatoris* Urban from Ecuador (Kuijt, 1986a, fig. 2), which also has basal sprouting and is parasitic on a *Phoradendron.* That this is not axillary branching from the nodes of a much shortened base is demonstrated by the usual lack of basal cataphylls, in contrast to what occurs elsewhere in the plant.

The explanation of the basal cushion almost certainly lies in the original haustorial disk of the seedling. It has recently been shown in an unrelated species of Viscaceae, *Viscum minimum* Harvey, that the margin of the haustorial disk regularly produces aerial shoots (Kuijt, 1986b). The same is true for *Viscum album* L. (Tubeuf, 1923), and for *Ixocactus hutchisonii* Kuijt of Loranthaceae (Kuijt, 1987). In *Phoradendron,* this feature would appear to have some taxonomic constancy in the group of species under discussion.

Additional specimen examined. COLOMBIA. ANTIOQUÍA: highway between Uramita and Cañasgordas, on *Phoradendron piperoides* (H.B.K.) Trel., *Barkley & Gutierrez 535457* (US).

5. **Phoradendron molinae** Kuijt, sp. nov. TYPE: Nicaragua. Madriz: cut over cloud forest area on Volcán Somoto, 10 km S of Somoto, 1,400 m, *Williams & Molina 20270* (holotype, US; isotype, F). Figure 7.

Internodia compressa carinataque, ad 6 cm longa; rami laterales paribus cataphyllorum basalium valde inferis singulis. Folia ad 10 × 4.5 cm; lamina tenuis, ovata, basi in petiolum insignem, cuneiformem, fere ad 1.5 cm longum abrupte contracta. Inflorescentia feminea solitaria, pari cataphyllorum sterilium praesente vel carente; pedunculus statu fructifero circ. 3 mm longus; spica fructifera circ. 3 cm longa, internodiis fertilibus 2 vel 3, floribus pro bractea fertili tribus, insertis paulum supra medium internodii. Fructus ovoideus, laevis, 3 × 2 mm, petala clausa.

Plants dioecious (only the female seen), stems with compressed, keeled internodes to 6 cm long, basal cataphylls one very low pair on lateral

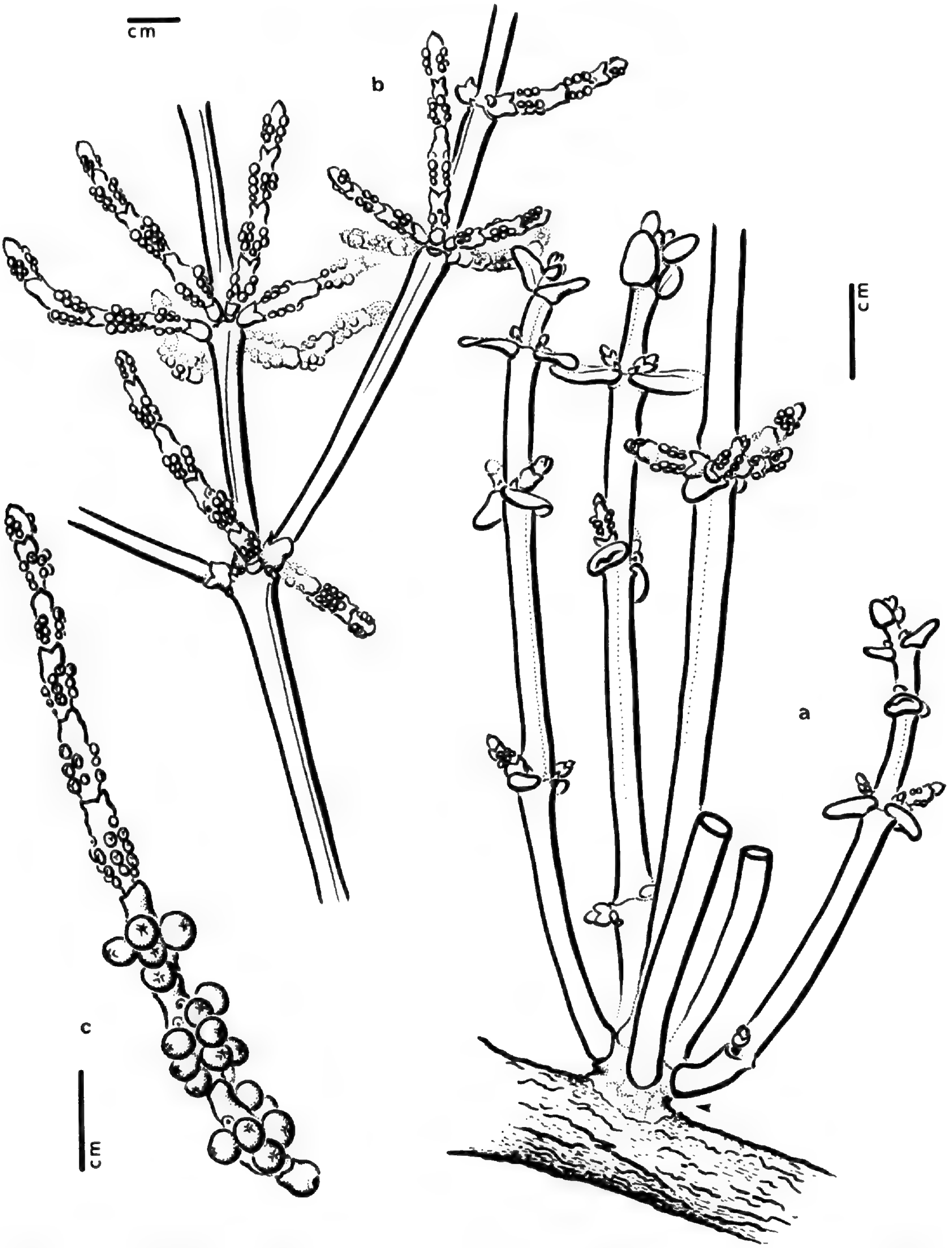

FIGURE 5. *Phoradendron fasciculatum* Kuijt (*Churchill & Kuijt 5106*).—a. Base of young plant, showing sprouting from basal cushion (arrow).—b. Habit of older plant.—c. Older inflorescence, the basal portion in fruit, the terminal portion proliferated and in flower.

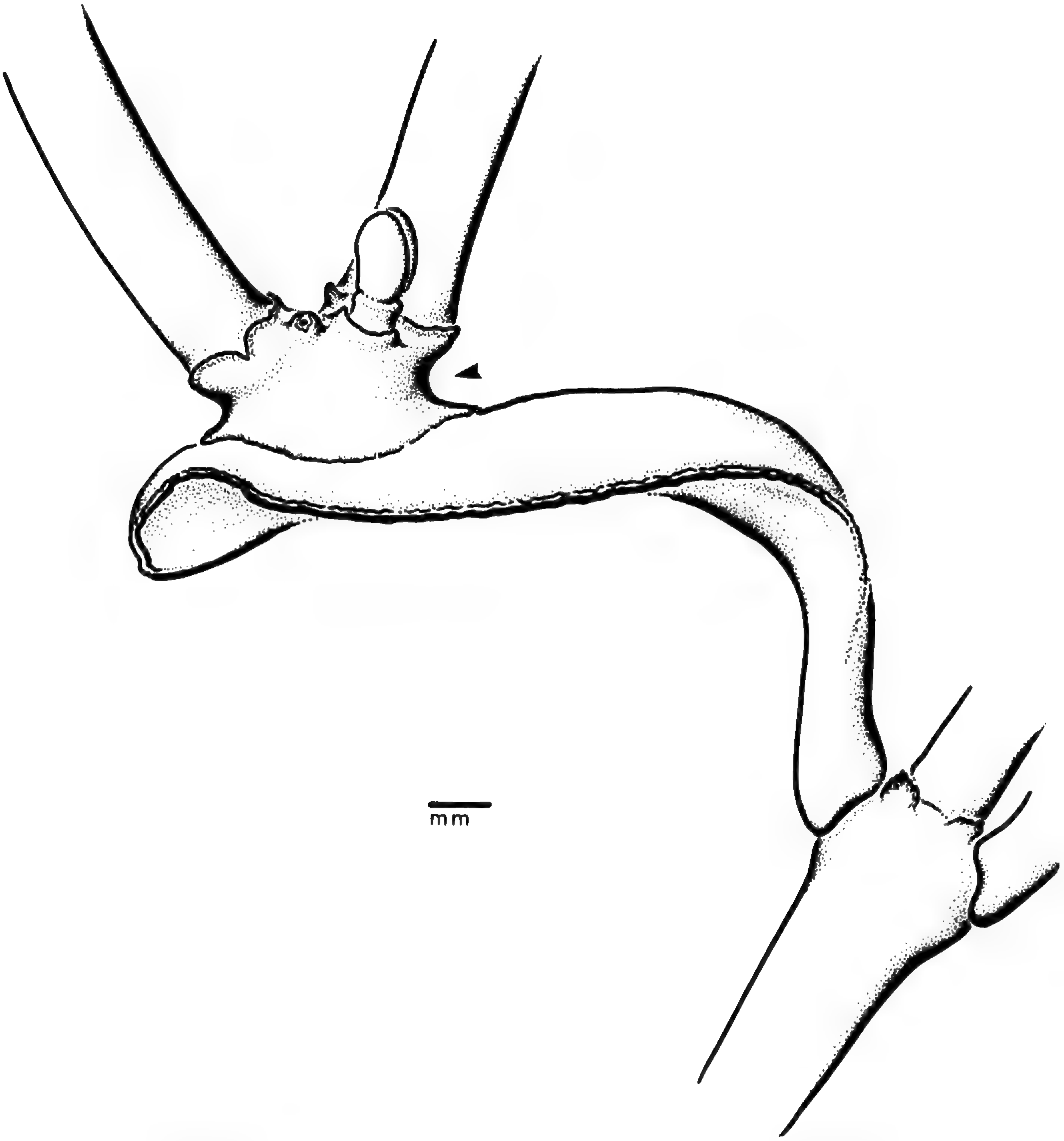

FIGURE 6. *Phoradendron dipterum* Eichler parasitic on *Phoradendron* sp., Nicaragua (*Stevens & Montiel 17931*, LEA). The hyperparasite is sprouting from a basal cushion (arrow) attached to a leaf of the primary host.

branches. Leaves to 10 × 4.5 cm; blade thin, more or less palmately veined, ovate, the base abruptly contracted into conspicuous, cuneiform petiole to nearly 1.5 cm long. Female inflorescence solitary, less than 2 cm long, often with a sterile pair of cataphylls; peduncle ca. 3 mm long in fruit; fruiting spike ca. 3 cm long, with 2–3 fertile internodes and 3 flowers per fertile bract just above the middle of the internode. Fruit ovoid, smooth, 3 × 2 mm; petals closed.

6. **Phoradendron nitens** Kuijt, sp. nov. TYPE: Costa Rica. Cartago: east side of continental divide between Tres Rios and Cartago, on Euphorbiaceae, *Kuijt 2465* (holotype, CR; isotype, UBC). Figure 19 in Kuijt (1964) and Figure 5 in Kuijt (1986a).

Planta magna, monoeca, carnosa, ramificatione saepe furcata; innovationes laterales cataphyllis basalibus magnis binis. Ramuli novelli aliquantum compressi, demum teretes. Folia usque ad 15 × 7 cm vel ultra, statu vivo crassa et nitentia, rigida, obovata vel fere elliptica, basi angustata vel abrupte contracta; petiolus validissimus, planus, ad 6 mm latus. Flores masculi rarissimi, inferiores seriatim dispositi; spica ad 4 cm longa, cataphyllis nullis, internodia fertilia 3 vel 4, flo-

FIGURE 7. *Phoradendron molinae* Kuijt (*Williams & Molina 20270*). —a. Habit. —b. Fruiting inflorescence. —c. Basal cataphylls.

res pro bractea 6–9, biseriati. Fructus flavus, 3 × 1.5 mm, ellipsoideus; petala clausa.

Plants fleshy, monoecious, the branching mostly forked, where percurrent perhaps with a pair of intercalary cataphylls. Lateral shoots with a large pair of basal cataphylls just above the axil; stems somewhat compressed when young, becoming terete. Leaves to 15 × 7 cm or larger, thick and shiny when fresh, rigid, obovate to nearly elliptical; base tapering or abruptly contracted; petiole very stout and flat, to 6 mm wide. Spike to 4 cm long, lacking cataphylls, fertile internodes 3–4, with flowers 6–9 per bract, biseriate; male flowers very rare, lowest in series. Fruit yellow, 3 × 1.5 mm, ellipsoid; petals closed.

Additional specimens examined. NICARAGUA. ZELAYA: Município de Siuna, Río El Bambú, arriba, 200–400 m, *Ortiz 1665* (HNMN, MO); Rosa Grande, Río Labú (río abajo), 300 m, *Ortiz 1031* (HNMN, MO); Cerro Waylawas (Peñas Blancas), 5 km al S de Wany, costado oeste del cerro, on Crescentia, *Grijalva & Burgos 1665* (HNMN, MO); Municípío de Rama, camino desde "Santa Julia" hasta "La Palmera," 60–95 m, *Robleto 680* (HNMN, MO). (Also see the specimens listed under *Phoradendron obliquum* (Presl) Eichler in Kuijt, 1964).

This species, which in Mesoamerica has been erroneously referred to *Phoradendron obliquum* (Presl) Eichler, is often extremely difficult to separate from vigorous specimens of *P. robustissimum* Eichler if only herbarium material is available. In the fresh condition, its usually larger shiny leaves and yellowish berries contrast sharply with those of the latter species. *Phoradendron robustissimum* is also strictly dioecious, but the rarity of male flowers in *P. nitens* can be very misleading. *Phoradendron obliquum* is presently placed in synonymy under *Dendrophthora obliqua* (Presl) Wiens (Kuijt, 1986a).

The species is now known from Panama, Costa Rica (Kuijt, 1964), and Nicaragua, and has been reported recently from Ecuador (Kuijt, 1986a, as *Phoradendron* #5, fig. 5). We may thus anticipate that it will be found in Colombia.

7. **Phoradendron tardispicum** Kuijt, sp. nov. TYPE: Panama. Chiriquí: bridge over Río San Felix, on Panama Hwy., 50 m, on *Ficus* along river directly S of bridge, *Churchill & Kuijt 5107* (holotype, MO; isotypes, BM, LEA, MEXU, PMA). Figure 8.

Plantae dioeca (pistillatae solum visae), vivae obscure virides, glabrae. Caules deinde teretes; internodia recta, 5–9 cm longa. Cataphylla basalia plerumque par unum vel paria dua, valde inconspicua. Cataphylla intercalaria praesentia, paria singula paribus foliorum interspersa sed ad caules irregulariter distributa, ad internodia nonnulla carentia. Folia amplexicaulia, cordata, viva nitida, usque ad 7.5 × 6 cm, margine undulata, venatione pinnata. Inflorescentiae sat graciles, 6–8 cm longae, fere omnes ad internodia vetustiora defoliata, aliquot pro nodo, spica quaque paribus duobus cataphyllorum sterilium basalium internodiisque fertilibus circ. 7; flores biseriati, ad 10 pro bractea fertili. Fructus ovoideus, luteo-viridis, 3 mm longus, petalis clausis.

Plants dioecious (only the female seen), bright, dark green when fresh, glabrous, 1–2 m diam., somewhat pendulous. Upper part of internode slightly flattened when young, soon becoming terete; internodes straight, 5–9 cm long. Basal cataphylls mostly 1 or 2 pairs, very inconspicuous, if 1 pair present nearly axillary, if 2 pairs present the second pair to 20 mm above axil, rarely to 4 pairs. Intercalary cataphylls present, one pair between successive pairs of foliage leaves but irregularly distributed along the branch, absent from some internodes, always inconspicuous. Leaves amplexicaul, cordate, shiny when fresh, to 7.5 × 6 cm, rather thin; margin undulate; venation pinnate but obscure. Inflorescences rather slender, 6–8 cm long, nearly all on older, leafless internodes, several per node, rarely one in axils of intercalary cataphylls; spike with 2 pairs of sterile basal cataphylls less than 5 mm above base, followed by ca. 7 fertile internodes. Flowers biseriate, to 10 per fertile bract, yellowish green, each fertile internode with stalk and flowerless tip 2–4 mm long. Fruit ovoid, yellowish green, 3 mm long, the petals closed.

This is a remarkable species for its irregularly distributed intercalary cataphylls and for late development of inflorescences. It is difficult to see what known species might be related. As far as I am aware, only in *Phoradendron paradoxum* Urban from Venezuela do intercalary cataphylls alternate in occurrence, but there this pattern seems to be regular (Trelease, 1916). That species and the closely related *P. fendlerianum* Eichler, however, have triseriate flowers and long-petioled leaves and do not seem closely related. In the newly described *P. balslevii* Kuijt from Ecuador (Kuijt, 1986a), a similar irregularity exists, but there 0–3 cataphylls may be present on an "internode"; nor does this species seem to be closely related to *P. tardispicum.*

8. **Phoradendron zelayanum** Kuijt, sp. nov. TYPE: Nicaragua. Zelaya: N of abandoned airstrip near Alamikamba, along tributary of Caño Alamikamba, 10 m, gallery forest among savanna, on *Symphonia globulifera* L.f., *Stevens 21717* (holotype, MO; isotypes, HNMN, LEA). Figure 9.

Planta monoeca, dichotoma, apice abortivo. Caules teretes; innovationes laterales cataphyllis infra positis binis. Folia late ovata vel orbicularia, lamina ad 8 × 8 cm, palmato-venosa; petiolus validus, planus, supra expansus. Inflorescentia cataphyllis sterilibus nullis; in-

FIGURE 8. *Phoradendron tardispicum* Kuijt (*Churchill & Kuijt 5107*).—a. Habit.—b. Inflorescence.

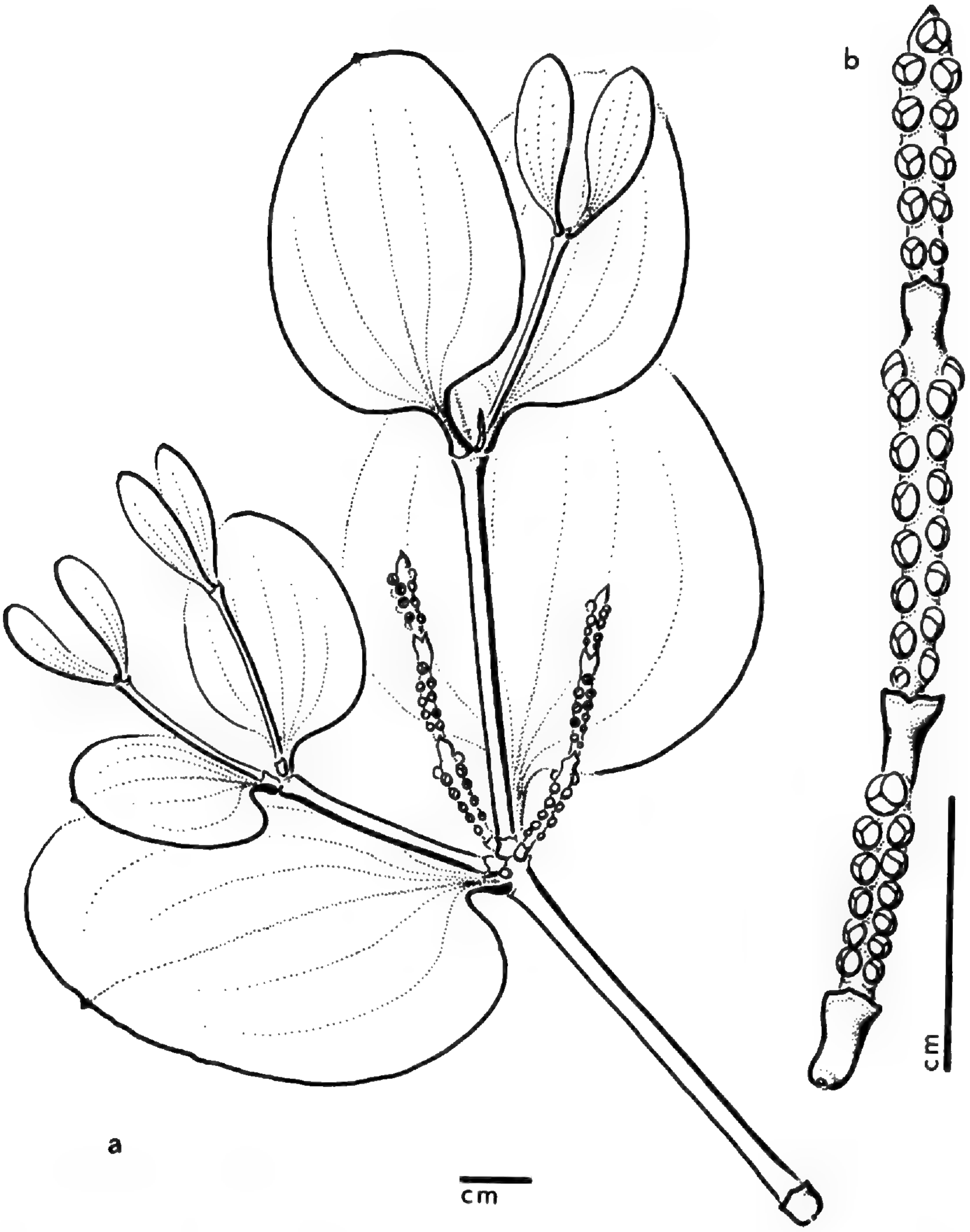

FIGURE 9. *Phoradendron zelayanum* Kuijt (*Stevens 21717*).—a. Habit.—b. Inflorescence.

ternodia fertilia tria; flores 13–15 pro bractea fertili, biseriati; spica 4 cm longa; spicae hermaphroditae.

Plants monoecious, forking, the apex aborting, the inflorescences and young shoots dull golden-yellow. Stems terete, stout; internodes to 8 cm long; the lateral shoots with one low pair of cataphylls. Leaves broadly ovate to orbicular; blade to 8 × 8 cm, with 5 or 7 very conspicuous palmate veins running far towards the apex; petiole stout, ca. 8 mm long, flat and expanding distally. Inflorescences bisexual, lacking sterile cataphylls, the peduncle 3 mm long, this followed by 3 fertile internodes each with 13–15 biseriate flowers per fertile bract, the entire spike 4 cm long.

9. **Psittacanthus angustifolius** Kuijt, sp. nov. TYPE: Nicaragua. Madriz: 0.5 km al S de San José de Cusmapa, 1,200 m, parasitando en un *Pinus*, *Moreno 24419* (holotype, MO; isotype, HNMN, LEA). Figure 10.

Caules acute quadrangulares. Folia bina, anguste falcata, tenua, venatione pinnata; lamina ad 17 × 2.5 cm, basi acuta, apice graciliter attenuata, petiolus ad 5 mm longus. Inflorescentia terminalis, e triadis 4 vel 6 consistens. Pedunculi triaderum circ. 1 cm longi, inferiores bracteis foliaceis ad 2 cm longis; pedicelli cupula terminali notabili. Petala aurantiaca, 7.5–8 cm longa; alabastrum rectum vel aliquantum curvatum. Ligulae et pili staminum nulli, sed apices petalorum crista centrali, carnosa liguliformi ornati. Stamina dimorpha, 5 cm longa, antherae 6 mm longae. Stigma antheras superans, capitatum.

FIGURE 10. *Psittacanthus angustifolius* (*Moreno 24419*).—a. Habit.—b. Tip of petal.

Stems sharply quadrangular. Leaves paired, narrowly falcate, thin; the blade to 17 × 2.5 cm, venation pinnate, the base acute, the apex slenderly attenuate; petiole to 5 mm long. Inflorescences terminal, consisting of 4 or 6 triads; triad peduncles ca. 1 cm long, the lowest ones with foliaceous bracts to 2 cm long; pedicels 1.5 cm long, with conspicuous terminal cupule, the calyculus smooth. Bud stout, more or less straight or somewhat curved; base and tip 5 and 4 mm wide, respectively, the latter blunt. Petals orange, 7.5–8 cm long; inner part of flower hairless, the petal base 5 mm wide, without ligule; petal apices 4 mm wide, blunt, each with a fleshy, ligule-like median crest extending inwards. Stamens dimorphic; filaments attached at ca. 2.5 cm above petal base, 5 cm long; anthers 6 mm long. Ovary 5 × 6.5 mm. Stigma placed above anthers, very small, capitate. Fruit unknown.

Additional specimen examined. Same data as type, *Soza et al. 155* (HNMN, MO).

This is an extremely distinctive species, known from what is essentially a single collection. Whether the species is restricted to *Pinus,* as apparently is *Psittacanthus pinicola,* can only be shown by further fieldwork. The two species cannot be confused, as *P. pinicola* is dyadic and has irregularly whorled, blunt, more leathery leaves. The type locality suggests that the species may well be present in neighboring Honduras.

10. **Psittacanthus minor** Kuijt, sp. nov. TYPE: Nicaragua. Matagalpa: SW slopes of Cerro El Pilón and adjacent Laguna Tecomapa, roadside, low thorn scrub and pastures on rocky slopes, on ant acacia, *Stevens 9466* (holotype, MO; isotypes, HNMN, LEA). Figure 11.

Plantae parva, caulibus teretibus, foliis binis. Folia tenua; lamina ad 5.5 × 3.5 cm, ovata, utraque extremitate obtusa vel fere; petiolus 3–5 mm longus. Inflorescentia terminalis, paribus triadarum 4–6. Petala circ. 3.7 cm longa, rubro-aurantiaca; area ligulae paulum distincta. Alabastrum rectum, basi haud dilatatum, calyculus laevis. Stamina dimorpha; antherae 3 mm longae, series duae vix imbricantes; filamenta circ. 16 mm longa; stylus petalis fere aequilongus; stigma aegre distinguendum.

Stems terete, phyllotaxy paired. Leaves thin, the blade to 5.5 × 3.5 cm, ovate, the apex and base obtuse or nearly so; venation more or less palmate; petiole 3–5 mm long. Inflorescences terminal, consisting of 4–6 pairs of triads on peduncles ca. 12 mm; pedicels 10 mm long. Buds straight, not dilated at base. Petals ca. 3.7 cm long, red-orange; ligular area weakly differentiated. Stamens dimorphic; the anthers 3 mm long, dorsifixed, the 2 series scarcely overlapping, the filaments attached ca. 21 mm above the base, some 16 mm long. Ovary more or less cylindrical, 4 × 2 mm; style nearly as long as the petals; stigma weakly differentiated; calyculus smooth. Fruits ovoid, 1.5 × 1 cm, with conspicuous calyculus, blackish.

Additional specimens examined. NICARAGUA. MATAGALPA: Puertas Viejas, 2 km al N sobre la Carretera Panamericana, "San Vicente," 600 m, on *Acacia, Moreno 18288* (HNMN, LEA, MO); same, San Juanillo, 8 km al SE de Ciudad Dario, 500 m, on Fabaceae, *Grijalva 2618* (HNMN, LEA, MO); same, Entrada Paso de Carretera, quebrada, 460–480 m, on Bignoniaceae, *Moreno 16698* (HNMN, LEA, MO). MANAGUA: camino Dario-Presa Santa Barbara, 8 km al NW de Ciudad Dario, on Leguminosae, *Grijalva 2693* (HNMN, LEA, MO).

Psittacanthus minor is closely related to *P. mayanus* Standley & Steyerm., which appears to be limited to the Yucatán region, has quadrangular stems, and fruits which are about half as large as those of *P. minor. Psittacanthus mayanus* is much smaller in general.

11. **Psittacanthus pinicola** Kuijt, sp. nov. TYPE: Belize. Belize: Manatee Pine Ridge, on pine, 1931–32, *Gentle 82* (holotype, GH; isotype, MO). Figures 12, 13.

Caules plus minusve teretes; folia symmetrica, ter verticillata, ad 11 × 2.5 cm, anguste elliptica vel lanceolata, apice rotundata, basi in petiolum circ. 5 mm longum angustata. Inflorescentiae laterales, ad nodos, umbellulas e dyadis 2 vel 3 formantes. Petala circ. 4 cm longa, rubra, apice luteo-viridescentia, medio aurantiaca, basi ligula prominente; alabastrum supra aliquantum curvatum, circum ovarium ad latitudinem circ. 5 mm dilatatum, ad apicem tenuissimum, leviter curvatum, circ. 1.5 mm latum angustatum; calyculus laevis. Stamina dimorpha; antherae dorsifixae, dorso paulo pilosae. Ovarium plus minusve cylindricum, 4.5 mm longum; stylus longus, basi aliquantum torsus; stigma ellipsoideum, subtiliter papillosum. Fructus ellipsoideus, calyculo inconspicuo, 13 × 5 mm, saturate purpureus.

Stems more or less terete, becoming coarsely fissured and blackish when old; leaves symmetrical, in (often somewhat irregular) whorls of 3, to 11 × 2.5 cm, narrowly elliptical to lanceolate; apex rounded; base tapering into petiole ca. 5 mm long. Inflorescences lateral, axillary, often also on older, leafless stems, each being an umbel of 2 or 3 dyads; inflorescence peduncle to 13 mm long; dyad peduncles and floral pedicels 5–7 mm

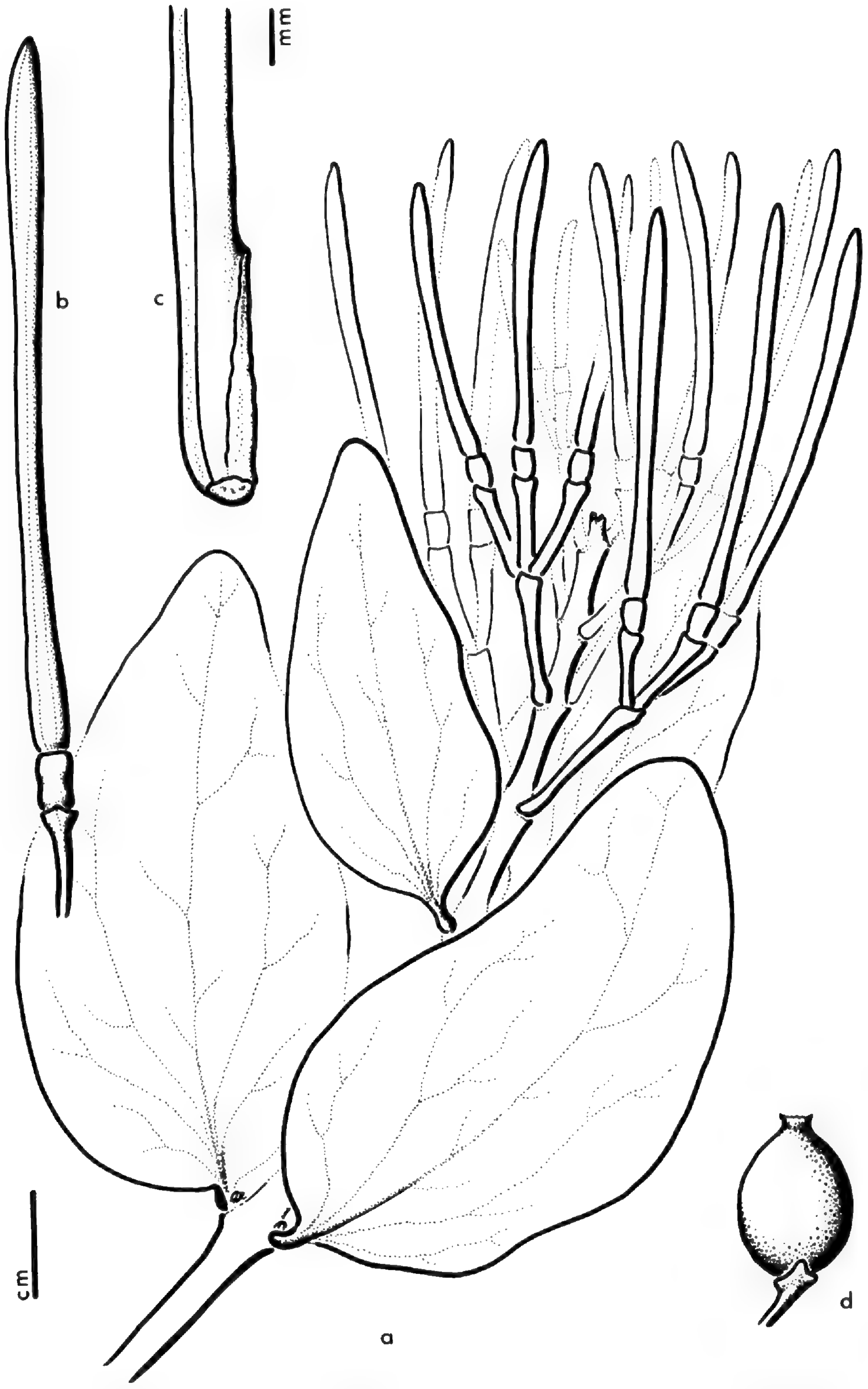

FIGURE 11. *Psittacanthus minor* Kuijt (*Stevens 9466*).—a. Habit, with immature inflorescence.—b. Mature bud.—c. Base of petal.—d. Fruit (*Moreno 18288*).

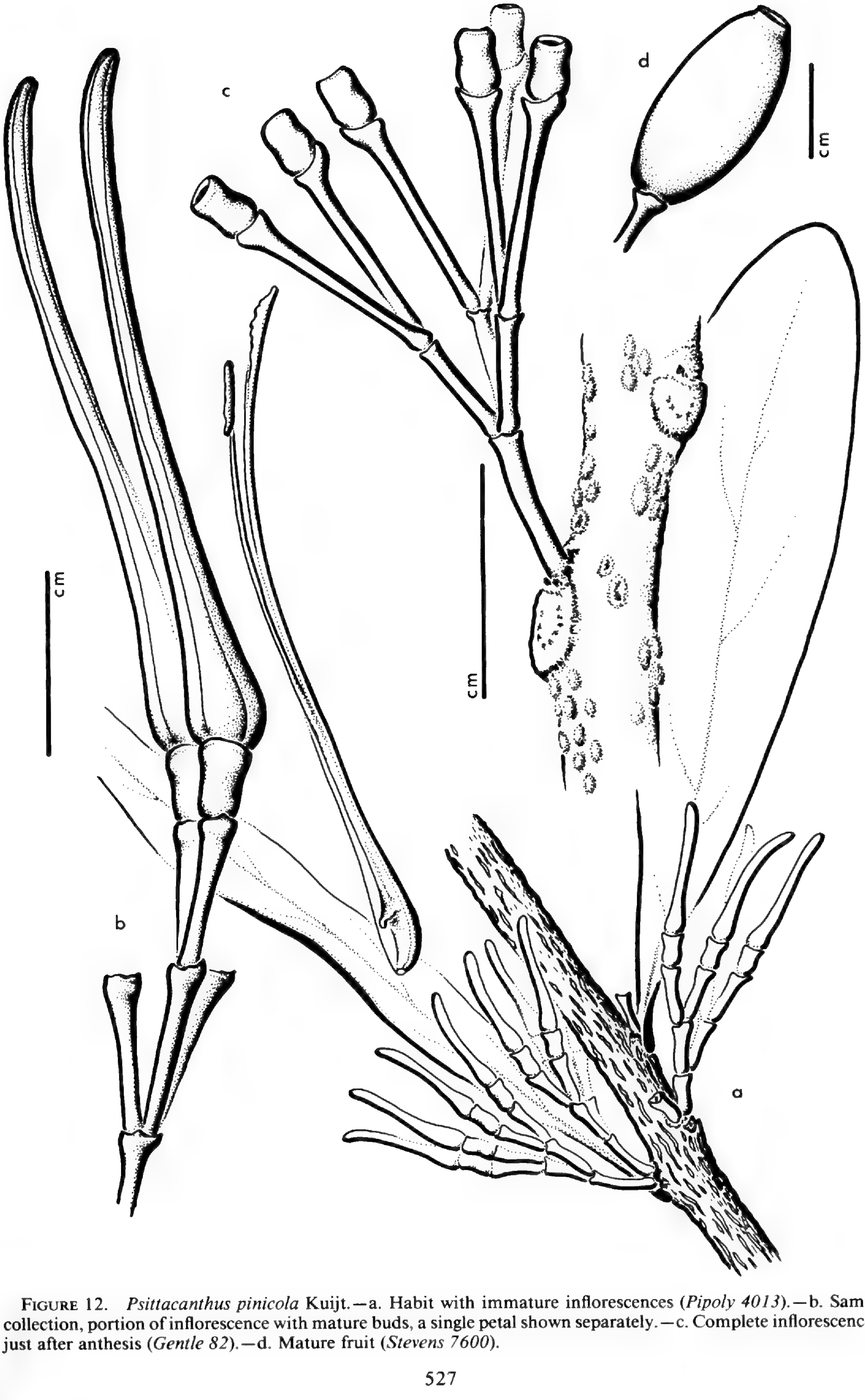

FIGURE 12. *Psittacanthus pinicola* Kuijt.—a. Habit with immature inflorescences (*Pipoly 4013*).—b. Same collection, portion of inflorescence with mature buds, a single petal shown separately.—c. Complete inflorescence just after anthesis (*Gentle 82*).—d. Mature fruit (*Stevens 7600*).

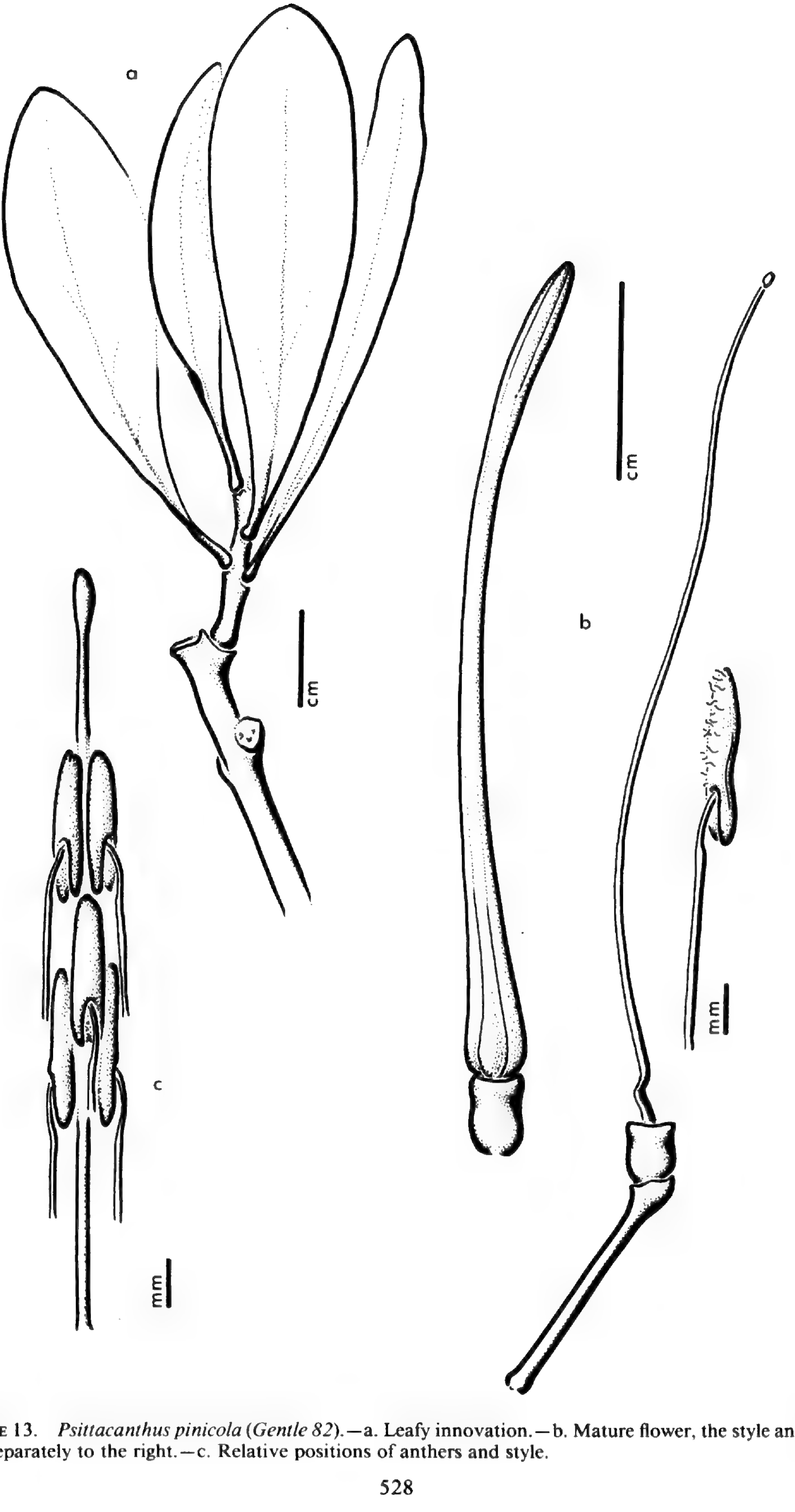

FIGURE 13. *Psittacanthus pinicola* (*Gentle 82*).—a. Leafy innovation.—b. Mature flower, the style and anther shown separately to the right.—c. Relative positions of anthers and style.

long, the latter scarcely expanded at the tip. Petals ca. 4 cm long, red with yellow-green tip, orange in the middle, prominently ligulate at the base. Buds somewhat curved above, inflated at the ovary to a width of nearly 5 mm, tapering to a very slender, slightly curved tip ca. 1.5 mm wide. Stamens dimorphic, sometimes apparently nearly trimorphic (Fig. 13c); filaments of the longer type attached 1.5 cm above the base, 1.5 cm long; anthers 3–4 mm long, dorsifixed, sparsely pubescent on back. Ovary more or less cylindrical, green, 4.5 mm long, 2 mm diam. below, expanding slightly above; calyculus smooth. Style 4.6 cm long more or less straight, but the base somewhat twisted; stigma ellipsoid, finely papillate. Fruit ellipsoid, with inconspicuous calyculus, 13 × 5 mm, "deep purple."

Additional specimens examined. BELIZE. BELIZE: western highway, Mile 30, beside track, on pine, *Whitefoord 2442* (MO); same, The Place, on pine, *Whitefoord 2562* (MO). DISTR. UNKNOWN: P. Cayo, in roadside park on ridge area overlooking 1,000 ft. falls, in area of *Pinus caribea*, Mountain Pine Ridge area, *Huston 615* (MO). NICARAGUA. ZELAYA: Río Troncera at junction with carretera between Waspam and Puerto Cabezas, elevation less than 200 m, poorly developed gallery forest in savanna, on *Pinus caribea*, *Pipoly 4013* (HNMN, LEA, MO); near Tala Has and Puente Mango (over Río Kisalaya), 40–60 m, pine savanna, on *Pinus caribea*, *Stevens 7600* (LEA, MO); Comarca del Cabo, Kornuk Creek above Puente Pozo Azul, old bridge, *Robbins 5831* (LEA, MO). NUEVA SEGOVIA: El Jícaro, 7 km sobre la carretera a Murra entrada al Quebracho, 600–620 m, on pine, *Moreno 8305* (HNMN, LEA, MO).

Other dyadic species north of Panama are *P. sonorae* (Watson) Kuijt, *P. palmeri* (Watson) Barlow & Wiens, *P. nudus* (Molina) Kuijt & Feuer, and *P. ramiflorus* (DC.) G. Don. *Psittacanthus pinicola* is similar to the last species but seems more closely related to *P. dichrous* (Martius) Martius (see Eichler, 1868, especially Pl. 5). Not only inflorescence structure and general appearance indicate this affinity, but even the peculiar curvature of the stylar base is seen in both.

12. **Psittacanthus rhynchanthus** (Bentham) Kuijt, comb. nov. *Loranthus rhynchanthus* Bentham, Bot. Voy. Sulphur 102–103. 1845. TYPE: "*Dr. Sinclair*," Tiger Island (Honduras, Bay of Fonseca) (K). Figure 14d–f.

Psittacanthus chrismarii Urban, Bot. Jahrb. 24: 331. 1897. TYPE (here designated): Costa Rica. Forêts de Nicoya, *Tonduz 13706* (hololectotype, US; isolectotypes, CR, GH).

Psittacanthus calyculatus auct., non (DC.) G. Don, Gen. Syst. 3: 415. 1834. TYPE: Mexico. Cuernavaca: *Berlandier 1150* (G-DC).

An attractive *Psittacanthus* in which the buds are distinctively curved and beaked occurs throughout Mesoamerica, at low elevations from southern Mexico to Venezuela. In the past, this species has been called *P. calyculatus* (DC.) G. Don or, earlier, *P. chrismarii* Urban. After studying the types of both *Loranthus rhynchanthus* Bentham and *L. calyculatus* DC., I conclude that these are two distinct species. Consequently, the name *P. rhynchanthus* must be applied to the wide-ranging species mentioned above. True *P. calyculatus* seems limited to Mexico, the type originating from the area of Cuernavaca, further collections having been seen from Puebla and Morelia.

Notwithstanding their general similarity, the two species may be consistently separated mostly on the basis of floral features. The mature, unopened bud of *Psittacanthus calyculatus* is very nearly straight and has a rather blunt tip; that of *P. rhynchanthus* shows a distinctive curvature in the distal portion, the apex being sharply acute, and more beaklike. *Psittacanthus rhynchanthus* has smooth pollen sacs behind which are borne long, conspicuous, reddish stamen hairs; the pollen sacs of *P. calyculatus* are distinctly lobed, and stamen hairs are lacking. Furthermore, the stylar base in *P. rhynchanthus* bears low protuberances, and each adjacent petal base shows a ligule consisting of a low, V-shaped ridge; the stylar base in *P. calyculatus* is smooth, and ligules are absent. Leaves of *P. calyculatus* tend to be smaller (to 8 × 4 cm), mostly less than twice as long as wide, and approximately symmetrical, while those of *P. rhynchanthus* are usually larger (to 12 × 4 cm), more than twice as long as wide, and strikingly falcate.

In Venezuela, at least some individuals of the latter species have extremely narrow leaves; these plants belong to *Psittacanthus rhynchanthus* var. *wurdackii* (Rizzini) Kuijt, comb. nov. (*P. calyculatus* (DC.) G. Don var. *wurdackii* Rizzini, Rodriguésia 41: 15. 1976). I have not yet encountered the species from the Caribbean lowlands of Colombia, but it would be surprising if it were not present there.

13. **Struthanthus subtilis** Kuijt, sp. nov. TYPE: Panama. Coclé: near continental divide along lumbering road, 2.2 km beyond sawmill in forest above El Copé, 900 m, *Hammel 998*

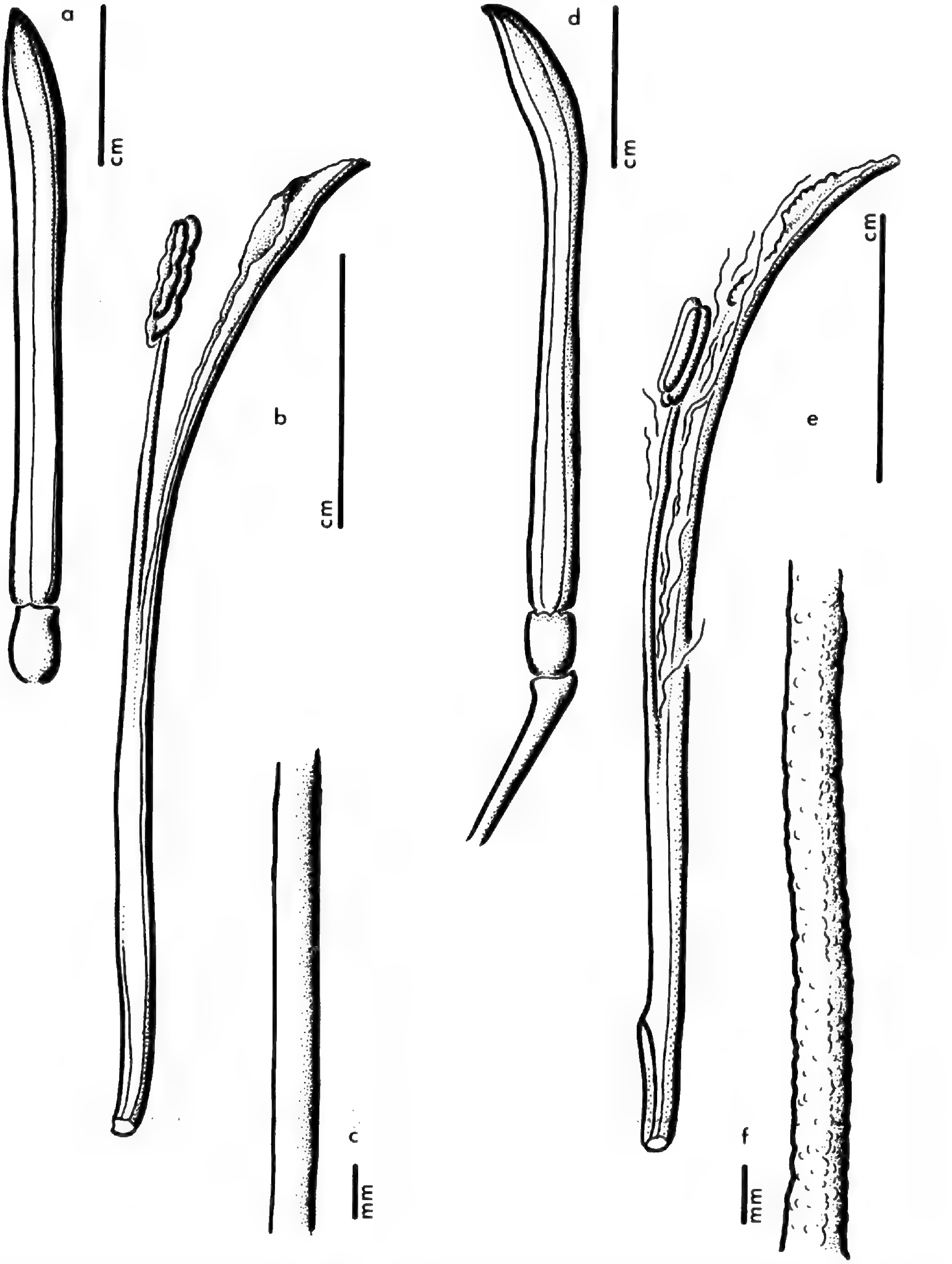

FIGURE 14. *Psittacanthus calyculatus* (DC.) G. Don (a–c; Mexico, Puebla, slopes of Popocatepetl, *Ugent et al. 1359*, WIS) and *P. rhynchanthus* (Bentham) Kuijt (d–f; Nicaragua, Managua, Cuatro Esquinas, *Moreno 4400*, LEA).—a, d. Mature buds.—b, e. Petals.—c, f. Stylar bases.

(holotype, MO; isotypes, LEA, PMA). Figure 15.

Plantae inconspicuae, subtiles; caulis gracilis, plus minusve teres. Folia tenua; venatio manifesta, pinnata; lamina anguste lanceolata ad late ovata, 4–12 cm longa, 2–6 cm lata, apice caudiformis, petiolus circ. 3 × 1 mm. Inflorescentiae singulae, axillares, bracteis triadarum 2 vel 4 constitutentes; pedunculus communis ad 8 mm longus, triadarum ad 5 mm, uterque 0.5 mm

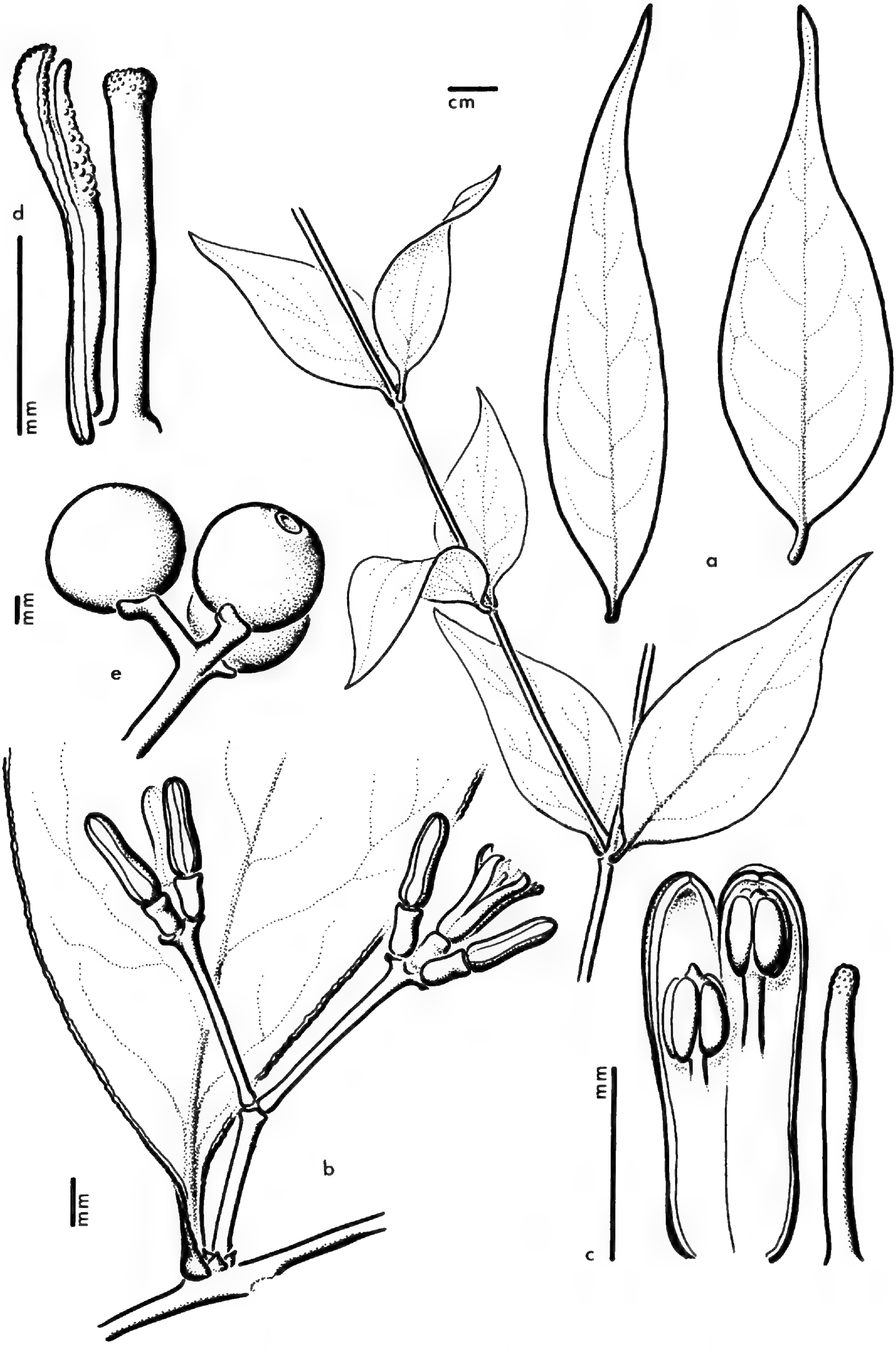

FIGURE 15. *Struthanthus subtilis* Kuijt.—a. Leafy shoot (*Croat 49004*) and leaves (*Croat 44584*).—b. Inflorescence (*Folsom & Lantz 1894*).—c. Same collection, petals and style, male flower.—d. Same collection, petals and style, female flower.—e. Mature fruits (*Hammel 998*).

vel minus crassus; flores laterales anthesi pedicellis 0.5 mm longis; bracteae bracterolaeque minutae, caducae; petala 2–2.5 mm longa; stigma cristis indistinctis papillosis 6. Fructus aurantiacus, subglobosus, 5 mm diam., calyculo inconspicuo; pedicelli fructuum lateralium ad 3 mm elongati.

Plants inconspicuous, rather delicate, branched. Stems slender, more or less terete; stem roots occasional, thin. Leaves thin, blade narrowly lanceolate to broadly ovate, always with caudate tip, 2–6 × 4–12 cm, the evident venation pinnate; petiole ca. 3 × 1 mm. Inflorescences pale green, solitary in leaf axils, subtended by 4 minute, probably caducous bracts, consisting of a raceme of 2 or 4 triads; inflorescence peduncle to 8 mm long; triad peduncles to 5 mm, both 0.5 mm or less thick. Lateral flowers on pedicels 0.5 mm long at anthesis; bracts and bracteoles minute, caducous. Petals 2–2.5 mm long. Stamens dimorphic; upper portion of sterile stamens papillate; anthers 0.4 mm long; style 2 mm long, the stigma with 6 indistinct papillate crests. Fruits orange, nearly spherical, 5 mm diam.; calyculus inconspicuous; pedicels of lateral fruits elongated to 3 mm.

Additional specimens examined. PANAMA. COCLÉ: near continental divide along lumbering road, 1.5 mi. N of El Copé, *Croat 44584* (CR, LEA, MO); El Copé–El Potrosa, Atlantic slope of Alto Calvario, 700–850 m, *Folsom & Lantz 1894* (LEA, MO, PMA); along road from La Pinteda to El Copé by way of Piedras Gordas, sawmill above El Copé, cloud forest, 100 m, *Hammel 2640* (LEA, MO); along road between Llano Grande and Coclesito (N of Pintada), 4 mi. N of Llano Grande, 600 m, *Antonio 3575* (LEA, MO); trail from Caño Blanco del Norte to continental divide N of El Copé, on *Hedyosmum*, 400 m, *Davidse & Hamilton 23654* (BM, LEA, MEXU, MO, PMA); El Copé, Atlantic side, 1,200 m, *Antonio 1153* (LEA, MO); between continental divide above El Copé and El Potroso sawmill and the Río Blanco to the north, 330 m, *Sytsma et al. 2409* (EAP, LEA, MO); El Copé, along gravel road to the right before sawmill, 800 m, *Antonio 2207* (LEA, MO, NY, PMA); Alto Calvario cloud forest, 5.3 km above El Copé, continental divide, above sawmill, 930 m, *Antonio 3044* (LEA, MO, PMA); above El Potroso sawmill at continental divide, 1,200–1,300 m, *Sytsma 1820* (LEA, MO). VERAGUAS: along Santa Fé–Calovebora road beyond Escuela Agricola Alto Piedra, along first major stream, 3 mi. from fork in road at school, 700 m, *Croat 49004* (LEA, MO).

This species was previously listed as *S.* aff. *dichotrianthus* Eichler (Kuijt, 1978). *Struthanthus dichotrianthus* (and *S. phyllyraeoides* (Kunth) Blume) are indeed related to *S. subtilis*, as is *S. quercicola* (Cham. & Schlecht.) Blume of western Panama to Mexico, but the extreme slenderness and small racemes of our plant, the leaf size, and especially the consistently caudate to acuminate leaf apex, leave little doubt that this is a distinct species. *Struthanthus subtilis* appears to be endemic to the Coclé-Veraguas region.

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A REVISION OF *DILODENDRON* (SAPINDACEAE)[1]

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ABSTRACT

Dilodendron of Brazil and adjacent regions and *Dipterodendron* of Central America and northern South America are congeneric. Here we discuss their relationships, present a key to the three species that we recognize in the combined genus, and make the appropriate new combinations for *Dilodendron costaricense* (Radlk.) Gentry & Steyerm. and *D. elegans* (Radlk.) Gentry & Steyerm.

Dilodendron Radlk., a monotypic genus of the dry areas of subequatorial South America, is closely related to *Cupania* L. and *Matayba* Aubl., from both of which it differs strikingly in having bipinnate leaves. According to Radlkofer (1892–1900, 1895) the other main differentiating features of subtribe Cupanineae are that the petals of *Cupania* and *Matayba* (as well as closely related monotypic *Vouarana* Aubl.) have two squamae, whereas those of *Dilodendron* lack squamae. Two other monotypic genera, Brazilian *Scyphonychium* Radlk. and Guianan *Pentascyphus* Radlk., have an intermediate bifid or emarginate petal scale. The final genus of subtribe Cupanineae, *Tripterodendron* Radlk., likewise monotypic and restricted to Brazil, is unique in having tripinnate leaves and the small subcupular calyx and bisquamate petals of *Matayba*. Generic limits in subtribe Cupanineae are generally not clearly defined, and *Cupania* and *Matayba,* the only significant genera (indeed the only nonmonotypic genera) recognized by Radlkofer (1892–1900), are notoriously difficult to tell apart.

When Radlkofer (1892–1900) published his *Flora Brasiliensis* treatment, *Dilodendron* was known from Brazil and Bolivia, and from a single sterile collection from Costa Rica. *Dilodendron bipinnatum* has also since been collected in Paraguay and disjunct in the dry part of the Río Urubamba Valley in Convención Province of Cuzco Department, Peru (Macbride, 1956), but the Costa Rican collection was subsequently determined not to be congeneric.

Dipterodendron Radlk. is a small genus of three described species previously reported from Costa Rica, Panama, and northwestern Venezuela (Radlkofer, 1933; Steyermark, 1952; Croat, 1976). *Dipterodendron* was described by Radlkofer (1914) on the basis of three Costa Rican collections. He recognized two species separated by rather tenuous differences: leaflets smooth and drying bright green in *D. costaricense* Radlk. vs. leaflets dark green and papillose and appressed puberulous below in *D. elegans* (Radlk.) Radlk. The sterile Oersted collection now recognized as *D. elegans* had originally been described as a variety of *Dilodendron bipinnatum* in the *Flora Brasiliensis* by Radlkofer.

A third species, *D. venezuelense* Steyerm. was described in 1952 from Merida State in northwestern Venezuela, representing the first report of *Dipterodendron* for South America. Like that of *D. elegans* before it, the type of *D. venezuelense* was sterile. The Venezuelan plant was distinguished from *D. elegans* by larger, more coarsely toothed leaflets 2.3–4.5 cm long and 0.6–1.5 cm wide, and because of its geographic disjunction. However, recent collections from Costa Rica also have leaflets reaching 4 cm long and 1.5 cm wide. Some Costa Rican collections have leaflets with coarse teeth and others with fine teeth. Coarse teeth appear to reflect juvenile state rather than a consistent specific difference. Moreover, we have recently closed the geographic gap by collecting *Dipterodendron* in northern Colombia. Thus, we regard *D. venezuelense* as conspecific with *D. elegans.* Croat (1976) has already suggested that all three *Dipterodendron* species might prove conspecific, pointing out that *D. venezuelense* seems intermediate between *D. costaricense* and *D. elegans.* While the vegetative differences—mainly a more strongly appressed-puberulous leaflet undersurface in *D. elegans*—might be inadequate to justify maintaining *D. costaricense* as a species separate from *D. elegans,* there are also previously unreported fruit

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differences. Thus, we refer all Central American and northern South American material of *Dipterodendron* to two rather than three very closely related species, both of which range from Costa Rica to northern Venezuela.

The similarities between *Dipterodendron* of northern South America and monotypic *Dilodendron* of subequatorial South American dry forests suggest that even more merging is in order. This study was initiated when one of us recently collected a bipinnate-leaved Sapindaceae tree as a tree plot voucher at the Tambopata Nature Reserve in geographically intermediate Amazonian Peru. The Peruvian plant was recognized in the field as a species of *Dipterodendron,* representing a very large range extension of the genus. However, the equally striking vegetative similarity between the Peruvian plant and *Dilodendron* was subsequently discovered in the herbarium when an attempt was made to identify it to species. This led to an examination of the taxonomy of the entire complex, which has never been monographed except for a recopying of Radlkofer's earlier descriptions and commentary in his posthumous (1933) *Pflanzenreich* treatment. It turns out that *Dipterodendron* was never adequately differentiated from *Dilodendron* in the first place. Radlkofer (1914), who had seen no flowers, suggested that *Dipterodendron* is intermediate between *Dilodendron* and *Tripterodendron* but differentiated it only from the latter (which has tripinnate leaves and a thick oily aril, and lacks saponiferous cells in the embryo) rather than from the former even though he had earlier referred the first *Dipterodendron* collection to *Dilodendron.* Later (1933) he emphasized slight differences in radicle position. Aristeguieta (1973) questioned the validity of separating *Dipterodendron* from *Dilodendron,* noting that according to the literature *Dipterodendron* usually lacks petals and has the radicle on the margin of the cotyledon, while *Dilodendron* has 3–5 petals and the radicle descending down the middle of the dorsal side of the cotyledons. He ultimately assigned the Venezuelan material to *Dipterodendron* essentially on geographic grounds. Later, Steyermark (in herb.) identified sterile collections from Bolívar State in eastern Venezuela as *Dilodendron bipinnatum,* which would virtually eliminate the geographic discontinuity.

Although *Dipterodendron* might be retained as distinct on the basis of its apetalous flowers, vestigial petals are sometimes present. Moreover, in *Dilodendron* the very small petals are variable in number, mostly 3–4 but sometimes making up a full complement of 5, and sometimes vestigial (Radlkofer, 1892–1900). In fact, male flowers can lack petals altogether, just as in *Dipterodendron.* Since number of petals and even their presence or absence is variable in the single species *D. bipinnatum,* there seems no compelling reason to separate *Dipterodendron* from *Dilodendron* on this basis. There is ample precedent for including in the same genus otherwise similar species that differ in presence or absence of petals, e.g., in *Swartzia, Licania,* or *Combretum*; moreover, other Sapindaceae genera like *Alectryon* and *Mischocarpus* have both petaliferous and apetalous species. Although interpretation of floral sexuality in Sapindaceae from herbarium specimens is very tricky, in the case of *Dipterodendron* loss of petals (only in male flowers?) might reflect a shift to full dioecy. We conclude that *Dipterodendron* should be united with *Dilodendron* to reflect best their extreme similarity. Indeed we are suspicious that monotypic *Tripterodendron,* of which we have examined only sterile material, might also be congeneric with *Dilodendron.* At any rate, some collections of *Dilodendron* have incompletely tripinnate leaves or squamellate petals, and the other distinguishing characters of disk margin, aril consistency, and lack of saponiferous cells in the embryo seem weak.

Dilodendron Radlk., Sitzungsber. Math.-Phys. Cl. Konigl. Bayer. Akad. Wiss. München 8: 355. 1878. TYPE: *D. bipinnatum.*

Dipterodendron Radlk., Smithsonian Misc. Collect. 61(24): 5. 1914. TYPE: *D. costaricense.*

Medium to large dioecious trees. Leaves alternate, bipinnate (rarely in part tripinnate), multifoliolate, the leaflets sessile or subsessile, serrate or dentate. Inflorescence a narrow (often almost subspiciform) panicle, usually borne clustered near the end of a branch and flowering precociously or with the newly expanding leaves. Flowers tiny, the sepals 5, the petals smaller than sepals, sometimes absent, when present variable in number and often in part vestigial, the stamens typically 8 but often fewer, the short anthers inflexed in bud, conspicuously exserted on slender filaments at anthesis, the ovary puberulous, trigonal-ovoid, (2–)3-locular, the style terminating in minute 2–3-lobed stigma. Capsule 2–3-lobed, loculicidally (2–)3-valved, the valves woody or subwoody, the 1–2(–3?) seeds ellipsoid, with a thin, shiny, dark brown testa, scarious aril (fide

Radlkofer), and basal hilum. Embryo (fide Radlkofer) subcircinately curved, the thick carnose cotyledons saponiferous, the radicle dorsal.

KEY TO THE SPECIES OF *DILODENDRON*

1a. Outer margin of leaflet teeth convex, the leaflet margin noticeably ciliate, the lower midrib and lateral nerves with spreading hairs; flowers usually with small well-developed petals; calyx lobes apically rounded; leaves with 5–10, often opposite pinnae; Brazil to southern Peru .... 1. *D. bipinnatum*

1b. Outer margin of leaflet teeth straight, the leaflets not ciliate-margined, the lower midrib and lateral nerves glabrous or strigillose with a few appressed hairs on midrib nerves; flowers apetalous; calyx lobes acute; leaves with 8–16, usually alternate pinnae; Costa Rica to Venezuela and Peru.

  2a. Fruit trigonal-globose, at dehiscence the valves not splitting to the base nor reflexed; inside of valves densely pilose, the outer surface dull, puberulous, and lenticellate; leaflets glabrous beneath, the tertiary venation visibly reticulate .... 2. *D. costaricense*

  2b. Fruit laterally compressed, at dehiscence the valves splitting to the base and reflexing; inside of valves glabrous or sparsely pilose, the outer surface elenticellate, drying black and shiny, the scattered minute trichomes hardly visible on the verruculose surface; leaflets densely strigillose beneath, the tertiary venation usually not evident .... 3. *D. elegans*

1. **Dilodendron bipinnatum** Radlk., Sitzungsber. Math.-Phys. Cl. Konigl. Bayer. Akad. Wiss. München. 8: 355. 1878. SYNTYPES: Brazil. Minas Gerais: *St. Hilaire 1586, Martius s.n., Riedel 1090, Warming s.n.* (US).

Tree 8–20 m tall, to 40 cm dbh, the branchlets usually somewhat angled and/or longitudinally ridged, puberulous with both long and short (in part gland-tipped) hairs when young, becoming glabrescent, lenticels absent or minute and inconspicuous. Leaves bipinnate with 5–10 subopposite or alternate pinnae, rarely the basal leaflets of the lower pinnae completely divided and the leaf subtripinnate, the rachis puberulous with crisped trichomes, flattened adaxially toward base, usually ending in a naked tip extended beyond base of uppermost pinna, the pinnae 3–16-foliolate, the usually alternate leaflets narrowly ovate or oblong-ovate, obtuse to narrowly acute, 1.5–9 cm long, 0.5–3 cm wide, smaller at base and apex of each pinna, the margin rather ciliate and deeply toothed, the outer tooth margin strongly convex, sometimes with 1 or 2 marginal notches (= doubly toothed), puberulous with erect or suberect (sometimes in part gland-tipped) trichomes, above glabrescent except the main veins, below ± persistently pubescent over surface but concentrated on main veins, the tertiary venation somewhat prominulous below, the petiole 6–12 cm long. Inflorescence a terminal fascicle of narrow panicles, usually borne in the axils of fallen leaves at apex of a leafless branchlet, 3–36 cm long, tannish puberulous with trichomes of different lengths, the flowers sessile or subsessile, borne singly or in widely spaced, few-flowered clusters along and at tips of the lower branches (only at apex of the much-reduced upper lateral branches), subtended by bracteoles. Flowers greenish to cream or yellowish, 2–3 (male) to 5 (female, fide Radlkofer) mm long; sepals 5, ovate, unequal, sparsely appressed-puberulous and lepidote, the margins ± ciliate; petals reduced, shorter than sepals, 3–4(–5), sometimes completely lacking in male flowers, broadly obovate, contracted to basal claw, puberulous at least on 2 tiny lateral projections (= scales) near apex of basal stalk; disk glabrous except for tuft of hairs between filament bases; stamens exserted, (6–)8(–9, fide Radlkofer), radiating from center of disk, the filaments ca. 3 mm long, much narrower at apex, the anthers 1–1.5 mm long, reddish; the female flowers (not seen, fide Radlkofer) with puberulous disk, short thick style, and obtuse 3-lobed stigma. Capsule trigonal-obovoid, 1.5–2 cm long, splitting open somewhat unequally to near base, 3-valved, the valves woody, 3–4 mm thick, pubescent inside, glabrous or glabrate outside, drying black, the surface rugulose.

Additional specimens examined. BRAZIL. BAHIA: 10 km W of Barreiras, 500 m, (fr), *Irwin et al. 31317* (F, NY, US). DISTRITO FEDERAL: Bacia do Rio São Bartolomeu, Brasilia, (fl), *Heringer et al. 4530* (MO, NY), (fr), *Heringer et al. 5224* (NY), (fl), *Heringer et al. 7011* (MO). GOIAS: 15 km N of Veadeiros, (fl), *Prance & Silva 58264* (MO, NY, US); Zona do calcareo, corrego Maranhão, (fl), *Pires et al. 9472* (F). MATO GROSSO: Campinapolis, (st), *Haridasan 72* (F); 270 km N of Xavantina, 8 km E of base camp, (fl), *Ratter et al. 1874* (NY). MINAS GERAIS: Ituiutaba, (fl), *Macedo 761* (MO, US); 15 km de Grão Mogol, estr. Montes Claros-Grão Mogol, (fl), *Pirani et al. s.n.* (*CFCR 880*) (NY); Lagoa Santa, (st), *Warming s.n.* (US).

PARAGUAY: prope Concepción, (fl), *Hassler 7393* (MO).

BOLIVIA. BENI: Lake Rogagua, 300 m, *Rusby 1686* (NY). SANTA CRUZ: Río Yapacani, (fl), *Kuntze s.n.* of June 1892 (NY, US); Velasco, (fl), *Kuntze s.n.* of July 1892 (NY, US); Provincia del Sara, Montes de Dolores, Cantón Buena Vista, 450 m, (fl), *Steinbach 2515* (NY);

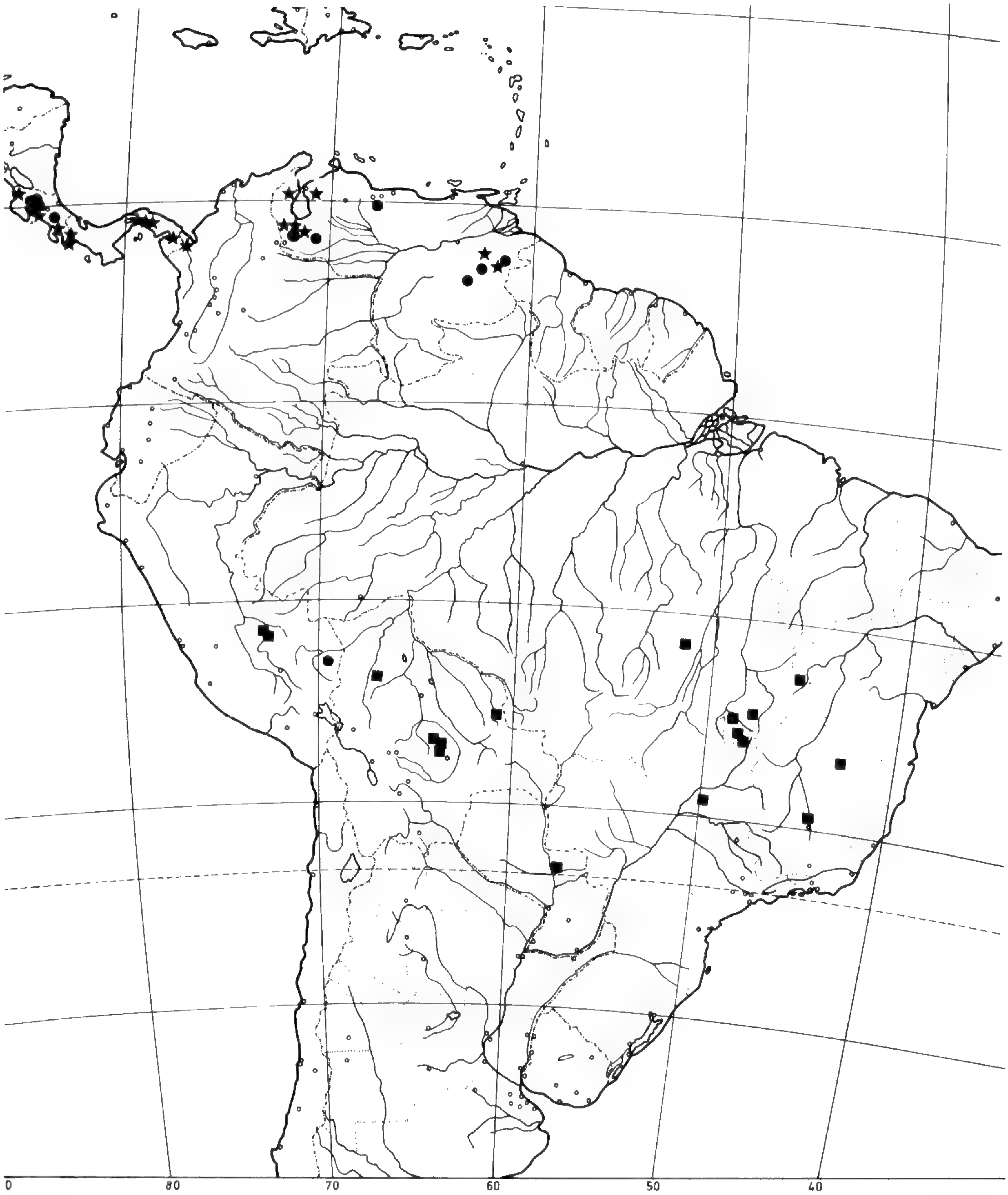

FIGURE 1. Distribution of *Dilodendron*. Squares = *D. bipinnatum*, stars = *D. costaricense*, circles = *D. elegans*.

Buenavista, Prov. Sara, 450 m, (fl), *Steinbach 6479* (F, MO, NY).

PERU. CUZCO: Santa Ana, 900 m, (fl), *Cook & Gilbert 1468* (US), *1617* (US); Potrero, Prov. Convención, 1,500 m, (fl), *Vargas 8228* (US); Santa Ana, Prov. Convención, (fl), *Weberbauer 5020* (F), (fr), *Weberbauer 5020* (F).

Vernacular names. Brazil: *Maria pobre, moniha, pão pobre, farinha secca.* Bolivia: *cuta.* Peru: *sumbayllo hembra, sumbaillo.*

2. **Dilodendron costaricense** (Radlk.) A. Gentry & Steyerm., comb. nov. *Dipterodendron costaricense* Radlk., Smithsonian Misc. Collect. 61(24): 7. 1914. TYPE: Costa Rica. Alajuela:

La Balsa de Río Grande, *Pittier 3645* (holotype, US; isotype, US).

Tree 14–35 m tall, to 45 cm dbh, with buttresses and flat spreading crown, the branchlets glabrescently finely puberulous, minutely and inconspicuously lenticellate. Leaves bipinnate with 8–14 alternate or subopposite pinnae, the rachis puberulous with crisped trichomes, slightly flattened adaxially, often subwinged when young, the pinnae 5–32-foliolate (or the leaflets of the uppermost incompletely differentiated), the alternate leaflets elliptic to oblong-elliptic, obtuse to acutish when mature, often subacuminate when young, 1–4.5 cm long, 0.3–1.5 cm wide, slightly smaller at base and extreme apex of each pinna (or the terminal leaflets incompletely differentiated when young), the margin not ciliate, serrate with relatively even teeth (occasionally almost entire and typically more deeply dentate when young), the outer tooth margin nearly straight, above glandular-punctate, puberulous on midvein, below glabrous or with very few inconspicuous trichomes near base, the tertiary venation visible and often ± prominulous below; petiole 2–9 cm long. Inflorescences several per branch, 5–15 cm long, each a few-branched, narrow panicle arising from axil of fallen leaf, borne below leaves near branch apex in fruit (presumably as in *D. elegans* when in flower), puberulous with crisped and subappressed trichomes. Flowers unknown, presumably 8-staminate from the vestiges at base of young fruits (fide Radlkofer). Capsule trigonal-globose (even when only 2 fertile seeds), 2–3.4 cm long and diam., splitting open only partially, 3-valved, the valves woody, 2–4 mm thick, densely pilose inside, puberulous and minutely raised lenticellate outside, drying dull brownish with tannish lenticels, the seeds bean-shaped, 1.8–2 cm long with a shiny brown testa and a basal hilum.

Additional specimens examined. COSTA RICA. ALAJUELA: La Balsa de Río Grande, (fr), *Pittier 3645* (US); El Coyolar, near San Mateo, 100 m, (fr), *Pittier 3681* (coll. *Werckle*) (US); El Coyolar, 240 m, (st), *Standley 40056* (US); vic. of Capulín, Río Grande de Tarcoles, 80 m, (st), *Standley 40159* (US). GUANACASTE: Santa Rosa National Park, 200–300 m, 10°51′N, 85°37′W, (st), *Janzen 10683* (MO), *Liesner 4236* (MO). PUNTARENAS: Palmar Norte de Osa, 0 m, (fr), *Allen 5738* (US).

PANAMA. CHIRIQUI: Progreso, (st), *Cooper & Slater 280* (NY, US); W of San Bartolo Limite, (st), *Croat 22159A* (MO). DARIEN: Cerro Coasí, Río Coasí, (seed), *Duke 15629* (MO); Yaviza, (fr), *Pittier 6589* (US). PANAMA: El Llano, (fr), *Duke 5818* (MO); Río Tapía, (st), *Standley 28087* (US), *28282* (US); Juan Díaz, (st), *Standley 30574* (US); Río Tapía, (st), *Standley 41186* (US).

COLOMBIA. BOLIVAR: San Juan Nepomuceno, 200 m, 9°58′N, 75°10′W, (fr), *Cuadros & Gentry 3617* (MO). CHOCO: Municipio de Riosucio, Peye, 60 m, (st), *Forero 1781* (COL, MO).

VENEZUELA. BOLIVAR: 48 km NE del caserio Los Rosos, 17 km de Upata, (st), *Blanco 334* (MO, NY, VEN); Altiplanicie de Nuria, ESE of Villa Lola, 315 m, (st), *Steyermark 86364* (NY, VEN). MERIDA: El Vigía-Panamericana, 100–120 m, (st), *Bernardi 2093* (NY). ZULIA: Dtto. Colón, 14–25 km NO de Pto. Chama, (fr), *Bunting & Drummond 6324* (VEN); El Toro, 8 km SSO de El Consejo, (fr), *Bunting & Alfonzo 7054* (VEN); Misión de Tucuco, 105–250 m, (fr), *Ijjasz 88* (NY); La Cocha, Mun. Uribarri, (fr), *Trujillo 12211* (F).

Vernacular names. Costa Rica: *lupinsacca.* Panama: *guavino.* Venezuela: *tamarindo de monte, machirio tamirindo.*

The seeds are said to be edible (*Bernardi 2093*).

3. **Dilodendron elegans** (Radlk.) A. Gentry & Steyerm., comb. nov. *D. bipinnatum* var. *elegans* Radlk., in Mart. Fl. Bras. 13(3): 597. 1900. *Dipterodendron elegans* (Radlk.) Radlk., Smithsonian Misc. Collect. 61(24): 7. 1914. SYNTYPES: Costa Rica. Alajuela: prope Alajuela, *Oersted 4, 5* (C, not seen).

Dipterodendron venezuelense Steyerm., Fieldiana, Bot. 28: 346. 1952. TYPE: Venezuela. Merida: between San Isidro Alto and Santa Cruz de Mora, 760–1,800 m, *Steyermark 56569* (holotype, F; isotype, VEN).

Tree 8–25 m tall, the branchlets longitudinally striate-ridged or slightly angled, minutely puberulous with erect or subappressed trichomes, glabrescent, the lenticels small, inconspicuous and scattered or essentially lacking. Leaves bipinnate with 10–16 frequently opposite or subopposite pinnae, the rachis puberulous with crisped trichomes, grooved above; pinnae (5–)9–23-foliolate, the alternate to subopposite leaflets oblong-elliptic, obtuse to acute, 1–6(–7) cm long, 0.3–2 cm wide, smaller at apex and base of each pinna (or the terminal leaflets incompletely differentiated), the margin not ciliate, serrate with relatively even teeth, the outer tooth margin nearly straight, the upper surface rather glandular and shiny, drying dark, the midrib puberulous, the lower surface drying olive, ± conspicuously strigillose with appressed trichomes, the tertiary venation usually not evident; petiole 3–17 cm long. Inflorescences few-branched, very narrow, subspiciform panicles, typically arising in clusters at the end of a leafless branch from the axils of fallen leaves and often accompanying a cluster of unexpanded new leaves, in fruit ± clustered at the base of the now fully expanded leaves, 3–26 cm long, tannish puberulous with ± appressed trichomes, the flowers mostly in subsessile or short-stalked clusters along it. Flowers reddish, apetalous, the sepals 5, ovate, less than 1 mm long, puberulous; disk flat, densely puberulous; stamens exserted at anthesis, 6–7(–8?), the expanded filaments ca. 2.5 mm long, the short, thick anthers ca. 1 mm long; female flowers similar to immature male flowers, with the 1 mm long densely puberulous ovary tapering into a long, narrow style and surrounded by ca. 6–8 subsessile sterile stamens, the stigma minutely 2-lobed. Capsule compressed-obovoid, 1–1.8 cm long, 1–2 cm wide, splitting to base at dehiscence with the valves reflexed, 2-valved, the valves subwoody, ca. 2 mm thick, sparsely pilose or ± glabrate inside, outside with sparse and inconspicuous scattered trichomes, drying black (red when fresh) with a minutely wrinkled-verrucose surface, elenticellate; seeds mostly 1 per fruit, flattened ovoid, 1 cm long, with shiny dark brown testa and a tan basal hilum.

Additional specimens examined. COSTA RICA. ALAJUELA: Camino de San Ramón, (st), *Brenes 4351a* (NY); La Palma (San Miguel) de San Ramón, 900–1,000 m, (fl), *Brenes 5351* (F, NY); San Pedro de San Ramón, (fl), *Brenes 15041* (F, NY); El Rodeo, (fl), *Lankester 1300* (F); El Rodeo, 900 m, (st), *Pittier 1578* (US); San Pedro, pres San Ramón, 1,300–1,400 m, (fr), *Tonduz 17667* (US). SAN JOSÉ: Basin of El General, 675–900 m, (fl), *Skutch 4850* (F, MO, NY), (fr), *4876* (MO, NY, US).

VENEZUELA. BARINAS: Barinitas, (st), *Bernardi 3337* (VEN). BOLIVAR: between Tumeremo and El Dorado, 29 km N of El Dorado, 220 m, (st), *Steyermark 86570* (NY, VEN); savanna de los Chacharros, 4 km upstream from Raudal Cotua, Río Asa, (st), *Steyermark 86773* (NY, VEN); 2 km SE of Los Patos, 30 km S of El Manteco, 365 m, (st), *Steyermark 86957* (NY, US, VEN). CARABOBO: carretera Maracay–Magdaleno–Guigue, Cuesta de Yuma, 450 m, (fr), *Bunting 4349* (NY). TRUJILLO: Cerro Gordo, sandstone soil on ridge, 9°45′N, 70°15′W, 1,000 m, (fr), *Steyermark & Carreno 111646* (MO, NY, US). ZULIA: Dtto. Colón, carretera Machiques–La Fria entre La Redoma y Placita, (fl), *Bunting & Alfonzo 6930* (VEN).

PERU. MADRE DE DIOS: Tambopata, 12°49′S, 69°18′W, 280 m, (st), *Gentry et al. 46217* (AMAZ, MO, USM).

Vernacular names. Costa Rica: *lorito, gallinazo.* Venezuela: *caro montañero.*

As thus constituted, *Dilodendron* is a small genus of three species with one species (*D. bipinnatum*) mostly in the subequatorial dry areas of the Brazilian shield and adjacent regions, a second (*D. costaricense*) in northern South America extending northward into southern Central America, and a third (*D. elegans*) widespread from Costa Rica to Venezuela and Amazonian Peru. *Dilodendron elegans* and *D. costaricense* are apparently ecologically separated. In Central America *D. elegans* occurs in wet forest, whereas *D. costaricense* occurs in moist forest with a strong dry season and exclusively on the Pacific slope; similarly, in Colombia and Venezuela, *D. costaricense* occurs mostly in drier forests and *D. elegans* in wetter ones.

Dilodendron provides an excellent example of the importance of sterile collections. Not only was the original Peruvian collection that led to this entire revision sterile, but so are most of the other collections of the former *Dipterodendron.* Of the 22 collection numbers of *D. costaricense,* all but six are sterile and six of the ten state records from which it is known, including the only report from Colombia, are based only on sterile collections; the flowers are still unknown. Described from a sterile collection, *D. elegans* is now known from 17 collection numbers from eight different states in three countries; however, only nine of the collections are fertile and the only records for several states as well as for the country of Peru are based on sterile material. Large tropical forest trees like *Dilodendron* will never be understood until more collectors (and collecting institutions) get over their prejudice against sterile collections.

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UNA NUEVA ESPECIE DEL GENERO *DIOSCOREA* (DIOSCOREACEAE) DEL ESTADO DE QUERETARO, MEXICO[1]

O. Tellez V.[2] y B. G. Schubert[3]

Resumen

Se describe *Dioscorea matudae,* una nueva especie del estado de Queretaro, México. Se discuten sus características en relación al sentido seccional dado por Knuth en 1924.

Como parte del proyecto "Desarrollo del Herbario Nacional" en el Instituto de Biología, U.N.A.M., se han hecho colecciones por diferentes regiones de México, una de éstas es en el estado de Queretaro, en donde fue encontrada una especie del género *Dioscorea* que después de un análisis, se determinó como nueva especie para la ciencia y la cual se describe a continuación.

Dioscorea matudae O. Téllez & B. G. Schubert, sp. nov. TIPO: México. Queretaro: 4 km al E del poblado Arroyo Seco, carretera a Jalpan, alt. 840 m, selva baja caducifolia, 20 Oct. 1982, *P. Tenorio L. & C. Romero de T. 2265* (holotipo, MEXU; isotipos, A, ENCB, F, MEXU, MO, XAL).

Herba tenella. Caules sinistrorsum volubiles. Folia ovata, (2.7–)3.5–5.8 cm longa, (1.5–)2–4.3 cm lata, 7-nervia. Inflorescentiae staminatae 4–12 cm longae; flores 2–4(–6) quoque cyma; stamina 6, introrsa. Inflorescentiae pistillatae 2.4–11 cm longae; staminodia 6. Fructus samaroideus ex capsula proveniens, 2 loculis abortivis, 1 evoluto; semen 4 × 3 mm, ala abortiva vel vestigialiter semen circundanti.

Herbácea trepadora glabra. Tallo sinistrorso 1–1.5 mm, ligeramente angulado a lineado. Hojas (2.7–)3.5–5.8 cm de largo, (1.5–)2–4.3 cm de ancho, alternas, ovadas, la base cordada, el ápice agudo a larga y abruptamente acuminado; 7-nervias, prominentes en el envés, ocasionalmente escasa y cortamente serruladas, las más externas bifurcadas; pecíolo (0.7–)1–2 cm de largo, ligeramente angulado, cortamente serrulado. Inflorescencia estaminada 1 ó 2 racimos de cimas o panículas de cimas de 4–12 cm de largo por axila; raquis angulado y conspicuamente serrulado; flores 2–4(–6) por cima; pedicelo ca. 1 mm de largo, conspicuamente angulado, serrulado; bráctea exterior 1–2 mm de largo, 1 mm de ancho, ovado-lanceolada, acuminada; bráctea interior 1 mm de largo, 0.5–1 mm de ancho, ovada. Perianto 1–1.5 mm, verdoso a amarillento; tépalos 1–1.3 mm de largo, 0.5 mm de ancho, oblongos a elípticos; estambres 6, 1 mm de largo, insertados en la base de los tépalos; anteras introrsas, las tecas coherentes; pistilodio 0.2–0.4 mm de alto, cónico a triangular, inconspicuo. Inflorescencia pistilada 1 racimo de 2.4–11 cm de largo por axila; raquis angulado, conspicuamente serrulado; flores solitarias; pedicelo 1–2(–3) mm de largo; bráctea exterior 1.5–2 mm de largo, 0.5–1 mm de ancho, ovado-lanceolada, acuminada; bráctea interior 1–1.5 mm de largo, 0.5 mm de ancho, lanceolada. Perianto 1–1.3 mm, verdoso a amarillento, los tépalos 1–1.3 mm de largo, 0.5 mm de ancho, oblongos a elípticos; estaminodios 6, ca. 0.5 mm de largo, insertados en la base de los tépalos, anteríferos o no; columna estilar 0.8–1 mm de alto, los estilos bífidos, rollizos, delgados. Cápsulas 9–12 mm de largo y ancho, con dos de los lóculos abortados, en algunos casos incompletamente y no se producen semillas (con los dos lóculos completamente abortados 7–8 × 2–5 mm, o con los lóculos desarrollados 9–12 × 6–9 mm), suborbiculares a orbiculares, membranosas; pedicelo acrescente en el fruto 4–6 mm de largo, cortamente serrulado; semilla 4 mm de largo, 3 mm de ancho, suborbicular, parda, solo una semilla en el lóculo desarrollado, el ala casi completamente abortada u ocasionalmente presente como vestigios cerca al hilo.

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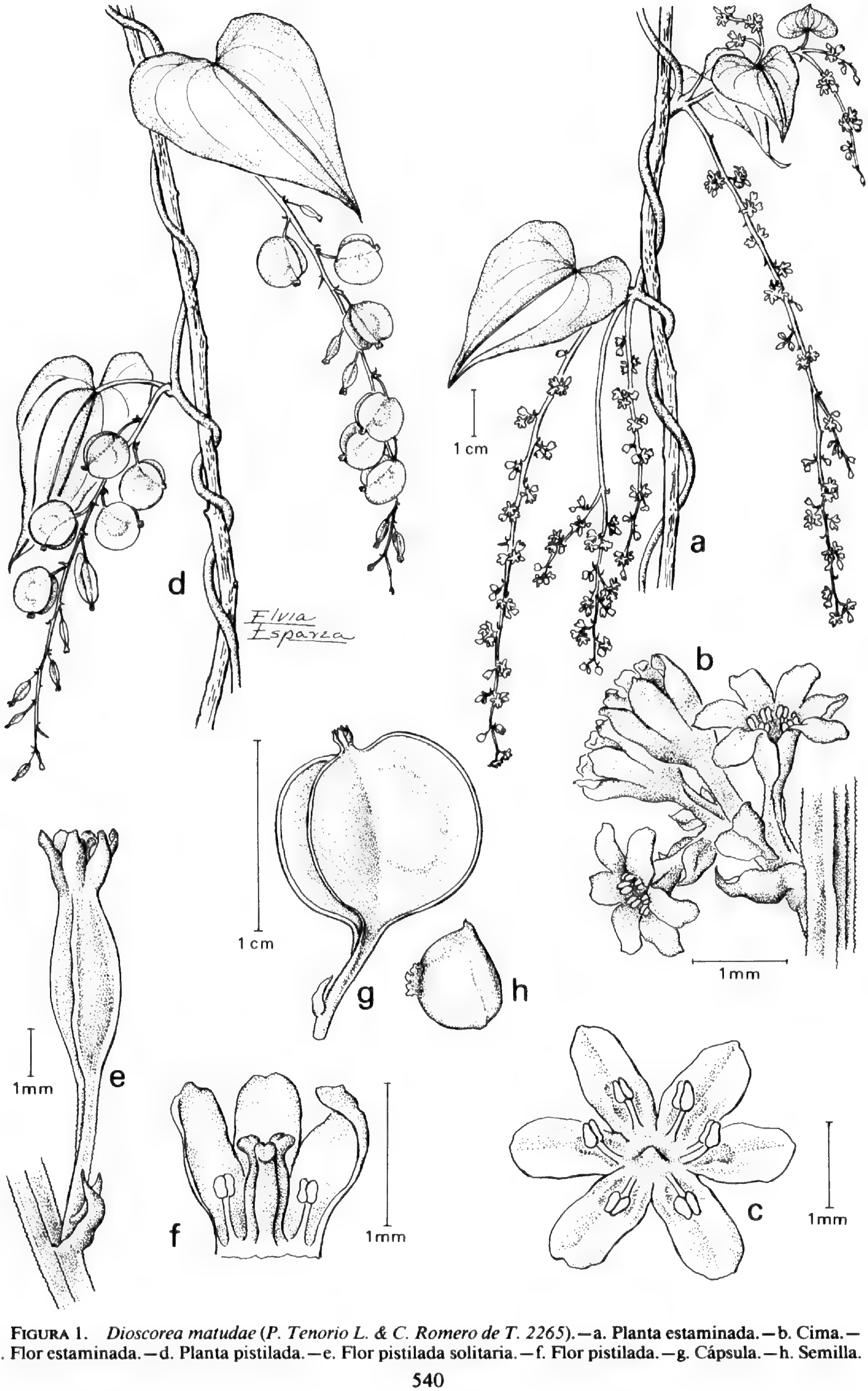

FIGURA 1. *Dioscorea matudae* (*P. Tenorio L. & C. Romero de T. 2265*).—a. Planta estaminada.—b. Cima.—c. Flor estaminada.—d. Planta pistilada.—e. Flor pistilada solitaria.—f. Flor pistilada.—g. Cápsula.—h. Semilla.

Especie interesante y a la vez dificil de relacionar con las especies cercanas en el sentido seccional dado por Knuth (1924). Un conjunto de características permiten distinguirla fácil mente de cualquier otra especie. Estas son la presencia de seis estambres introrsos insertados en la base de los tépalos; pistilodio cónico a triangular, conspicuo, semejante a los observados en la sección *Macrogynodium* Uline; el habito herbáceo delicado; los tallos sinistrorsos; las hojas pequeñas y glabras, semejantes a las de algunas especies con tres estambres y tres estaminodios encontradas en varias secciones del subgénero *Dioscorea* Pax.; su cápsula con dos de los lóculos abortados; la semilla con el ala completamente a casi completamente abortada; y el pedicelo acrescente en el fruto. Estos caracteres hasta ahora conocidos de *D. cyphocarpa* Robinson ex R. Knuth y *D. tacanensis* Lundell de la sección *Polyneuron* Uline, pero que difieren de *D. matudae* por sus tres estambres formando una columna estaminal insertada en el centro del toro.

Lo anterior evidencia con gran probabilidad la presencia de estructuras homólogas en el grupo. Burkill (1960) y Téllez et al. (en prep.) hacen referencia a estas estructuras, interpretándolas como paralelismo en diferentes líneas dentro del género, lo cual probablemente ha dificultado en gran medida determinar las relaciones de sus taxa en una forma objetiva.

Con gran probabilidad ésta especie podría dar origen a una nueva sección por si misma o quedar integrada a algunas de las antes mencionadas con las que comparte las características vistas.

El epíteto específico está dedicado al Dr. Eizi Matuda, quien contribuyó en forma sustancial al conocimiento de las especies mexicanas de éste género.

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SYSTEMATICS OF THE SOUTHERN AFRICAN GENUS *HEXAGLOTTIS* (IRIDACEAE–IRIDOIDEAE)[1]

PETER GOLDBLATT[2]

ABSTRACT

Hexaglottis is a genus of six species occurring along the west and south coast of southern Africa, an area of predominantly winter rainfall. It is a member of tribe Irideae subtribe Homeriinae, which is characterized by a cormous rootstock and secondarily bifacial leaves. *Hexaglottis* is defined largely by an unusual flower structure with shortly clawed subequal tepals and completely divided filiform style arms. This revision includes three new species, *H. namaquana, H. riparia,* and *H. brevituba,* and three that were described before 1800. On the basis of chromosome cytology, experimental hybridization, and vegetative morphology, *H. nana* is excluded from *Hexaglottis*; it is probably allied to the genus *Rheome.* The relationships and history of *Hexaglottis* are discussed, and, following a detailed presentation of taxonomically important characters including chromosome cytology, *Hexaglottis* is analyzed cladistically. *Hexaglottis namaquana* is suggested to be an isolated and primitive relict and the sister species of the remainder of the genus. The southern African genus *Homeria* is probably the closest ally and sister group of *Hexaglottis.* The putative ancestry of these two genera is traced back to a group of species of *Moraea* section *Moraea.* Basic chromosome number in *Hexaglottis* is $x = 6$, while *H. nana* has $x = 10$, a number shared with *Rheome* and basic for *Moraea.*

Hexaglottis is a small genus of Iridaceae tribe Irideae restricted to the winter rainfall area of southern Africa (Fig. 1). It has linear, bifacial, and usually channeled leaves; corms of the *Moraea* type composed of a single swollen internode and apically rooting bud; and umbel-like inflorescence units (rhipidia) enclosed in large, opposed, herbaceous bracts (spathes). This series of characteristics establishes its systematic position in the predominantly southern African subtribe Homeriinae (Goldblatt, 1976b: 661, 1980) of the Old World tribe Irideae. The floral structure is distinctive and, although not unique, defines the genus. The subequal tepals have short erect claws and horizontally extended limbs, and the styles are short with branches divided almost to the base into paired filiform arms that extend outwards on either side of the subtending anther. The flowers are yellow and fugacious, lasting only a few hours. Additional features are firm, brown- to blackish-reticulate corm tunics and a basic chromosome number of $x = 6$.

Moraea hexaglottis (Goldblatt, 1986) has a similar flower structure, but the flowers are blue, unlike *Hexaglottis,* and the basic chromosome number is $x = 10$. A second species, described by H. M. L. Bolus as *H. nana,* has flowers essentially identical to those of other species of *Hexaglottis,* but it has dark brown, unbroken corm tunics, unusual fasciculate rhipidia, and a base number of $x = 10$. It is here excluded from *Hexaglottis.* Crossing studies, chromosome morphology (detailed below), and vegetative morphology indicate that it is related to the small genus *Rheome,* comprising *R. maximiliani* and *R. umbellata,* and probably also to *Moraea linderi* and *M. margaretae,* which recent unpublished investigation has indicated are closely allied to *Rheome.*

The peculiar *Hexaglottis* type of flower is thus believed to have evolved independently three times. It defines *Hexaglottis* only in combination with the vegetative and chromosomal features mentioned above.

RELATIONSHIPS

Hexaglottis is probably most closely allied, within the Homeriinae, to *Homeria,* and avail-

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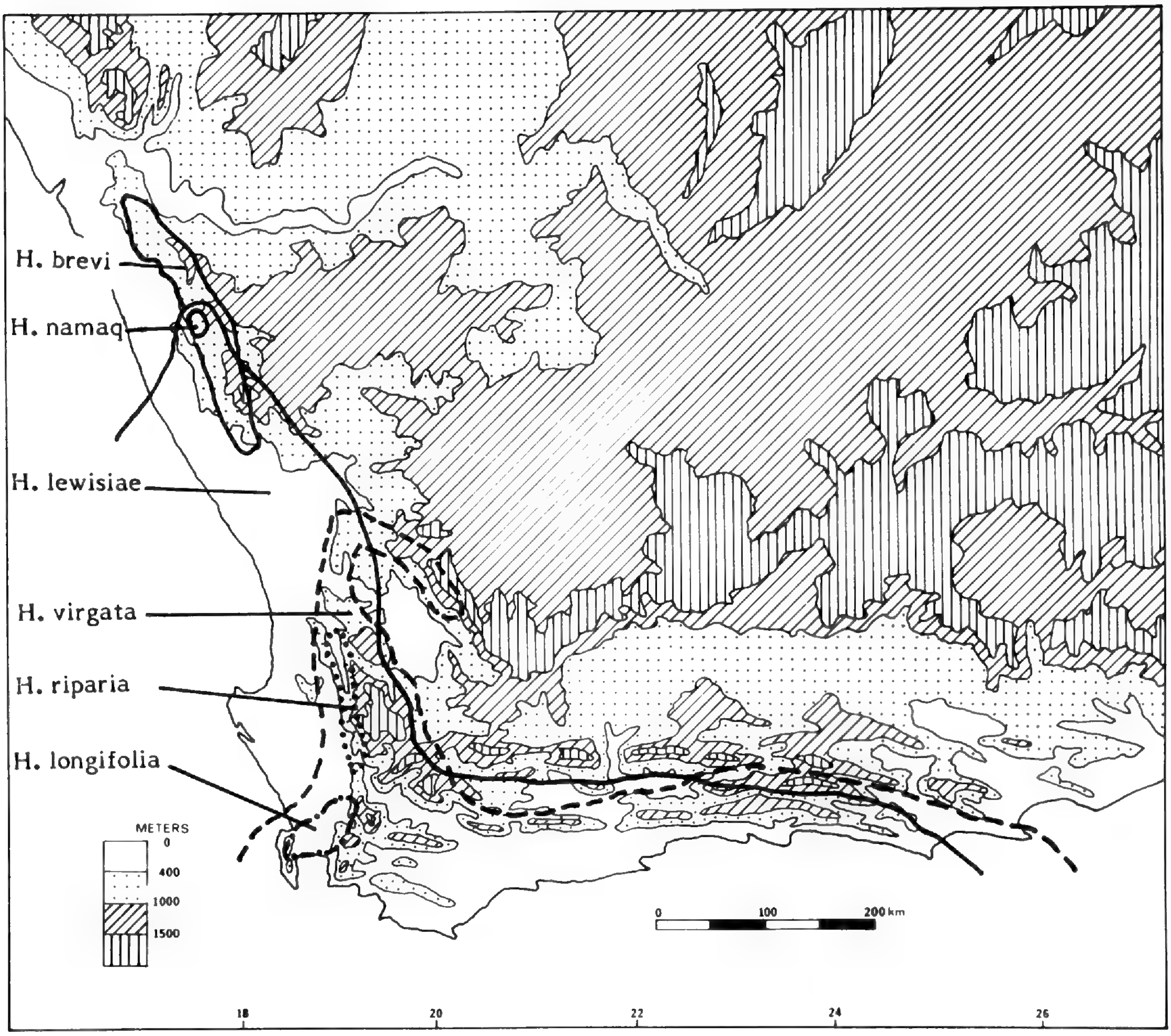

FIGURE 1. Geography of *Hexaglottis*.

able morphological and cytological data suggest that the two genera have as a common ancestor (Fig. 5) probably a species or group of species of *Moraea* allied to *M. flexuosa* (Goldblatt, 1982). The characteristics that *Homeria* and *Hexaglottis* share include subequal tepals, the claws of which cup the lower part of the filaments, and style branches reduced from the elaborate flattened structures basic for Homeriinae (Goldblatt, 1980, 1986) and probably for the entire tribe Irideae (Goldblatt, in prep.). The two genera also share a similar and derived karyotype with $x = 6$ comprising strongly acrocentric to subacrocentric chromosomes. Genome size (Goldblatt et al., 1984) is similar, 22–29 pg DNA in *Homeria* and 20.6 pg DNA in *Hexaglottis namaquana*, the only species of the genus for which this is known. *Moraea flexuosa* has a comparable karyotype. Other members of *Moraea* that appear less closely related include a part of the heterogeneous section *Moraea*, $x = 10$, and section *Polyanthes*, $x = 6$, the latter distinguished by having blue to violet flowers (a derived condition in *Moraea*). The karyotype in section *Polyanthes* is also somewhat different in comprising acrocentric and submetacentric chromosomes (Goldblatt, 1980).

HISTORY OF *HEXAGLOTTIS*

The taxonomic history of *Hexaglottis* has been described by G. J. Lewis (1959) in detail, and it is reviewed here briefly. The first of the species now admitted to *Hexaglottis* was described by Nicholas Jacquin in 1776 as *Ixia longifolia*. The excellent figure that now serves as the type of the species is unmistakably this Cape Peninsula species, often confused with the more common and widespread *H. lewisiae*. Shortly afterward, the younger Linnaeus described a second species as *Moraea flexuosa* (Linnaeus fil., 1781). This name is now regarded as nomenclaturally superfluous and illegitimate, and a new name, *H. lewisiae*, was proposed for the species in 1971 (Goldblatt, 1971a) (see discussion under this species).

The very distinctive, late-flowering *Hexaglottis virgata* was described in 1791 by Jacquin, this species also being assigned to *Moraea.* As with Jacquin's earlier species of *Hexaglottis,* a fine illustration leaves no doubt about its identity. Thus, all three common southwestern Cape species of the genus were known and described by the beginning of the nineteenth century when E. P. Ventenat erected the genus in 1808. Ventenat made no transfers to his new genus, mentioning only *Ixia longifolia* Jacq. by name, "*Ixia longifolia* Jacq. etc.," which leaves one wondering whether he had further species in mind. The genus soon gained acceptance, and combinations were made for *H. longifolia* by R. A. Salisbury (1812) and for *H. virgata* and the illegitimate *H. flexuosa* by Sweet (1830). One more species was collected in the nineteenth century, *H. riparia,* discovered by C. F. Ecklon & C. L. Zeyher (their *Irid. 30*), but the collection was consistently assigned to *H. flexuosa.*

The three described species of *Hexaglottis* were regarded as a single taxon by Klatt (1866) under the name *Homeria spicata* (Ker) Sweet, the type of which is conspecific with the earlier *Homeria elegans* (Jacq.) Sweet (Goldblatt, 1981). Later, Klatt (1882: 52, 1895: 159) recognized *Hexaglottis* with *H. longifolia* (including *H. lewisiae*) and *H. virgata.* Baker's (1896) definitive nineteenth century floristic treatment of the Iridaceae in *Flora Capensis* is identical, but he understood *Hexaglottis* so inadequately (Lewis, 1959) that his work on the genus must be disregarded.

Louisa Bolus added one more species to *Hexaglottis* in 1932, the west coast *H. nana,* which, although common, was apparently only discovered in the 1920s. *Hexaglottis nana* as already outlined differs markedly in its vegetative morphology, cytology, and crossing relationships from *Hexaglottis* and is now excluded from the genus (for comparison of *H. nana* with *H. lewisiae* see Fig. 2).

Lewis's (1959) revision of *Hexaglottis* admitted four species to the genus and two new varieties, *H. virgata* var. *lata* and *H. longifolia* var. *angustifolia,* neither of which is recognized here.

Collecting since the publication of Lewis's revision, especially in the arid country to the north of the Cape Floristic Region, has substantially expanded the knowledge of *Hexaglottis.* I discovered a new species, *H. namaquana,* in the Spektakel Mountains of northern Namaqualand in 1974 and extended the range of *H. lewisiae* into these mountains west of Springbok. The distinctive new *H. brevifolia* of northern Namaqualand and the Richtersveld is now recognized, specimens previously having been placed in *H. lewisiae* and *H. virgata* by Lewis, and a new subspecies of *H. virgata,* subsp. *karooica,* has been described from the Roggeveld Escarpment in the western Karoo. Lastly, plants treated as *H. longifolia* var. *angustifolia* by Lewis (1959) have been re-collected and are regarded as a distinct species described here as *H. riparia.*

The picture in 1959 of *Hexaglottis* as a small genus essentially of the Cape Floristic Region with minor extensions of *H. lewisiae* and *H. virgata* to the north into semi-arid Namaqualand has changed fundamentally. *Hexaglottis* must now be viewed as centered along the interior Cape West Coast with extensions south and east into the Cape Floristic Region.

MORPHOLOGY

Rootstock. Species of *Hexaglottis* have a corm of the *Moraea* type (Goldblatt, 1976b: 670, 1981: 428) consisting of a single swollen internode with an apical primordium from which both shoot and roots are produced. This organ is one of the two major specializations defining subtribe Homeriinae. The corm originates from an axillary bud near the base of the flowering stem. The corm tunics are basically like those found in *Homeria* and several species of *Moraea* subgenus *Moraea* and consist of a coarse open network of hard, wiry, dark brown to black fibers. In *Hexaglottis* the mealy substance between the fibers often persists and clings to the fibers, imparting a lighter color to them. The outer tunic layers are usually paler in color and characteristically medium brown in many collections of *H. virgata* and *H. lewisiae.* The two moisture-loving species, *H. riparia* and *H. longifolia,* have softer-textured tunics, the outer layers of which become light brown and the fibers are relatively fine.

Leaves. The leaves are bifacial with a sheathing base and more or less linear and channeled, this being the basic leaf type for Homeriinae. The leaves of *Hexaglottis namaquana* are the most distinctive, being relatively broad, almost prostrate, strongly undulate, lightly twisted with the

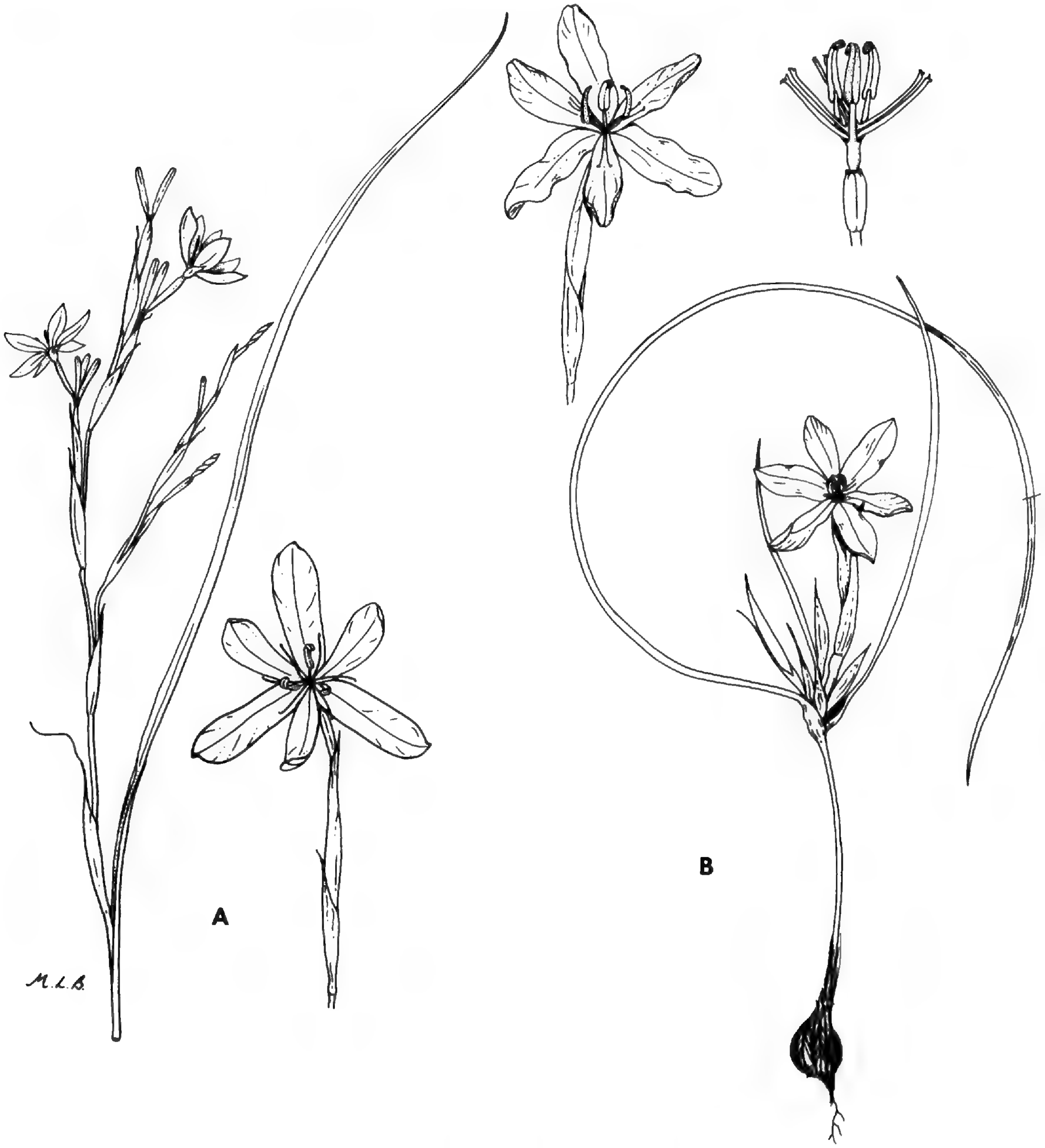

FIGURE 2. Habit and flowers of *Hexaglottis lewisiae* (A) and for comparison the vegetative and floral morphology of *'Hexaglottis' nana* (B). Compare for example, Figures 6 and 11. Habits ×0.5; single flowers full size; separated stamens and style branches ×2.

margins sometimes somewhat crisped. The leaf condition in *H. namaquana* must be regarded as derived from the much more common erect linear leaf with straight margins found in the other species of the genus and thus represents one or possibly two autapomorphies. The leaves of *H. virgata* may be lightly coiled distally, a feature obscure in herbarium material. There are usually two to three foliage leaves per plant, but the number depends on growing conditions, so that fewer leaves are produced in drier seasons. Plants always produce more leaves in the greenhouse than in the wild. Under optimal conditions *H. longifolia, H. riparia,* and *H. virgata* subsp. *karooica* have four or five leaves. The leaves are inserted fairly close together near or slightly below ground level, but in *H. lewisiae* subsp. *secunda,* the leaf or leaves may be inserted some distance above the ground.

Flowering stem, sheathing bract leaves, and *branching patterns.* The flowering stem is more or less erect, particularly so in *Hexaglottis virgata,* but willowy and nodding in *H. longifolia* and *H. riparia.* There may be up to three or four major branches, each stalked and bearing a few to several sessile lateral rhipidia (the inflorescence units). The exception is *H. namaquana* in which all the rhipidia are stalked, presumably the ancestral condition, and thus terminal on the main or lateral branches. The sessile lateral rhipidia are a derived feature, and a synapomorphy separating the main group of species of *Hexaglottis* from *H. namaquana.*

A sheathing bract leaf with a closed sheath subtends each branch or lateral rhipidium. In the latter, the sheathing bract leaf resembles the inflorescence spathes, which it may completely conceal. Each sheathing bract leaf generally overlaps the one above, except in *H. longifolia,* the cauline internodes of which are comparatively long. Lewis (1959) used this feature as an important character for distinguishing *H. longifolia.*

Rhipidia. The inflorescence units are of the basic type for Iridaceae, consisting of compressed cymose umbels enclosed in two large, opposed, sheathing spathes, the inner of which exceeds the outer except in the lateral rhipidia of *H. longifolia,* where they are nearly equal, a presumably specialized condition. Individual flowers are pedicellate and subtended by a single membranous bract contained within the spathes. The flowers are produced serially, a few days apart, at which time the pedicels elongate to raise the flowers out of the spathes. In *Hexaglottis brevituba* and *H. virgata* the pedicels are short and the ovaries are included in the spathes, but the flowers have a perianth tube that serves the same function as the pedicel in extending the flowers beyond the spathes. The spathes are initially herbaceous with dry attenuate apices, but towards the middle of the flowering season they begin to dry out and become light brown and chaffy towards the middle. The short pedicels, included ovaries, and perianth tube are important synapomorphies separating *H. brevituba* and *H. virgata* from the rest of the genus.

Flower. The flower is almost uniform throughout *Hexaglottis,* except for the presence of a tube in *H. brevituba* and *H. virgata,* and is unusual in Iridaceae in the structure of the style and style branches and the relationship of the latter to the stamens. The shortly clawed tepals are pale to deep yellow and subequal, or those of the inner whorl are slightly smaller. The claws, 1–2 mm long, are erect and form a cup around the base of the filaments, while the relatively long limbs spread horizontally. The filaments are united below for 1–3 mm into a column, at the apex of which the style divides into three branches, each opposite a stamen. The branches divide almost immediately to form two long, filiform, apically stigmatic arms which extend outwards more or less horizontally to either side of the subtending stamen. The flowers are short-lived, opening in the mid to late afternoon and fading about three hours later. The unusual structure of the style of this flower has led to the placement of all species with this character together in a single genus, but data presented in this revision indicate that *H. nana,* described by Louisa Bolus in 1932, is distantly related to the other species of *Hexaglottis* and must have acquired its *Hexaglottis*-like flower by convergence. A similar flower has also evolved in *Moraea hexaglottis* (Goldblatt, 1986). The divided style branches and filiform ascending arms are the primary characters separating *Hexaglottis* from other genera of Homeriinae, to which should perhaps be added the partly free filaments, a probable reversal from an ancestral condition with apically free filaments as in the putative relatives *Moraea flexuosa* and *Homeria* (Fig. 5). The free part of the filaments allows the long anthers to be displayed prominently and also well separated from the style branches which almost always in Homeriinae divide at the top of the united part of the filaments.

As already mentioned in the paragraph dealing with rhipidia, flowers of *Hexaglottis virgata* and *H. brevituba* have short pedicels and included ovaries. In other species the pedicels are about as long as the spathes, and at anthesis the ovary is almost always exserted.

Fruit. Capsules of *Hexaglottis* species vary considerably and are important in recognizing species and in assessing phylogenetic relationships. The capsules are typically exserted from the spathes and are basically ellipsoid in shape, as in *H. namaquana* and *H. lewisiae* subsp. *secunda.* In the latter, the capsule has a short beak, a feature not always evident in populations from Namaqualand but strongly expressed in plants from the northwest Cape. *Hexaglottis lewisiae* subsp. *lewisiae* has trigonous, more or less cylindric capsules, while obovoid to clavate capsules distinguish *H. riparia* and *H. longifolia.* The capsules of *H. longifolia* are relatively large, 12–16 (–23) mm long, but only 6–10(–12) mm long in *H. riparia,* the smaller size presumably basic and consistent with capsule dimensions of other

TABLE 1. Chromosome numbers in *Hexaglottis* and *Rheome*. Original counts are marked with an asterisk. Previous counts were reported by Goldblatt (1971b, 1980).

Species	Haploid Number	Collection Data
		HEXAGLOTTIS
H. namaquana Goldbl.	6*	Spektakel Pass, west of Springbok, *Goldblatt 3059* (MO).
H. lewisiae Goldbl. subsp. *lewisiae*	6*	Tulbagh Cemetery, *Goldblatt 5224* (MO); Cape Town, Kirstenbosch Gardens (wild plants), *Goldblatt 5104* (MO).
subsp. *secunda* Goldbl.	6	Loeriesfontein road, north of Nieuwoudtville, *Goldblatt 108* (J).
	6*	Spektakel Pass, west of Springbok, *Goldblatt 6513* (MO); granite outcrops SW of Skuinskraal, near Hondeklipbaai, *van Berkel 453* (MO); near Nieuwoudtville, *Goldblatt 6535* (MO).
H. riparia Goldbl.	6*	Olifants R. bank at Citrusdal, *Goldblatt 6555* (MO).
H. longifolia (Jacq.) Sweet	12*	Cape Town, Kirstenbosch Gardens (wild plants), *Goldblatt 5934* (MO), *Malan 120* (NBG).
H. brevituba Goldbl.	12*	Near the Kosies road, NW of Steinkopf, *Goldblatt 5748* (MO).
H. virgata (Jacq.) Sweet subsp. *virgata*	5	Signal Hill, Cape Town, *Goldblatt 71* (J).
	5*	Slopes near parking area, Signal Hill, Cape Town, *Goldblatt 6747* (MO); Signal Hill, near Sheik's tomb, *Goldblatt 6768* (MO); lower slopes of Devils Peak, *Goldblatt 6717* (MO).
	6*	Hills west of Riversdale, *Goldblatt 5436* (MO); Franskraal, near the coast, *Goldblatt 5368* (MO); near Misgund, *Goldblatt 6792* (MO); between Bredasdorp and Napier, *Goldblatt 6937* (MO); between Doorn River and Bidouw road, *Goldblatt 5941* (MO).
subsp. *karooica* Goldbl.	7*	Roggeveld, near Voelfontein farm, *Goldblatt 6336* (MO); Blomfontein farm west of Middelpos, *Snijman 765* (MO, NBG).
'*Hexaglottis*' *nana* L. Bolus	10*	Olifants River valley near Alpha, *Goldblatt 5120* (MO); Pakhuis Pass, near Soldaat Kop, *Goldblatt 5158* (MO).
		RHEOME
R. maximiliani (Schltr.) Goldbl.	10	Brandewyn River near Travellers Rest, *Goldblatt 3884* (MO).
R. umbellata (Thunb.) Goldbl.	10*	East end of Du Toits Pass, *Goldblatt 5907* (MO).
	15	Paarl Golf Course, *Goldblatt 4414* (MO).
	15*	Piketberg, top of Versveld Pass, *Goldblatt 5163* (MO); foot of the Elandskloof Mts. at Elandsberg farm, *Goldblatt 5853* (MO).

species. The capsules of *H. virgata* and *H. brevituba* are included in the spathes and are narrowly fusiform. They remain enclosed by the spathes through ripening and dehisce only in the upper part.

The seeds are brown and basically angular, but elongate in *H. virgata* and *H. lewisiae* subsp. *lewisiae,* both of which have narrow capsules (seeds of *H. brevituba* are not known). Seeds of *H. longifolia* are unusually large, a feature possibly relating to its polyploid state. *Hexaglottis lewisiae* subsp. *secunda* can usually be distinguished by the raised and winglike angles of the seeds. The seeds are known from only a few populations of this subspecies, and I hesitate to regard the winglike angles as characteristic of the taxon until more is known about their occurrence.

CHROMOSOME CYTOLOGY

The cytology of *Hexaglottis* was investigated extensively for this study. The method followed here is the same as that outlined for similar in-

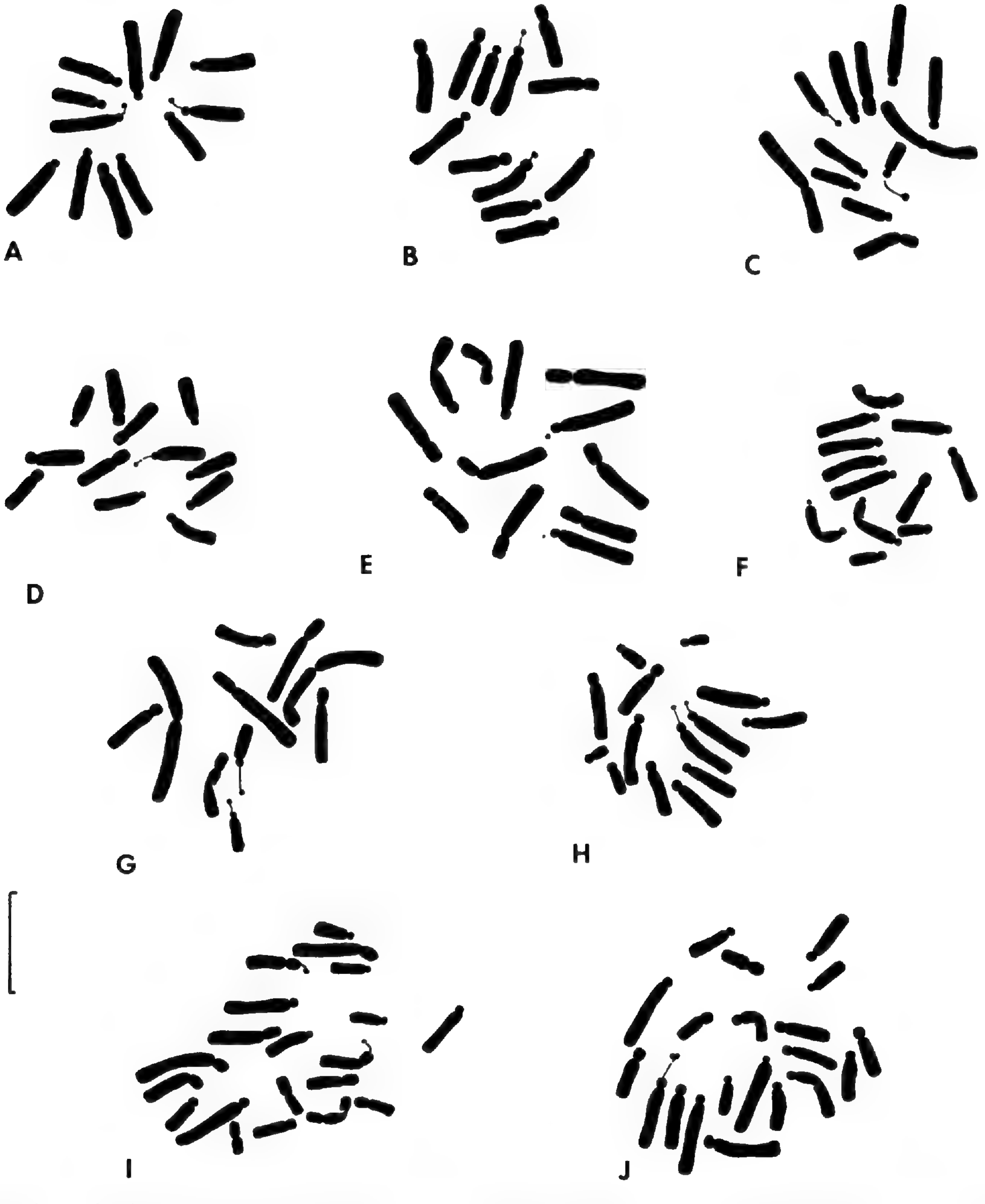

FIGURE 3. Mitotic metaphase configurations of *Hexaglottis* species.—A. *H. namaquana.*—B. *H. lewisiae* subsp. *lewisiae.*—C. *H. lewisiae* subsp. *secunda.*—D. *H. riparia.*—E. *H. virgata* subsp. *virgata,* $2n = 12$ (Franskraal, *Goldblatt 5368*).—F. subsp. *virgata* $2n = 12$ (Doorn R.–Bidouw, *Goldblatt 5941*).—G. subsp. *virgata* $2n = 10$ (Signal Hill, *Goldblatt 6747*).—H. *H. virgata* subsp. *karooica,* $2n = 14$.—I. *Rheome umbellata,* $2n = 20$.—J. '*Hexaglottis*' *nana,* $2n = 20$. Scale = 10 µm.

vestigations in Iridaceae (Goldblatt, 1979, 1980). The results are presented in Table 1. Base number in *Hexaglottis* is $x = 6$, this originally suggested on the basis of one count for *H. lewisiae* (as *H. flexuosa*), $2n = 12$ (Goldblatt, 1971b), while a single count for the specialized *H. virgata,* $2n = 10$, suggested that this species was a derived aneuploid. Several additional counts for *Hexaglottis* have confirmed $x = 6$ as basic. *Hexaglottis lewisiae, H. namaquana, H. riparia,* and three populations of *H. virgata* all have $2n = 12$. The two known populations of *H. virgata* subsp. *karooica* both have $2n = 14$, while *H. longifolia* is tetraploid with $2n = 24$.

The two populations of *Hexaglottis nana* examined cytologically were found to have a diploid number of $2n = 20$ and a karyotype exactly like that of the diploid *Rheome maximiliani*

(Goldblatt, 1980). Basic chromosome number in *Rheome,* already established (Goldblatt, 1980) as $x = 10$, has been confirmed here, with additional counts for *R. umbellata.* This species was originally thought to be triploid, $2n = 30$, but one diploid population has been discovered, as well as two more triploid populations (Table 1).

The chromosomes of *Hexaglottis* species are fairly large, ranging in size in the basic karyotype from 5 to 9 μm with the method used here. The basic karyotype as exemplified in the least specialized species, *H. namaquana,* consists of acrocentric to nearly telocentric chromosomes with a satellite on the distal end of the short arm of the third or fourth longest pair (Fig. 3A).

Hexaglottis lewisiae subsp. *lewisiae* and *H. riparia* (Fig. 3B, D) have a similar karyotype, but the satellite is located on one of the longest chromosome pairs. Size differences are relatively small, and the shortest chromosomes are only ±35% smaller than the longest (Fig. 3A–C; see also Goldblatt, 1971b: 364, fig. 14E). *Hexaglottis longifolia* is tetraploid, $2n = 24$, but otherwise has a karyotype comparable to that of *G. riparia* and *G. lewisiae* subsp. *lewisiae.*

The Namaqualand populations of *Hexaglottis lewisiae* subsp. *secunda* (Fig. 3C) have an apparently derived karyotype. The longest chromosome pair is metacentric and about 12.5 μm long, nearly twice as long as the next in size, an acrocentric pair. The third or fourth pair is submetacentric, while the smallest pair has a large satellite (Fig. 3C) and is only 5 μm long, about one-third as long as the long metacentric. This karyotype has been found in two widely separated Namaqualand populations of this poorly sampled subspecies (Table 1), but a population from Nieuwoudtville, well to the south, has a karyotype of acrocentric chromosomes, unusual only in having a satellite on the end of a long arm of a long chromosome pair. The single plant that I examined was structurally heterozygous, having only one satellite present.

In the specialized *Hexaglottis virgata,* there is unexpected intraspecific variation in the karyotype. The presumed basic karyotype (Fig. 3E) as found in southern Cape populations of subsp. *virgata* consists of six pairs of acrocentrics, the first and third of which have a distinctly longer short arm. The satellite is located on the second longest and strongly acrocentric pair. A northern population of *H. virgata* (*Goldblatt 5491*) can be distinguished cytologically by having satellites on the distal end of the long arm of the longest and strongly acrocentric pair (Fig. 3F). The northern populations may be a separate cytological race, but more material needs to be examined. Cape Peninsula populations of *H. virgata* are aneuploid, $2n = 10$ (Goldblatt, 1971b), and have a karyotype exhibiting considerable structural rearrangement. The longest pair (Fig. 3G) is metacentric and about 12 μm long, while unusually large satellites are located on the shortest and acrocentric pair, the satellite being longer than the short arm. Robertsonian fusion of two acrocentric, medium-sized pairs and the translocation of the satellite to the smallest pair would account for the modified karyotype.

Hexaglottis virgata subsp. *karooica* is unusual in the genus in its diploid number of $2n = 14$ (Fig. 3H). Three individuals of both known populations were examined. The chromosomes are more strongly acrocentric than in the basic $2n = 12$ cytotype of subsp. *virgata* and there are two, rather than a single, small pairs. The origin of the extra small pair is unknown. Satellites in the subspecies are located on the ends of the short arms of a large chromosome pair.

Karyotype evolution in *Hexaglottis* appears to have proceeded from a basic, rather uniform, acrocentric set of chromosomes to increasing symmetry with the development of greater size differences and, in *H. lewisiae* subsp. *secunda* and the Cape Peninsula populations of *H. virgata* subsp. *virgata,* the evolution of large metacentrics, in the latter with a decrease in base number to $x = 5$. *Hexaglottis virgata* subsp. *karooica* seems to be one of the rare examples in Iridaceae of an increase in base number, as the karyotype of this specialized and rare taxon is almost certainly derived from ancestors with $x = 6$. The origin of the extra pair of small chromosomes is problematic. The tetraploid *H. longifolia* may have evolved by amphipolyploidy, and its large size, especially in vegetative and fruit characters, may be a direct result of its polyploidy. *Hexaglottis brevifolia* has the same base number as the genus but details of its karyotype were not seen in the poor material available.

HYBRID STUDIES

A crossing program involving three species of *Hexaglottis, H. nana,* and *Rheome maximiliani* in the spring of 1982 produced results (Fig. 4) that confirm the indications from cytology that *H. nana* is allied to *Rheome* rather than to *Hexaglottis. Rheome maximiliani* could be crossed readily to emasculated flowers of *H. nana,* while

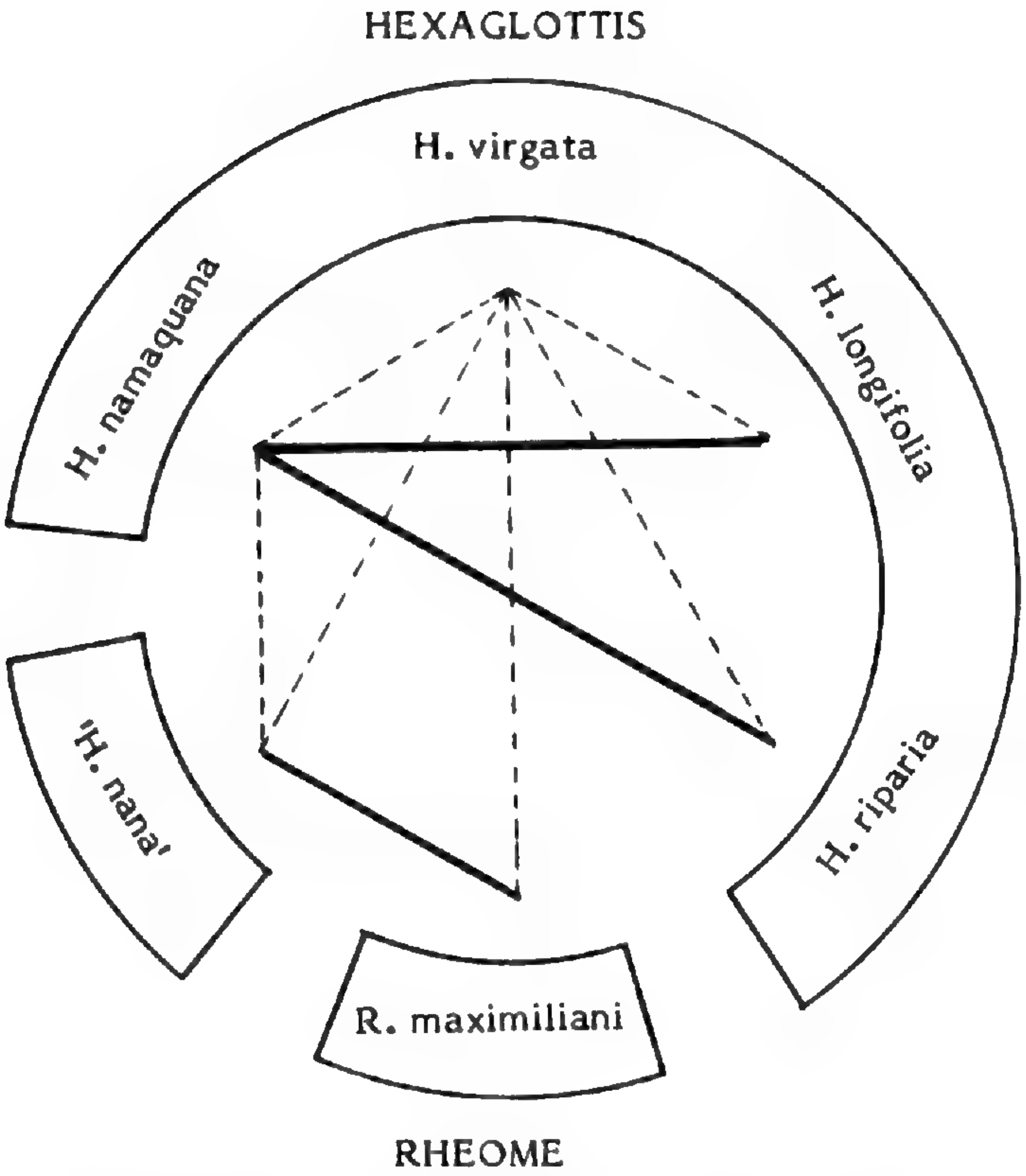

FIGURE 4. Crossing relationships in *Hexaglottis*, '*H.*' *nana*, and *Rheome maximiliani*. Heavy lines indicate successful crosses; dotted lines indicate crosses were attempted but failed.

repeated attempts to cross both of these species with three species of *Hexaglottis* used in the study failed. Attempts to make interspecific crosses between other species of *Hexaglottis* produced mixed results. Successful crosses were made between *H. longifolia*, *H. riparia*, and *H. namaquana*, but all attempts to cross *H. virgata* with these species failed. The study was not extended to the species of *Moraea* that are most similar to *Rheome*, namely *M. linderi* and *M. margaretae*, as neither was available in cultivation.

REPRODUCTIVE BIOLOGY AND POLLINATION

The *Hexaglottis* flower is relatively small and inconspicuous, especially for Iridaceae, but as plants typically grow in fairly dense colonies and produce several flowers each day, they often make an effective display. Individual flowers of all species last only a few hours, opening at constant times depending on the species or population, in mid to late afternoon and closing in the early evening. All species except *H. longifolia* are strongly self-incompatible (*H. brevifolia* unknown). Very rarely a few undersized capsules are produced on plants by autogamy late in the flowering season, but normally flowers do not set seed by their own pollen, even though a small quantity of pollen is usually deposited on the stigmas while the flowers are open. The exception, *H. longifolia*, is self-compatible and autogamous. Plants produce numerous full capsules with fertile seed without cross-pollination.

The pale to deep yellow stellate flowers of *Hexaglottis* are typically pollinated by bees. The small nectaries, located at the base of the outer tepals, produce a limited quantity of nectar which is retained in the space between the short, erect tepal claws and the filaments. The nectar, however, seems to be of secondary importance, and the insect visitors appear to be attracted primarily to the pollen, a large amount of which is produced in the relatively long anthers.

Although the flowers of all species are very similar, there is a considerable difference in the response of bees to the flowers of the three species, *H. lewisiae*, *H. virgata*, and *H. longifolia*, for which I have careful observations. *Hexaglottis longifolia* is totally unattractive to bees, which ignore open flowers even when they pass close to them. The same bees, however, visit the opening flowers of *H. lewisiae* subsp. *lewisiae* growing within a few meters of *H. longifolia*. Bees gather around populations of *H. lewisiae* in the middle of the afternoon about the time its flowers normally open, and they begin to gather pollen as soon as the flowers open.

Hexaglottis virgata is similarly attractive to bees, but pollinator activity was always less intense than in *H. lewisiae*. Honeybees (Apidae) and species of Anthophoridae were observed pollinating *Hexaglottis* flowers.

PHYLOGENY

Cladistics affords the most objective and critical method of assessing the phylogeny of a group, and the results of a cladistic analysis of *Hexaglottis* and its immediate allies are presented below. The cladogram (Fig. 5) was constructed manually following concepts of clustering by shared derived characteristics (synapomorphies) and parsimony established by Hennig (1966) and adapted by several botanists recently (Bremer, 1976; Humphries, 1981; Funk, 1982; Goldblatt, 1985). As discussed in the preceding pages, *Hexaglottis* (excluding *H. nana*) is believed to be a natural (monophyletic) assemblage distinguished by a number of specialized features, their polarity determined by outgroup comparison and by generally accepted trends in Iridaceae. The characters used for the cladistic analysis are presented in Table 2, and most of them are discussed

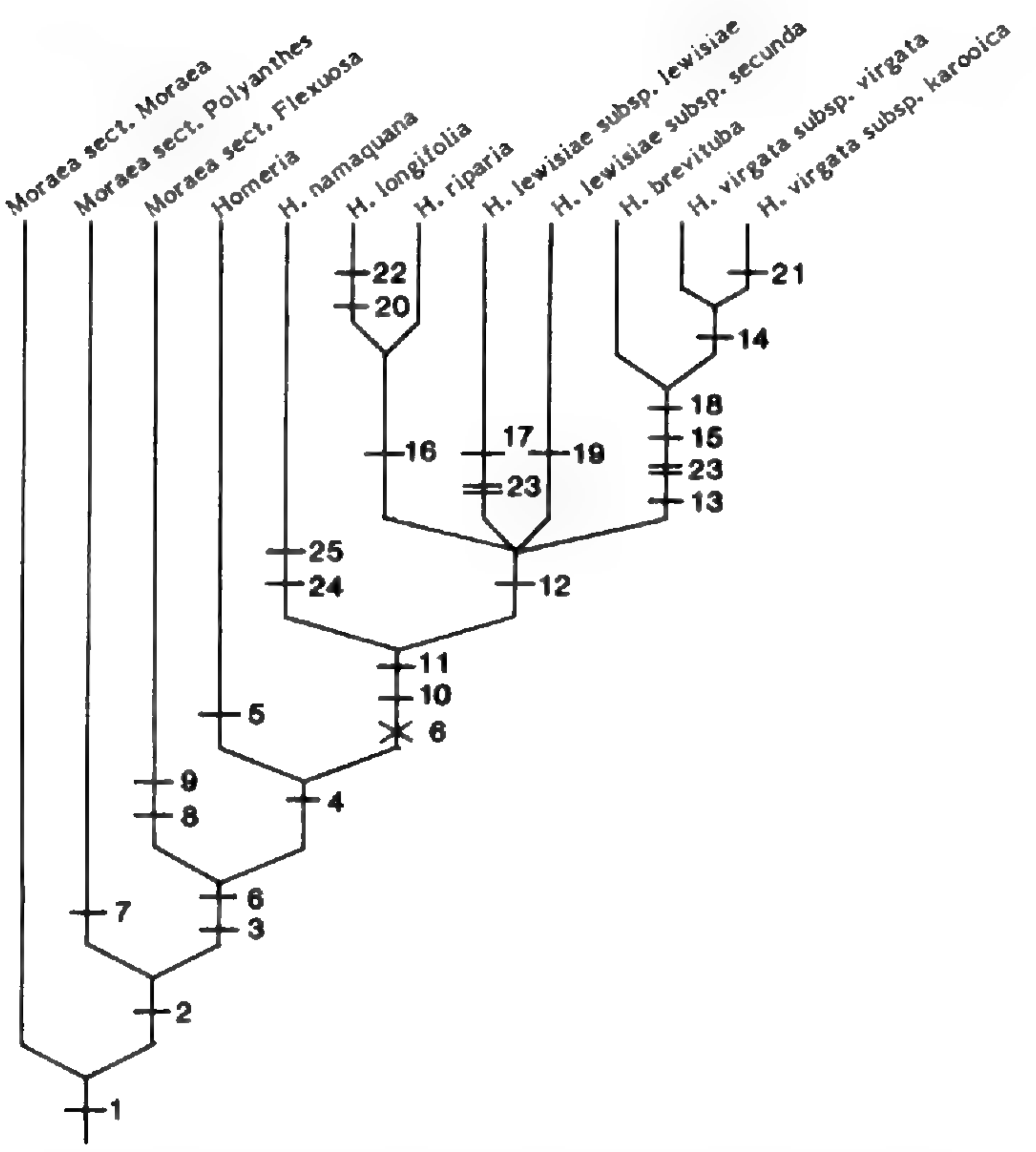

FIGURE 5. Cladogram of *Hexaglottis* and its relatives in subtribe Homeriinae indicating the possible phylogeny of the genus and of the species within *Hexaglottis*. The characters (synapomorphies) are listed in Table 2. Character states evolved independently (parallelisms) are indicated by double lines and a probable reversal by a cross.

in more detail in the pages dealing with morphology and cytology of *Hexaglottis*. The basic structure of the *Moraea* flower and the reduction and specialization in *Homeria* and some species of *Moraea* have been discussed at length elsewhere (Goldblatt, 1980, 1986). Reasons for considering $x = 10$ the basic chromosome number in *Moraea* and its allies have been presented in two studies (Goldblatt, 1971b, 1976a) dealing primarily with chromosome cytology.

The immediate sister group of *Hexaglottis* is probably *Homeria*, and the genera share a series of derived and reduced floral features as well as the same chromosome number and karyotype. Their common ancestor is probably a species group in *Moraea*, a genus of some 120 species, from which have been segregated several smaller genera that stand out phenotypically in a variety of unusual features. A study in progress suggests that each of these segregates is related to a species or section of *Moraea*. *Homeria* and *Hexaglottis* together are probably related to *M. flexuosa* of the monotypic section *Flexuosa*, in turn most likely derived from species at present placed in section *Moraea*. The sole synapomorphy that

TABLE 2. Characters used in the cladogram (Fig. 5), the derived (apomorphic) state listed first, followed by the presumed ancestral (plesiomorphic) condition.

1. Corm tunics composed of hard, wiry, blackish fibers forming an open reticulum—tunics composed of straw-colored fibers forming a fine reticulum.
2. Basic chromosome number $x = 6$—basic number $x = 10$.
3. Karyotype comprising only acrocentric chromosomes—karyotype comprising submetacentric pairs as well as acrocentrics.
4. Style branches narrow and not petaloid—style branches broad and petaloid.
5. Nectaries and nectar guides present on inner and outer tepals—nectaries and nectar guides present on outer tepals only.
6. Filaments united entirely (or free near the apex)—filaments united in the lower half.
7. Flowers shades of blue to violet—flowers shades of yellow.
8. Stem flexuose—stem more or less straight.
9. Tepal claws longer than the limbs—tepal claws about as long as or shorter than the limbs.
10. Style branches divided to the base—style branches forked apically, usually above the stigma lobe.
11. Arms of the style branches filiform, apically stigmatic—arms of the style (if present) flat and curving outwards.
12. Lateral rhipidia sessile and enclosed in the sheathing bracts—lateral rhipidia borne on discrete stalks exceeding the subtending bracts.
13. Hypanthium tube present, at least 1 mm long—tepals free from the base.
14. Hypanthium tube at least 3 mm long—tube 1–2 mm long.
15. Ovary enclosed in the spathes—ovary exserted from the spathes.
16. Capsule narrowly obovoid to clavate-truncate—capsule ellipsoid.
17. Capsule more or less cylindric-trigonous—capsule ellipsoid.
18. Capsule elongate-ellipsoid and enclosed in the spathes—capsule ellipsoid and exserted.
19. Capsule beaked—capsule not beaked.
20. Plants polyploid ($2n = 24$)—plants diploid ($2n = 12$).
21. Basic chromosome number $x = 7$—basic number $x = 6$.
22. Plants self-compatible and autogamous—plants self-incompatible.
23. Seeds angular-fusiform—seeds broadly angular.
24. Leaves spreading and undulate—leaves ascending to erect and more or less straight.
25. Leaf margins undulate to lightly crisped—leaf margins straight.

unites these species is the corm tunic which consists of coarse, dark brown to black, netted fibers. Within the group with coarse black corm tunics, *Hexaglottis, Homeria, Moraea* section *Flexuosa,* and *Moraea* section *Polyanthes* appear to form a monophyletic alliance that shares the derived basic chromosome number of $x = 6$ and a karyotype of predominantly to exclusively acrocentric chromosomes. Section *Polyanthes* has blue flowers, an apomorphic character in *Moraea,* and some subacrocentric chromosomes, while *Hexaglottis* and *Homeria* have flowers with nectar guides on both inner and outer tepals and have style branches reduced from the basic petaloid condition. The species of section *Moraea* belonging to this alliance include *M. namaquamontana, M. serpentina, M. tortilis,* and their close allies, all except *M. namaquamontana* being united by having included ovaries and capsules. The detailed relationships of the species in section *Moraea* are not dealt with further and will be the subject of a future study.

Hexaglottis itself stands out in having specialized style branches and having a possible reversal in the filaments being free in the upper half (see discussion under Flower in the section dealing with Morphology). *Hexaglottis namaquana* stands out in the genus as unspecialized and taxonomically isolated. It is probably close to the ancestor of the genus and, given its very local distribution, must be regarded as a relict species. It is the sister species to the other species of the genus, which all have sessile lateral rhipidia, an important synapomorphy in *Hexaglottis.* The included ovary and hypanthium tube are synapomorphies uniting *H. brevifolia* and *H. virgata,* the latter distinguished by its longer tube and particularly short pedicel. *Hexaglottis virgata* subsp. *karooica* has unusually large flowers (probably a specialized condition but not reflected in the cladogram) and the derived chromosome number of $2n = 14$. *Hexaglottis riparia* and *H. longifolia* form another species pair, linked by the derived capsule shape. *Hexaglottis longifolia* stands out here in having large capsules, autogamous reproduction, and in being polyploid. The two subspecies of *H. lewisiae* apparently share no synapomorphy, or at least none that I have been able to identify. However, they are too similar morphologically to be regarded as separate species. Further study may throw more light on their relationship and will perhaps indicate the presence of specialized features linking them.

The parallelism shared by *Hexaglottis lewisiae* subsp. *lewisiae* and the *H. virgata–H. brevituba* clade, narrow fusiform seeds (character 23), suggests a possible alternative phylogeny with these taxa forming a single clade. This is an attractive hypothesis, suggesting as it does the derivation of the species with a perianth tube and cylindric, included ovary (i.e., *H. virgata* and *H. brevituba*) from an ancestor like subsp. *lewisiae,* which at least has an unusually narrow ovary. The separation of *H. lewisiae* subsp. *secunda* from subsp. *lewisiae* that would result from such an interpretation is difficult to accept given their otherwise similar morphology.

One significant conclusion that is evident from the cladistic analysis is that *Moraea* as presently defined is shown to be paraphyletic, consisting of a number of discrete lineages, some of which are treated as distinct genera. The analysis of the relationships of the main species groups in the whole alliance is in progress and there will likely be some changes to the taxonomy of *Moraea* and its segregates. Such changes may include *Hexaglottis* but it seems preferable, nevertheless, to publish the revision according to the present taxonomy. The species, *H. nana,* is not reassigned to any genus, as this would be premature given the prevailing uncertainty about the relationships of species in *Moraea* itself.

SYSTEMATIC TREATMENT

Hexaglottis Ventenat, Decades Generum Novorum 6, no. 3. 1808. TYPE SPECIES: *H. longifolia* (Jacq.) Salisb., lectotype, designated by Lewis (1959: 219–222).

Important references: Baker, Handbook Irid. 75–76. 1892 et Flora Cap. 6: 31–32. 1896; Lewis, Flora Cape Peninsula 225. 1950; J. S. African Bot. 25: 215–230. 1959.

? *Plantia* Herbert, Edwards Bot. Reg. 30: Misc. 89. 1844. TYPE SPECIES: *P. flava* Herb. [The identity of *P. flava,* treated by Lewis (1959) as conspecific with *H. virgata,* is uncertain. No type material is known. The protologue seems to match *Hexaglottis* and single-leafed species of *Homeria* sections *Homeria* and *Conanthera* equally well. *Plantia* is cited here as doubtfully congeneric with *Hexaglottis.*]

Plants variable in size, 12–120 cm high. *Corm* globose, ± symmetric, 10–20 mm diam. or larger if surrounded by accumulated tunic layers, the tunics consisting of dark brown to blackish layers of thick vertical ribs connected by fine cross-fibers, the older layers increasingly fibrous and dissected. *Leaves* usually 2–3, occasionally only 1, linear, usually ascending and longer than the stems, often trailing distally, or ± prostrate, flat or channeled, usually inserted towards stem base or at some distance above the ground, the margins plane or undulate. *Stem* erect, straight to slightly flexuose, branched, with only one main axis or with 2–6 diverging secondary axes; lateral rhipidia (inflorescence units) either stalked on short branches (*H. namaquana*) or sessile and partly enclosed by the subtending stem bract, this usually as long or longer than spathes. *Rhipidia* stalked (*H. namaquana*) or sessile except the terminal, 2–several-flowered; *spathes* herbaceous, or partly to entirely dry and pale at flowering time, attenuate, except in *H. namaquana,* the outer often concealed by the sheathing stem bracts and membranous below, ½–⅔ as long as the inner (subequal in the lateral rhipidia of *H. longifolia*); in sessile rhipidia the upper part of inner visible above bracts except in *H. longifolia. Flowers* stellate, upright or facing sidewards, yellow, scented or not, the nectar guides deeper yellow and usually surrounded by small dark spots, larger on the outer tepals, located near the base of the limbs, the tepals free or united below as a closed tube; *perianth tube* (when present) cylindric, 1–7 mm long, narrow, usually curving slightly outward, partly enclosed in the spathes; *tepals* with short erect claws 1–2 mm long, forming a narrow cup enclosing base of filaments or filament column; the outer slightly larger than the inner and with a small nectary on the claw; limbs extended horizontally, the outer ± ovate to oblong, the inner oblong to cuneate. *Filaments* 4–6 mm long, monadelphous, united for 1–2(–3) mm, weakly diverging above; *anthers* 3–9 mm long, linear, initially erect, curling inwards and partly collapsing after anthesis. *Ovary* narrowly ellipsoid to ± cylindric or wider above, exserted or included in the spathes; *style* dividing at apex of the united part of the filaments into 3 short branches, each divided almost to the base into 2 filiform (microscopically grooved) arms, extending outwards on either side of the subtending filaments, ciliate and stigmatic only at the apex. *Capsule* ellipsoid, obovate to clavate, or ± cylindric, exserted or included in the spathes, usually only 1 per inflorescence in *H. virgata*; *seeds* angular, sometimes narrowly so. *Basic chromosome number* $x = 6$; diploid numbers $2n = 12, 14, 24$.

Distribution. Winter rainfall parts of southern Africa, from Port Elizabeth in the east, to the Cape Peninsula and north throughout Namaqualand, also locally on the Roggeveld Escarpment in the western Karoo.

KEY TO *HEXAGLOTTIS* AND OTHER AFRICAN IRIDACEAE WITH A *HEXAGLOTTIS*-TYPE FLOWER

1a. Rhipidia 2–several, arranged in a fascicle, each on a short stalk; outer inflorescence spathes usually not entirely sheathing, but with a diverging apex .... *'Hexaglottis' nana*
1b. Rhipidia many, not fasciculate but in spicate or racemose arrangement, each either sessile or stalked; outer inflorescence spathes entirely sheathing.
    2a. Lateral rhipidia stalked.
        3a. Flowers blue-violet; style arms 2.5–3 mm long .... *Moraea hexaglottis*
        3b. Flowers yellow; style arms about 4 mm long; leaves comparatively broad and short, to 11 mm wide, spreading on the ground and twisted, the margins undulate and often crisped .... 1. *H. namaquana*
    2b. Lateral rhipidia sessile, spicately arranged on the main axes.
        4a. Tepals free to base; ovary and capsule partly to well exserted from the spathes.
            5a. Capsules narrowly ellipsoid to cylindric-trigonous; rarely more than 3 mm at the widest point, plants of open and dry habitats .... 2. *H. lewisiae*
            5b. Capsules obovoid to clavate, truncate above; 4–8 mm at the widest point; plants of moist habitats, streamsides, and seeps.
                6a. Capsules 12–16(–23) mm long and 6–8 mm wide; inner spathe of lateral rhipidia usually shorter than outer and concealed by the sheathing bract leaves ... 4. *H. longifolia*
                6b. Capsules 6–10(–12) mm long and ca. 4 mm wide; inner spathe of the lateral rhipidia usually longer than outer and not concealed .... 3. *H. riparia*
        4b. Tepals united into a tube below the claws; ovary and capsule enclosed within the spathes.
            7a. Perianth tube 1–2 mm long; upper part of the ovary often emerging from the spathes; plants of northern Namaqualand and the Richtersveld .... 5. *H. brevituba*
            7b. Perianth tube (3–)4–9 mm long; ovary entirely included; plants of the northwest, western, and southern Cape and western Karoo .... 6. *H. virgata*

1. **Hexaglottis namaquana** Goldbl., sp. nov. TYPE: South Africa. Cape: Namaqualand, top of Spektakel Pass, stony clay soil among patches of quartzite, *Goldblatt 3059* (holotype, MO; isotypes, K, NBG). Figure 6.

Plantae 15–30 cm altae, foliis 2–3 prostratis undulatis, marginibus undulatis vel crispis, omnibus rhipidiis pedunculatis ex bracteis vaginantibus caulium exsertis, tepalis liberis, ca. 2 cm longis, ovario 4–5 mm longo plerumque exserto, capsulis oblongo-ellipsoideis ca. 8–10 mm longis.

Plants 15–30 cm high. *Corm* 1–1.5 cm diam., the tunics fibrous, dark brown to black, extending above into short stiff bristles. *Leaves* 2–3, all ± basal, 8–15 cm long, to 11 mm wide, ± prostrate, irregularly undulate or twisted, the margins undulate or crisped. *Stem* several-branched and all branches (on plants in full bloom) stalked, the branches subtended by dry, sheathing bracts 17–21 mm long. *Rhipidia* stalked, exserted from the subtending bracts; *spathes* herbaceous or becoming dry above, acute, the inner 2.5–3 cm long, the outer about half as long. *Flowers* yellow, stellate with free, spreading tepals; *tepals* about 2 cm long with claws about 2 mm long, the outer tepal limbs to 5 mm wide, the inner narrower. *Filaments* united only at very base (seemingly free), 3–4 mm long; *anthers* about 3 mm long, straight and suberect before dehiscence. *Ovary* 4–5 mm long, usually just exserted from spathes, the style arms spreading, about 4 mm long. *Capsules* narrowly oblong-ellipsoid, 8–10 mm long; *seeds* angular, about 1 mm diam. *Chromosome number* $2n = 12$.

Flowering time. Late September to October; flowers opening in the mid afternoon, after 3:00 P.M. and fading near sunset.

Distribution. *Hexaglottis namaquana* is known only from the eastern slopes of the Spektakelberg, some 16 miles west of Springbok in northern Namaqualand (Fig. 6). It is found towards the top of Spektakel Pass, in hard, stony, clay soil, sometimes covered with white quartzite pebbles of the Nama System. Outcrops of Nama shales and quartzites are rare in Namaqualand, where granites and granitic sands are the rule. *Hexaglottis namaquana* may be found in other parts of Namaqualand where there are similar outcrops of the Nama System. The species is sympatric with *H. lewisiae,* which on Spektakel Pass is a tall slender, narrow-leafed plant, blooming very late in the day. Its flowers open at about 5:30 P.M. and last about three hours. The flowers of *H. namaquana* open at about 3:00 P.M. and begin to fade at 5:30. They are further isolated reproductively by a shift in flowering season. *Hexaglottis namaquana* blooms from late September into mid October, whereas *H. lewisiae* in this area blooms from mid October to late November.

Diagnosis and relationships. *Hexaglottis namaquana,* discovered only in 1974, is a remarkable member of the genus. It has the small yellow flowers that characterize *Hexaglottis,* but unlike all the other species, the lateral rhipidia are borne on long branches rather than being sessile. The former feature must be regarded as primitive for the genus and separates *H. namaquana* from the other species. Members of this species are fairly short and are unusual also in having the leaves strongly undulate to crisped. The capsule is unspecialized in being well exserted from the spathes and in being ellipsoid. In other species of *Hexaglottis* the capsule is either elongated and sometimes linear or is shortly stalked and enclosed within the spathes.

Additional specimens examined. SOUTH AFRICA. CAPE–29.17 (Springbok): Spektakel Pass, west of Springbok (DA), *Goldblatt 5172* (MO, NBG); rocky eastern slopes near the top of Spektakel Pass, *Goldblatt 6672* (MO).

2. **Hexaglottis lewisiae** Goldbl., J. S. African Bot. 37: 234. 1971. TYPE: South Africa. Cape: *Thunberg s.n.* "*Moraea flexuosa* b" [holotype, Herb. Thunberg 1217, UPS (this is the specimen selected by Lewis, 1959: 224 as the lectotype of the invalid *M. flexuosa*)]. Figure 7.

Moraea flexuosa L. f., Suppl. Pl. 100. 1782; Ker, Bot. Mag. 19: tab. 695. 1803, nom. illeg. superf. pro *Ixia longifolia* Jacq. *Sisyrinchium flexuosum* (L. f.) Spreng., Syst. Veg. 1: 167. 1825, nom. illeg. bas. illeg. *Homeria flexuosa* (L. f.) Sweet, Hort. Brit. 1: 395. 1827, nom. illeg. bas. illeg. *Hexaglottis flexuosa* (L. f.) Sweet, Hort. Brit. ed. 2: 498. 1830; Lewis, J. S. Afr. Bot. 25: 223. 1959 et Fl. Cape Peninsula 225. 1950, nom. illeg. bas. illeg. TYPE: as for *Ixia longifolia* (= *Hexaglottis longifolia*).

Hexaglottis longifolia (Jacq.) Salisb. sensu Baker, Flora Cap. 6: 32. 1896, pro parte (excluding the type of *H. longifolia*).

Homeria spicata (Ker) Sweet sensu Klatt, Linnaea 34: 626. 1866, pro parte [excluding the type of *H. spicata,* this now placed in *Homeria elegans* (Jacq.) Sweet, cf. Goldblatt, 1981: 462–464]. Klatt's (1866) concept of *H. spicata* included *Hexaglottis virgata, H. longifolia,* and *H. lewisiae.*

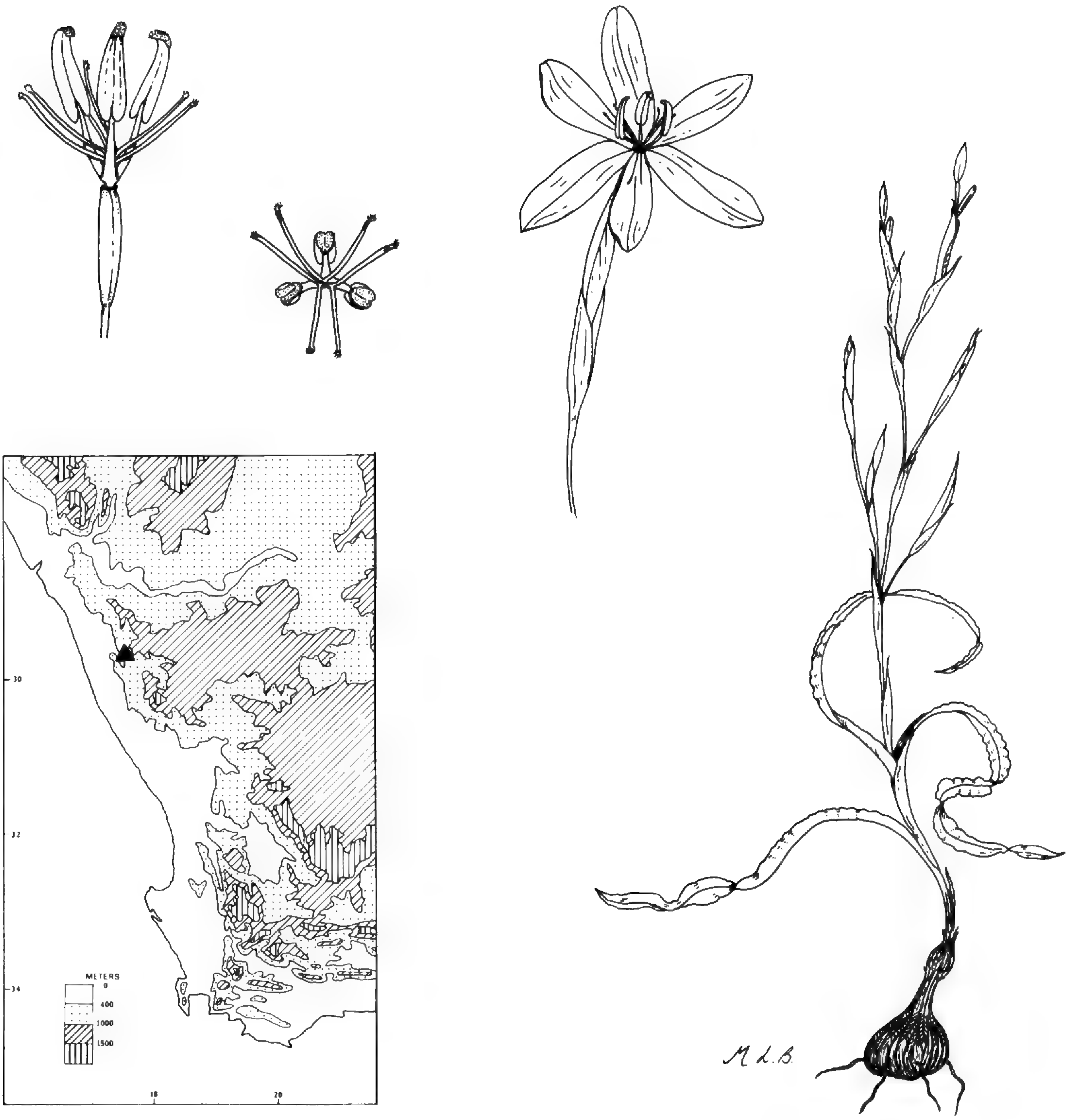

FIGURE 6. Morphology and distribution of *Hexaglottis namaquana.* Habit ×0.5; flower full size; side and top view of the stamens and style branches ×2.

Plants variable in size, (12–)20–60 cm high. *Corm* 15–20 mm diam., symmetric, the tunics (pale–)dark brown, fibrous, occasionally produced upwards into a neck. *Leaves* 1–3(–4), inserted towards the base (sometimes shortly above the ground), ascending, linear, channeled, the margins sometimes inrolled or rarely undulate and the leaves rather short, normally much exceeding the stem and trailing above. *Stem* usually bearing 1–3 secondary branches near the base, often flexuose, the lateral rhipidia sessile, usually overlapping the rhipidium above, subtended by a sheathing stem bract concealing at least the lower part of the spathes, and usually about two-thirds their length. *Rhipidia* sessile except the terminal; *spathes* herbaceous, dry above, (2.5–) 3–4.5 cm long, attenuate, the inner slightly longer than the outer. *Flower* golden yellow with a strong sweet scent, stellate with free tepals, the outer often feathered brownish on the reverse, the nectar guides deeper yellow, usually surrounded by several small dark greenish spots; *tepals* 19–24 mm × 7–10 mm (subsp. *lewisiae*), 24–30 mm × 10–13 mm (subsp. *secunda*), the claws 1.5–2

FIGURE 7. Morphology of *Hexaglottis lewisiae* subsp. *lewisiae* and the distribution of both subspecies of *H. lewisiae*. Habit, corm, and fruiting branch ×0.5; flower full size; seeds much enlarged.

mm long, the limbs horizontal, the outer ovate, the inner more or less cuneate, about as long to 2 mm shorter than the outer. *Filaments* 4–6 mm long, united for 1–1.5 mm; *anthers* 5–7 mm long before collapsing. *Ovary* (5.5–)6–12 mm long, usually partly to entirely exserted at flowering, rarely entirely included (*Barker 2558*); style about 2 mm long, the style arms spreading and 6–7 mm long. *Capsule* triangular in section and narrowly cylindric, 11–16(–20) mm long (subsp. *lewisiae*) or terete and ellipsoid, 8–13 (–15) mm long (subsp. *secunda*), then often shortly beaked, dehiscing in the upper third to half only; *seeds* angular, sometimes narrowly so and tapering at both ends, 1.2–2 mm long, 0.7–1 mm at the widest, winged in northern populations. *Chromosome number* $2n = 12$.

Flowering time. (September–)October–November; flowers opening between 3:00 and 4:00 P.M. in the south and beginning to fade towards 7:00 P.M., only opening towards sunset in the Namaqualand populations and fading at about 8:00 P.M.

Distribution and biology. Hexaglottis lewisiae is widespread in the southern African winter rainfall area (Fig. 7). It extends from Springbok in the north through the southwestern Cape as far east as the Humansdorp district. It is common only in the western Cape and has a scattered distribution to the north of Piketberg and east of Bredasdorp. It is found in dry and exposed sites, often on stony ground, and occurs on sandy and clay soils.

Like most species of *Hexaglottis, H. lewisiae* is pollinated by bees, but pollination has been studied in most detail in this species, and my observations are summarized here. The relatively small and seemingly inconspicuous flowers appear to be very attractive to small bees. When the flowers open in mid afternoon, bees rapidly appear around the plants and begin to gather pollen. They visit the same flowers several times, collecting pollen as soon as it is exposed in the anther sacs, which dehisce slowly from the apex. Pollen is the primary reward and only occasionally is some nectar also taken. The small quantity of nectar produced seems to be of minor interest to the pollinators. Fruit and seed production is very successful in *H. lewisiae,* and plants develop several full capsules from each of the many inflorescences.

Diagnosis and relationships. Hexaglottis lewisiae is a diploid and self-incompatible. Its yellow flowers are almost identical to those of all other species of *Hexaglottis,* except that unlike *H. virgata* and *H. brevituba,* the tepals are free to the base. It shares with all but *H. namaquana* the similar vegetative feature of sessile lateral rhipidia. It is most easily confused with *H. riparia* and *H. longiflora,* but these have obovoid or clavate capsules, thus always broadest in the upper third and markedly flat-topped, unlike the cylindric or ellipsoid, and sometimes beaked, capsules of *H. lewisiae. Hexaglottis riparia* and *H. longifolia* grow in moist situations and, possibly as a consequence, have more and longer leaves than is usual in *H. lewisiae.* The combination of their three or four leaves, obovate-clavate capsules, moist habitats, and sometimes even smaller flowers makes it unlikely that *H. riparia* and *H. longifolia* will be confused with *H. lewisiae.*

History. Hexaglottis lewisiae has been known since the younger Linnaeus (1782) described the species as *Moraea flexuosa* based on material collected by Carl Peter Thunberg a few years earlier. The epithet is regarded today as superfluous and illegitimate since Linnaeus cited as a synonym *Ixia longifolia* Jacq., now *H. longifolia.* The combination *Hexaglottis flexuosa* was made by Sweet in 1830, and the species, usually including *H. longifolia,* was known by this name for several years. The later nineteenth century botanists generally did not recognize *H. flexuosa.* F. W. Klatt included it, together with *H. virgata* and *H. longifolia,* in *Homeria spicata,* this a synonym of *Homeria elegans* (Goldblatt, 1981). Later, Klatt (1882) recognized *Hexaglottis,* including *H. virgata* and *H. longifolia* (presumably but not explicitly including *H. lewisiae*). J. G. Baker (1896) included *H. flexuosa* in *H. longifolia,* and the distinction between the two species was only reestablished by Lewis in 1950. The new name *H. lewisiae* was proposed in 1971 by the present author for the species that until this time was known by the illegitimate name *H. flexuosa.*

Variation. There appear to be two major forms of *Hexaglottis lewisiae,* the southern and typical, treated here as subsp. *lewisiae,* which extends from the western Cape coast eastwards through the southern Cape to Humansdorp. It has medium-sized flowers with tepals 19–24 mm long and distinctive long slender capsules 11–20 mm long that tend to dehisce only in the upper part. The seeds are also comparatively small as a result of the need to be accommodated in the narrow locules. The karyotype in this form appears to be uniform and consists of four strongly acrocentric chromosome pairs and two acro- to submetacentric pairs.

Populations to the north of the Olifants River mountains, from Clanwilliam north to Springbok, treated as subsp. *secunda,* comprise plants with larger flowers, the tepals 24–30 mm long, somewhat shorter ellipsoid capsules 8–13(–15) mm long, and larger seeds. The chromosome cytology of this series of populations is not as well known, but two Namaqualand populations examined have karyotypes with a large metacentric chromosome pair. This northern form is morphologically variable. Namaqualand plants have a single leaf in the wild, but two leaves in cultivation, and slightly smaller flowers than those from the northwest Cape. The extensive populations from the western Karoo near Nieuwoudtville have capsules with a beaklike apex, a feature weakly developed and often obscure in Namaqualand plants. Capsules in populations from Clanwilliam and Vanrhynsdorp are unknown, and karyotypes have been determined for one northwest Cape population. The flowers of the Namaqualand populations have a different phenology, opening between 5:30 and 6:00 P.M., whereas all other forms of *H. lewisiae* open between 3:00 and 4:00 P.M. and fade at about 6:00 P.M.

KEY TO THE SUBSPECIES OF *HEXAGLOTTIS LEWISIAE*

1a. Capsules ellipsoid, 8–13(–15) mm long, often distinctly beaked; outer tepals 24–30 mm long, flowers usually secund .... 2A. subsp. *secunda*
1b. Capsules cylindric or nearly so, 11–16(–20) mm long, not beaked; outer tepals 19–24 mm long, flowers usually upright .... 2B. subsp. *lewisiae*

2A. subsp. **secunda** Goldbl., subsp. nov. TYPE: South Africa. Cape: stony east-facing slopes near the top of Spektakel Pass, west of Springbok, *Goldblatt 6673* (holotype, PRE; isotypes, K, MO, NBG, S, US, WAG).

Planta 30–60 cm alta, floribus usitate secundis tepalis 24–30 mm longis 10–13 mm latis, ovario 5.5–9 mm longis, capsulis ellipsoideis 8–13(–15) mm longis saepe rostratis.

Plants 30–60 cm high. Flowers usually secund; *tepals* 24–30 mm long, 10–13 mm wide. *Ovary* 5.5–9 mm long, usually at least partly exserted at flowering. *Capsule* terete and ellipsoid, 8–13 (–15) mm long, dehiscing for at least half its length; *seeds* angular, narrowly winged on the ridges, about 2 mm long, ca. 1 mm at the widest.

Distribution. Subspecies *secunda* has a scattered distribution throughout the northwest Cape and Namaqualand. Records extend from Clanwilliam north through the Olifants River Valley to Vanrhynsdorp, to the Karoo north and east of Nieuwoudtville, and into Namaqualand, where it has been recorded west of Garies, in the Kamieskroon district, and on the Spektakelberg, west of Springbok. Plants grow in rocky ground, either in clay soil, as on the Spektakelberg and in the Karoo, or in sand.

Additional specimens examined. SOUTH AFRICA. CAPE–29.17 (Springbok): stony east-facing slopes near the top of Spektakel Pass, west of Springbok (DA), *Goldblatt 6613* (MO).

30.17 (Hondeklipbaai): Klip Vlei, between Kamieskroon and Garies (BD), *Thorne s.n.* (SAM 49973); roadside between Brakdam and Rietkloof, *Pearson 5664* (K); 0.5 km SW of Skuinskraal farm, Hondeklipbaai road (DB), *van Berkel 453* (MO, NBG).

31.18 (Vanrhynsdorp): Zandkraal, sandveld (DB), *Acocks 14826* (K), *Barker 5665* (NBG), *Snijman 889* (MO, NBG); flats below the Gifberg, 12 km south of Vanrhynsdorp, *Goldblatt 6992* (MO, PRE); slopes of the Olifants River Bridge, south of Klawer, rocky sandstone soil (DC), *Goldblatt 6991* (K, MO, NBG, PRE).

31.19 (Calvinia): Loeriesfontein road, ca. 2 miles north of the Waterfall (AC), *Goldblatt 108* (J); karroid hills northeast of the Klip Koppies, Nieuwoudtville, *Goldblatt 7073* (MO); red clay soil among ironstone boulders, Glenlyon farm, Nieuwoudtville, *Goldblatt 6535* (MO); Nieuwoudtville, rocks on top of kopies, *Galpin 11137* (K, PRE).

32.18 (Clanwilliam): 10 km north of Clanwilliam, rocky sandstone soil (BB), *Goldblatt 6990* (MO, PRE, STE, US).

2B. Subsp. **lewisiae.**

Plants (12–)20–60 cm high. Flowers usually upright; *tepals* 19–24 mm long, 7–10 mm wide. *Ovary* 8–10 mm long, usually partly to entirely exserted at flowering, rarely entirely included. *Capsule* terete to triangular in section, narrowly cylindric, 11–15(–20) mm long, dehiscing in the upper third to half only; *seeds* angular-ellipsoid, tapering at both ends, 1.2–1.4 mm long, ca. 0.7 mm at the widest.

Distribution. Subspecies *lewisiae* extends from the Cape west coast east through the southern Cape to Humansdorp. It appears to be common only in the west and records are very scattered east of Bredasdorp. Figure 7.

Specimens examined. SOUTH AFRICA. CAPE–32.18 (Clanwilliam): NE edge of Verlorenvlei (AD–BC), *Pil-*

lans 7803 (BOL); De Hoek, Piketberg (DD), *Barker 2558* (NBG).

33.18 (Cape Town): Mamre hills (AD), *Compton 9828* (NBG); Porterville (BB), *Loubser 466* (NBG); ca. 10 km north of Malmesbury (BC), *Goldblatt 6173* (MO, S, US); mountains around Cape Town (CD), *Ecklon & Zeyher s.n.* (84) (S); foot of Lions Head, *Pappe s.n.* (SAM 70674); Oudekraal, Cape Peninsula, *Goldblatt 163* (J); Bakoven, *Lewis 971* (SAM); Camps Bay, *Moss 13403* (BM); Table Mountain (CD), *Ecklon 536* (BM, K, MO, PRE); Wynberg Hill, *Pillans 10198* (MO, US); Kirstenbosch, *Lewis 672* (NBG, SAM); Kirstenbosch, slopes near the herbarium, *Goldblatt 5104* (MO); Kirstenbosch, near the temporary offices, *Goldblatt 6634* (BR, MO, PRE, WAG); below Pearson House, Kirstenbosch, *Goldblatt 6634* (BR, MO, PRE, WAG); near Bishopscourt, *Salter 9002* (BOL); behind Groot Schuur, *Wolley Dod 360* (BM, BOL, K); Rosebank, *H. Bolus 3801* (BOL, K); Tygerberg Nature Reserve (DC), *Loubser 3059* (MO); Langverwacht, above Kuils River, *Oliver 4803* (K, MO, PRE, STE); Stellenbosch Flats (DD), *Garside 66* (K); between Klapmuts and Paarl, *Acocks 3677* (S); Berg River near Paarl, *Drège s.n.* in 1840 (K, S), *Barker 8797* (NBG).

33.19 (Worcester): Gydo Pass (AB), *Wall 705* (S); Worcester, beim Wasserfall (AC), *Ecklon & Zeyher Irid. 29* (1.11) (LD, MO); near Tulbagh, *Leighton 1317* (BOL); Tulbagh plains, *Marloth 9575* (PRE); Tulbagh Cemetery, *Goldblatt 5224* (MO); Wolseley, *Barker 2072* (NBG); du Toits Kloof (CA), *Stokoe s.n.* (SAM 60126); Worcester Veld Reserve (CB), *Olivier 204* (STE).

33.21 (Ladismith): 5 mi. west of Ladismith (AC), *Rycroft 3030* (NBG).

33.22 (Oudtshoorn): Ruigtevlei, near Swart R., George (DC), *Fourcade 1525* (BOL).

33.24 (Steytlerville): Essenbosch hills (CD), *Fourcade 4420* (K).

34.18 (Simonstown): Simons Bay (AB), *Wright 269* (K); Hout Bay, *Wall s.n.* (S); Noordhoek, *Barker 2728* (BOL, NBG); Bergvliet Farm, *Purcell 124* (SAM).

34.19 (Caledon) Elgin (AA), *Dahlstrand 1164* (PRE); Dwarsberg-Somerset Sneeukop, *Stokoe s.n.* (SAM 55728); Genadendal (AB), *Prior s.n.* (K); between Houw Hoek and Kleinmond (AC), *Werdemann & Oberdieck 678* (B, K, PRE); Hemel en Aarde (AD), *Gillett 90* (STE); 8 mi. from Stanford on the road to Elim, *Gillett 4506* (BOL, K); Klippiesbaai, Vogelklip, Hermanus, *S. Williams 873* (C, MO, WAG); near Napier (BD), *Leipoldt 3551* (BOL); between Baardscheerdersbos and Elim (DA), *Goldblatt 7107* (MO, PRE).

34.22 (Mossel Bay): along the river at Great Brak River (AA), *Young s.n.* (BOL 5541); between George and Great Brak River (?AB), *Burchell 6151* (K).

34.24 (Humansdorp): Oudebosch flats (AA), *Fourcade 960* (BOL).

Without precise locality: Cape of Good Hope (CBS), *Forster s.n.* (BM); *Thunberg s.n.* "*Moraea edulis* Ker," "*Moraea polyanthos*" (S "Herb. Casstrom," "Herb. Swartz"); rock crevices above forest plantation, Clanwilliam, *Galpin s.n.* (BOL).

Introduced: Réunion, Trou aux Cerfs, *Vaughan 3255* (SAM), *Lorence 15764* (K).

3. **Hexaglottis riparia** Goldbl., sp. nov. TYPE: South Africa. Cape: along the Olifants River at Citrusdal campsite, after fire, *Goldblatt 6706* (holotype, NBG; isotypes, K, MO, PRE, STE). Figure 8.

Hexaglottis longifolia var. *angustifolia* Lewis, J. S. African Bot. 25: 222. 1959, pro parte (excluding the type of var. *angustifolia,* this placed in *H. longifolia* in the present paper).

(*Plantia flava* Herb., Edwards Bot. Reg. 30: misc. 89. 1844 is a possible synonym. See discussion below under History.)

Planta 45–90 cm alta, foliis (2–)3 linearibus, rhipidiis lateralibus sessilibus, bracteis caulis imbricatis longioribus quam internodis, spathis exterioribus usitate in bracteis caulis inclusis, tepalis liberis 16–21 mm longis 6–8 mm latis, ovario 5–7 mm longo exserto, capsulis obovato-clavatis 6–10(–12) mm longis.

Plants 45–90 cm high. *Corm* 13–20 mm diam., the tunics of fine, light brown fibers. *Leaves* (2–)3, linear, 3–5 mm wide, ascending, channeled, the margins incurved, usually bent and trailing above, the lowermost longest, about as long as the stem, the upper decreasing in length and width. *Stem* straight, simple or 1–3-branched from the lower nodes, the lateral rhipidia sessile at each node, subtended by a sheathing stem bract often entirely concealing the inflorescence spathes, these as long or somewhat longer than the internode and overlapping the next bract. *Rhipidia* sessile, except the terminal; *spathes* herbaceous, attenuate, dry apically, 3.3–3.8 cm long, about as long as the subtending stem bract, the outer shorter than the inner, often hidden. *Flowers* stellate with free tepals, deep yellow, strongly scented; *tepals* 16–21 mm long, 6–8 mm wide, with claws about 2 mm long, the limbs spreading, the inner slightly shorter than but as wide as the outer. *Filaments* 4–6 mm long, united for 1.5–2.5 mm; *anthers* 5–6 mm long. *Ovary* 5–7 mm long, exserted; style arms 5–6 mm long, extended horizontally. *Capsules* obovoid-clavate, somewhat truncate, 6–10(–12) mm long, about 4 mm wide; *seeds* angular, 1–1.5 mm long, 1 mm at the widest diam. *Chromosome number* $2n = 12$.

Flowering time. October–November; flowers open at about 5:00 P.M. and begin to fade after 7:30 P.M.

Distribution. Hexaglottis riparia has a limited range, occurring in valleys of the western Cape mountains between Tulbagh Kloof in the south and Clanwilliam in the north (Fig. 9). It appears to be restricted to streambanks and possibly edges of marshes. Such areas are frequently overgrown with tall vegetation, and *H. riparia* accordingly blooms only after fires or heavy graz-

FIGURE 8. Morphology of *Hexaglottis riparia*. Habit, flowering, and fruiting branches × 0.5; single flower and capsule full size.

ing when the habitat has been opened up considerably.

Diagnosis and relationships. *Hexaglottis riparia* has flowers typical of the genus. It is distinctive largely in its small obovoid to clavate fruits and in its slender, often willowy stems. The capsules are 6–10 mm long, or occasionally in robust plants up to 12 mm. *Hexaglottis longifolia* has similarly shaped capsules but they are much larger, usually 16–23 mm long. The similarity in capsule shape prompted Lewis (1959) to include the only collection of *H. riparia* known to her in *H. longifolia* var. *angustifolia.* The type of the latter has unusually narrow leaves but in other respects the type corresponds well to typical *H. longifolia.* This species differs further from *H. riparia* in having pale yellow, unscented flowers and in being self-compatible, autogamous, and tetraploid with $2n = 24$. The flowers of *H. riparia* are deep yellow and scented, and, like other members of the genus, it is self-incompatible and diploid with $2n = 12$. The similar capsule shape in *H. riparia* and *H. longifolia,* a derived feature, probably indicates that they are closely related.

History. This species was apparently collected first by Ecklon & Zeyher in the Tulbagh district in the 1820s, and rarely since then. It was initially assigned to *Hexaglottis longifolia* and subsequently cited by Lewis (1959) under *H. longifolia* var. *angustifolia.* There is a possibility that the species described as *Plantia flava* may be the same as *H. riparia.* Baker (1896) and Lewis (1959) treated the monotypic *Plantia* as congeneric with *Hexaglottis.* The type is, however, unknown, and the description is ambiguous and could apply as well to some species of *Homeria* as to *Hexaglottis. Plantia flava* was grown and flowered in England from corms collected by George Synnot, who lived in the Clanwilliam district from 1821 to 1825 (Gunn & Codd, 1981). If *Plantia flava* is a species of *Hexaglottis,* it is probably conspecific with *H. riparia,* the only species of *Hexaglottis* in the northwest Cape with capsules that correspond with Herbert's description of the capsules as obovate.

Specimens examined. SOUTH AFRICA. CAPE–32.18 (Clanwilliam): river banks, Clanwilliam (BB), *Galpin 11483* (BM, K, PRE, UPS); Clanwilliam, *Leipoldt 376* (SAM).

32.19 (Wuppertal): along the Olifants river at Citrusdal campsite (CA), *Goldblatt 6555* (K, MO, NBG), *6706* (K, MO, NBG, PRE, STE).

33.19 (Worcester): Worcester, Tulbaghskloof, etc., *Ecklon & Zeyher Irid. 30* (77.9) (K, MO).

4. **Hexaglottis longifolia** (Jacq.) Salisb., Trans. Hort. Soc. 1: 313. 1812; Baker, Flora Cap. 6: 32. 1896, in part excl. *H. lewisiae* (as *H. flexuosa*); Lewis, Flora Cape Peninsula 225. 1950 et J. S. African Bot. 25: 223–225. 1959. *Ixia longifolia* Jacq., Hort. Vindob. 3: 47 & tab. 90. 1776. *Moraea longifolia* (Jacq.) Pers., Syn. Pl. 1: 49. 1805. *Moraea flexuosa* L. f., Suppl. Pl. 100. 1782, nom. illeg. superf. pro

Ixia longifolia Jacq., applied to *H. lewisiae. Sisyrinchium flexuosum* (L. f.) Spreng., Syst. Veg. 1: 167. 1825, nom. illeg. bas. illeg. *Homeria flexuosa* (L. f.) Sweet, Hort. Brit. 1: 395. 1827, nom. illeg. bas. illeg. *Hexaglottis flexuosa* (L. f.) Sweet, Hort. Brit. ed. 2: 498. 1830; Lewis, J. S. African Bot. 25: 223. 1959, nom. illeg. bas. illeg., applied to *H. lewisiae.* TYPE: South Africa. Cape: illustration in Hort. Vindob. 3: tab. 90. Figure 9.

Hexaglottis longifolia var. *angustifolia* Lewis, J. S. African Bot. 25: 222. 1959. TYPE: South Africa. Cape: Du Toits Kloof, *Pillans 8436* (BOL, holotype), pro parte (including only the type, other specimens here treated as *H. riparia*).

Plants 60–150(–200) cm high. *Corm* 15–20 mm diam., the tunics of fine, light brown fibers. *Leaves* 3–4(–5), linear, ascending, the lower longest, 50–100 cm long, the upper decreasing in size, 6–12 (–20) mm wide, flat or channeled, usually bent and trailing distally. *Stem* straight, simple or 1–3-branched from the lower nodes; lateral inflorescences sessile at each node, subtended by a sheathing stem bract often entirely concealing the spathes, as long, longer, or shorter than the internode. *Rhipidia* sessile, except the terminal; *spathes* herbaceous, attenuate, dry at apex, 3.5–5.5(–7.5) cm long, the inner about as long as the subtending stem bract, the outer shorter, often hidden. *Flowers* pale yellow, odorless or with a very faint odor, stellate, with free tepals, the nectar guides usually only on the outer tepals, inconspicuous; *tepals* with claws about 2 mm long, the outer with limbs 19–27 mm long, 8–11 mm wide, the inner 16–23 mm long, 6–9 mm wide. *Filaments* 4–6 mm long, united for 2–3 mm; *anthers* 5–6 mm long before anthesis. *Ovary* 8–12 mm long, exserted, the style arms comparatively short, 4–6 mm long, ascending, reaching only to the base of the anthers. *Capsules* well exserted, obovoid-clavate, truncate, 12–16(–23) mm long, 6–8 mm wide, dehiscing for ½–¾ their length; *seeds* angular, 2–2.3 mm long and up to 1.5 mm at the widest. *Chromosome number* $2n = 24$.

Flowering time. Mid October–November; flowers opening (2:00–)2:15–2:45 P.M. and beginning to fade ca. 6:00 P.M.

Distribution and biology. Hexaglottis longifolia is restricted to the Cape Peninsula and a few valleys in the mountains between Somerset West and Paarl. It grows along streams and in marshes or shady and damp sites (Fig. 9).

It is the only polyploid species in the genus and further unusual in *Hexaglottis* in being self-compatible and normally autogamous. Although the flowers appear to the human eye similar to those of the bee-pollinated *H. lewisiae, H. longifolia* is seldom visited by insects. Plants of *H. longifolia* growing a few feet away from *H. lewisiae* are ignored by bees gathering pollen from the latter species. Flowers of *H. longifolia* placed among those of *H. lewisiae* are consistently avoided by bees. Clearly to these insects, the odorless flowers of *H. longifolia* are very different to those of *H. lewisiae,* which are strongly scented. Possibly there are significant differences in ultraviolet patterning as well.

Diagnosis and history. The good illustration of Jacquin's *Ixia longifolia* accompanying the protologue and now regarded as the type of the species corresponds unmistakably to the tall, pale yellow-flowered *Hexaglottis* of damp shady sites on the Cape Peninsula. The painting shows clearly the characteristic pale yellow flowers, six rather short style branches, and the large, obovoid to clavate capsules. Despite this clear illustration, *H. longifolia* has often been associated with the very different *H. lewisiae* (as *H. flexuosa*) (Klatt, 1895; Baker, 1896), which has deep yellow, scented flowers, long style branches, and linear cylindric capsules. Lewis (1959) has explained in detail this historical confusion and has elaborated the several differences between these two quite distinct species. No further discussion seems necessary here.

Lewis (1959) recognized two varieties of *Hexaglottis longifolia* in her revision, the typical, and var. *angustifolia,* the latter distinguished by narrower, stiff, and strongly channeled leaves, shorter spathes, and smaller capsules. Her decision to treat this somewhat smaller form as a variety of *H. longifolia* was evidently based on similarity of general appearance, including the shape of the capsules, which, although smaller, are obovoid and truncate, and by the habitat: moist places along streams and rivers. The type, from du Toits Kloof, seems to me merely a slightly smaller specimen of *H. longifolia* and can be matched in size by some collections from the Cape Peninsula. It does not appear to warrant taxonomic recognition. However, the other collection cited, *Galpin 11483,* from the Olifants River Valley, is a different species treated here as *H. riparia.* It has smaller capsules and the flowers, examined live from this area, are unlike those of *H. lon-*

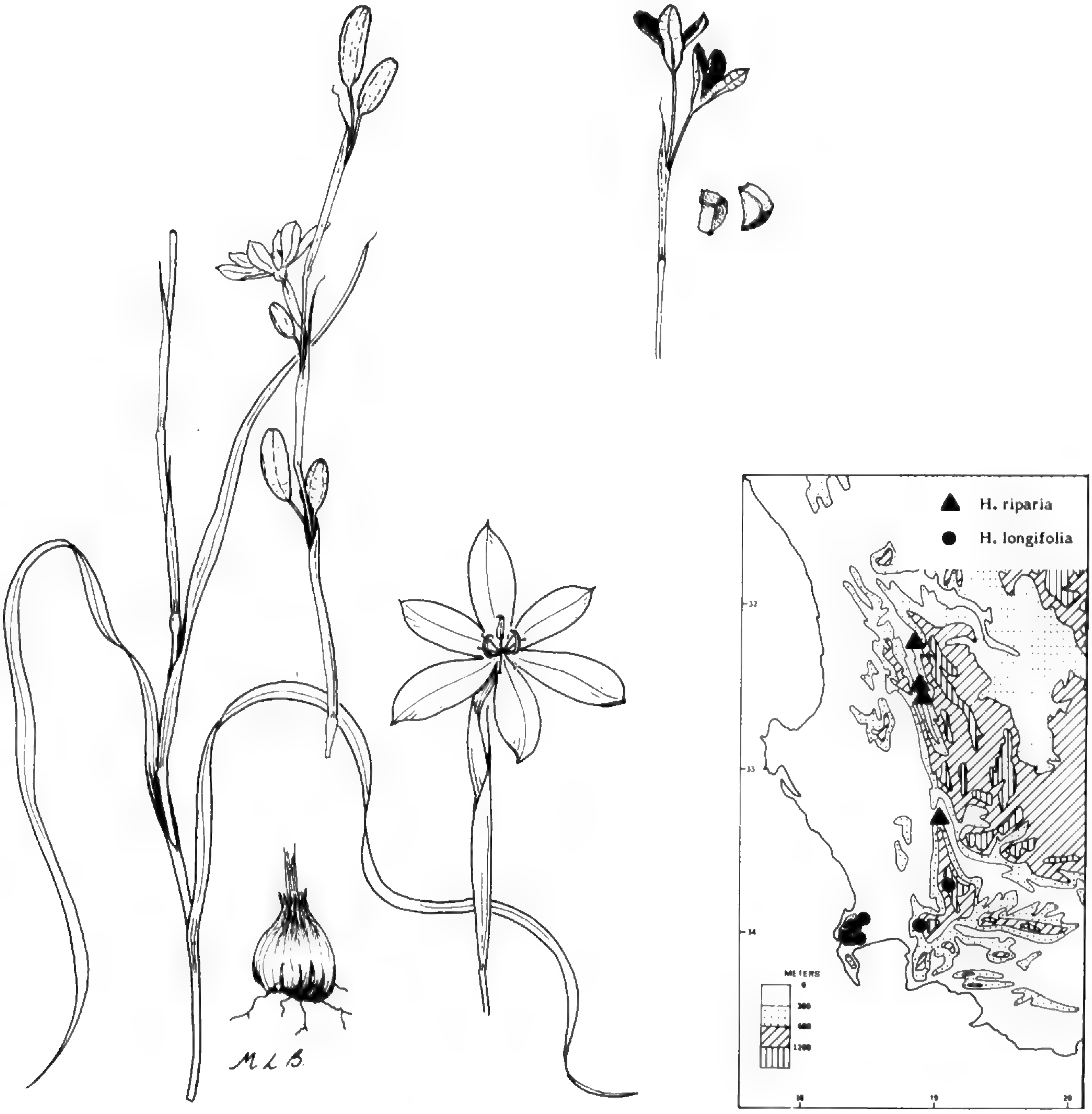

FIGURE 9. Morphology of *Hexaglottis longifolia* and distribution of *H. longifolia* and *H. riparia*. Habit, flowering and fruiting branches, and corm ×0.5; flower ± full size; seeds much enlarged.

gifolia. They are bright yellow and strongly scented, in both characteristics corresponding better to *H. lewisiae* and in conflict with *H. longifolia* with its pale yellow, scentless flowers. In addition, *H. riparia* is diploid, $2n = 12$, and self-incompatible, in contrast to the tetraploid and autogamous *H. longifolia*.

Specimens examined. SOUTH AFRICA. CAPE–33.18 (Cape Town): Liesbeek River, below Fernwood (CD), *Salter 8973* (NBG), *8775* (NBG, SAM), *8999* (NBG); Kirstenbosch, *Lewis 673* (NBG, PRE, SAM), *Goldblatt 5934* (MO); Kirstenbosch, below Pearson House, *Malan 120* (NBG), *Goldblatt 6635* (K, MO, PRE, WAG); below Fernwood, *Salter 9377* (BM); above Rhodes Drive, *Salter 9354* (BM); Table Mt., east base in damp soil, *Pillans 10262* (BR, MO); Jonkershoek (DD), *Werdermann & Oberdieck 722* (B, K).

33.19 (Worcester): du Toits Kloof (CA), *Pillans 4836* (BOL).

34.18 (Simonstown): Orange Kloof, swamp (AB), *Wolley Dod 3479* (BM, BOL, K, PRE); shady roadside cutting below Constantia Nek on the road to Groot Constantia, *Goldblatt 6640* (MO, PRE, S).

Without precise locality: *Thunberg s.n.* (S "Herb. Casstrom").

5. **Hexaglottis brevituba** Goldbl., sp. nov. TYPE: South Africa. Cape: Richtersveld, Sabiesies, on the road to Cornelsberg, *Viviers s.n.* in 1983 (holotype, NBG; isotypes, K, MO, PRE). Figure 10.

Planta 40–55 cm alta, foliis 2–4, rhipidiis sessilibus, spathis imbricatis longioribus quam internodis, spathis exterioribus ex bracteis caulis exsertis, tepalis infra connatis, tubo 1–2 mm longo, ovario 8–10 mm longo supra ex bracteis exserto, pedicellis 4–10 mm longis.

Plants 40–55 cm high. *Corm* 12–18 mm diam. or larger if surrounded by accumulated tunic layers, the tunics of coarse, dark brown to blackish fibers. *Leaves* 2–4, linear, ascending, longer than the stems and trailing distally, channeled with margins incurved, inserted towards stem base. *Stem* with 1 main axis or with 2–3 diverging secondary axes, straight or rarely slightly flexuose; lateral rhipidia sessile, partly enclosed by the somewhat shorter subtending stem bracts. *Rhipidia* sessile except the terminal, 3–4-flowered; *spathes* herbaceous, or partly to entirely dry and pale at flowering time, attenuate, (20–)25–30 mm long, exserted from the stem bracts, often membranous below, the outer half to two-thirds as long as the inner. *Flowers* stellate, upright or secund, pale yellow, evidently odorless; tepals united below into a short closed tube; *perianth tube* 1–2 mm long, exserted from the spathes; *tepals* 16–19 mm long, the claws about 1 mm long, the limbs extended horizontally, 5–8 mm wide, the outer larger, narrowly ovate, the inner smaller. *Filaments* 3–4 mm long, united for about 1 mm; *anthers* 7–8 mm long. *Ovary* 8–11 mm long, cylindric, often curved outwards, the upper 1 mm narrow and sterile, the apex often exserted from the spathes; pedicel 4–10 mm long, the style arms about 6 mm long. *Capsule* and *seeds* not known. *Chromosome number* $2n = 12$.

Flowering time. September to October; flowers opening mid afternoon and fading after 7:00 P.M.

Distribution. *Hexaglottis brevituba* is known from only a few sites in central and northern Namaqualand, from Garies to Steinkopf (Fig. 10). There is only a single record from the central part of Namaqualand, at Stinkfontein south of Garies, and other collections are from the Springbok area and north to the Richtersveld, where the type collection was made. *Hexaglottis brevituba* is probably more common than the present record indicates. It is inconspicuous except when in bloom, and the flowers are open for only a few hours in the mid afternoon of a few weeks, usually towards the end of spring.

Diagnosis and relationships. *Hexaglottis brevituba* is clearly allied to the widespread *H. virgata,* which has similar vegetative and floral morphology but is readily distinguished by its flowers with a well-developed perianth tube some 4–7 mm long and an entirely included ovary with a pedicel 4–6 mm long. In *H. brevituba* the perianth tube is only 1–2 mm long; the ovary is often apically exserted and the pedicel (4–)7–10 mm long.

History. The first record of *Hexaglottis brevituba* was made by Rudolf Schlechter in 1897 and the collection was identified only as *Hexaglottis.* In Lewis's revision of the genus she placed it in *H. virgata* var. *lata,* the type and only other collection being from the Biedouw Valley. A third collection, made by G. J. Lewis near Springbok, was assigned to *H. lewisiae* (as *H. flexuosa*) by Lewis, who did not notice the characteristic short perianth tube in the poorly preserved flowers. The perianth tube can, however, be seen in this collection when buds are examined carefully. The range of the species was substantially extended to the Stinkfontein Mountains in the Richtersveld by Mike Viviers in 1983. This, the only adequate collection of *H. brevituba,* has been selected as the type.

Specimens examined. SOUTH AFRICA. CAPE: 28.16 (Vioolsdrif): Richtersveld, Sabiesies, on the road to Cornelsberg (CA), *Viviers s.n.* (K, MO, NBG, PRE), *1337* (NBG).

29.17 (Springbok): north of Steinkopf, near Kosies road in kloof northeast of Rabas (BA), *Goldblatt 5748* (MO); near Springbok (DB), *Lewis 743* (SAM).

30.18 (Kamiesberg): Stinkfontein (on the Groot Doorn R.) (CC), *Schlechter 114876* (BOL).

6. **Hexaglottis virgata** (Jacq.) Sweet, Hort. Brit. ed. 2: 498. 1830; Baker, Flora Cap. 6: 32. 1896, pro parte; Lewis, Flora Cape Peninsula 225. 1950 et J. S. African Bot. 25: 225. 1959. *Moraea virgata* Jacq., Ic. Pl. Rar. 2: tab. 228. 1791 et Coll. Bot. 3: 194. 1791. *Ixia virgata* (Jacq.) Willd., Sp. Pl., 1: 202. 1798. *Homeria virgata* (Jacq.) Sweet, Hort. Brit. ed. 1: 395. 1827. TYPE: South Africa. Cape: cultivated in Vienna, illustration in Jacq., Ic. Pl. Rar. 2: tab. 228. Figure 11.

Plants variable in size, 12–85 cm high. *Corm* 13–18 mm diam., or larger if surrounded by accumulated tunic layers, the tunics of coarse, dark brown to blackish fibers. *Leaves* usually 2–3, occasionally only 1, rarely 4, linear, ascending, longer than the stems and trailing distally, channeled with margins curving inward, occasionally loosely coiled above, inserted towards the stem base. *Stem* with 1 main axis or with 1–3(–6) fairly

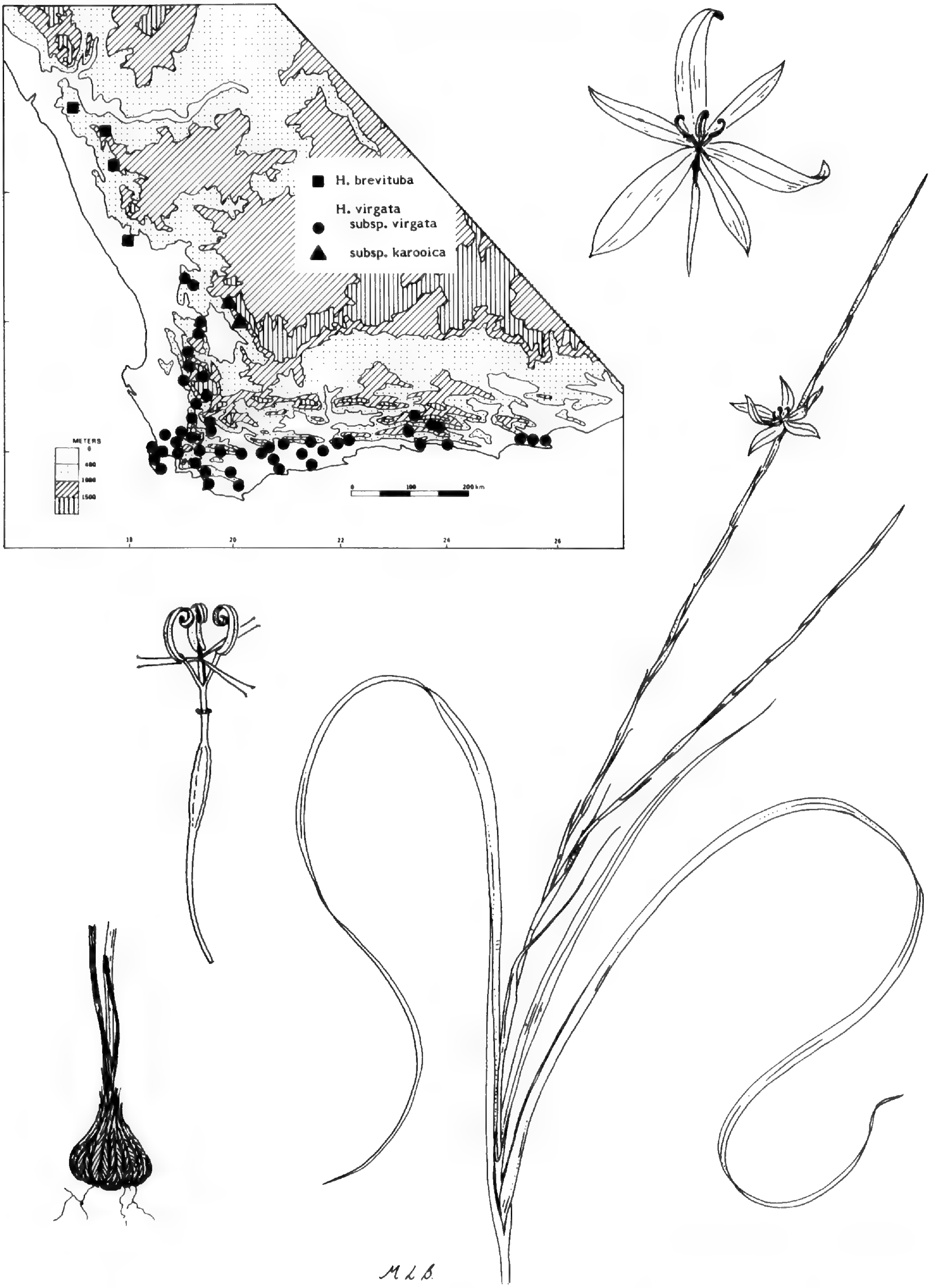

FIGURE 10. Morphology of *Hexaglottis brevituba* and the distribution of *H. brevituba* and *H. virgata.* Habit ×0.5; flower and corm full size; detail of stamens, ovary, and style branches ×2.

long, strongly diverging secondary branches, straight to slightly flexuose, the lateral rhipidia sessile, each partly to almost entirely enclosed by the subtending stem bract, this usually as long or longer than spathes. *Rhipidia* sessile except the terminal, 2–3-flowered; *spathes* herbaceous, or partly to entirely dry and pale at flowering time, attenuate, 22–30(–37) mm long, the outer concealed by a stem bract, often membranous below, ½–⅔ as long as the inner, upper part of the inner extending above the bracts. *Flowers* stellate with the tepals united below into a closed tube, upright or secund, pale yellow, evidently odorless, the nectar guides deeper yellow; *perianth tube* cylindric, narrow, usually slightly curving outward, (3–)4–6(–9) mm long, usually at least partly enclosed in the spathes; *tepals* 14–25 (subsp. *virgata*), 23–32 (subsp. *karooica*) mm long, with short claws 1–1.5 mm long, the limbs extended horizontally, 4–8(–11) mm wide; the outer larger, lanceolate to ovate, the inner smaller, lanceolate to cuneate. *Filaments* 3.3–6 mm long, united for 1–2 mm; *anthers* initially 6–9 mm long. *Ovary* 8–16(–20) mm long, the upper 1–2 mm narrow and sterile, cylindric, included in the spathes, the pedicel short, 5–6 mm long; style arms 5–6 mm long. *Capsule* narrowly spindle-shaped, included in the spathes, 9–13 mm × 2–3 mm (subsp. *virgata*), or 16–22 mm × 4 mm (subsp. *karooica*), only 1 (rarely 2) developed in each rhipidium; *seeds* narrowly angular, 0.7–1 mm wide and 1–2 mm long. *Chromosome number* $2n = 12, 10$ (subsp. *virgata*), or $2n = 14$ (subsp. *karooica*).

Flowering time. (Late September–)October–December(–mid January); flowers opening 3:00–3:30 P.M. (or up to 4:00 P.M. on cooler days), beginning to fade ca. 6:30 P.M., usually collapsed by 7:00 P.M.

Distribution. *Hexaglottis virgata* is widespread in the southern African winter rainfall area, extending from the Nieuwoudtville district in the northwest through the western and southern Cape to Port Elizabeth in the east (Fig. 10). It is rather scattered in the west of its range, but common from Malmesbury and the Cape Peninsula eastwards through the southern Cape. It is found more often on heavier soils, particularly shales of the Malmesbury System, but also occurs on granitic substrates. Occasionally *H. virgata* is found on sandy soils of the Cape System. Subspecies *karooica* occurs inland on the Roggeveld Escarpment, where it favors sheltered and damp situations.

Diagnosis and relationships. *Hexaglottis virgata* is a distinctive species, unmistakable in its slender, relatively long perianth tube some 4–7 mm in length and very straight stems with strongly diverging lateral branches. The historic confusion about the identity of this species has been due to the poor observation that resulted in overlooking the perianth tube or confusing it with the slender ovary (Lewis, 1959). In fact the upper part of the ovary is narrow, sterile, and tubular, but this is clearly different from the perianth tube from which it is separated by an abscission layer. The only other species of *Hexaglottis* with a perianth tube is *H. brevituba*, described in this paper. *Hexaglottis brevituba* has a much shorter tube, only 1–2 mm long, compared with a tube (3–)4–7 mm long in *H. virgata*. The two species differ in several other features. *Hexaglottis virgata* has an ovary entirely included in the spathes on a short pedicel up to 5 mm long, while *H. brevituba* has a longer pedicel 7–10 mm long, and the ovary is curved and usually just exserted from the spathes.

Two subspecies of *Hexaglottis virgata* are recognized here. The typical and most common, subsp. *virgata*, has relatively small flowers and capsules. It has a wide distribution extending over almost the entire range of the species. Subsp. *karooica*, known only from two isolated sites on the Roggeveld Escarpment, has unusually large flowers, spathes, and capsules.

History. The earliest existing records of *Hexaglottis virgata* are those made by the Swedish botanists Carl Peter Thunberg and Anders Sparrman in the 1770s, but this common southwestern Cape species must surely have been collected earlier than this. However, it was Nicholas Jacquin who first described the species in 1791, based on plants grown in Vienna, and probably sent to him some years earlier by Franz Boos and Georg Schol, the collectors who provided Jacquin with many of the Cape plants that he illustrated and described. The painting that accompanies the description and serves as the type in the absence of preserved material is excellent and leaves no doubt about the identity of what Jacquin called *Moraea virgata*. After the genera *Homeria* and *Hexaglottis* were recognized as distinct from *Moraea* by E. P. Ventenat in 1808, *M. virgata* was

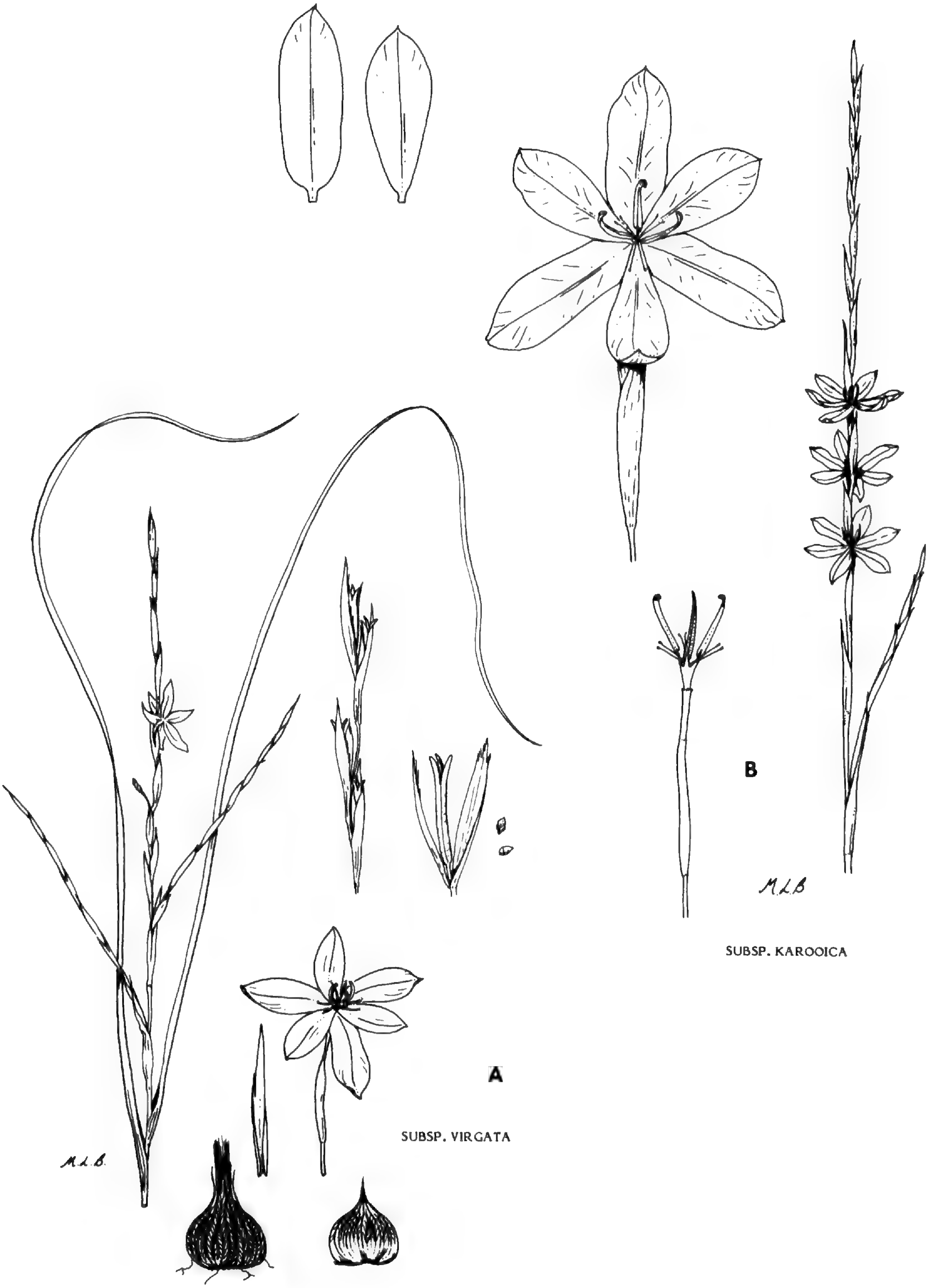

FIGURE 11. Morphology of *Hexaglottis virgata*.—A. Subsp. *virgata*.—B. Subsp. *karooica*. Habits ×0.25; corms ×0.5; flowers, fruiting branch (subsp. *virgata*), separated tepals, and detail (subsp. *karooica*) of androecium and gynoecium full size; single capsule and seeds (subsp. *virgata*) ± ×2.

transferred to *Homeria* (Sweet, 1827) and shortly afterward to *Hexaglottis* (Sweet, 1830). J. G. Baker included *H. lewisiae* (as *H. flexuosa*) and *H. longifolia* in *H. virgata* in *Flora Capensis* (1896). This unsatisfactory treatment was corrected by G. J. Lewis in 1950.

KEY TO THE SUBSPECIES OF *HEXAGLOTTIS VIRGATA*

1a. Outer tepals 14–22(–25) mm long × 5–7 (–11) mm wide; spathes (at least the terminal) 22–28(–32) mm long; foliage leaves 1–3, rarely more .... 6A. subsp. *virgata*
1b. Outer tepals 23–32 mm long × 7–10.5 mm wide; spathes (at least the terminal) 32–37 mm long; foliage leaves (2–)3–5 .... 6B. subsp. *karooica*

6A. Subsp. **virgata.** Figure 11A.

Hexaglottis virgata var. *lata* G. Lewis, J. S. African Bot. 25: 228–229. 1959. TYPE: South Africa. Cape: Welbedacht, Bidouw Valley, *Lewis 2514* (holotype, SAM 61821; isotypes, BOL, PRE, SAM).

Plants 12–50(–70) mm high. *Leaves* 1–3(–4). *Spathes* 22–28(–32) mm long. *Flowers* with perianth tube (3–)4–5.5(–7) mm long; *tepals* 14–22(–25) mm long. *Filaments* 3.3–6 mm long; *anthers* 5–8 mm long. *Ovary* 8–12 mm long; *capsules* 9–13 mm long. *Chromosome number* $2n$ = 12, 10.

Distribution. The distribution of subsp. *virgata* is the same as that for the species, except that it does not occur on the Roggeveld Escarpment (Fig. 10).

Variation. As circumscribed here, subsp. *virgata* includes the variety *lata,* described by G. J. Lewis for somewhat larger-flowered plants with comparatively wide tepals, from the Biedouw Valley. When this was described in 1959, no other population of *H. virgata* was known from the northwestern Cape, and only one was known from Namaqualand, a poorly preserved specimen, which Lewis included in var. *lata* despite the distorted flowers that could not be accurately measured. *Hexaglottis virgata* is now known from several sites in the northwest Cape, from the Olifants River Valley and adjacent Pakhuis Mountains to the Nieuwoudtville Escarpment. Variation in flower dimensions in these populations is considerable and covers the whole range from typical rather small-flowered subsp. *virgata* (tepals 14–20 × 5–8 mm; spathes 22–28 mm long), which occurs in the Cape Peninsula and southern Cape, to the type of var. *lata* and very similar plants from Nieuwoudtville (tepals 20–25 × 9–11; spathes 23–30 mm long). The rationale for recognition of the variety has thus disappeared. These northwestern populations do, however, appear to represent a distinct race. Plants from two populations from the northwestern area have a karyotype with strongly acrocentric chromosomes (Fig. 3F) that contrast with the presence of acrocentrics and submetacentrics in the most common southern cytotype (Fig. 3E).

Populations examined from the Cape Peninsula have n = 5, and a very different karyotype from those with n = 6 (Fig. 3G) (see discussion under Cytology). There seems to be no corresponding morphological difference in the Cape Peninsula plants.

Specimens examined. SOUTH AFRICA. CAPE–31.19 (Calvinia): Grasberg road northwest of Nieuwoudtville, renosterveld (AC), *Goldblatt 7071* (K, MO, NBG, PRE, US); 2–3 km from Nieuwoudtville on the north side of the road to the escarpment, *Goldblatt 7411* (MO); 8 km south of Nieuwoudtville on sandstone slopes, *Goldblatt 7395* (MO).

32.18 (Clanwilliam): 10 km south of Clanwilliam, clay road bank (BB), *Goldblatt 6705* (MO, PRE); 12 km south of Clanwilliam, stony clay bank, *Goldblatt 6989* (K, MO, NBG, PRE, WAG); clay hillside just south of the Alpha turnoff, on the National Road to Citrusdal (BD), *Goldblatt 3028* (MO).

32.19 (Wuppertal): between Doorn River and Bidouw Valley turnoff, stony clay (AA), *Goldblatt 5941* (MO); Welbedacht, Bidouw Valley, *Lewis 2514* (BOL, PRE, SAM).

33.18 (Cape Town): Table Mountain (CD), *Tyson 2488* (SAM), *Bayliss 3054* (UC); kloof between Lions Head and Table Mountain, *Burchell 252* (K); slopes of Devils Peak, above de Waal Drive, Cape Town, *Goldblatt 6717* (MO); near Bishopscourt, *Salter 9001* (BOL); Wynberg Hill, *Pillans 10819* (MO, UPS), *Salter 8978* (SAM), *9545* (BM); Signal Hill, *Lewis 665* (SAM), *Goldblatt 71* (J), *6747* (MO, S), *6748* (MO), *Marloth 7234* (PRE); Camps Bay, *Moss 13403* (J); Observatory grounds, *Davis s.n.* (SAM 61050); Tygerberg Nature Reserve (DC), *Loubser 3004* (MO); Stellenbosch (DD), *Boucher 3392* (PRE, STE); 4 miles from Faure on the Stellenbosch road, *Lewis 2340* (SAM); Groot Drakenstein und fuss Paarlberg, *Drège s.n.* (S).

33.19 (Worcester): farm Waterval, near Porterville (AA), *Loubser 966* (NBG); Tulbagh Cemetery (AC), *Goldblatt 5225* (K, MO, S); 9 miles along the Leeuwfontein road (AD), *Pearson 3508* (K); Bains Kloof (CA), *Schlechter 9106* (BM, BOL, BR, G, K, MO, PRE, S), *2597* (PRE); 8 miles west of Worcester, near the Breede R. (CB), *Lewis 5309* (NBG, PRE); Karoo Garden, Worcester, *Compton 17849* (NBG), *Lewis 5304* (NBG); Pokkraal, Rawsonville, *le Roux s.n.* (PRE); between Worcester and Robertson (DA–DB), *Zinn s.n.* (SAM 65673).

33.20 (Montagu): pasture below 10 O'Clock Mt., Swellendam (CD), *Wurts 486* (NBG).

33.21 (Ladismith): south entrance to Attaquas Kloof (DD), *Thompson 1636* (PRE); Attaquaskloof, Mossel Bay, *Barker 7692* (NBG).

33.23 (Willowmore): hills near Uniondale (CA), *H. Bolus 2484* (K); Prince Alfreds Pass (CC), *Wall 18* (LD); near Misgund (CD), *Goldblatt 6792* (MO); between Misgund and Nieuweplaats (DC), *Fourcade 5485* (PRE, STE); Kliprivier, Tsitsikamma Park, *Bower 625* (PRE); hills near Joubertina (DD), *Fourcade 2374* (BOL, K); Joubertina, Bokkeveld hill, *Esterhuysen 6772* (BOL).

33.25 (Port Elizabeth): Van Staadens Hoogte (CC), *MacOwan 2055* (BM, K); Greenbushes (CD), *Holland 4051* (BOL); Baakens River Valley, Port Elizabeth (DC), *Olivier 1739* (WAG); Port Elizabeth, *Long 502* (K), *Paterson sub Rogers 2414* (J).

34.18 (Simonstown): Steenberg (AB), *Compton 1665* (NBG); Bergvliet, *Purcell s.n.* (BOL 1638, SAM), *124* (SAM); Somerset West, on stiff clay soil (BB), *Parker 4388* (BOL, K, MO, NBG).

34.19 (Caledon): Houw Hoek (AA), *Penther 572* (K, S); Greyton-Genadendal (AB), *Lindeberg s.n.* (S); Napier Ruggens (BD), *Marloth 10006* (PRE); between Napier and Bredasdorp (CA), *Goldblatt 6937* (MO); Franskraal, along the coast above the beach (CD), *Goldblatt 5368* (MO); sandy soil on slopes near Avoca (DA), *Goldblatt 6939* (MO, PRE, S, WAG); Bredasdorp Poort (DB), *Esterhuysen 19580* (BOL).

34.20 (Bredasdorp): Storms Vlei Kloof (AA), *Leipoldt 3549A* (BOL); Bontebok Park, Swellendam (AB), *Liebenberg 6710* (STE); Zuurbraak (BA), *Barker 5029* (NBG); Grootvadersbos, paths in wood (BB), *Willems 88* (NBG); shale hills west of Heidelberg, *Goldblatt 7416* (MO); Potteberg (BC), *David s.n.* (NBG); Malgas, Swellendam distr., *Leipoldt 3550* (BOL).

34.21 (Riversdale): hill top 5 km west of Riversdale (AA), *Goldblatt 5436* (MO); Still Bay, limestone hills (AD), *Esterhuysen 19538* (BOL, PRE); limestone hills south of Albertinia, Stilbaai road on turnoff to Riethuiskraal, *Goldblatt 7428* (MO); Onverwacht, Albertinia (BA), *Muir 1207* (BOL).

34.23 (Knysna): Plettenberg Bay (AB), *Rogers 28241* (K), *26762* (K).

Without precise locality: CBS, *Alexander s.n.* (BM, K); *Sparrman s.n. Iris edulis* (S); *Thunberg s.n. Iris edulis* (S).

6B. Subsp. **karooica** Goldbl., subsp. nov. TYPE: South Africa. Cape: eastern border of farm Blomfontein, 22 km from Middelpos towards de Hoop, *Snijman 765* (holotype, NBG; isotypes, K, MO, PRE). Figure 11B.

Planta robusta, 30–85 cm alta, foliis (2–)4–5, spathis 32–37 mm longis, tubo perianthii 6.5–9 mm longo, tepalis 23–32 mm longis, 7–11 mm latis, antheris 6–8 mm longis, capsulis 16–22 mm longis.

Plants robust and 30–85 cm high. *Leaves* usually 4–5, rarely 2–3. *Spathes* 32–37 mm long. *Flowers* with perianth tube 6.5–9 mm long; *tepals* 23–32 mm long, 7–11 mm wide. *Filaments* 4–6 mm long; *anthers* 6–8 mm long. *Ovary* 15–20 mm long. *Capsules* 16–22 mm long. *Chromosome number* $2n = 14$.

Distribution. Subsp. *karooica* is known from two widely separated localities along the Roggeveld Escarpment, near Blomfontein west of Middelpos in the north, and on the slopes of Sneeukrans on the farm Voelfontein northwest of Sutherland, some 50 km to the south. The habitat at both sites is moist, the plants growing among large rocks near seepage zones.

Variation. The subspecies is variable in flower size. Plants from the Middelpos area have very large tepals 28–32 mm long while those from Voelfontein have smaller flowers with the tepals somewhat narrower and only 23–24 mm long. Despite this variation, other features, including large spathes and capsules, higher leaf number, and the unusual karyotype with $2n = 14$, in both populations indicate that subsp. *karooica* is indeed a distinct geographical variant of *Hexaglottis virgata*.

Specimens examined. SOUTH AFRICA. CAPE–31.20 (Williston): Roggeveld Escarpment, 71 km SE of Calvinia on Middelpos road via Blomfontein (CC), *Goldblatt 4612* (MO, NBG); eastern border of farm Blomfontein, 22 km from Middelpos towards de Hoop, *Snijman 765* (K, MO, NBG, PRE).

32.20 (Sutherland): Roggeveld, Sneeukrans south of Voelfontein farm, ca. 4,500 ft., in wet site (AD), *Goldblatt 6336* (MO), *7126* (MO).

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NOTES ON THE VARIATION AND TAXONOMY OF *WATSONIA BORBONICA* (*W. PYRAMIDATA, W. ARDERNEI*) (IRIDACEAE) IN THE SOUTHWESTERN CAPE, SOUTH AFRICA[1]

Peter Goldblatt[2]

Abstract

Lomenia borbonica Pourret (1788) is an earlier name for the common Cape species formerly called *Watsonia pyramidata*, and the new combination in *Watsonia* is made here. Significant and unusual variation in the stamen and style orientation, either declinate or arcuate, characterizes southern and northern races which otherwise seem indistinguishable. The white-flowered *W. ardernei* is considered an albino sport of the northern race and is reduced to synonymy. Other synonyms of *W. borbonica* are discussed and the complete nomenclature of the species is presented.

The name *Watsonia borbonica* is a new combination based on *Lomenia borbonica* Pourret (1788), only species of *Lomenia* Pourret. The epithet was given to a plant believed to have been collected on the Isle de Bourbon, now called Réunion. *Lomenia* has long been misunderstood and was for a time considered a synonym of *Freesia* Klatt, a southern African genus. During a study of *Freesia* (Goldblatt, 1982), I discovered that *Lomenia* was congeneric with *Watsonia*. Based on the illustration in the protologue, I considered *L. borbonica* conspecific with *W. marginata* (L. f.) Ker, the basionym of which predates *Lomenia*. Later, I found the type specimen of *L. borbonica* at the Paris Herbarium (P) in 1985. The specimen is in excellent condition, and there can be no doubt that it is identical with the species presently known as *W. pyramidata* (Andrews) Klatt, and in the *Flora Capensis* as *W. rosea* Ker (Baker, 1896). The type collection is attributed to Philibert Commerson, who collected in the Mascarene Islands in 1770–1774. Commerson is thought not to have visited the Cape (Gunn & Codd, 1981), and the provenance of this and a few other Cape plants attributed to Commerson's collection remains unknown.

Nothing could be more inappropriate than for a native southwestern Cape species to have a specific epithet '*borbonica*'. However, there is no alternative but to use the earliest valid and legitimate name for a species as mandated by the 1983 Code of Botanical Nomenclature.

Habitat and Variation

Watsonia borbonica is a fairly common and well-known species of *Watsonia* of the southwestern Cape, South Africa. It is usually found in mountain habitats and is locally common and conspicuous after fires on lower slopes, but it also occurs on sandy flats and at relatively high altitudes up to 1,000 m. Its range extends from the Cape Peninsula eastward to Bredasdorp and locally north through the du Toits Kloof mountains to the Breede River floodplain near Romans River. Plants flower in the early summer, from October to early December and at high elevations into January. They prefer rocky sandstone soils but may be found on soils derived from granite.

Although *Watsonia borbonica* is not particularly variable, what may be called the northern and southern races differ in one unusual feature, the orientation of the stamens and style. The southern and typical populations have declinate stamens that lie against the lower (anterior) tepal, and when the style is receptive it lies below the stamens. Northern populations from Paarl Mountain, du Toits Kloof, and the Breede River valley have unilateral stamens that lie horizontal to somewhat arched under the upper (posterior) tepal, and the style lies between the stamens and the upper tepal. In all other features the plants appear to be morphologically identical and cannot be distinguished even on close inspection.

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The diagnostic features of *Watsonia borbonica* are its large flowers with subequal, pink tepals 30–36 mm long; a short, flared upper perianth tube 8–12 mm long; robust and branched habit (1–2 m tall); oblong-ovate capsules 20–30 mm long; and seeds with two wings. Pink-flowered specimens of the northern form have always been included in *W. borbonica* (as *W. pyramidata*). However, a white-flowered sport believed to have come from the northern part of its range has been recognized as *W. ardernei,* a plant that has been in cultivation for close to 100 years and is the best-known cultivated *Watsonia* species. *Watsonia ardernei* is here reduced to synonymy in *W. borbonica.*

The significance of the variation in stamen and style orientation is uncertain. It is clear that declinate stamens and style are unusual in *Watsonia,* occurring in only six other species. Arcuate stamens are more common and are found in all but one of the remaining ca. 45 species of the genus and in many other genera of Ixioideae. Presumably the declinate condition, rare in Iridaceae, is derived directly from the more common arcuate state and not independently from an ancestor with symmetrically disposed stamens. Despite the apparently gross morphological difference in stamen and style orientation between the northern and southern races of *W. borbonica,* I believe that they should be treated as a single species. I defer recognition of intraspecific taxa until my monograph of *Watsonia,* currently in preparation, is completed.

Other Synonyms

Among other species I regard as synonyms of *Watsonia borbonica* is *W. cooperi* G. Lewis, based on the illegitimate homonym *Tritonia cooperi* Baker. The type is a fragment comprising a lateral branch of the spike and three poorly pressed flowers. The leaf mounted with the flowering material has three conspicuous veins and is clearly misplaced, belonging either to a species of *Anapalina* N. E. Br. or *Tritoniopsis* L. Bolus. However, the flowering material seems to belong to *W. borbonica.* The tube and tepals are much distorted, but the stamens seem declinate, and the dimensions of the tepals and perianth tube accord with *W. borbonica.*

The reasons for treating *Watsonia ardernei* Sander and *W. ardernei* Hort. ex Mathews & L. Bolus as conspecific with *W. borbonica* have already been outlined, but the existence of the homonyms applied to the same species is puzzling. Possibly Mathews & Bolus believed that the name as described by Sander in a nurseryman's catalogue was not valid, hence their formal recognition of a name already in use. The white-flowered form, originally collected at Romans River near Wolseley, on which *W. ardernei* (both of Sander and of Mathews & Bolus) is based is no longer known in the wild. It probably comprised one or a few individuals that were introduced into gardens and then multiplied. The plant named *W. iridifolia* var. *obrienii* by N. E. Brown is based on cultivated plants from the same source as the type material of *W. ardernei.*

The complete synonymy of *W. borbonica* is outlined below. All type specimens cited have been seen.

Synonymy

Watsonia borbonica (Pourret) Goldbl., comb. nov. *Lomenia borbonica* Pourret, Hist. & Mem. Acad. Roy. Sci. Toulouse (Acta Acad. Sci.) 3: 74 & tab. 5. 1788. TYPE: said to have been collected on Réunion (Ile de France) but clearly from the SW Cape, *Commerson s.n.* (holotype, P).

Gladiolus pyramidalis Lam., Encyc. Meth. 2: 726. 1786. hom. illeg., non Burm. f. (1768), which is *Ixia patens* Aiton (Lewis et al., 1972: 302). TYPE: South Africa. Cape: precise locality unknown, collector unknown (holotype, P—Herb. Lamarck).

Gladiolus iridifolius varietas speciosa floribus roseis Jacq., Ic. Rar. Pl. tab. 235. 1793.

Neuberia rosea (Ker) Ecklon, Top. Verz. 37. 1827, nom. illeg., genus sine descr.

Watsonia pyramidata (Andrews) Klatt, Durand & Schinz, Consp. Fl. Africa 5: 194. 1895; Stapf, Bot. Mag. sub tab. 9261. 1931; L. Bolus, Fl. Pl. Africa 25: tab. 974. 1946; Lewis, Flora Cape Peninsula 238.1950. *Gladiolus pyramidatus* Andrews, Bot. Rep. 5: tab. 335. 1803. *Watsonia rosea* Banks ex Ker, Konig & Sims, Ann. Bot. 1: 230. 1804, Bot. Mag. tab. 1072. 1807; Baker, Handbk. Irid. 158. 1892, Flora Cap. 6: 177. 1896, nom. illeg. superfl. pro *Gladiolus pyramidatus* Andrews. TYPE: South Africa. Cape: precise locality unknown, illustration in Bot. Rep. tab. 335 (lectotype here designated).

Watsonia striata Klatt, Abh. Nat. Ges. Halle 15: 352. (Erganz. 18). 1882. TYPE: South Africa. Cape: Cape Town, *Spielhaus s.n.* (holotype, B—Herb. Lubeck, believed destroyed). Identity determined from description only.

Watsonia iridifolia var. *obrienii* N. E. Br., Gard. Chron. ser. 3, 6: 350. 1889; Klatt, Durand & Schinz, Conspect. Fl. Africae 5: 193. 1895. TYPE: South Africa. Cape: not known; authentic material present at Herb. Kew (probably originally from Romans River farm, Tulbagh Div., flowered at Kew from plants sent from St. George's Park, Port Elizabeth).

W. obrienii van Tubergen, Gard. Chron. ser. 3, 16: 701. 1894, nom. nud. (not a valid combination based on *W. iridifolia* var. *obrienii* as suggested by Marais, Kew Bull. 35: 172. 1980).

Tritonia cooperi Baker, Handbk. Irid. 192. 1892, Flora Cap. 6: 122.1896, hom. illeg., non Klatt (1882), which is *Tritonia cooperi* (Baker) Klatt. *Watsonia cooperi* L. Bolus, J. Bot. 67: 135. 1929; Lewis, J. S. African Bot. 7: 55. 1941. *Tritonia quinquenervata* Foster, Contr. Gray. Herb. 114: 46. 1936, nom. nov. pro *T. cooperi* Baker, hom. illeg. TYPE: South Africa. Cape: Worcester Div., *Cooper 3182* (holotype, K, sketch at BOL). (The type sheet comprises a flowering stem and poorly pressed flowers of *W. borbonica* and a leaf of a species of *Anapalina* or *Tritoniopsis*.)

Watsonia ardernei Sander, New Plants for 1897: 18, 20 & fig. 1897, Catalogue 44. 1899. TYPE: not known, figure in New Plants for 1897 (lectotype here designated).

Watsonia ardernei Hort. ex Mathews & L. Bolus, Ann. Bolus Herb. 4: 25–26. 1925; Fl. Pl. Africa 19: tab. 750. 1939, hom illeg., non *W. ardernei* Sander (1897). TYPE: South Africa. Cape: Romans River farm, Tulbagh Distr. (cult. Kirstenbosch), *Tredgold s.n.* (lectotype, BOL 17839, here designated; isolectotypes, BM (as *Arderne s.n.*), BOL).

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NOTES ON THE FLORAL BIOLOGY, CYTOLOGY, AND EMBRYOLOGY OF *CAMPYNEMANTHE* (LILIALES: CAMPYNEMATACEAE)[1]

PORTER P. LOWRY II,[2] PETER GOLDBLATT,[3] AND HIROSHI TOBE[4]

ABSTRACT

Field observations of the endemic New Caledonian genus *Campynemanthe* (Liliales: Campynemataceae) indicate that at least *C. neocaledonica* and *C. viridiflora* are strongly protandrous and have an unusual postanthesis recurving of the filaments. A chromosome number of $n = 11$ has been determined for both species from meiosis in pollen mother cells, these being first records for the genus and family. Endosperm formation in *C. neocaledonica* is nuclear rather than helobial as in several genera of the putatively related Melanthiaceae.

Campynemanthe Baillon comprises three species restricted to the Pacific island of New Caledonia. Goldblatt (1986) recently revised the genus along with the closely related, monotypic Tasmanian endemic *Campynema* Labill. and followed Dahlgren & Clifford (1982) and Dahlgren & Lu (1985) in placing both genera in Campynemataceae. The family, which appears to occupy an unspecialized position in Liliiflorae, is possibly most closely related to Melanthiaceae of the order Liliales (sensu Dahlgren & Clifford, 1982) or Melanthiales (as recently circumscribed by Dahlgren et al., 1985). Campynemataceae are distinguished from most other Liliales by their small greenish flowers with persistent and accrescent tepals, partly inferior ovaries, and free stylodia. The embryology of both genera of Campynemataceae is of the basic type for the monocots (Dutt, 1970; Dahlgren & Lu, 1985), except that the endosperm development is now known to be nuclear, a derived condition.

We report here some observations on the floral biology of two species of *Campynemanthe,* including the occurrence of protandry and an unusual postanthesis behavior of the persistent filaments. We also record the first chromosome counts for the genus and family, and we observed nuclear endosperm development, an aspect of the embryology of Campynemataceae previously unknown.

FLORAL BIOLOGY

Recent field observations indicate that *Campynemanthe neocaledonica* (Rendle) Goldblatt is strongly protandrous. This phenomenon was initially observed in December 1985, in a population of about 100 individuals covering an area of ca. 20 m^2 located at 900 m on the Plateau de Dogny (*Lowry 3945*). Many individuals were bearing both flowers and young fruits. The flowers exhibited discrete male and female phases of sexual expression. In the initial, male phase the straight filaments are erect to ascending and are usually twisted slightly counterclockwise so that the oblong to ovate anthers alternate with the tepals (Fig. 1a). During this phase the three small stylodia are erect and closely appressed, forming a short beak, with the undeveloped adaxial stigmatic surfaces unexposed. Following abscission of the anthers, the persistent filaments become nearly spreading to horizontal and twist further (Fig. 1b). At this time the stylodia elongate considerably and recurve to expose the whitish stigmatic surfaces.

While there appears to be no overlap in the sexual phases within a single flower, flowers of

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ANN. MISSOURI BOT. GARD. 74: 573–576. 1987.

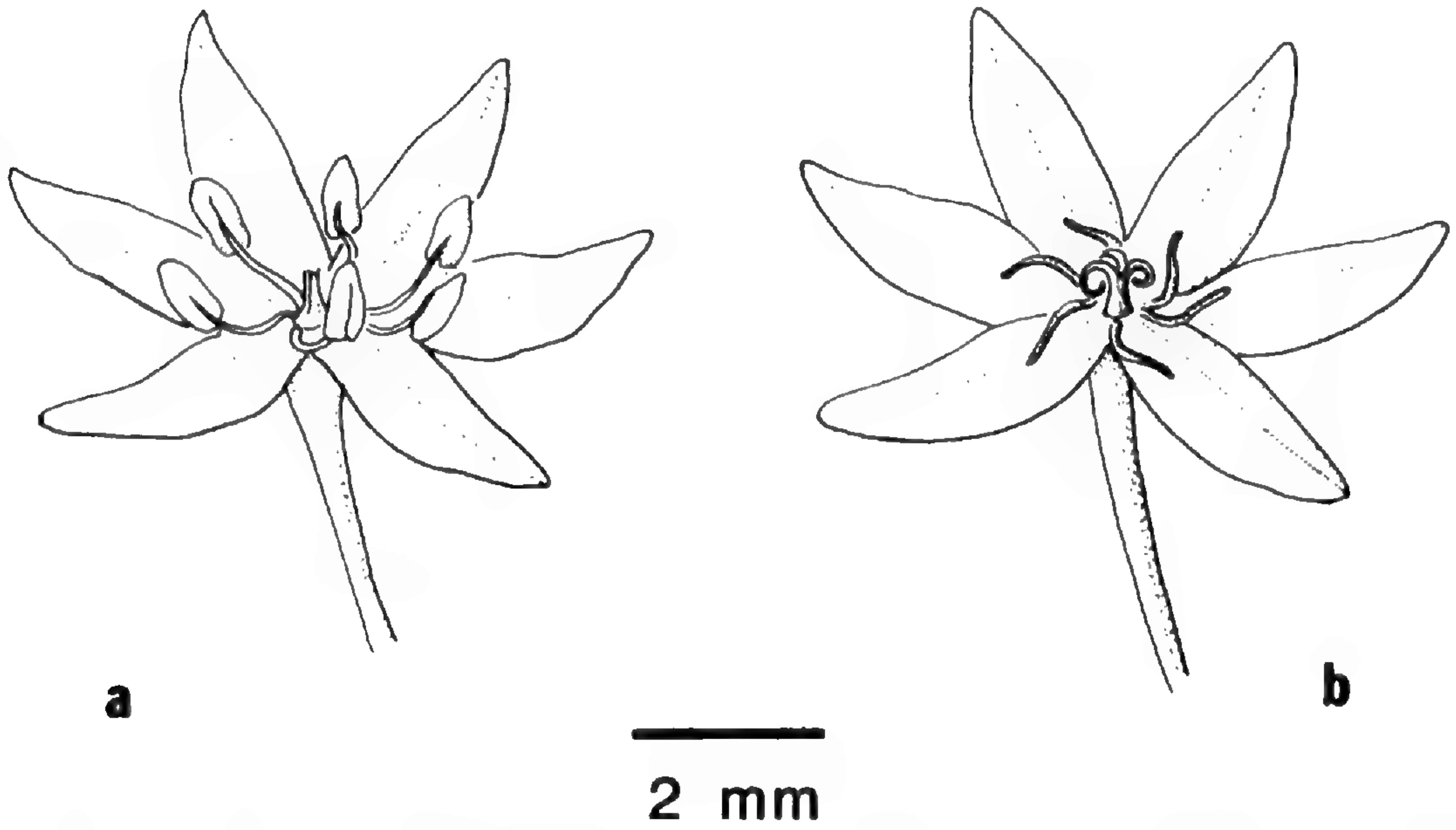

FIGURE 1. Flowers of *Campynemanthe neocaledonica* (*Lowry 3945*).—a. Male phase.—b. Female phase.

both phases frequently occur within individual inflorescences. Geitonogamy thus appears possible, assuming at least some self-compatibility. There did not appear to be synchrony of flowering among the individuals in the population, although observations were made on only a single day.

It has since been possible to confirm protandry in another population of *Campynemanthe neocaledonica* from Haute Ouinné (*Lowry & Suprin 3698*) from photographs taken in the field. Similarly, two distinct floral phases can be seen in photographs of *C. viridiflora* Baillon taken at 950 m on the Montagne des Sources (*Lowry 3762*) and at 1,350 m on Mt. Humboldt (*Lowry 3812*), indicating that this species is dichogamous and almost certainly protandrous. Unfortunately, we have not been able to determine whether protandry occurs in the third member of the genus, *C. parva* Goldblatt, or in *Campynema lineare* Labill. In the latter the filaments also recurve after abscission of the anthers, as figured by Dahlgren & Lu (1985) and reported by Goldblatt (1986).

Bawa & Beach (1981) and Lloyd & Webb (1986), who have reviewed the evolutionary aspects of dichogamy in general, and protandry in particular, concluded that dichogamy in self-compatible species permits pollen and stigmas to be positioned close to one another without high levels of self-pollination. They also pointed out that protandry is by far more common than protogyny in biotically pollinated species, which is presumably the case for *C. neocaledonica*. We did not observe floral visitors on species of *Campynemanthe*.

CHROMOSOME NUMBER

A haploid chromosome number of $n = 11$ was determined from pollen mother cells in flower buds of *Campynemanthe neocaledonica* and *C. viridiflora*. Inflorescences of these species were fixed in the field with 3 : 1 ethanol–acetic acid and squashed with FLP orcein. The relatively large chromosomes were ca. 3 μm long at meiotic metaphase but exhibited no distinctive details.

Chromosome numbers in Melanthiaceae are diverse. The counts summarized in Table 1 were taken from the *Index to Plant Chromosome Numbers* series (Goldblatt, 1985, et praec.) and unpublished work (Ambrose, 1975; Bodkin, 1978). Tofieldieae apparently have $x = 15$, the only known base number in the monotypic genera *Pleea* and *Harperocallis*, and the most common one in *Tofieldia*. *Tofieldia coccinea* Richards. has $x = 16$, a count confirmed by a number of workers, but several other species have $x = 15$. Counts of $n = 14$ and $n = 15$ have been reported for *T. calyculata* (L.) Wahlenb. *Japanolirion*, which perhaps belongs in Tofieldieae (Utech, 1984), has $n = 12$.

In Melanthieae $x = 8$ is the most frequent base number and the only one in *Melanthium*, *Schoenocaulon*, and *Veratrum*. There are two distinct series in *Zigadenus*: $n = 16$ in *Z. elegans* Pursh, *Z. glaucus* Nutt., *Z. sibiricus* (L.) A. Gray ex S. Wats., *Z. nuttallii* A. Gray ex S. Wats., and *Z. volcanicus* Benth.; and $n = 11$ in *Z. fontanus*

Eastw., *Z. fremontii* (Torr.) Torr. ex S. Wats., *Z. brevibracteatus* (M. E. Jones) Hall, and *Z. venenosus* S. Wats. *Amianthium* has $x = 16$ (Utech, 1986), and *Stenanthium* has $x = 8$ and a puzzling second base of $x = 10$.

Narthecieae, the largest tribe in the family, appears to be paleotetraploid. *Narthecium, Aletris, Nietreria,* and *Metanarthecium* have $x = 13$, while *Helonias* and *Heloniopsis,* now usually segregated as a distinct tribe (Utech, 1984) or even family, have $x = 17$. *Lophiola,* perhaps allied to Narthecieae, has $n = 21$.

The curious genus *Chionographis,* placed in Chionographideae (Dahlgren et al., 1985), has $n = 12$ in *C. koidzumiana* Ohwi and *C. japonica* (Willd.) Maxim. var. *japonica,* but *C. japonica* var. *kurohimensis* Ajima & Satomi has $n = 22$, and subspp. *minoensis* (Hara) Hara and *hisuachiana* (Okuyama) Hara have $n = 21$. The most parsimonious interpretation here is a base number of $x = 12$, with reduction to $x = 11$ and polyploidy resulting in $n = 22$, then reduction to $n = 21$. The taxonomically isolated *Xerophyllum* (Xerophylleae) has $x = 15$.

Summarizing, the available counts suggest to us a possible ancestral base number of $x = 8$ for Melanthiaceae, persisting only in *Melanthium, Schoenocaulon, Veratrum,* and *Stenanthium* (all Melanthieae). Other genera and tribes are apparently paleotetraploid, with Tofieldieae having $x = 15$ (or 16) and Narthecieae perhaps with $x = 13$. *Chionographis* most likely has $x = 12$, and *Xerophyllum* $x = 15$. The base number of $x = 17$ reported in *Helonias* and *Heloniopsis* is difficult to reconcile with other members of the Narthecieae. The odd counts of $n = 11$ in *Zigadenus,* which has several species with $x = 16$, and $n = 20$ in *Stenanthium,* which also has $n = 8$, remain to be explained as well.

Our report of $n = 11$ for Campynemataceae, which suggests a base number of $x = 11$, does not fit with any assemblage of Melanthiaceae. Campynemataceae do, however, appear to be paleotetraploid but have a lower base number than any genus or tribe of Melanthiaceae, with the exception of the paleodiploid *Veratrum.* This may indicate a derived condition, with $x = 11$ presumably being secondary to the higher numbers in the tetraploid series $x = 16, 14, 13, 12, 11$.

TABLE 1. Chromosome numbers recorded in Campynemataceae and basic chromosome numbers for genera of Melanthiaceae summarized from the *Index to Plant Chromosome Numbers* (Goldblatt, 1985, et praec.) and supplemented by data in Ambrose (1975), Bodkin (1978), and Utech (1984, 1986).

Taxon (species counted/total species)	Base Number	Haploid Numbers
Campynemataceae		
Campynema (0/1)	Uncounted	
Campynemanthe (2/3)		
C. neocaledonica[1]	11	11
C. viridiflora[1]	11	11
Melanthiaceae		
Tofieldieae		
Pleea (1/1)	15	15
Harperocallis (1/1)	15	15
Tofieldia (9/20)	15	15, 14, 16, 30
Japanolirion (1/1)	12	12
Melanthieae		
Veratrum (11/25)	8	8, 16, 40, 48
Zigadenus (8/15)	16	16, 11
Schoenocaulon (8/10)	8	8
Stenanthium (2/2)	8	8, 10
Melanthium	8	8
Amianthium	16	16
Narthecieae		
Narthecium (2/5)	13	13, 26
Aletris (7/25)	13	13, 26
Metanarthecium (1/2)	13	26
Nietreria	13	13
Ypsilandra (0/5)	Uncounted	
Helonias (1/1)	17	17
Heloniopsis (5/5)	17	17
Lophiola (1/1)	21 (or 7)	21
Chionographideae		
Chionographis (2/5)	12	12, 21, 22
Xerophylleae		
Xerophyllum (2/2)	15	15

[1] Voucher data for original counts: *C. neocaledonica,* New Caledonia, Plateau de Dogny, 900 m, *Lowry 3945* (MO, NOU, P); *C. viridiflora,* New Caledonia, Mt. Mou, 1,150 m, *Lowry 3857* (MO, NOU, P).

EMBRYOLOGY

Although it was not possible to pursue the details of early endosperm development in *Campynemanthe,* the available fixed material of *C. neocaledonica* (*Lowry 3945*), which comprised nearly 100 seeds that had developed past the 64-nucleate stage, indicates that the endosperm of this species is nucleate and not helobial (Stenar,

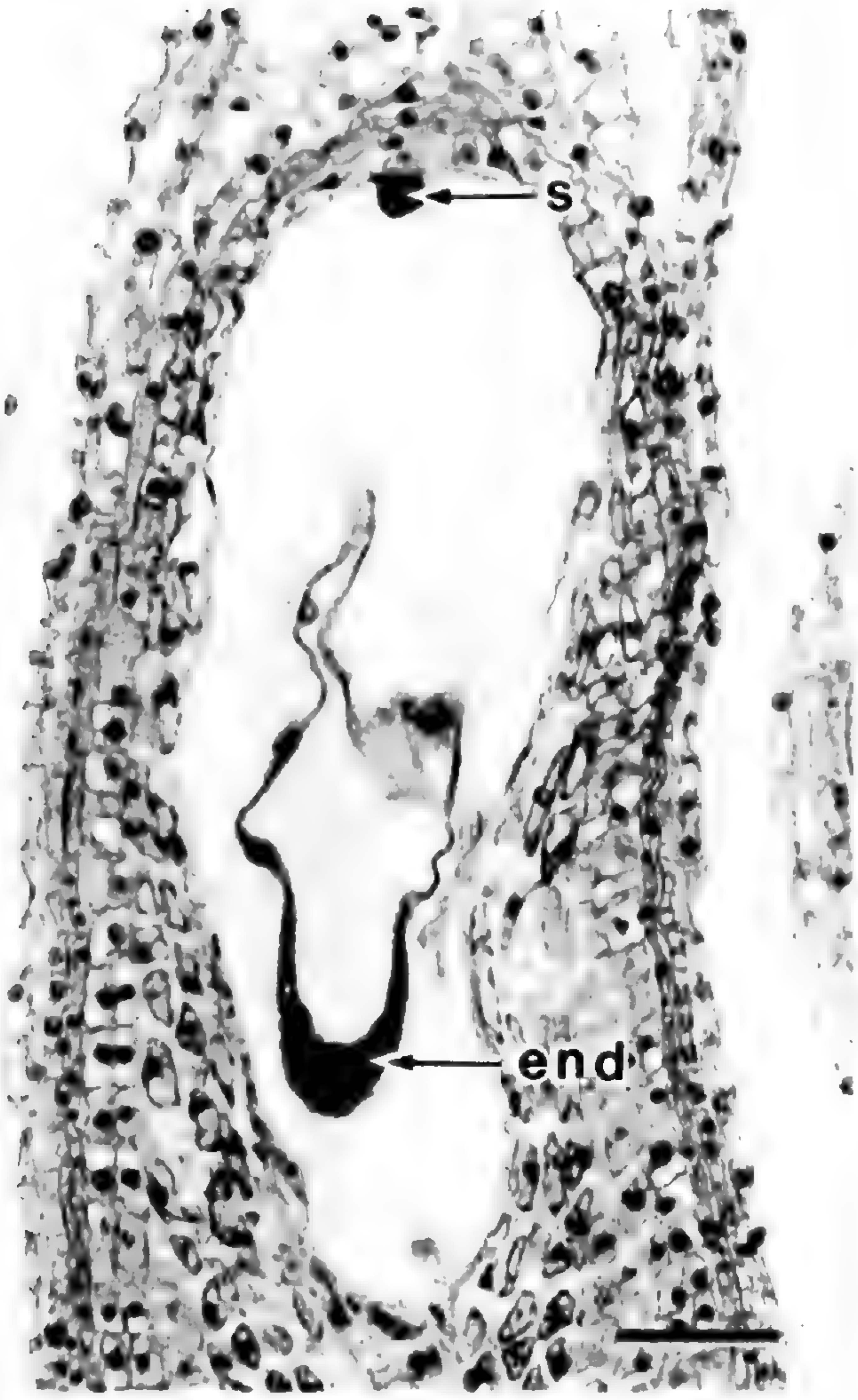

FIGURE 2. Longitudinal section of a young seed of *Campynemanthe neocaledonica* showing free endosperm nuclei at the 64-nucleate stage. s, synergid; end, endosperm nucleus. Scale = 50 μm.

1949; Eunus, 1951) as in other Melanthiaceae in which this embryological feature is known (including *Tofieldia, Narthecium, Heloniopsis, Metanarthecium, Aletris, Zigadenus, Veratrum,* and *Amianthium*). In *Amianthium muscaetoxicum* Walt. the embryo sac in postfertilization stages forms a micropylar and chalazal endosperm chamber characteristic of the helobial type; in an earlier stage the micropylar chamber contains 16 nuclei, and the chalazal chamber 8 nuclei (Eunus, 1951, fig. 31). In *Campynemanthe,* however, there appears to be no such chalazal chamber, nor is there a distinct aggregate of endosperm nuclei at the chalazal end. All of the endosperm nuclei occur within a single cell (i.e., embryo sac), although they are more abundant toward the chalazal end (Fig. 2). The presence of nuclear endosperm in *C. neocaledonica* suggests that this character may be useful in distinguishing Campynemataceae from Melanthiaceae.

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A REVIEW OF THE NEW WORLD SPECIES OF *ORTHROSANTHUS* SWEET (IRIDACEAE)[1]

JAMES E. HENRICH[2] AND PETER GOLDBLATT[3]

ABSTRACT

Orthrosanthus, a genus of some 9 species of Iridaceae—Sisyrinchieae, occurs in Australia and South and Mesoamerica. This review, arising out of research for floristic treatments for *Flora Mesoamericana* and *Flora de Nicaragua,* deals with the systematics and nomenclature of the New World species. We recognize five American species: *O. acorifolius* and *O. occissapungus* are endemic in South America; *O. chimboracensis* occurs in South and Mesoamerica; and *O. monadelphus* and *O. exsertus* are restricted to Mesoamerica and Mexico. The taxonomic history of *Orthrosanthus* in the New World is outlined followed by a key, and the nomenclature, brief descriptions, and distribution ranges for each species are provided.

The genus *Orthrosanthus* comprises nine species of Iridaceae, tribe Sisyrinchieae Baker. It has an unusual disjunct distribution, occurring in Australia and central Mexico to South America, a pattern shared in the family only with *Libertia,* although the latter does not extend into Mesoamerica. In the New World the taxonomy of *Orthrosanthus* has long been confused, with several authors recognizing different numbers of species, subspecies, and varieties (Baker, 1892; Steyermark, 1948; Ravenna, 1977). *Orthrosanthus* is usually regarded as closely allied with *Libertia* and *Sisyrinchium* and is distinguished from them by an oblong to cylindric, included, and often sessile to subsessile ovary and capsule. *Sisyrinchium* and *Libertia* have globose to subglobose capsules borne on slender pedicels, typically well exserted from the subtending bracts and spathes. Further, *Orthrosanthus* has angular seeds, whereas *Libertia* and *Sisyrinchium* have spherical seeds without prominent angular ridges.

Preparing a treatment of Iridaceae for *Flora Mesoamericana* and *Flora de Nicaragua,* we have reviewed the literature dealing with *Orthrosanthus* and have examined the ample herbarium material now available. Our conclusions regarding the systematics of *Orthrosanthus* appear to merit the review presented here, since they differ extensively from currently accepted taxonomy, as represented in most major herbaria. Also, information about *Orthrosanthus* is scattered in the literature and there is no modern summary of the systematics and geography of the genus in the New World. Cooke (1986) treated *Orthrosanthus* for *Flora of Australia,* where four species are now admitted. We recognize five New World species (Fig. 1): *O. acorifolius* (Kunth) Ravenna, *O. chimboracensis* (Kunth) Baker, *O. exsertus* (R. Foster) Ravenna, *O. monadelphus* Ravenna, and *O. occissapungus* (Ruiz ex Klatt) Diels. A short history of *Orthrosanthus* in the New World is outlined below, followed by a diagnostic key for the species and a review of their systematics and nomenclature.

HISTORICAL REVIEW

Orthrosanthus was erected by Robert Sweet (1827) for the Australian *O. multiflorus* Sweet. The first New World species ultimately assigned to *Orthrosanthus* were described by Kunth (1815) as *Moraea* (a distantly related African genus, tribe Irideae). Kunth described three species now recognized as *Orthrosanthus*: *Moraea chimboracensis, M. gladioloides,* and *M. acorifolia.* Baker (1876: 113) was the first to include New World species in *Orthrosanthus,* recognizing *O. chimboracensis* (Kunth) Baker (with *M. acorifolia* as a synonym and *M. gladioloides* as a variety) and a second species *O. spicatus* (Baker) Baker from South America. The latter is a short plant with a winged flowering stem and congested, sessile inflorescence units (rhipidia). The flowers have a short perianth tube, and the globose capsules are carried on slender pedicels above the subtending bracts as in *Sisyrinchium* and *Phaiophleps.* Ravenna (1968) placed the species in *Phaiophleps* as *P. brasiliensis,* but we doubt that it belongs in this heterogeneous alliance. It should

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be referred back to *Sisyrinchium*, pending critical study of its affinities. Baker's (1892) later, more detailed treatment recognized seven species in *Orthrosanthus*, the same two in the New World and five in Australia.

In contrast to Baker's treatment, Klatt (1861) first placed New World species of *Orthrosanthus* in *Sisyrinchium*. He described the distinctive central Andean *O. occissapungus* and a synonym of *O. chimboracensis*, *S. moritzianum*. Later, Klatt (1882) placed New World *Orthrosanthus* in *Solenomelus* Miers, recognizing *Solenomelus chimboracensis* (including *M. acorifolia* and *Sisyrinchium moritzianum*) and *Solenomelus gladioloides* (including *Sisyrinchium occissapungum*). At the close of the nineteenth century Rusby (1896) described *O. nigrorhynchus*, not realizing that *Sisyrinchium occissapungum* was an earlier name for the plant, and two years later Kuntze described the conspecific *O. tunariensis*. *Orthrosanthus occissapungus* has white flowers, characteristic long narrow capsules, and typically single- to few-flowered rhipidia.

A review of *Orthrosanthus* by Steyermark (1948) is consistent with Baker's earlier treatment in recognizing only one American species (at least he makes no reference to *O. occissapungus* or its synonyms). Steyermark's contribution is noteworthy for recognizing four varieties and two forms distinguished by capsule size, degree of exsertion of the capsule from the subtending bracts, flower color, inflorescence characters, leaf dimensions, and geographical distribution.

Recently, Ravenna (1965) described *Orthrosanthus monadelphus* (= *O. chimboracensis* var. *centro-americanus* Steyerm.) and made the combination *O. monadelphus* subsp. *exsertus* (R. Foster) Ravenna. Ravenna (1969) also reduced *O. occissapungus* to subspecific status as *O. chimboracensis* subsp. *tunariensis* (Kuntze) Ravenna. Without mentioning Steyermark's (1948) treatment of the genus, in particular *O. chimboracensis* var. *acorifolius*, Ravenna (1977) transferred *Moraea acorifolia* to *Orthrosanthus* as *O. acorifolius* (Kunth) Ravenna. In 1981 he indicated that he regarded *Orthrosanthus* as comprising four species and one subspecies.

TAXONOMY

Orthrosanthus Sweet, Flora Australasica, t. 11. 1827; Baker, Handbk. Irid. 117–119. 1892; Cooke, Fl. Australia 46: 10–13. 1986. TYPE: *O. multiflorus* Sweet.

Elvetria Raf., Fl. Telluriana 4: 30. 1838. TYPE: *E. multiflora* (Sweet) Raf. (= *O. multiflorus* Sweet).

Evergreen tufted perennials with short, persistent, creeping rhizomes. Leaves several, mostly basal, ensiform and equitant, linear to linear-lanceolate, coriaceous, without a midvein, crowded at the apex of the rhizome. Flowering stem erect, branched, the branches ascending, either long or short, terminating in single rhipidia, or the branches crowded distally. Rhipidia relatively short; spathes subequal. Flowers actinomorphic, subsessile or shortly stalked, blue or white; tepals free (united in a short tube in some Australian species), subequal, spreading horizontally from the base; filaments free or united in the lower half; anthers erect; ovary included in the spathes, ± sessile, or exserted in *O. exsertus*; style short, dividing into 3 relatively long branches extending between the stamens, the branches stigmatic apically. Capsules ellipsoid to cylindric, sometimes pubescent, included or exserted; seeds angular to fusiform.

Species: 9; highland areas from Mexico to Panama, the Coastal Cordillera of Venezuela, and through Andean South America to Bolivia and northern Argentina (Fig. 1), and in Australia.

KEY TO THE NEW WORLD SPECIES

1a. Capsules with pedicels (vestigial–)5–15(–25) mm long; capsule glabrous.
  2a. Spathes usually enclosing a single flower; capsules slender, (15–)22–30 mm long; seeds elongate-angular, 2.5–3 mm long, 0.5 mm wide (Peru, Bolivia, and northern Argentina) .... 5. *O. occissapungus*
  2b. Spathes enclosing (2–)3 or more flowers; capsules oblong to ellipsoid, 10–18 mm long; seeds angular to irregularly globose, 1.2–2 mm long and wide.
    3a. Mature capsules borne well above the subtending bracts; pedicels 15–25 mm long (central Mexico: Mexico, Puebla, Distrito Federal, Tamaulipas, Nuevo León, Michoacán) .... 3. *O. exsertus*
    3b. Mature capsules usually included; pedicels 5–10 mm long (Costa Rica, Venezuela, Colombia, Ecuador, Peru) .... 2. *O. chimboracensis*
1b. Capsules sessile or with short pedicels less than 5 mm long; capsule surface pubescent, sometimes densely so.
  4a. Capsules 7–13 mm long; leaves 2–4 mm wide (southern Mexico to northern Panama, except Belize and Nicaragua) .... 4. *O. monadelphus*
  4b. Capsules 8–11 mm long; leaves 4–12 mm wide (Venezuela) .... 1. *O. acorifolius*

FIGURE 1. Distribution of the species of *Orthrosanthus* in the New World.

1. **Orthrosanthus acorifolius** (Kunth) Ravenna, Mus. Nac. Hist. Nat. Santiago Notic. Mens. 21: 7–9. 1977. *Moraea acorifolia* Kunth, Nov. Gen. & Sp. Pl. 1: 323. 1815. *Orthrosanthus chimboracensis* var. *acorifolius* (Kunth) Steyerm., Lloydia 11: 19. 1948. *Marica acorifolia* (Kunth) Martens & Galeotti, Bull. Acad. Brux. 10: 110. 1843 (misapplied, probably to *O. monadelphus*). TYPE: Venezuela. Distrito Federal: in crepidinibus montis Silla de Caracas, ca. 1,250 m, *Bonpland & Humboldt s.n.* (lectotype, P—General Herbarium; the sheet is designated "Herbier Bonpland," here designated). The lectotype specimen has locality data, "Silla de Caracas," approximating that published in the protologue, but also the number *1129*; more type material probably existed and may be found.

Orthrosanthus chimboracensis var. *acorifolius* f. *albus* Steyerm., Lloydia 11: 19. 1948. TYPE: Venezuela. Trujillo: La Quebrada Cortijo, by boundary line Lara-Trujillo, above Humocaro Bajo, *Steyermark 55339a* (holotype, F).

Plants to 65 cm tall. Leaves to 50 cm long, (0.4–)0.9–1.2 cm wide, broadly linear, gradually acuminate. Flowering stem about as long as the leaves; rhipidia several-flowered. Flowers ca. 3 cm diam., blue or rarely white. Capsules 8–11 mm long, sessile or with short pedicels to 5 mm long, pubescent; seeds angular to somewhat rounded, ca. 1–1.2 mm at the widest diameter.

Distribution. Orthrosanthus acorifolius is apparently restricted to the Coastal Cordillera and Andes of Venezuela and eastern Colombia.

This species is usually very robust and has comparatively broad leaves sometimes matched in *Orthrosanthus* by those of *O. chimboracensis.* The ovary and young capsules are heavily pubescent, as in *O. monadelphus,* to which *O. acorifolius* is probably most closely related.

2. **Orthrosanthus chimboracensis** (Kunth) Baker, Gard. Chron. n. ser. 6: 67–68. 1876. *Orthrosanthus chimboracensis* var. *typicus* Steyerm., Lloydia 11: 15–16. 1948. *Moraea chimboracensis* Kunth, Nov. Gen. & Sp. Pl. 1: 322. 1815. TYPE: Ecuador. Tunguragua: regni Quitensis ad radices montis Chimborazo inter pagum Calpi et rupem Yana-Urcu, ca. 1,640 m, *Bonpland & Humboldt s.n.* (lectotype, P—Herb. Bonpland, here designated). More type material may be found; the sheet we have designated as lectotype has the data "Chimborazo" only and the number *3188.*

Moraea gladioloides Kunth, Nov. Gen & Sp. Pl. 1: 322. 1815. TYPE: Peru. Cajamarca: locis frigidis Peruviae inter Caxamarcam et Micuipampam, ca. 1,480 m, *Bonpland & Humboldt s.n.* (lectotype, P—Herb. Bonpland, here designated). The lectotype specimen has the locality data "Peruvia," partially corresponding to the protologue; we expect that other type material may exist, hence the designation of a lectotype.

Sisyrinchium moritzianum Klotzsch ex Klatt, Linnaea 31: 378. 1861. TYPE: Venezuela (as Colombia). Merida: Paramo de la Culata, *Moritz 1204* (isotype, K).

Plants (20–)60–115 cm tall. Leaves 15–70 cm long, 8–12 mm wide, narrowly lanceolate to linear. Flowering stem longer than the leaves; rhipidia several-flowered and regularly spaced; spathe margins hyaline. Flowers 2–2.6 cm diam., blue. Capsules 14–18 mm long, glabrous, the pedicels 5–10(–15) mm long; seeds angular, 1.2–2 mm at the longest axis.

Distribution. *Orthrosanthus chimboracensis* ranges from Costa Rica and Venezuela southward through the Andes from Colombia to Peru. It is a montane species seldom occurring below 2,000 m.

Plants are typically less robust than *Orthrosanthus acorifolius* and can be recognized by a sparsely pubescent to glabrous ovary and completely glabrous capsule with a short pedicel 5–10 mm long.

3. **Orthrosanthus exsertus** (R. Foster) Ravenna, Wrightia 7: 10. 1981. *Orthrosanthus chimboracensis* var. *exsertus* R. Foster, Contr. Gray Herb. 155: 49. 1945. TYPE: Mexico. Distrito Federal: on the sides of ravines near Eslava, *Pringle 8827* (holotype, G; isotypes, C, CAS, F, G, GH, MEXU, MO, NY, O, S, TEX, UC, US).

Orthrosanthus chimboracensis var. *exsertus* f. *albus* Steyerm., Lloydia 11: 17. 1948. TYPE: Mexico. Tamaulipas: Santa Rita, Ranch Tamaulipas, 1,500 m, *Runyon 875* (holotype, US; isotype, TEX).

Plants 40–70 cm tall. Leaves 40–55 cm long, 3–8 mm wide, narrowly acuminate. Flowering stem somewhat longer than the leaves; rhipidia several-flowered. Flowers to 2.5 cm diam., blue, or occasionally white; ovary exserted from the spathes shortly after anthesis. Capsules 1–1.7 cm long, glabrous, broadly acuminate apically, well exserted from the spathes on pedicels 15–25 cm long; seeds angular to somewhat rounded, 1.2–1.5 mm at the widest diameter.

Distribution. *Orthrosanthus exsertus* is endemic to highland areas of southern and central Mexico (Nuevo León, Tamaulipas, Puebla, Michoacán, Distrito Federal, México).

The smallest of the New World species of *Orthrosanthus, O. exsertus* is distinctive in having comparatively narrow leaves and glabrous capsules exserted from the spathes and bracts on pedicels 15–25 mm long. Recognized only in 1981 as a distinct species, and first as a variety in 1948, *Orthrosanthus exsertus* was recorded as early as 1829 or 1830 by Schiede and a few years later by Liebmann. Their collections are among the three syntypes cited by Klatt for *Sisyrinchium occissapungum,* now *O. occissapungus,* and neotypified here by a collection from Peru.

4. **Orthrosanthus monadelphus** Ravenna, Bol. Soc. Argentina Bot. 10: 317. 1965. TYPE: Guatemala. Baja Verapaz: cumbre El Chol, ca. 2,200–2,500 m, *Ravenna 266* (holotype, Herb. Ravenna, not seen; isotypes, F, HBG).

Orthrosanthus chimboracensis var. *centro-americanus* Steyerm. Lloydia 11: 19. 1948. TYPE: Guatemala. Jutiapa: exposed rocky slopes on summit, Volcán Suchitán, northwest of Asunción Mita, *Steyermark 31913* (holotype, F).

Orthrosanthus chimboracensis var. *intermedius* Steyerm., Lloydia 11: 19–20. 1948. TYPE: Costa Rica. Cartago: Volcán Irazu, *Allen 674* (holotype, F).

Plants (15–)30–60 cm tall. Leaves 30–45 cm long, 8–10 mm wide, linear. Flowering stem to 60 cm; rhipidia several-flowered and spaced somewhat irregularly along the stem; spathe margins narrowly hyaline. Flowers 1.4–3 cm diam., blue. Capsules 10–13 mm long, usually pubescent, sessile or nearly so, only the apices exceeding the spathes; seeds angular to somewhat rounded, 1.2–1.5 mm at the widest diameter.

Distribution. *Orthrosanthus monadelphus* is common in highland areas of Mesoamerica. It is recorded from southern Mexico to Guatemala and El Salvador, and locally to the south in Costa Rica and northern Panama.

This species is probably most closely allied to the Venezuelan *Orthrosanthus acorifolius,* with which it shares a similar, nearly sessile, and pubescent ovary and capsule. The filaments are united in the lower half, not much more so than in the other American species. Although first recognized as a distinct subspecies in 1948, and as a species in 1965, it is interesting to note that the collection cited by Martens & Galeotti (1843) as *Marica acorifolia* may be the first record for *Orthrosanthus monadelphus* [Mexico: Oaxaca, rochers gneissiques de Penoles, Misteca alta, ca. 2,150–2,300 m, *Galeotti 5368* (?BR, not seen)].

5. **Orthrosanthus occissapungus** (as *O. ocisapunga*) (Ruiz ex Klatt) Diels, Engler & Prantl, Nat. Pflanzenfam. ed. 2. 15a: 478. 1930. *Sisyrinchium occissapungum* Ruiz ex Klatt, Linnaea 31: 379. 1861. NEOTYPE: Peru. La Libertad: along the Río Negro 3 km south of Huamachuco, *West 8113* (neotype, MO; isoneotypes, GH, UC). The three cited syntypes of *S. occissapungum* have not been found and are presumed destroyed, hence our designation of a neotype. For completeness, the syntypes are cited here as follows: Peru. Huanuco: ad Pillao etc., *Ruiz* ex Herb. Lambertii (B, not seen); Mexico. Oaxaca: Chinantla, *Liebmann 310* (location unknown) (? = *O. exsertus*); Mexico. Veracruz: Jalapa, *Schiede 1029* (location unknown) (? = *O. exsertus*).

Orthrosanthus nigrorhynchus Rusby, Mem. Torrey Bot. Club 6: 126. 1896. TYPE: Bolivia. Cochabamba: near Cochabamba, *Bang 1074* (lectotype, NY, here designated as the best preserved and most complete of three sheets at NY, the institution where Rusby worked; isolectotypes, BM, F, G, GH, K, MO, NY).

Orthrosanthus tunariensis Kuntze, Rev. Gen. Pl. 3: 309. 1898. TYPE: Bolivia. Cochabamba: im Tunarigebirge, 3,600 m (collector and location of the type not in the protologue and unknown to us). *Orthrosanthus chimboracensis* subsp. *tunariensis* (Kuntze) Ravenna, Revista Inst. Munic. Bot. (Buenos Aires) 2: 30. 1969.

Orthrosanthus chimboracensis sensu Rusby, non (Kunth) Baker, in Bull. Torrey Bot. Club 29: 224. 1901.

Plants to 80 cm tall. Leaves 30–50 cm long, 3–8 mm wide, narrowly linear, sharply acute. Flowering stem to 80 cm; rhipidia typically single-flowered. Flowers 2.6–3.4 cm diam., white. Capsules (15–)22–30 mm long, glabrous, extending above the spathes on pedicels to 5 mm long; seeds elongate-angular, 2.5–3 mm at the longest axis.

Distribution. *Orthrosanthus occissapungus* is restricted to northwestern Argentina, Bolivia, and Peru, where it grows at elevations above 3,200 m.

The most unusual of the New World species of *Orthrosanthus, O. occissapungus* can be recognized by its one- to few-flowered spathes, long slender capsules, and elongate seeds. The flowers are always white in *O. occissapungus* and only occasionally so in other species in the New World.

As indicated in the nomenclature above, we have been unable to locate the original type material of *Sisyrinchium occissapungum.* The syntype from Peru, collected by Ruiz, had the manuscript epithet "*occissapungum*" according to Klatt. It was housed in the Berlin Herbarium and must be presumed destroyed. It was almost certainly conspecific with *O. nigrorhynchus* described in 1896. The two other specimens cited in the protologue are from Mexico: *Schiede 1029* (also presumed destroyed) from Jalapa in Veracruz, and *Liebmann 310* from Chinantla, Oaxaca. The latter specimen is cited as "Herb. mihi" by Klatt, that is, in his own herbarium, which was at one time at Berlin but is now at Stockholm. No Liebmann collection with this number has, however, been located at either place. Duplicates of the Liebmann collection at Copenhagen, where Liebmann's main collection is preserved, likewise do not include the missing type number. Other Liebmann specimens at Copenhagen and at Paris collected at the same locality and time are the Mexican *Orthrosanthus exsertus* and represent the first collections of that species.

We are regarding *Orthrosanthus occissapungus* as a valid combination made by Diels (1930: 478) but recognize that it would not be accepted according to the current Code of Botanical Nomenclature if made today. Diels did not cite a basionym or indicate in any way that he was making a combination in citing the species as *O. ocisapunga* (sic) Ruiz. Nevertheless, there can be no doubt that he was placing *Sisyrinchium occissapungum* Ruiz ex Klatt in *Orthrosanthus* as the earliest name for the species known until this time as either *O. nigrorhynchus* or *O. tunariensis,* neither of which he mentioned in his enumeration of the species of *Orthrosanthus.* The name *O. occissapungus* was accepted by Macbride (1936) and Vargas (1944) but was attributed by both authors to Diels (as *O. ocisapunga* Ruiz ex Diels). We do not believe that Diels intended to describe the species, and therefore we cannot accept this treatment. We also note that it was not Diels's practice to cite the authors of species in later combinations e.g., his listing of *O. chimboracensis* Bak. [instead of (Kunth) Baker], and so there is no inconsistency in his not mentioning the authors of the basionym for *O. occissapungus.*

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PATCH FORMATION AMONG ISRAELI CRUCIFERS: HOW DO THEY GET AWAY WITH IT?[1]

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ABSTRACT

Many crucifers in the Mediterranean and desert floras of Israel frequently form large monospecific patches but do not suffer severe herbivore damage. This situation is unexpected from some recent theory of insect–plant interactions which predicts that such resource concentration should attract high herbivore loads, and that herbaceous plants should rely on unpredictability in time and space as a defense against herbivores. In Israel, Mediterranean crucifers flower earlier than members of other species-rich families with similar growth forms (Lamiaceae, Asteraceae, Liliaceae, Solanaceae, Poaceae, Papilionaceae, Apiaceae). This is not true for desert crucifers; their phenologies are unpredictable from year to year. We hypothesize that their displaced phenologies and possession of potent allelochemicals allow Mediterranean patch-forming species to produce monocultures while not sustaining high levels of herbivory. In contrast, desert patch-forming crucifers rely on unpredictable phenologies as well as allelochemicals as defenses against herbivores. Patch formation may be reinforced by plant–pollinator interactions. Among Mediterranean crucifers, patch formers are taller and have larger petals than do non-patch formers. In addition, patch formation is correlated with high levels of floral ultraviolet reflectance and patterning. These differences may result from reduced interspecific but enhanced intraspecific competition for pollinators among patch formers. These patterns are not found among desert species, although desert patch formers do initiate flowering before other crucifers.

The family Brassicaceae (Cruciferae) has figured prominently in the development of theory concerning insect–plant interactions. Responses of phytophagous insects to experimental manipulations of one or a few crucifer species (e.g., Tahvanainen & Root, 1972; Root, 1973; Slansky & Feeny, 1977), as well as considerations of family-wide attributes (Feeny, 1976, 1977), comprise much of the empirical and theoretical support for concepts such as "associational resistance" (Tahvanainen & Root, 1972) and "plant apparency" (Feeny, 1976). Feeny (1977) also cited family-wide attributes of crucifers to support his contention that escape in time and space and allelochemic diversity protect herbaceous plants from potential herbivores. Several characteristics of crucifers make them particularly amenable for studies of herbivore–plant interactions. They are well represented in floras of many regions of the world (Hedge, 1976), all species thus far examined contain glucosinolates (Kjaer, 1976), and many species are important cultivated crops.

The family contains approximately 400 genera and 3,000 species, most of which are annual herbs (Vaughan et al., 1976). The Irano-Turanian region is home to about 900 crucifer species and was probably the center of origin for at least the Old World taxa (Hedge, 1976). Brassicaceae is a dominant and conspicuous family in terms of species diversity and abundance in both the Mediterranean and desert regions of Israel, particularly in late winter and early spring (Shmida & Auerbach, 1983). Most of the 111 or more species native to Israel are Irano-Turanian or are descendants of Irano-Turanian stock (Zohary, 1973).

Crucifers frequently form enormous monospecific patches in Israel without sustaining extensive herbivore damage. This situation is unexpected from some current theory of insect–plant interactions which predicts that such resource concentration should attract high herbivore loads, and that herbaceous plants should rely on unpredictability in time and space as a defense against herbivores. Here, we examine the crucifer flora of Mediterranean and desert regions of Israel in terms of plant morphology, phenology, and propensity of some species to occur naturally in large monocultures. In partic-

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ular, we address the question, "how do patch formers avoid colonization by a high density and/or diversity of phytophages"?

ISRAELI CRUCIFERS

We obtained data on plant species from *Flora Palaestina* (Zohary & Feinbrun-Dothan, 1966), herbarium records of the Hebrew University Department of Botany, Hebrew University, field observations from January to June 1983, more than 10 years of vegetation samples taken by A.S., and phenological records from ECOPAS. The last is a computer data base compiled by members of the Department of Botany, Hebrew University, and the Society for the Protection of Nature in Israel. Each month phenological records are submitted by a network of observers, resulting in a comprehensive record of Israel's flora.

Tables 1 and 2 list species of native crucifers growing in the Mediterranean (76 species) and desert regions (37 species) of Israel (two species are listed in both regions). For each species we show growth form, floral characteristics, pubescence, abundance in Israel, and a subjective measure of size of monospecific patches. Within both assemblages we excluded extremely rare species that we never encountered in the field (approximately 20 species).

We must clarify one entry in Tables 1 and 2. Our index of patch formation ranges from "+ + +" (largest patches) to "−" (no patches). Although this categorization is subjective, we classified species as patch formers only if they formed large monospecific associations. A patch in our usage is not a clump of several individuals of one species; rather, it is an extensive single-species association. Patches range from approximately ten meters to several kilometers on a side. For instance, in spring 1983 (highest spring rainfall in 30 years), we measured patches of *Erucaria hispanica* L., near Arad, Israel, and *Sinapis arvensis* L., near Bet She'an, Israel, that extended several hundred meters from secondary roads and ran parallel to the roads for greater than three kilometers (further descriptions of locations can be found in Shmida & Auerbach, 1983). We combined all patch formers for statistical analyses.

Using these data, we compared phenological attributes of the Brassicaceae with those of seven other species-rich families with similar growth forms in Israel (Table 3). Phenological comparisons were based on peak flowering time (month in which most individuals of a species produce most of their flowers) and on range of flowering time (range of months in which flowers have been observed for each species). For each family we constructed cumulative frequency distributions of flowering range and peak and compared the resultant distributions using a nonparametric test of association (Kolmogorov-Smirnov 2 sample test, Conover, 1980). We also compared average month of peak flowering between the Brassicaceae and other families with a parametric test (Welch approximation of the *t*-test, Remington & Schork, 1970), since these data were approximately normally distributed. We limited these comparisons to Mediterranean species because desert species are constrained to flowering over a short, variable period when rains occur. Comparisons were done on all species and the subset of annual species for each family, except for Liliaceae which only has one annual species.

We then compared morphological and phenological attributes of patch- and non-patch-forming crucifers. These analyses were conducted separately for Mediterranean and desert species. We compared phenologies based on cumulative frequency distributions of flowering range and flowering peak and average month of peak flowering. In addition, we compared the average month of start of flowering using a parametric test (Welch approximation of *t*-test). Average plant height and petal size from ECOPAS were compared using *t*-tests, whereas analyses of associations of pubescence and ultraviolet patterns with patch formation were based on two-by-two contingency tables.

RESULTS

INTERFAMILY DIFFERENCES

Comparison of the phenology of Mediterranean crucifers with members of other families indicates that in general crucifers flower earlier in the year, both in terms of flowering range and flowering peak (Table 3). The single exception is no significant difference between the peak flowering time of the Brassicaceae and Liliaceae (Table 3). The average duration of flowering of all crucifers differs from that of all Lamiaceae, Asteraceae, Solanaceae, and Poaceae (Table 3). Among all families we examined, medians of flowering range and peak occur earlier for annual species than for perennials except for the Solanaceae, in which the situation is reversed. Peren-

TABLE 1. Morphological and ecological attributes of crucifer species in the Mediterranean flora of Israel. Growth form: A = annual; H = hemicryptophyte; CHN = between hemicryptophyte and chamaephyte; CH = chamaephyte. Flower phenology = months in which a species flowers (1 = Jan., 2 = Feb., etc.). Flower color: W = white; Y = yellow; CY = pale yellow; C = cream; F = flesh; P = purple; PP = pink; CP = pale pink. Relative abundance: O = 1–3 occurrences; RR = very rare; R = rare; C = common; LC = locally common; CC = very common.

Species	Growth Form	Mean Height (cm)	Pubes-cence	Flower Phenology	Flower Color	Petal Length (mm)	Relative Abun-dance	Patchiness
Aethionema carneum (Banks et Sol.) B. Fedtsch.	A	12	–	2–3	PP	2	RR	–
A. heterocarpum Gay	A	12	–	2–3	PP	2	C	–
Alyssum damascenum Boiss. et Gaill.	A	8	+	2–4	C	2	C	–
A. minus Rothm.	A	10	+	1–3	C	2	CC	–
Arabidopsis pumila (Stephan ex Willd.) Busch	A	13	–	2–3	C	2	O	–
A. thaliana Schur	A	15	–	2–3	W	2	RR	–
Arabis aucheri Boiss.	A	17	+	2–4	W	5	R	–
A. caucasica Schltr.	H	20	+	4–5	W	13	O	–
A. nova Villars	A	12	–	2–3	W	4	O	–
A. turrita L.	H	60	++	4–6	F	11	RR	–
A. verna (L.) R. Br.	A	15	+	3–4	W	7	C	–
Biscutella didyma L.	A	27	+	1–4	CY	3	CC	–
Brassica cretica Guss.	CHN	60	–	4–5	C	12	O	–
B. nigra (L.) Koch	A	120	–	4–6	Y	10	LC	+++
B. tournefortii Gouan	A	80	–	2–4	C	7	CC	+
Cakile maritima Scop.	A	30	–	3–11	P	9	CC	+
Calepina irregularis (Asso) Thell.	A	18	–	1–3	W	3	C	–
Capsella bursa-pastoris (L.) Medikus	A	18	–	12–4	W	2	CC	–
C. rubella Reuter	A	15	–	1–2	W	2	O	–
Cardamine hirsuta L.	A	20	–	2–4	W	2	RR	–
Cardaria draba (L.) Desv.	H	27	+	3–4	W	3	LC	+++
Carrichtera annua (L.) DC.	A	15	++	3–4	CP	9	LC	–
Chorispora purpurascens (Banks et Sol.) Eig	A	25	+	3–4	P	18	RR	+
Clypeola aspera (Grauer) Turrill	A	10	+	1–3	C	2	R	–
C. jonthlaspi L.	A	8	++	1–3	C	2	CC	–
C. lappacea Boiss.	A	10	++	1–3	C	2	RR	–
Conringia orientalis (L.) Andrz.	A	50	–	3–4	Y	10	O	–
Coronopus squamatus (Forsskal) Asch.	A	10	–	2–4	W	2	LC	+
Crambe hispanica L.	A	65	+	3–4	W	3	C	+
Descurainia sophia (L.) Webb ex Prantl	A	25	+	2–4	C	3	O	–
Diplotaxis erucoides (L.) DC.	A	40	–	1–3	W	15	C	+++

TABLE 1. Continued.

Species	Growth Form	Mean Height (cm)	Pubescence	Flower Phenology	Flower Color	Petal Length (mm)	Relative Abundance	Patchiness
D. viminea (L.) DC.	A	10	–	12–2	C	3	LC	–
Enarthrocarpus arcuatus Labill.	A	25	+	1–4	CP	13	LC	+
Erophila minima C. A. Meyer	A	6	–	1–3	W	2	CC	–
E. verna (L.) Besser	A	7	–	1–3	W	2	LC	–
Eruca sativa Miller	A	40	–	2–3	CP	17	LC	++
Erucaria hispanica (L.) Druce	A	50	–	2–4	P	12	LC	+++
Erysimum crassipes Fischer et C. Meyer	H	50	+	5–6	C	8	C	–
E. repandum L.	A	20	+	3–4	Y	7	R	–
Fibigia clypeata (L.) Medikus	CHN	35	++	2–4	Y	15	LC	++
Hesperis pendula DC.	H	55	++	4–6	F	17	R	–
Hirschfeldia incana (L.) Lagr.-Fossat	A	60	–	3–5	Y	10	CC	+++
Hymenolobus procumbens (L.) Nutt. ex Torrey et A. Gray	A	13	–	1–2	W	1	RR	–
Iberis acutiloba Bertol.	A	8	–	2–4	W	2	RR	–
Isatis lusitanica L.	A	50	–	2–4	Y	4	C	++
Lepidium latifolium L.	H	70	–	5–8	W	2	RR	–
L. ruderale L.	A	15	–	2–3	W	1	O	–
L. sativum L.	A	45	–	3–5	W	2	RR	+
L. spinescens DC.	A	40	–	3–5	P	2	LC	+
L. spinosum Ard.	A	25	–	3–5	W	2	R	–
Malcolmia chia (L.) DC.	A	15	+	2–4	P	10	C	–
M. crenulata (DC.) Boiss.	A	12	–	1–3	W	20	C	–
Maresia nana (DC.) Battand.	A	10	+	2–3	P	4	R	–
M. pulchella (DC.) O. Schulz	A	15	–	1–3	P	12	C	+++
Matthiola longipetala (Vent.) DC.	A	40	++	3–4	P	18	R	–
M. tricuspidata (L.) R. Br.	A	20	++	3–9	P	15	C	–
Myagrum perfoliatum L.	A	40	–	3–4	Y	4	O	–
Nasturtium officinale R. Br.	H	30	–	2–12	W	3	C	++
Neslia apiculata Fischer, C. Meyer et Avé-Lall.	A	40	+	2–3	Y	3	R	–
Ochthodium aegyptiacum (L.) DC.	A	70	–	2–4	Y	4	C	++
Peltaria angustifolia DC.	H	65	–	3–5	W	4	LC	++
Raphanus aucheri Boiss.	A	45	+	4–5	Y	11	C	–
R. raphanistrum L.	A	55	–	1–4	CP	18	C	++

TABLE 1. Continued.

Species	Growth Form	Mean Height (cm)	Pubescence	Flower Phenology	Flower Color	Petal Length (mm)	Relative Abundance	Patchiness
R. rostratus DC.	A	60	–	2–4	P	20	LC	++
Rapistrum rugosum (L.) All.	A	60	–	3–4	Y	8	C	++
Ricotia lunaria (L.) DC.	A	22	–	1–3	P	15	LC	++
Rorippa amphibia (L.) Besser	H	40	–	4–5	Y	5	O	–
Sinapis alba L.	A	100	+	3–4	Y	12	CC	++
S. arvensis L.	A	50	+	2–5	Y	9	C	+++
Sisymbrium damascenum Boiss. et Gaill.	A	45	–	2–4	Y	5	RR	+
S. irio L.	A	40	–	1–5	Y	3	CC	+
S. officinale (L.) Scop.	A	40	+	3–4	C	4	R	–
S. orientale L.	A	50	+	3–4	Y	9	R	–
Thlaspi arvense L.	A	30	–	3–3	W	4	RR	–
T. perfoliatum L.	A	8	–	1–3	W	3	CC	–
Turritis laxa (Sibth. et Smith) Hayek	H	60	–	4–6	W	5	RR	–

nials also have longer average durations of flowering than annuals, except in the Solanaceae.

INTRAFAMILY COMPARISONS

Tables 1 and 2 show that most crucifer species in Israel, as in other areas, are annuals. As mentioned above, the few perennial species in both the Mediterranean and desert floras generally flower later and longer than the annuals, although exceptions do exist (e.g., *Fibigia clypeata* L.). Additionally, a distinct guild can be recognized among both Mediterranean and desert species. This *Erophilla* or 'pygmy' guild is characterized by small plants (5–15 cm), with small, generally white or cream-colored flowers that appear early in the year (mid January through February). Within the two floral associations, we conducted all statistical analyses on crucifers four times: all species, annuals only, pygmy guild excluded, and perennials and pygmies excluded.

For the Mediterranean crucifers, patch-forming species are taller than non-patch-forming species (Table 4). In addition, height of patch formers generally paralleled our rank of patch formation (+++ > ++ > + > –, cases 3 and 4; ++ > +++ > + > –, cases 1 and 2, Table 4). In three of four comparisons, patch formers also had significantly larger petals than did non-patch formers (Table 4), with patch rank generally paralleling petal size (++ > +++ > + > –, all cases). Few systematic differences exist among phenologies; patch formers generally do not flower earlier or longer than non-patch formers, although there are a few exceptions. There is no dominant flower color among Mediterranean patch-forming species; yellow, white, cream, and purple flowers are all common. Pubescence is significantly associated with non-patch-forming species in all analyses.

Unlike Mediterranean species, the desert patch-forming species are neither taller nor have larger petals than non-patch formers (Table 4). Although patch formers initiate flowering earlier than non-patch formers, the overall distributions of flowering peaks and ranges, and average durations of flowering generally do not differ between the groups.

Patch formers in the desert, with the exception of pygmy species, generally have purple flowers (8 of 12 species). Once again, pubescence is significantly associated with non-patch-forming species (Table 4).

Horovitz & Cohen (1972) analyzed ultraviolet

TABLE 2. Morphological and ecological attributes of crucifer species in the desert flora of Israel. See legend of Table 1 for abbreviations.

Species	Growth Form	Mean Height (cm)	Pubescence	Flower Phenology	Flower Color	Petal Length (mm)	Relative Abundance	Patchiness
Alyssum dasycarpum Stephan ex Willd.	A	10	+	2–4	C	3	RR	–
A. linifolium Stephan ex Willd.	A	10	–	1–3	W	2	R	–
A. marginatum Steudel ex Boiss.	A	10	+	2–4	C	2	R	–
A. minus (L.) Rothm.	A	10	+	2–3	C	2	C	–
Anastatica hierochuntica L.	A	5	+	2–4	W	3	R	++
Carrichtera annua (L.) DC.	A	15	++	3–4	C	9	LC	–
Cordylocarpus muricatus Desf.	A	37	+	3–4	C	8	O	–
Diplotaxis acris (Forsskal) Boiss.	A	35	–	1–4	P	10	C	++
D. harra (Forsskal) Boiss.	A	35	+	2–6	Y	9	CC	–
Enarthrocarpus strangulatus Boiss.	A	30	+	1–4	C	12	LC	+
Eremobium aegyptiacum (Sprengel) Asch. et Schweinf. ex Boiss.	P	15	+	2–6	PP	6	C	–
Erucaria boveana Coss.	A	35	–	2–4	P	10	CC	++
E. uncata (Boiss.) Asch. et Schweinf.	A	32	–	3–4	P	11	R	++
Farsetia aegyptiaca Turra	CH	35	+	1–11	F	12	CC	–
Isatis microcarpa Gay ex Boiss.	A	20	–	3–4	Y	3	RR	–
Leptaleum filifolium (Willd.) DC.	A	4	–	1–3	PP	7	C	++
Lobularia arabica (Boiss.) Muschler	A	12	–	1–4	W	4	LC	–
L. libyca (Viv.) Webb et Berth.	A	15	+	1–3	W	4	R	–
Malcolmia africana (L.) R. Br.	A	16	+	2–4	P	8	R	–
Maresia pygmaea (Del.) O. Schulz	A	7	–	3–4	P	9	R	–
Matthiola arabica Boiss.	H	40	++	3–5	F	12	RR	–
M. aspera Boiss.	A	30	++	2–4	P	13	LC	+++
M. livida (Del.) DC.	A	33	++	2–4	F	12	C	–
M. parviflora (Schousboe) R. Br.	A	17	++	3–4	P	8	R	–
Morettia canescens Boiss.	CH	23	+++	2–10	W	8	LR	–
M. parviflora Boiss.	CH	20	+++	2–10	W	4	LR	–
Moricandia nitens (Viv.) E. A. Durrand et G. Barratte	CH	32	–	1–12	P	18	CC	+
M. sinaica (Boiss.) Boiss.	CH	60	–	3–4	P	12	RR	–
Nasturtiopsis arabica Boiss.	A	15	–	2–4	Y	3	CC	+++
Notoceras bicorne (Sol.) Caruel	A	5	+	1–3	C	2	CC	+
Pseuderucaria clavata (Boiss. et Reuter) O. Schulz	A	30	–	2–4	P	17	LR	+++

TABLE 2. Continued.

Species	Growth Form	Mean Height (cm)	Pubescence	Flower Phenology	Flower Color	Petal Length (mm)	Relative Abundance	Patchiness
Reboudia pinnata (Viv.) O. Schulz	A	23	−	1–4	PP	9	CC	++
Savignya parviflora (Del.) Webb	A	20	−	2–4	P	5	LC	+
Schimpera arabica Hochst. et Steud. ex Boiss.	A	25	−	2–4	Y	3	LC	++
Sisymbrium erysimoides Desf.	A	30	−	1–5	Y	4	C	++
Torularia torulosa (Desf.) O. Schulz	A	15	+	2–4	W	3	LC	−
Zilla spinosa (L.) Prantl	P	35	−	2–9	P	13	CC	+++

characteristics of the flowers of 22 species of crucifers native to Israel (17 Mediterranean, 5 desert). Among these, high ultraviolet reflectance and/or patterning is positively associated with patch formation ($G_{adj.} = 12.3$, $P < 0.001$). The same is true for the subset of Mediterranean species ($G_{adj.} = 6.59$, $P < 0.025$), but not the desert ones ($G_{adj.} = 0.5$, $P > 0.05$).

DISCUSSION

WHY NOT FORM PATCHES?

Several lines of evidence suggest that patch formation should increase the susceptibility of a plant species to insect attack. Many herbivores, particularly those with narrow host ranges, are more likely to find, to remain on, and to reproduce on hosts that are concentrated in space (Root, 1973; Risch, 1981). This is one reason why monocultures of herbaceous plants frequently support greater densities of insect pests than do polycultures (Pimentel, 1961; Root, 1973; Feeny, 1976; Altieri et al., 1977; Risch, 1981). The diversity and abundance of phytophagous insects attacking a plant species in a given area are also influenced by the botanical diversity of the area (Strong et al., 1984). Members of a mixed-species plant assemblage often escape attack because increased species diversity reduces the susceptibility of each plant species to discovery. This phenomenon has been referred to as "associational resistance" (Tahvanainen & Root, 1972) or "plant defense guilds" (Atsatt & O'Dowd, 1976). Considerations of alternative resource availability for phytophagous insects as well as their frequent use of visual or chemosensory cues in host-plant location suggest that this form of escape should increase in effectiveness as phytophage dietary specialization increases (Root, 1973; Atsatt & O'Dowd, 1976).

Rhoades & Cates's (1976) and Feeny's (1976) general theories of plant defensive chemistry expand the concept of plant escape from enemies in ecological time into evolutionary arguments concerning selection for different classes of allelochemicals. Both postulate that as the occurrence of a plant species or tissue becomes more predictable (apparent) in space and time there should be greater selection for generalized, quantitative (dosage-dependent) defenses as opposed to specialized, qualitative defenses (toxins). Quantitative defenses are presumed to be more metabolically costly but harder for a herbivore to circumvent than qualitative ones. Thus, it is

TABLE 3. Comparison of phenologies of the Brassicaceae with other families in the Mediterranean flora of Israel. Months were converted to integers (Jan. = 1, Feb. = 2, etc.) for flowering range and peak analyses. Inequality signs indicate earlier (<) and later (>) in the growing season.

Family	Number of Species	Flowering Range (median month)	Flowering Peak (median month)	Flowering Duration (mean number months (s.d.))	Compared with Brassicaceae	
					Flowering Range (distribution)	Flowering Peak (distribution)
Brassicaceae	76	3.71	3.61	2.94 (1.47)		
Annual	64	3.46	3.52	2.88 (1.20)		
Perennial	12	5.50	4.75	—		
Lamiaceae	80	5.79	5.27	3.71 (1.49)*	>+	>+
Annual	17	4.86	4.42	3.35 (1.41)	>++	>++
Perennial	63	6.07	5.50	—	—	—
Asteraceae	169	5.74	4.88	3.43 (1.74)*	>+	>+
Annual	105	5.17	4.54	3.25 (1.69)	>++	>++
Perennial	64	6.63	5.83	—	—	—
Liliaceae	66	4.33	3.66	2.91 (1.34)	>+	=
Perennial	65	4.33	3.67	—	—	—
Solanaceae	15	6.96	6.50	5.13 (2.64)*	>+	>+
Annual	6	7.60	7.00	5.33 (0.82)**	>++	>++
Perennial	9	6.50	6.17	—	—	—
Poaceae	168	5.67	4.86	3.77 (1.95)*	>+	>+
Annual	111	5.18	4.59	3.40 (1.61)**	>++	>++
Perennial	57	6.65	5.68	—	—	—
Papilionaceae	206	4.52	4.19	3.13 (1.10)	>+	>+
Annual	173	4.33	4.08	2.92 (0.67)	>++	>++
Perennial	33	5.70	5.21	—	—	—
Apiaceae	87	5.35	4.83	3.03 (1.24)	>+	>+
Annual	48	4.93	4.55	2.77 (1.10)	>++	>++
Perennial	39	5.79	5.39	—	—	—

* = Significantly different from all, or annual (**) crucifer species (t-test, Welsh approximation, $P < 0.05$).

\+ = Significantly different from all, or annual (++) crucifer species (Kolmogorov-Smirnov 2 sample test, $P < 0.05$).

argued that a plant that is apparent by virtue of its growth form, abundance, and longevity, such as a common tree species, must invest a considerable amount of energy into quantitative defenses, whereas an annual herbaceous plant can invest less energy in qualitative defenses, provided it also remains unapparent in time and/or space. By definition, unapparent plants should have small patch sizes and low population density (Fox, 1981).

Escape in time and space should be effective against specialized herbivores in ecological time and against nonspecialized herbivores over evolutionary time. Specialized herbivores that have evolved a means of circumventing an allelochemic defense frequently respond to the allelochemicals as chemosensory cues for host location and phagostimulation; such herbivores have, over evolutionary time, turned an unapparent resource into an apparent one (see Courtney, 1985, for various interpretations of apparency). Once this occurs the plant benefits from anything that reduces its apparency to adapted enemies, such as having an irregular phenology or growing in multispecies assemblages. Against nonspecialized herbivores, escape in space and/or time reduces the frequency of encounters between potential enemy and plant tissue, thereby decreasing the likelihood of an herbivore evolving a detoxification mechanism.

Since most crucifers are short-lived herbs and contain qualitative allelochemicals, one might expect them to rely quite heavily on escape in time and space from phytophagous insects. In fact, Feeny (1977) regarded crucifers as typical unapparent plants and much of his theory of plant apparency is based on crucifers (see references in Feeny, 1976). Most Israeli crucifers do rely on escape on one time scale by nature of their annual growth form with concomitant short-term availability each year of leaves. However, the propensity of many species to form large monotypic patches confers a high degree of spatial predictability and resource concentration on these species. In addition, location of patches of Mediterranean patch-forming species frequently does not change from year to year. This situation would appear to be disadvantageous in light of the theory discussed above.

HOW DO THEY GET AWAY WITH IT?

Mediterranean patch-forming crucifers in Israel suffer little herbivore damage despite their short-term spatial predictability. During a season of sampling (1983), we never observed high densities or diversities of phytophages on patch-forming species. Neither high numbers of supported insect herbivores nor large amounts of leaf area removal were detected with spot censusing during ten years of vegetation sampling.

We suggest that Mediterranean patch-forming crucifers are able to grow and persist in dense monospecific associations owing to possession of glucosinolates (and other allelochemicals in some species), and because they flower earlier than other local species. Both displaced phenologies and glucosinolates prevent seasonal tracking and use of crucifers over evolutionary time by presently non-crucifer-adapted herbivores. By growing earlier than most other annual species, these crucifers have reduced the number of chance encounters with nonadapted phytophages; such occasional encounters deter or kill the insect. Therefore, we see a displaced phenology reinforcing defensive chemistry and thereby reducing the probability of evolved phenological and dietary shifts in phytophages. If patch formation occurred later in the growing season, more encounters between pest and potential host would ensue, and over evolutionary time one would expect an increase in diversity of insect species adapting to patch-forming crucifer species.

Many crucifers germinate, grow, and flower before the annual peak of insect biomass. Indeed, many of the patch-forming species flower before the annual appearance of crucifer-adapted herbivores, such as *Pieris brassicae, P. rapae,* and alticine flea beetles (Furth, 1979; Auerbach & Shmida, unpubl. data). Occasionally, these adapted herbivores do appear on patch formers during the late stages of flowering or seed set,

TABLE 4. Comparisons of morphological and phenological attributes of patch-forming (P) and non-patch-forming (NP) crucifer species in the (A) Mediterranean and (B) desert floras of Israel. In reference to phenological traits, the inequality signs indicate earlier (<) and later (>) in the growing season. Groups are defined as: (1) = all species; (2) = annuals; (3) = pygmy guild excluded; (4) perennials and pygmies excluded.

Group	Plant Height	Petal Size	Mean Flowering Duration	Flowering Peak (distribution)	Flowering Peak (mean)	Flowering Range (distribution)	Start of Flowering	Pubescence
				(A) MEDITERRANEAN				
1	P > NP***	P > NP**	P > NP*	P = NP	P = NP	P = NP	P = NP	NP > P*
2	P > NP***	P > NP***	P = NP	P = NP	P > NP*	P = NP	P = NP	NP > P*
3	P > NP*	P = NP	P = NP	P = NP	P = NP	P = NP	P < NP*	NP > P*
4	P > NP***	P > NP*	P = NP	P = NP	P = NP	P = NP	P = NP	NP > P*
				(B) DESERT				
1	P = NP	P = NP	P = NP	P = NP	P = NP	P = NP	P < NP*	NP > P**
2	P = NP	P = NP	P = NP	P = NP	P = NP	P = NP	P < NP*	NP > P*
3	P = NP	P = NP	P = NP	P = NP	P = NP	P = NP	P < NP*	NP > P**
4	P = NP	P = NP	P = NP	P = NP	P = NP	P = NP	P < NP**	NP > P*

* = Significant difference, $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

when herbivory has a minimal effect on the fitness of annuals.

Germination timing in the desert is far less predictable than in Mediterranean regions because of variable late-winter and early-spring rains (Shmida et al., 1985). Thus, desert crucifers are far more unpredictable in time than their Mediterranean counterparts. Year-to-year variation in composition, location, and size of patches is often tremendous. Despite these differences, flowering is still well under way by the time most herbivores, even crucifer specialists, arrive. Interestingly, pubescence, a characteristic frequently interpreted as a possible herbivore defense (Coley, 1983) as well as an adaptation that reduces rates of evapotranspiration (Lieberman & Lieberman, 1984), is more common among non-patch- than patch-forming species in both floristic regions.

We can only speculate why crucifer-adapted herbivores have not undergone phenological displacement to exploit early-season crucifers. Selection for synchrony may be countered by physiological constraints associated with early-season cold temperatures. The extremely variable phenologies of desert crucifers also may preclude herbivore synchrony. As Feeny (1977) noted, "Short growth season, shifting pattern of geographic distribution, and association with harsh and somewhat unpredictable climatic conditions are all characteristics which are likely to favor escape by plants from their adapted enemies"; this has been echoed elsewhere (Janzen, 1970; Rhoades & Cates, 1976; Feeny, 1976). In addition, selective pressure for phenological changes among Mediterranean crucifer-feeding insects may not be very great, since cruciferous hosts are available later in the season. There also may be phytochemical barriers that function with phenology in much the same manner as we envisage for nonadapted herbivores. Many crucifers contain diverse glucosinolates as well as other allelochemicals, and the performance of crucifer feeders frequently varies greatly among host plants (Root & Olson, 1969; Feeny, 1976; Rodman & Chew, 1980).

HOW ARE PATCHES FORMED?

The ability to form patches clearly involves more than early phenologies, since we found few significant phenological differences between Mediterranean patch- and non-patch-forming crucifers (Table 4). In Mediterranean and desert regions of Israel, late-winter rains initiate germination of seeds of crucifers and other annuals. By early spring, patches of various crucifers dominate the landscape of much of Israel (Shmida & Auerbach, 1983). Bell & Muller (1973) described similar patch formation by an introduced crucifer, *Brassica nigra*, in some annual California grasslands. There, *B. nigra* produces monospecific patches throughout the grasslands despite synchronous germination of all annual species following late-autumn rains. Bell & Muller (1973) found that patch formation by *B. nigra* involves production of potent allelopathic chemicals. We do not know if allelopathy is important in patch formation by Israeli crucifers. Growth rate appears to have a role in patch formation. Many crucifers in Israel and elsewhere (Feeny, 1977) mature and set seed extremely rapidly, a trait associated with their occurrence in environmentally harsh or disturbed sites. In addition, patch formation may involve differential responses to microsite variability in edaphic parameters and grazing pressure.

WHY FORM PATCHES?

Patch formation may be reinforced by competition for pollinators and increased pollination efficiency. Most crucifers, including Israeli species, are either facultative or obligate outcrossers (Fryxell, 1957; Crisp, 1976; D. Zohary, pers. comm.). Seasonally advanced flowering among Mediterranean crucifers may reduce interspecific competition for pollinators, provided flowering does not occur before pollinators are available. Patch formation among these species may also increase pollination success over that of solitary individuals if pollinators are limited. Thus, patch formation could be reinforced by pollination success.

While patch formation may concentrate resources and produce attractive displays for pollinators (Handel, 1983; Rathcke, 1983), intraspecific competition for pollinators among members of a patch may increase if patch size becomes sufficiently large. For example, Rathcke's (1983) density-visitation model envisages a facilitation in pollination as patch size increases up to the point where pollinators are saturated, and thereafter an increase in competition with expanding patch size. Intraspecific competition for pollinators may also increase if advanced phenologies result in flowering before the annual peak in pollinator availability

(Schemske et al., 1978). As intraspecific competition intensifies, selection for enhanced attractiveness may result in differences between patch- and non-patch-forming species in pollination-associated traits.

In our analyses, two morphological attributes frequently associated with pollination, plant height and petal size (Faegri & van der Pijl, 1979; Waddington, 1979; Waser, 1983a), did vary between non-patch- and patch-forming species. Among Mediterranean species, patch formers are taller and they generally have larger petals than do non-patch-forming species. Although we do not know the intensity of intraspecific competition for pollinators in patches, increases in height and petal size were also positively associated with our measure of patch size. In addition, plant height, petal size, and indices of patch size were positively correlated with propensity for outcrossing as measured by pollen/ovule ratios (Kunin, unpubl. ms.). Thus, taller patch formers appear to have a greater tendency towards outcrossing than do smaller patch formers, and species that do not form patches have the lowest tendency to outcross. That high levels of ultraviolet reflectance and patterning is positively correlated with patch formation found among Mediterranean species also suggests that patch formation may result in increased intraspecific competition for pollinators.

Differences in height and petal size do not occur among desert species; however, desert patch-forming species do begin flowering before non-patch formers, a difference observed among Mediterranean species only when the early-flowering pygmy guild is excluded from analyses. Advanced flowering among the desert patch formers may reduce interspecific competition for pollinators (Waser, 1983b) and possibly permit pollinator specialization. Some pollinators in other deserts are capable of synchronizing with the ephemeral phenologies of their hosts (Baker & Hurd, 1968; Crawford, 1981). With the exception of the pygmy guild, a high proportion of desert patch formers have purple flowers (67% patch vs. 27% nonpatch), which suggests possible pollinator specialization or segregation between patch- and non-patch-forming species.

In summary, we suggest that growing in patches aids in pollinator attraction, especially in conjunction with atypical phenologies. Displaced phenologies also may function to segregate pollinator and herbivore guilds temporally. If pollinator efficiency is high and seed dispersal low, patch formation may be self-perpetuating, because of concentration of seeds into localized seed banks.

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FLAVONOID SYSTEMATICS OF SEVEN SECTIONS OF *LUDWIGIA* (ONAGRACEAE)[1]

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ABSTRACT

Data are presented for the flavonoids of 24 species and seven sections of *Ludwigia,* all of which previously had been grouped in sect. *Myrtocarpus.* A total of eight flavonoids, three glycoflavones, and five flavonol glycosides based on quercetin was found in these species. Seven compounds, all but one acylated glycoflavone, are present in species of the revised sect. *Myrtocarpus.* The monotypic sections *Tectiflora* and *Humboldtia* have only flavonols, and the monotypic sections *Amazonia* and *Heterophylla* have only glycoflavones. Sections *Pterocaulon* and *Cinerascentes* have both flavonols and glycoflavones. Morphologically, sect. *Myrtocarpus* has the most generalized features within *Ludwigia,* which suggests that the presence of both glycoflavones and flavonols is a primitive feature for the genus as a whole. The lack of one or the other of these groups of flavonoids in four of the monotypic sections reported suggests that these sections are advanced in this feature, as does a general reduction of structural types and a reduction in the number of glycosidic substitutions in them.

As part of a comprehensive study of the flavonoids of Onagraceae, we are herein reporting results from seven sections of *Ludwigia.* As explained in earlier papers (Averett et al., 1978, 1979), the objectives of the overall study on Onagraceae are to provide an analysis of the flavonoids at the generic level for the entire family and to gain insight into the evolution of flavonoid compounds by correlating substitutional and structural changes with a phylogeny based on other systematic data. This is the first of several papers in which we shall present the results of flavonoid analyses of *Ludwigia.* The only previous report on flavonoids in *Ludwigia* is a brief summary of data for the whole genus (including that reported here) in Averett & Raven (1984).

Ludwigia is the only genus of the tribe Jussiaeeae and comprises approximately 82 species found in wet habitats in both temperate and tropical regions worldwide (Raven, 1963). *Ludwigia* appears to represent a branch of the family distinct from all other members (Eyde, 1977, 1978, 1981; Raven & Tai, 1979). It is therefore of particular interest to consider the evolution of features in this isolated evolutionary line.

This report deals with the species included in the original broad circumscription by Munz (1942; see also Raven, 1963) of sect. *Myrtocarpus,* a group of some 23 species centered in tropical and subtropical South America that appeared to be "phylogenetically central" in the genus (Raven, 1963). Based on his studies of the morphology, cytology, and crossing relationships of this complex, Ramamoorthy (1979) divided sect. *Myrtocarpus* into seven sections, commenting that the species had been grouped primarily on the basis of shared primitive characters. Subsequent work has suggested that his sect. *Michelia* is not distinct from sect. *Myrtocarpus* sensu stricto, and that *Ludwigia mexiae* (Munz) Hara is sufficiently distinct from other members of sect. *Pterocaulon* that it is best treated as the monotypic sect. *Cinerascentes* (Ramamoorthy & Zardini, 1987). Thus we now recognize seven sections in this group, delimited as follows: sect. *Myrtocarpus* with 20 species (14 examined herein), including some with the most primitive assemblages of characters in the genus; sect. *Pterocaulon* with five species that comprise a well-marked and rather homogeneous group of diploid annuals; and five monotypic sections—*Amazonia, Heterophylla, Tectiflora, Humboldtia,* and *Cinerascentes*—that are each specialized relative to sect. *Myrtocarpus* (Ramamoorthy & Zardini, 1987).

MATERIALS AND METHODS

Dried leaf materials from 24 species of seven sections of *Ludwigia* were examined for flavonoids. Approximately 120 populations in total

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and as many as 25 populations of some of the more variable species were sampled. The samples included most chromosomal races of the species concerned. Voucher specimens are listed in Table 1.

The leaf material was extracted overnight in 85% methanol and the resulting extract was examined by two-dimensional paper chromatography. Certain of the extracts were analyzed using TLC (polyamide and cellulose) as well. In some cases, the flavonoids were crudely separated on Sephadex LH 20 with a methanol/water system as described by Hiermann et al. (1978). For structural elucidation, replicate chromatograms were run and the isolated compounds cut from the paper for further purification and analysis. The quantity of leaf material varied according to usage, but approximate amounts were 0.5–1.0 g for general screening, 5–10 g for replicate chromatograms, and 20–30 g for column chromatography. Identifications of the glycosides, their aglycones, and sugars were made as previously described (Averett et al., 1978, 1979) and were compared with standard Rf values and absorption maxima (Averett, 1977). In addition, most of the aglycones and sugars were run, along with authentic reference compounds, by circular thin-layer chromatography as described by Exner et al. (1977). Base hydrolysis was employed to determine acylation but the acylating function was not determined.

RESULTS AND DISCUSSION

Eight flavonoids were found among the species sampled (Table 2): orientin (1), isoorientin (2), orientin-O-acylate (3), quercetin 3-O-rhamnoside (4), quercetin 3-O-arabinoside (5), quercetin 3-O-glucoside (6), quercetin 3-O-diglucoside (7), and quercetin 3-O-rutinoside (8). Compounds 1–3 are glycoflavones and compounds 4–8 are flavonol glycosides. All of the compounds are based on structures having two hydroxyl substituents in the B-ring.

Some infraspecific variation was found, especially in such variable species as *Ludwigia peruviana, L. elegans,* and *L. laruotteana.* Although variation was present, no flavonoid unique to any species was found in a single population. We also detected differences in concentrations of compounds between populations of some species, but made no attempt to document these differences. Interspecific variation within the larger sections is apparent but, like populational variation, is largely confined to the presence or absence of certain compounds. The more interesting variation is found in intersectional comparisons. Because of this, samples are arranged by species and grouped in their respective sections in Table 2.

Compound 3, the acylated glycoflavone, is found in only five species in three different sections, including the closely related sections *Cinerascentes* and *Pterocaulon.* Compounds 5 and 7 are the next most frequently absent, occurring in only six and seven species, respectively, and typically in low concentration when present. Compounds 1, 2, and 8 are the least variable and are found in 18, 20, and 19 of the species, respectively. Compound 2 is present in all species in which glycoflavones occur, and compound 8 is present in all species in which flavonols are found. Compounds 4 and 6 occur in 13 and 14 of the species sampled. Glycoflavones are found in 20 of the 24 species, flavonols in 19, both glycoflavones and flavonols in 15, only glycoflavones in five, and only flavonols in four.

All of the species have at least two compounds and none has more than seven. The average number of compounds per species is 5.37 for the entire group. The comparison of numbers of compounds at the sectional level is especially interesting. Species of sect. *Myrtocarpus,* which has relatively generalized features, and sect. *Cinerascentes* have an average of five compounds. The remaining sections have reduced numbers of compounds, with averages of 3.4 (*Pterocaulon*), 3.0 (*Humboldtia* and *Heterophylla*), and 2.0 (*Amazonia* and *Tectiflora*).

Flavonols are present throughout Onagraceae and glycoflavones are present in all tribes except Fuchsieae and Epilobieae (Averett & Raven, 1984). Glycoflavones are especially well represented in *Circaea* (Boufford et al., 1978; Averett & Boufford, 1985). The presence of glycoflavones is considered primitive relative to the presence of other groups of flavonoids (Harborne, 1977), and the distribution of these compounds within Onagraceae does not contradict that contention.

Except for *Ludwigia sericea,* which has only flavonols, all species examined of sect. *Myrtocarpus* and the single species, *L. mexiae,* of sect. *Cinerascentes* have both glycoflavones and flavonols. The remaining monotypic sections exhibit either glycoflavones only—sections *Heterophylla* and *Amazonia*—or flavonols only—sections *Humboldtia* and *Tectiflora.* Collectively, the species of sect. *Pterocaulon* exhibit both

TABLE 1. Voucher specimens of *Ludwigia* used for flavonoid analysis in this study. Specimens of all material deposited at MO, unless otherwise indicated.

- *Ludwigia* section *Amazonia* Ramamoorthy
  - *Ludwigia densiflora* (Micheli) Hara. BRAZIL. RONDONIA: *Duarte 7329* (MO, RB).

- *Ludwigia* section *Cinerascentes* Ramamoorthy & Zardini
  - *Ludwigia mexiae* (Munz) Hara. BRAZIL. PARA: *Ramamoorthy 652.*

- *Ludwigia* section *Heterophylla* Ramamoorthy
  - *Ludwigia inclinata* (L. f.) Gómez. MEXICO. OAXACA: *Breedlove & Raven 13686.* COSTA RICA. PUNTARENAS: *Stork & Horton 8912* (US). BRAZIL. AMAPA: *Froes & Black 27732* (IAN).

- *Ludwigia* section *Humboldtia*
  - *Ludwigia sedoides* (H. & B.) Hara. PANAMA. CANAL ZONE: *D'Arcy 12350.* BRAZIL. PARA: *Archer 8411* (RSA).

- *Ludwigia* section *Myrtocarpus* (Munz) Hara
  - *Ludwigia albiflora* Ramamoorthy. BRAZIL. GOIAS: *Ramamoorthy 545.* MINAS GERAIS: *Ramamoorthy 427* (MO, SP).
  - *Ludwigia bullata* (Hassler) Hara. BRAZIL. MATO GROSSO DO SUL: *Ramamoorthy 610* (MO, SP), *Ramamoorthy & Vital 640* (MO, SP).
  - *Ludwigia elegans* (Camb.) Hara. BRAZIL. GOIAS: *Ramamoorthy 532, 560, 564.* MINAS GERAIS: *Ramamoorthy 403, 410, 424*; *Ramamoorthy & Vital 140*; *Ramamoorthy et al. 148, 153, 161, 168, 176, 178, 179, 181* (MO, SP), *184, 195, 299, 301, 308, 309, 319.* RIO DE JANEIRO: *Ramamoorthy et al. 291.* SAO PAULO: *Ramamoorthy 379, 384, 395*; *Ramamoorthy & Vital 112*; *Ramamoorthy et al. 196.*
  - *Ludwigia hassleriana* (Chodat) Hassler. BRAZIL. MATO GROSSE DO SUL: *Ramamoorthy 629*; *Ramamoorthy et al. 271.*
  - *Ludwigia irwinii* Ramamoorthy. BRAZIL. MINAS GERAIS: *Ramamoorthy et al. 142.* SAO PAULO: *Ramamoorthy 80*; *Munz 15406* (NY, POM, US).
  - *Ludwigia laruotteana* (Camb.) Hara. BRAZIL. GOIAS: *Ramamoorthy 419, 420.* MINAS GERAIS: *Ramamoorthy 101*; *Ramamoorthy & Vital 90*; *Ramamoorthy et al. 143, 147, 160, 172, 188, 311.* SAO PAULO: *Ramamoorthy 69.*
  - *Ludwigia martii* (Micheli) Ramamoorthy. BRAZIL. MINAS GERAIS: *Glaziou 15949* (B, C, F, P, R).
  - *Ludwigia myrtifolia* (Camb.) Hara. BRAZIL. MINAS GERAIS: *Ramamoorthy 734.*
  - *Ludwigia nervosa* (Poir.) Hara. NICARAGUA. ZELAYA: *Stevens 8275.* BRAZIL. BAHIA: *Ramamoorthy et al. 328.* DISTRITO FEDERAL: *Ramamoorthy 526.* GOIAS: *Ramamoorthy 561*; *Ramamoorthy & Vital 544.* MATO GROSSO: *Ramamoorthy 571.* MATO GROSSO DO SUL: *Ramamoorthy 605, 607.* MINAS GERAIS: *Ramamoorthy et al. 170.* SAO PAULO: *Ramamoorthy 393* (MO, SP); *Ramamoorthy & Vital 78* (MO, SP).
  - *Ludwigia peruviana* (L.) Hara. BRAZIL. MINAS GERAIS: *Ramamoorthy 366.* PARANA: *Ramamoorthy 207, 275, 281.*
  - *Ludwigia pseudo-narcissus* (Chodat) Ramamoorthy. BRAZIL. PARANA: *Ramamoorthy et al. 283.*
  - *Ludwigia rigida* (Miq.) Sandwith. SURINAM: *Pulle 475.* VENEZUELA. COJEDES: *Pittier 11711* (B, US, VEN).
  - *Ludwigia sericea* (Camb.) Hara. BRAZIL. MINAS GERAIS: *Ramamoorthy 68*; *Ramamoorthy et al. 157, 158, 159, 169.* PARANA: *Ramamoorthy et al. 215, 216, 288, 289.* SANTA CATARINA: *Ramamoorthy et al. 240.* SAO PAULO: *Ramamoorthy 444.*
  - *Ludwigia tomentosa* (Camb.) Hara. BRAZIL. BAHIA: *Ramamoorthy et al. 336.* DISTRITO FEDERAL: *Ramamoorthy 513*; *Ramamoorthy et al. 349, 351.* GOIAS: *Ramamoorthy et al. 342, 344, 345, 506.* MATO GROSSO: *Ramamoorthy & Vital 579.* MINAS GERAIS: *Ramamoorthy 163, 164, 165, 405*; *Ramamoorthy et al. 187.*

- *Ludwigia* section *Pterocaulon* Ramamoorthy
  - *Ludwigia decurrens* Walt. NICARAGUA. ZELAYA: *Stevens 4916.* BRAZIL. MINAS GERAIS: *Ramamoorthy et al. 303, 306.* SANTA CATARINA: *Ramamoorthy et al. 258, 259.*
  - *Ludwigia erecta* (L.) Hara. MEXICO. OAXACA: *Breedlove & Raven 13669* (DS, MO). NICARAGUA. ZELAYA: *Stevens 8274.* CUBA. ORIENTE: *Ekman 6537* (S). COLOMBIA. HUILA: *Smith 1204* (GH, UC, US). SOUTHERN RHODESIA. NDANGA: *Goodier 977.*
  - *Ludwigia filiformis* (Micheli) Ramamoorthy. BRAZIL. GOIAS: *Ramamoorthy & Vital 555.* SAO PAULO: *Ramamoorthy 73.*
  - *Ludwigia longifolia* (DC.) Hara. BRAZIL. MINAS GERAIS: *Ramamoorthy & Vital 96*; *Ramamoorthy et al. 150.* SANTA CATARINA: *Ramamoorthy et al. 231, 233, 237.*
  - *Ludwigia major* (Micheli) Ramamoorthy. BRAZIL. RIO GRANDE DO SUL: *Ramamoorthy et al. 245.*

- *Ludwigia* section *Tectiflora* Ramamoorthy
  - *Ludwigia latifolia* (Benth.) Hara. NICARAGUA. RIO SAN JUAN: *Neill 3361.* GUYANA. WEST DEMARARA: *Maguire & Fanshave 22951* (NY, U, US). PERU. SAN MARTIN: *Ferreyra 18506, Williams 7153* (F, US).

TABLE 2. Distribution of flavonoids among seven sections of *Ludwigia*. + = flavonoid detected; 0 = flavonoid not detected. Key: 1 = orientin, 2 = isoorientin, 3 = orientin-O-acylate, 4 = quercetin-3-O-rhamnoside, 5 = quercetin-3-O-arabinoside, 6 = quercetin-3-O-glucoside, 7 = quercetin-3-O-diglucoside, and 8 = quercetin-3-O-rutinoside.

	Glycoflavones			Flavonols				
	1	2	3	4	5	6	7	8
Sect. *Amazonia*								
L. densiflora	+	+	0	0	0	0	0	0
Sect. *Cinerascentes*								
L. mexiae	+	+	+	0	+	0	0	+
Sect. *Heterophylla*								
L. inclinata	+	+	+	0	0	0	0	0
Sect. *Humboldtia*								
L. sedoides	0	0	0	+	0	+	0	+
Sect. *Myrtocarpus*								
L. albiflora	+	+	0	+	0	+	0	+
L. bullata	+	+	0	+	0	+	0	+
L. elegans	+	+	0	+	+	+	+	+
L. hassleriana	0	+	0	+	0	0	+	+
L. irwinii	+	+	0	+	+	+	+	+
L. laruotteana	+	+	0	+	+	+	+	+
L. martii	0	+	0	0	0	0	+	+
L. myrtifolia	+	+	0	+	0	+	0	+
L. nervosa	+	+	0	+	0	+	0	+
L. peruviana	+	+	0	+	+	+	+	+
L. pseudo-narcissus	+	+	0	0	0	0	0	+
L. rigida	+	+	0	0	0	0	0	+
L. sericea	0	0	0	+	0	+	0	+
L. tomentosa	+	+	0	+	+	+	0	+
Sect. *Pterocaulon*								
L. decurrens	+	+	0	0	0	+	+	+
L. erecta	+	+	+	0	0	0	0	0
L. filiformis	0	0	0	+	0	+	0	+
L. longifolia	+	+	+	0	0	0	0	0
L. major	+	+	+	0	0	0	0	0
Sect. *Tectiflora*								
L. latifolia	0	0	0	0	0	+	0	+

glycoflavones and flavonols, but only one species, *L. decurrens*, has both classes of compounds. One species, *L. filiformis*, has only flavonols, and the remaining three species have only glycoflavones. Thus, if sect. *Pterocaulon* is a monophyletic group derived from sect. *Myrtocarpus*, as is indicated from morphological studies, then within this section of five species one has lost the ability to produce glycoflavones and three to produce flavonols; that, at least, would be the most parsimonious explanation.

The five monotypic sections we are considering here do not appear to be more closely related to sect. *Myrtocarpus*, on the basis of their overall characteristics, than they do to any other part of *Ludwigia*. Additionally, they differ in many morphological features one from another, and there is no evidence of a direct relationship between any two. The overall similarity of flavonoids between sections *Tectiflora* and *Humboldtia* and between sections *Amazonia* and *Heterophylla* could not, then, be taken as an indication of relationship between those taxa. Rather, the similarity of flavonoids between these groups seems to reflect parallel and independent loss of particular classes of flavonoids and/or individual compounds, a trend that has characterized the evolution of the genus overall. A further evaluation of their relationships, which must be multidimensional, would need to take into account the remainder of the genus. It does appear, in terms of admittedly largely plesiomorphic characteristics, that sections *Pterocaulon* and *Cinerascentes* are more clearly related to sect. *Myrtocarpus* than are the others.

In summary, our analysis has revealed a pattern of loss of individual flavonoids and groups of flavonoids in the seven sections of *Ludwigia* that we have considered in this paper. Further resolution of the relationships of these species must await more detailed study.

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A CHEMOTAXONOMIC CLASSIFICATION OF THE SOLANACEAE[1]

PETER TÉTÉNYI[2]

ABSTRACT

Alkaloids and steroids in the Solanaceae are reported extensively in the literature. By examining the biosynthetic routes leading to different alkaloids, the pathways can be visualized as a spiral from which the various compounds can be derived. Arrangement of the genera of Solanaceae according to their chemical contents in relationship to this spiral supports traditional classifications of the family, but the Anthocercidoideae and Atropoideae must be recognized as new subfamilies due to their biochemical synthesis syndromes. Similarly, Solaninae and Physalinae must be accepted as separate subtribes of tribe Solaneae because of their differing and exclusive steroid synthesis. *Acnistus* and *Dunalia* must be allied with *Jaborosa* in tribe Jaboroseae.

Although solanaceous species are well known to afford an array of alkaloids and steroids, the family has not been arranged yet according to chemical features. Indeed, it is difficult to find reports of most features because, except for the occurrence of calcium oxalate crystals, only their absence is recorded. Thus Philipson (1977) concluded that a lack of iridioids characterizes the Solanaceae within the Unitegminae. Dahlgren (1975, 1980) came to similar conclusions, adding the deficiency of polyacetylenes as a characteristic. Sporne (1980) believed that absence of leucoanthocyanins and ellagitanins are chemical characteristics of the family and indicated that whether or not the seeds contain endosperm may or may not be significant.

In an investigation of the cytochrome-C and plastocyanin amino acid sequence, Boulter et al. (1979) placed the Solanaceae far from the Asteraceae in their family tree, and although they related it closely to the Scrophulariaceae, they surprisingly considered the Caprifoliaceae to be the most closely related family. This biochemical statement supports the earlier view of Chadefaud & Emberger (1960) that the Solanaceae and Caprifoliaceae are closely related based on embryological characters. Nevertheless, mature solanaceous plants are typical alkaloid-accumulators, whereas mature caprifoliaceous plants have phenol-glycosides (Hegnauer, 1973). In the same publication Boulter et al. (1979) put the tomato alongside the potato and separated tobacco and the woody *Solanum crispum* Ruiz & Pavón, and they held *Capsicum frutescens* L. to be significantly different from the preceding species based on the amino acid complement.

The use of active principles found in different Solanaceae to construct systematic schemes can be accepted only when it can be demonstrated that the biosynthetic routes leading to these chemical structures are homologous (Tétényi, 1973). The valid chemical patterns are in the various biosynthetic pathways and not in the substances accumulated. Thus I have summarized the branching and relationships of biosynthetic pathways in alkaloid production in the Solanaceae in Table 1 and Figure 1. Numbers in the following paragraphs correspond to those of Table 1 and Figure 1.

The first evidence supporting this scheme lies in the well-known, genetically determined chemical differentiation in infraspecific chemotaxa of *Duboisia myoporoides* R. Br. (Tétényi, 1970). The characteristic active alkaloid ingredient, nicotine (1), in one chemotaxon of this species is the result of the synthesis of ornithine and tryptophan to an alkaloid. Another chemotaxon of *D. myoporoides* is characterized by a splicing of the aspartate pattern (lysine) and acetyl-CoA to the alkaloid biosynthesis, and the main alkaloids are then anabasine (A) and isopelletierine (B). In a third infraspecific chemotaxon, an entirely different pattern occurs: an α-face nucleophilic attack instead of the β-face one of the N-methyl-Δ^1-pyrrolinium salt (Fig. 2; Leete, 1979) leads to the pathways indicated by the solalkoid spiral (Fig. 1), that is, the linking of ornithine and acetyl-CoA to hygrine (2) and then the development

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TABLE 1. Alkaloids of Solanaceae included in and arranged conforming to the solalkoid spiral.

Nicotine and its derivatives				
nicotine (1) $C_{10}H_{14}N_2$ [54-11-5]		anabasine (A) $C_{10}H_{14}N_2$ [494-52-0]		isopelletierine (B) $C_8H_{15}NO$ [539-00-4]
Tropane alkaloids				
hygrine (2) $C_8H_{12}N_2O_3$ [496-49-1]		hygroline (2) $C_8H_{17}NO$ [1617-83-0]		withasomnine (3) $C_{12}H_{15}N_2$ [10183-74-1]
	cuscohygrine (4) $C_{13}H_{24}NO_4$ [454-14-8]		belladonnine (4) $C_{34}H_{42}N_2O_4$ [6696-63-5]	
tropinone (5) $C_8H_{13}NO$ [532-24-1]		physoperuvine (5) $C_8H_{15}NO$ [60723-27-5]		tropine (5) $C_8H_{15}NO$ [120-29-6]
	isovaleryloxytropane (6) $C_{13}H_{23}NO_2$ [490-96-0]		senecioyloxytropane (6) $C_{13}H_{21}NO_3$ [77101-57-6]	
tigloidine (7) $C_{13}H_{21}NO_2$ [495-83-0]		tigloyloxytropane (7) $C_{13}H_{21}NO_3$ [55727-41-8]		valtropine (7) $C_{13}H_{23}NO_2$ [495-82-9]
scopolamine (8) $C_{13}H_{21}NO_4$ [51-34-3]		hyoscyamine (8) $C_{17}H_{21}NO_3$ [101-31-5]		physochlaine (8) $C_{17}H_{23}NO_3$ [54357-41-4]
Other alkaloids				
fabianine (—) $C_{14}H_{21}NO$ [6871-51-8]		β-carboline (C) $C_{15}H_{21}N_2O_3$ [244-63-3]		capsaicine (D) $C_{18}H_{27}NO_3$ [54357-41-4]
	betaine (E) $C_{15}H_{11}NO_2$ [107-43-7]		choline (E) $C_5H_{15}NO_2$ [62-49-7]	

Explanation: common name; symbols in parentheses refer to Figure 1
formula
[registry number]

of other simple and ester tropane alkaloids. Thus pyruvate-leucine yields valeroidine (6) with isovaleric acid; aspartate-isoleucine yields tigloidine (7) with tiglic acid; and finally, from phenylalanine and tropic acid, scopolamine (8) becomes the characteristic alkaloid of the third chemotaxon.

The genus *Duboisia* R. Br. provides further evidence of this kind of chemical differentiation separating the infraspecific taxa of *D. myoporoides* from one another. In *D. hopwoodii* F. Muell., nicotine (1) and its derivatives are synthesized by the β-face attack of ornithine, whereas in *D. leichhardtii* F. Muell.—the most economical source in the world for scopolamine—this alkaloid is accumulated through the converse formation. Thus the scheme in Figure 1 is true for *Duboisia* as a genus as well as for its components.

Two other genera examined in subfamily Anthocercidoideae (described on p. 607)—which includes *Duboisia*—show the same diversity in alkaloid biosynthesis, having a broad spectrum of alkaloids, and those from nicotine (1), anabasine (A), cuscohygrine (4), to tropine (5), valeroidine (6), tigloidine (7), and scopolamine (8) have been detected.

Alkaloid synthesis in subfamily Cestroideae Schldl. also proceeds according to Figure 1, but here the main stopping points are nicotine and its derivatives, a somewhat different picture from the Anthocercidoideae. Thus nicotine (1) is the sole product in the genus *Cestrum* L., whereas fabianine, a tetrahydroquinoline alkaloid arising from a biosynthesis preceding the pyridine-nucleotide cycle, is accumulated as well as nicotine in *Fabiana* Ruiz & Pavón. The aspartate-lysine path is switched in *Streptosolen* Miers, and anabasine is accumulated in addition to nicotine. The alkaloid spectrum of *Nicotiana* L. and *Salpiglossis* Ruiz & Pavón by intervention of acetyl-CoA, accumulates isopelletierine (B) in addition

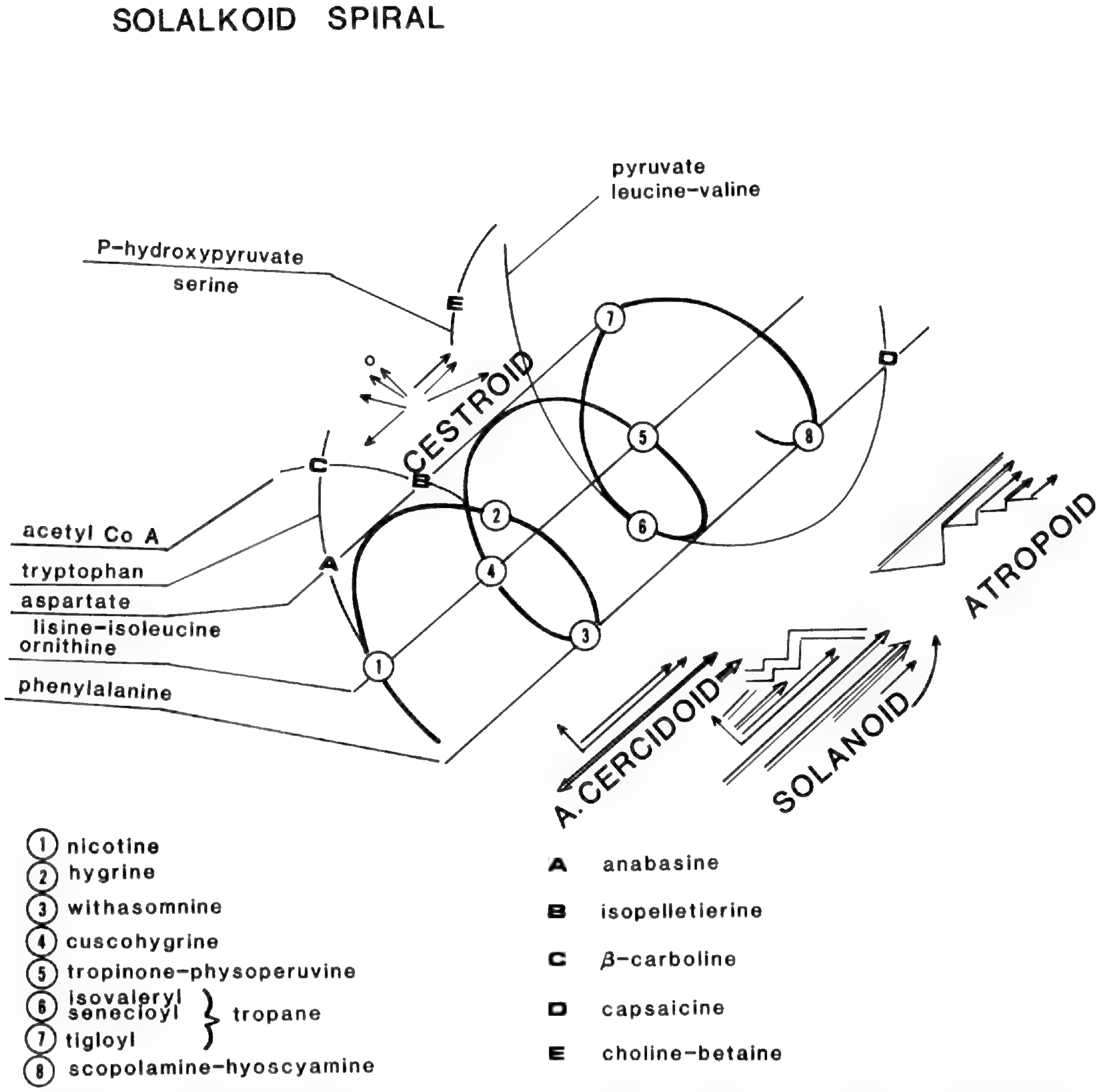

FIGURE 1. Solalkoid spiral based on characteristic biosynthetic patterns of most important alkaloids isolated from plants belonging to the Solanaceae. Amino acids represent starting and combined points. Patterns of alkaloid biosynthesis in subfamilies are clarified in the text.

to the above substances. *Nicotiana* is even enriched by betaine (E) through the hydroxypyruvate-serine pathway. Coupling of acetyl-CoA with tryptophan is the source of the simple indolalkaloid of *Vestia* Willd., which contains a β-carboline skeleton.

My scheme might not be tenable if the Cestroideae were not differentiated chemically also. In fact, the alkaloid biogenesis of hygrine derivatives is found in this subfamily too, although only *Brunfelsia* L. accumulates just cuscohygrine (4) and pyrrole-3-carboximidine, which was also detected in *Nierembergia* Ruiz & Pavón, whereas real tropane esters are synthesized in *Schizanthus* Ruiz & Pavón. However, the alkaloid spectrum in *Schizanthus* is unique in the whole family with its hygroline (occurring also in the Erythroxylaceae) and because the sencioyl and angeloyl tropane esters (6) are formed from pyruvate-leucine and ornithine. Formation of the alkaloid valeroidine in *Schizanthus* by this biosynthetic pathway is characteristic of the family Solanaceae as well as of *Anthocercis* Labill., *Cyphanthera* Miers, and *Duboisia*. However, taking into account the two kinds of hygrine synthesis, the predominance of nicotine in its various derivatives (A, B, C), and the primary substances brunfelsamine and fabianine, we can assert that the

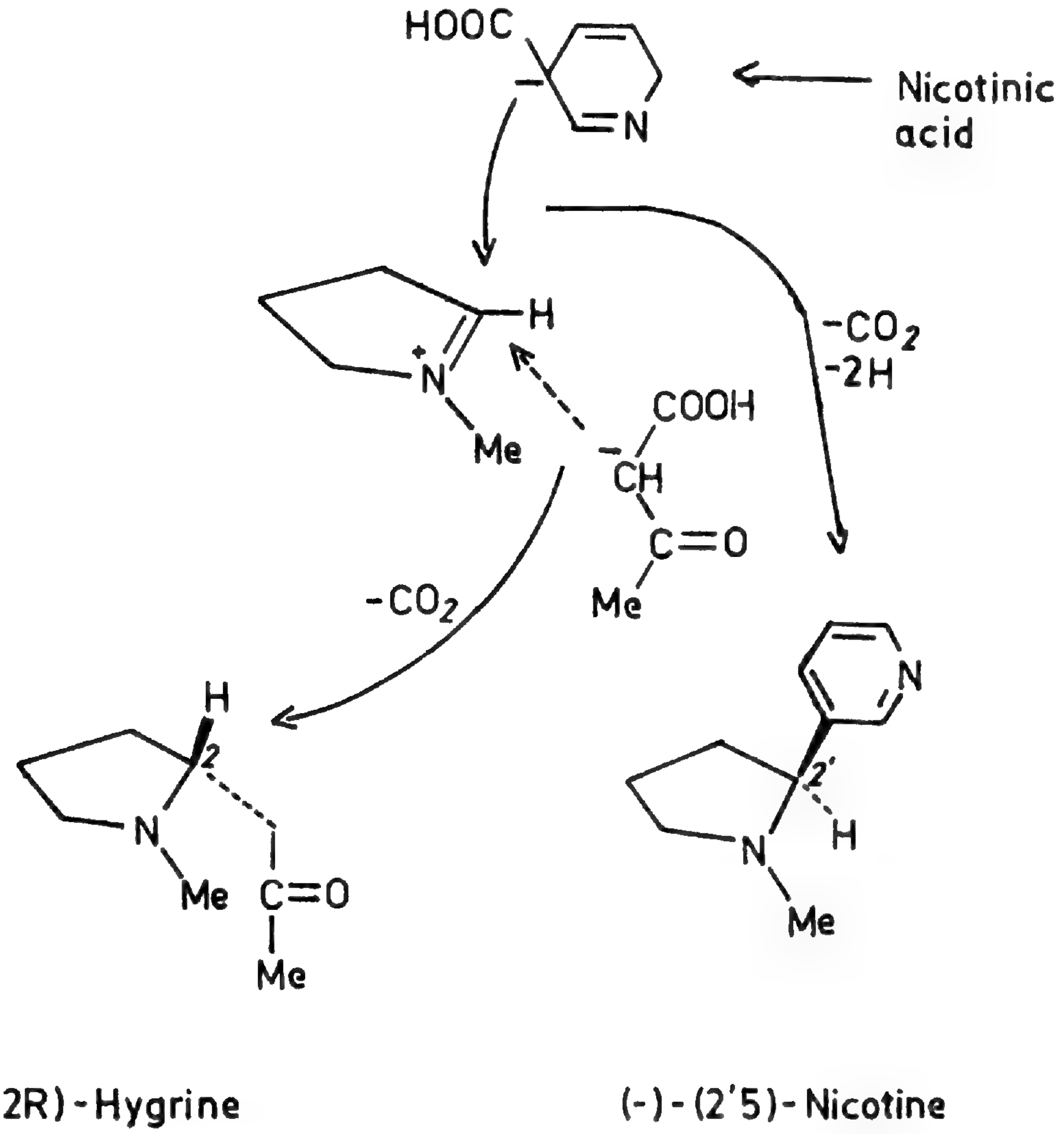

FIGURE 2. Nucleophilic attack of N-methyl-Δ^1-pyrrolinium salt from the α- and β-face (Leete, 1979).

chemical differentiation of the Cestroideae, in having an alkaloid synthesis with several similarities to that of the Erythroxylaceae, Rubiaceae, Elaeagnaceae, and Malpighiaceae, significantly surpasses that of the Anthocercidoideae.

Chemical differentiation in subfamily Solanoideae is of a different character than in the Cestroideae, for here the hygrine derivatives are always preponderant, and the differences are in the ever-increasing complexity of the molecular entities synthesized by the different genera as if overcoming a barrier. Similar to the case of *Brunfelsia* mentioned above, the *Solanum* L., *Jaltomata* Schldl. (*Saracha viscosa* Schrader), and *Margaranthus* Schldl. arrested at a certain stage, accumulate cuscohygrine (4) only. *Nicandra* Adans. starts from hygrine (2) and, like *Cyphomandra* Sendtner, reaches the formation of tropinone (5). The alkaloid physoperuvine (5) of *Physalis* L. is equivalent to this, although tigloidine (7), an alkaloid of this genus, is an ester but not with tropic acid. In *Withania* Pauquy aspartate-isoleucine and ornithine are synthesized to 3'-tigloyloxytropane without the presence of any tropic ester, but the alkaloid spectrum of this genus is very broad; thus withasomnine (3) is formed by coupling ornithine to phenylalanine. Isopelletierine (B) from lysine and acetyl-CoA and even the alkaloid choline (E) arise from the hydroxypyruvate synthesis pathway. These are only the main types represented. In the genera *Leucophysalis* Rydb. (*Physaliastrum japonicum* (Franchet & Savat.) Honda) and *Lycium* L. of this subfamily, the unique alkaloid detected so far is betaine (E), formed from the serine cycle in the same way as choline.

Affinity of subfamily Solanoideae with subfamily Anthocercidoideae is proven in the alkaloid spectra of *Brugmansia* Pers. and *Datura* L. On the one hand, these plants realize both synthetic routes from nicotine (1) to scopolamine (8), while on the other hand, they also form and accumulate the alkaloid valeroidine (6) like *Anthocercis* and *Duboisia*. In the genus *Solandra* Sw., valtropine (7), originating from the coupling of isoleucine with ornithine, follows a path of alkaloid biosynthesis homologous to that in *Cyphanthera* and *Grammosolen* Haegi. However,

TABLE 2. Differences of N-methyl-Δ^1-pyrrolinium derivative alkaloids in subfamily Atropoideae. Data from Romeike (1978) except where noted otherwise.

	Genus							
Alkaloids	*Atropa*	*Hyoscyamus*	*Scopolia*	*Whitleya*	*Mandragora*	*Przewalskia*	*Atropanthe*	*Physochlaina*
Physochlaine								+
Hyoscyamine	+	+	+	+	+	+	+	+
3'-tigloyloxytropane		+	+		+			
Belladonnine	+				+			
Tropine	+	+	+	+				
Tetramethylputrescine		+						
Δ-N-methylornithine (Hedges & Herbert, 1981)	+							

a related feature in the genus *Anthotroche* Endl. may be that hyoscyamine (8) predominates in the spectrum. The hygrine (2) of *Salpichroa* Miers also shows relationship to *Duboisia,* but here hyoscyamine (8) is the characteristic alkaloid, similar to the content of tigloidine (7) in *Acnistus* Schott and the small amount of scopolamine (8) in *Latua* Phil. The combination of pyruvate-valine and phenylalanine to capsaicine (D) supports the curious alkaloid biosynthesis and the isolation of *Capsicum* L. as stated by Boulter et al. (1979).

The system shown in Figure 1 is also supported by the alkaloid synthesis in subfamily Atropoideae (described on p. 607). In contrast to the Solanoideae, the simple alkaloid synthesis of the Atropoideae is subordinate to that of tropane esters. This is illustrated by the data in Table 2, for initially nicotine formation is only inhibited—as exemplified by *Atropa* L. and *Hyoscyamus* L.—and the genera *Scopolia* Jacq. and *Whitleya* Sweet (*Anisodus* Link) are the most advanced cases in which a simple tropane base could be detected. Occurrence of tigloyl ester (7) can be verified in *Mandragora* L. only by the presence of cuscohygrine (4) and a little scopolamine (8). *Przewalskia* Maxim. and *Atropanthe* Pascher accumulate mainly hyoscyamine (8), which is characteristic in the whole family and occurs in each genus. Although the result of the synthesis in *Physochlaina* G. Don is also predominantly hyoscyamine, its peculiar alkaloid, physochlaine (8), is the tropane ester of 4-methoxyphenylacetic acid, a phenylalanine derivative.

The alkaloid-forming distinctions of solanaceous taxa at various levels have been arranged according to Figure 1. The requirements were satisfied by this scheme, which we have termed the solalkoid spiral. One objection may be that I have not mentioned the connection between terpenoid and alkaloid biosynthesis. This is because the steroid synthesis that is characteristic of the family is exclusive, alternative, and without transition, in contrast to the process of alkaloid synthesis, which is gradual and proceeds by inhibition.

This is supported by the studies of infraspecific chemotaxa carried out with withanolides on *Withania somnifera* Dunal (Lavie, 1973) as well as our own analysis of steroidal alkaloid taxa of *Solanum dulcamara* L. (Tétényi et al., 1977). No instance of a steroidal alkaloid in a withanolide-containing species or the reverse is known, although this may be due to deficiency in our equipment or methods.

It seems that these two routes of steroid synthesis—steroidal alkaloids versus lactones—represent a phylogenetic branching alternative with cholesterol as its starting point. Oxidation leads to withanolides compared with partial etherification to neutral saponins, followed by cyclization to steroidal alkaloids.

Duboisia—subfamily Anthocercidoideae—synthesizes only neutral sapogenins, and *Cyphanthera, Anthotroche, Crenidium* Haegi ursolic acid only, a further feature pointing to their primordial endemism. Simple sapogenins were detected in subfamily Cestroideae: in *Combera* Sandw., *Fabiana, Nierembergia, Browallia* L.,

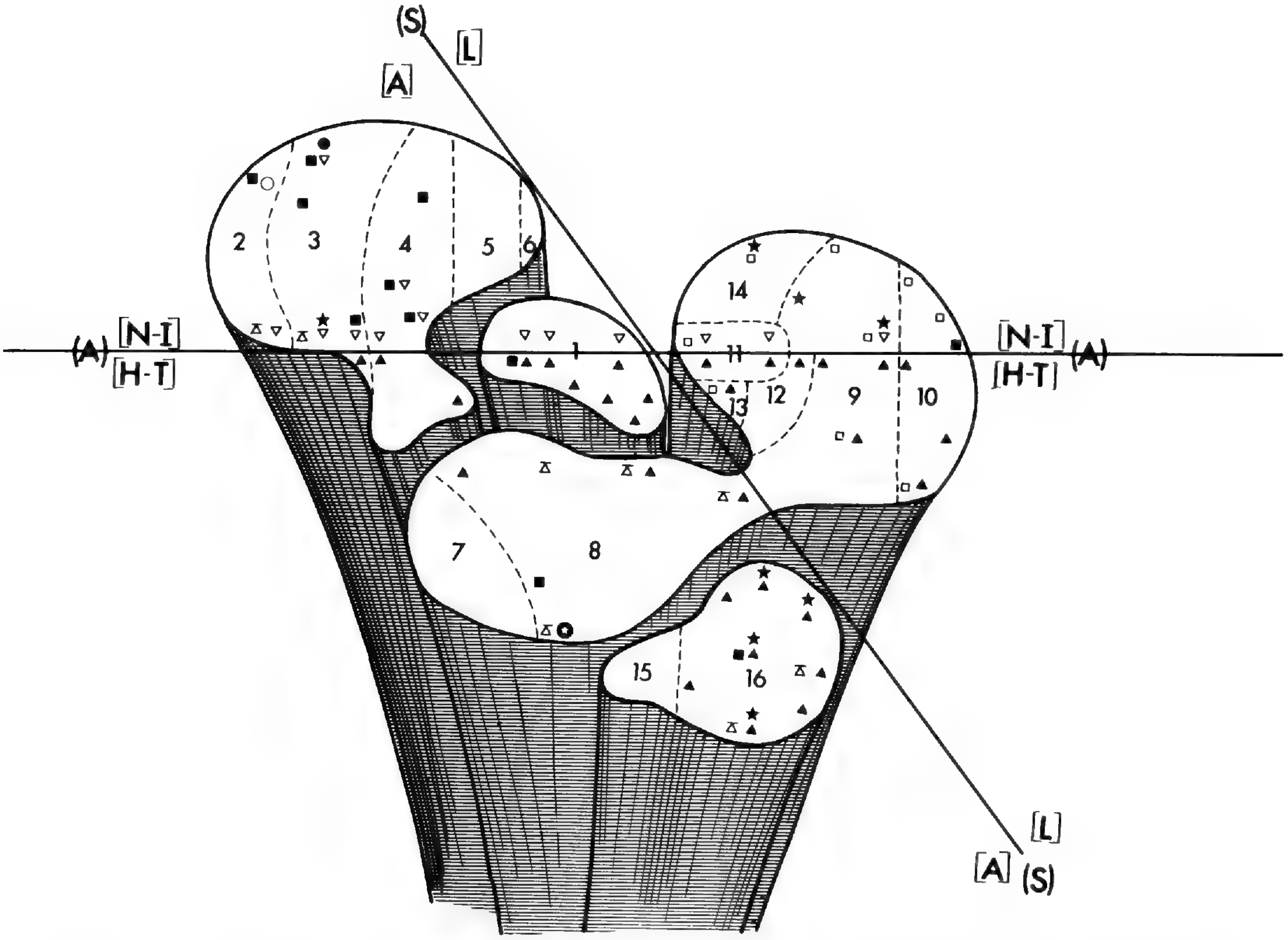

FIGURE 3. Chemotaxonomic system of the Solanaceae based on characteristic alkaloids and steroids of genera in four subfamilies containing 16 tribes and designed following Dahlgren (1975). Axes separate most important biosystematic systems. Steroid (S): ■ = sapogenin, ⊼ = alkaloid [A], □ = lactone [L]. Alkaloids (A): ▽ = nicotine-isopelletierine type [N-I], ○ = β-carboline, ● = isoquinoline, ★ = choline-betaine, ▲ = hygrine-tropane type [H-T], ⭘ = capsaicine. Anthocercoideae.—1. Anthocerceae G. Don. (7). Cestroideae.—2. Cestreae G. Don. (5).—3. Nicotianeae G. Don. (8).—4. Salpigloss[id]eae Benth. (7).—5. Schwenckieae A. T. Hunz. (3).—6. Parabouchetieae A. T. Hunz. (1). Solanoideae.—7. Juannulloeae A. T. Hunz. (8).—8. Solaneae–Solaninae (15).—9. Solaneae–Physalinae (9).—10. Jaboroseae Miers (7).—11. Datureae Reichb. (2).—12. Solandreae Miers (2).—13. Nicandreae Wettst. (1).—14. Lycieae A. T. Hunz. (3). Atropoideae.—15. Discopodiineae Baehni (2).—16. Atropeae Reichb. (9). Numbers in parentheses indicate numbers of genera.

Salpiglossis, Vestia, and *Streptosolen,* as well as in *Cestrum* and *Nicotiana,* but these two have steroidal alkaloids.

Subfamily Solanoideae, apart from *Exodeconus* Raf., shows a prevalence of steroidal alkaloids when the genera *Solanum, Cyphomandra, Capsicum,* and *Lycopersicon* Miller are considered. Because of their steroidal lactone synthesis, *Physalis, Withania, Witheringia* L'Hér., *Acnistus, Datura, Nicandra,* and *Lycium,* as well as *Dunalia* Kunth and *Jaborosa* Juss. and the sapogenin-containing *Trechonaetes* Miers, should be evaluated as quite distinct. This differentiated steroid synthesis divides subfamily Solanoideae. The connection between alkaloid and steroid biosynthesis is shown by the fact that *Solanum,* arrested at cuscohygrine, includes species accumulating steroidal alkaloids building in arginine released from the ornithine cycle in their genesis.

The genera *Physochlaina* and *Scopolia* of subfamily Atropoideae synthesize solanidine. *Hyoscyamus* synthesizes sapogenin, and thus the subfamily is nearer to the subtribe of the Solanoideae characterized by formation of the same steroids.

If we base a chemical classification of the Solanaceae on the facts mentioned above, we cannot accept the analysis of Evans (1979) or Romeike (1978), who considered only alkaloid properties in evaluating Wettstein's century-old system. I have developed in Figure 3 a chemotaxonomic classification of the Solanaceae. It

TABLE 3. Characteristic alkaloids and steroids for the chemotaxonomic system of the Solanaceae (corresponding to Fig. 3).

Tribe	Genus	Alkaloid	Steroid
1	*Anthocercis*	hyoscyamine,[10] scopolamine[13]	†
	Anthotroche	hyoscyamine[10]	
	Crenidium	hyoscyamine,[14] anabasine[14]	†
	Cyphanthera	scopolamine,[14] nicotine[14]	†
	Duboisia	scopolamine,[1] isopelletierine[1]	sapogenin[3]
	Grammosolen	scopolamine[10]	
	Symonanthus	tigloyl esters[10]	
2	*Cestrum*	nicotine[3]	solasodin[3]
	Vestia	β-carboline[17]	diosgenin[3]
3	*Combera*	—	sapogenin[3]
	Fabiana	nicotine, fabianine[3]	sapogenin[3]
	Nicotiana	betaine,[7] isopelletierine[1]	solasodin[3]
	Nierembergia	β-tigloyloxytropane + brunfelsamine[15]	sapogenin[4]
4	*Browallia*	—	sapogenin[3]
	Brunfelsia	cuscohygrine[3] + brunfelsamine[16]	—
	Salpiglossis	isopelletierine[1]	sapogenin[3]
	Schizanthus	senecioyloxytropan,[6] hygrolines[1]	—
	Streptosolen	anabasine[3]	sapogenin[2]
8	*Capsicum*	capsaicine[3]	solanidin[2]
	Cyphomandra	tropinone[1]	solasodin[1]
	Exodeconus	—	neotigogenin[3]
	Jaltomata	cuscohygrine[5]	—
	Lycopersicon	—	tomatin[7]
	Solanum	cuscohygrine (solamine)[8]	solasodin[3]
9	*Leucophysalis*	betaine[3]	—
	Margaranthus	cuscohygrine[8]	—
	Physalis	tigloidine,[1] physoperuvine[1]	physalin[3]
	Withania	choline, isopelletierine, 3′-tigloyloxytropane[1]	withanolide[3]
	Witheringia	—	physalin[9]
10	*Acnistus*	hyoscyamine[10]	withanolide[11]
	Dunalia	—	withanolide[11]
	Jaborosa	—	steroidlactone[11]
	Latua	hyoscyamine[1]	—
	Salpichroa	hyoscyamine[1]	—
	Trechonaetes	—	sapogenin[3]
11	*Brugmansia*	nicotine, scopolamine[1]	—
	Datura	nicotine, scopolamine[1]	withanolide[3]
12	*Solandra*	hyoscyamine[1]	—
13	*Nicandra*	tropinone[1]	withanolide[3]
14	*Lycium*	betaine[3]	withanolide[3]
16	*Atropa*	choline,[12] hyoscyamine[7]	—
	Atropanthe	hyoscyamine[1]	—
	Hyoscyamus	choline,[12] hyoscyamine[1]	sapogenin[3]
	Mandragora	hyoscyamine[1]	—
	Physochlaina	physochlaine[1]	solanidin[3]
	Przewalskia	hyoscyamine[1]	—
	Scopolia	choline,[12] hyoscyamine[1]	solanidin[3]
	Whitleya	choline,[12] hyoscyamine[1]	—

† Ursolic acids present.[14]

[1] Romeike, 1978; [2] Gibbs, 1974; [3] Hegnauer, 1973; [4] Lorenti et al., 1981; [5] Evans, 1979; [6] San Martin et al., 1980; [7] Paris & Moyse, 1971; [8] Evans & Somanabandhu, 1980; [9] Antoun et al., 1981; [10] Evans & Ramsey, 1981; [11] D'Arcy, 1979; [12] Gessner, 1977; [13] Evans & Ramsey, 1983; [14] El Imam & Evans, 1984; [15] Buschi & Pomilio, 1986; [16] Lloyd et al., 1985; [17] Faini et al., 1980.

considers the chemosyndrome of the Solanaceae, has reference to the cross-sectional presentation of Dahlgren (1975, 1980), and draws upon the systematic data of D'Arcy (1979), Haegi (1979, 1981), and Hunziker (1979).

The surface dimensions of the four subfamilies correspond to the number of included genera, while the curves involving the subfamilies label the affinity points of the homologous chemical qualities. The two main trends of alkaloid synthesis in the family—accumulation of nicotine-isopelletierine or hygrine-tropane type alkaloids—branch from the horizontal axis; the inclined axis separates the steroidal lactone and steroidal alkaloid taxa. Tribes of the subfamilies are shown by numbers and dotted lines. I have divided the tribe Solaneae Reichb. into subtribes Solaninae (Solanineae Dunal) and Physalinae (Physalidineae Reichb.) on the basis of different and exclusive types of steroid synthesis and considering the data of Baehni (1946) and others. *Acnistus* and *Dunalia* are placed in tribe Jaboroseae Miers in accordance with Baehni on the basis of their steroidal lactone content. *Latua* was similarly treated—its bent embryo agrees with this placement and its alkaloid chemistry precludes assigning it to subfamily Cestroideae.

The characteristic alkaloid or steroidal data for the genera shown in Figure 3 are also shown in Table 3. I have not found reliable recent data on the alkaloid or steroid active ingredient of four tribes and 43 genera; however, I feel justified in presenting this review, a novel chemotaxonomic evaluation of facts known to others, and a classification system for the Solanaceae.

This new system consists of four subfamilies. We must separate the Anthocercidoideae from the Cestroideae, and the Atropoideae from the Solanoideae because of differences in area of origin, morphology, flowers, and chemistry. The Anthocercidoideae have ancestral characteristics and are endemic to Australia. They differ morphologically from the Cestroideae by having long, narrow corolla lobes, finely striated corolla tubes, and distinctive sculptured pollen grains. Their chemosyndrome combines predominantly hygrine derivatives—characteristically scopolamine—with neutral sapogenins, while the Cestroideae have chiefly nicotine derivatives together with simple and complex steroidal alkaloids, and only one tropane ester alkaloid in common with the Anthocercidoideae.

The Atropoideae, which have a distinctive alkaloid-tropane ester synthesis relationship, differ also in having dispersed from their ancestral center. They are adapted to withstand cold seasons in Eurasia and have become isolated on islands or high mountains in Africa. The Atropoideae differ morphologically from the Solanoideae by having imbricate corolla lobes, whereas Solanoideae have valvate—sometimes twofold valvate—aestivation. The Atropoideae chemosyndrome combines highly derived tropane ester alkaloids with steroidal alkaloids, while the Solanoideae possess one of these biosyntheses but have the other only in inhibited form as simple tropanes or as steroidal lactones. These evolutionary patterns are sufficient to warrant recognition of the taxa as subfamilies.

Subfamily ANTHOCERCIDOIDEAE Tétényi, subfam. nov.

Plantae frutescentes caulibus lignosis in Australia habitantes. Aestivatio valvato-aperta. Corolla regulariter quinquelobata. Lobi involuti, prope nervum medianum strigillati, tubo longiores vel breviores sed numquam aequilongiores. Stamina epipetala in tubo profundae didynama vel aequaliter longa. Antherae extrorsae longitudinaliter dehiscentes. Fructus capsulares aut baccatus. Embryo parum curvus. Plantae praecipue alcaloidam "Scopolamin" et steroid-saponinem continentes.

Woody shrubs inhabiting Australia. Corolla with rolled, inflexed-valvate aestivation of the 5 lobes, these striated along main veins, varying in length but never as long as the tube. Stamens didynamous or equal, epipetalous low in corolla tube, the anthers dehiscing extrorsely by longitudinal slits. Fruit capsular or baccate. Embryo only slightly curved. Plants containing predominantly the alkaloid scopolamine and steroid saponins. Type: *Anthocercis* Labill.

Subfamily ATROPOIDEAE Tétényi, subfam. nov.

Plantae ex orbe antiquo oriundae. Herbae locis calidis excepto occurentes, aut plantae lignosae endemicae regionis montium excelsium vel insularum. Corolla tubulosa vel campanulata. Lobi corollae aestivatione imbricati. Stamina quinque aequalia. Fructus baccatus vel capsularis. Embryo circuliter vel spiraliter curvatus. Plantae praecipue alcaloidam "Hyoscyamin" et steroidalcaloidam continentes.

Herbaceous plants of the Old World, occurring exceptionally as endemic woody shrubs on mountains or islands in warmer regions. Corolla tubular or campanulate, the aestivation of lobes imbricate. Stamens 5, equal. Fruit baccate or capsular. Embryo curved circularly or in a spiral.

Plants containing predominantly the alkaloid hyoscyamine and steroidal alkaloids. Type: *Atropa* L.

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FLORA OF THE VENEZUELAN GUAYANA—III[1]

JULIAN A. STEYERMARK[2]

ABSTRACT

Continued studies of various families of the flora of the Venezuelan Guayana have resulted in the following new taxa: *Stegolepis albiflora, S. huberi, S. humilis* (Rapateaceae); *Panopsis cuaensis, P. parimensis, Roupala paruensis* (Proteaceae); *Guapira amacurensis, G. ayacuchae, G. bolivarensis, G. davidsei, G. glabriflora, G. marcano-bertii, G. sancarlosiana, G. sipapoana, Neea amaruayensis, N. bernardii, N. bracteosa, N. brevipedunculata, N. cedenensis, N. clarkii, N. davidsei, N. guaiquinimae, N. huachamacarae, N. ignicola, N. liesneri, N. mapourioides, N. marahuacae, N. parimensis, N. robusta, N. sebastianii, N. subglabrata, N. tepuiensis* (Nyctaginaceae); *Brunellia neblinensis* (Brunelliaceae); *Matayba ptariana* subsp. *guaiquinimae* (Sapindaceae); *Catostemma clarkii, C. ebracteolata, C. hirsutula, C. marahuacensis, C. pubistyla, C. sancarlosiana, Scleronema neblinensis* (Bombacaceae); *Bonnetia bolivarensis, B. euryanthera, B. guaiquinimae, B. ptariensis, B. tristyla* subsp. *nervosa, Laplacea fruticosa* var. *chimantae* (Theaceae); *Daphnopsis guaiquinimae, D. nevlingiana, Schoenobiblus amazonica* (Thymeleaceae); *Symplocos acananensis* (Symplocaceae); *Chomelia glabricalyx, Coccocypselum huberi,* and *Perama dichotoma* var. *monocephala* (Rubiaceae), a total of 50 species, 3 subspecies, and 1 variety. Keys are provided for the Venezuelan Guayanan species of Proteaceae, *Guapira, Neea, Catostemma, Symplocos,* and newly described taxa of *Bonnetia.*

RAPATEACEAE

STEGOLEPIS

Stegolepis albiflora Steyermark, sp. nov. TYPE: Venezuela. Bolívar: Meseta de Jaua; Cerro Sarisariñama, northeastern part, 4°41′40″N, 64°13′20″W, 1,410 m, 10 Feb. 1974, *Steyermark et al. 108873* (holotype, VEN; isotype, NY).

Herbae perennes usque 1.5 m; vaginis prope apicem manifeste tenuiterque multinervatis eligulatis; pedunculis 7–18 axillaribus 4.5–7 dm longis 0.8–1.5 mm diam.; capitulis globosis 1.8–2.5 cm diam., spiculis 6–14 maturis lanceolatis acutis 7–10 mm longis 2–3 mm latis; petalis albidis.

Herbaceous perennials up to 1.5 m tall. Sheaths eligulate, finely and many-nerved near the apex or along one side, 20–25 cm long, 4–6 cm wide. Leaf blades rich green both sides, 58–70 cm long, 3.5–5 cm wide, the nerves and midrib on lower side somewhat more prominent than on upper side. Peduncles numerous, 7–18, 45–70 cm long, 0.8–1.5 mm diam., many-sulcate. Heads globose, tan or tawny, 1.8–2.5 cm diam. Spikelets spreading in various directions, lanceolate, acute, 7–10 mm long, 2–3 mm wide. Bracteoles 14–15, graduate, the lower outer ones ovate-suborbicular, 2–2.5 × 2–2.5 mm, the middle ones obtuse, the upper ovate-lanceolate, obtuse to subacute, 7 × 4 mm. Sepals lanceolate, subacute, 6–7 mm long, 2.5–3 mm wide. Petals white, oblanceolate or lanceolate, acute, recurved, 5.5–7 mm long, 1.5–2 mm wide toward the middle. Anthers linear, 3.5 × 0.4 mm. Ovary depressed-globose, 1 mm high. Style 1 mm long. Seeds buff, barrel-shaped, rounded at both ends, 1.5 × 1 mm.

Paratypes. VENEZUELA. BOLÍVAR: Cerro Sarisariñama, summit, W-central part, 4°45′N, 64°26′W, 1,922–2,100 m, 22–27 Feb. 1967, *Steyermark 97839* (VEN); Meseta de Jaua, Cerro Jaua, summit, SW part, gallery forest, tributary of Río Marajano 4°48′50″N, 64°34′10″W, 1,750–1,800 m, 22–28 Feb. 1974, *Steyermark, Carreño & Brewer-Carias 109391* (VEN); Meseta de Jaua, Cerro Jaua, summit, SW part, 4°47′22″N, 64°33′35″W, 2,228–2,250 m, 27 Feb. 1974, *Steyermark, Carreño & Brewer-Carias 109581* (VEN); Meseta de Jaua, Cerro Jaua, summit, E-central part, 4°35′N, 64°15′W, 14 Feb. 1981, *Steyermark, Brewer-Carias & Liesner 124320* (VEN), *124321* (VEN); trail to Sima menor, Cerro Sarisariñama, *Ravelo 17* (MY).

This species is remarkable for having white petals and is the only white-flowered member of the otherwise yellow-petaled genus *Stegolepis.* Maguire (1976) identified all the collections from the Meseta Jaua (Cerro Jaua and Cerro Sarisariñama) as *S. choripetala,* a species originally described from Cerro Sipapo and not known elsewhere. The new taxon differs from *S. choripetala* not only in the white petals, but also in the smaller mature spikes, the greater number of more slender, shorter peduncles, and in the finely nerved sheath in the apical portion.

The collections cited were obtained from various parts of the huge Meseta de Jaua, indicating that the species is well distributed over the whole

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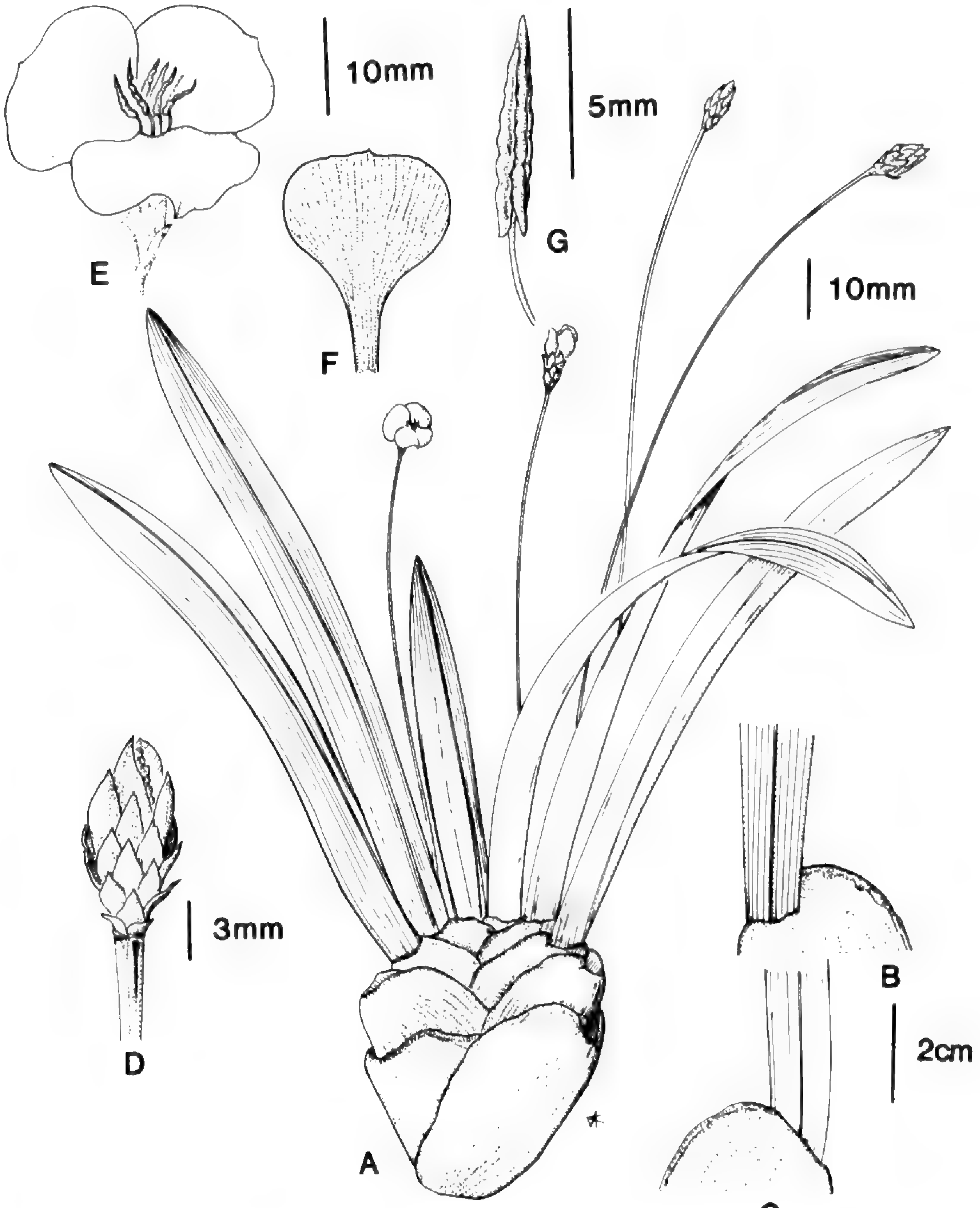

FIGURE 1. *Stegolepis humilis.* — A. Habit. — B, C. Base of leaf with auricle of sheath. — D. Spikelet. — E. Flower, natural position. — F. Petal. — G. Stamen. Based on holotype.

summit and is autochthonous to that table mountain.

Stegolepis huberi Steyermark, sp. nov. TYPE: Venezuela. Bolívar: Kukenán tepui, 5°16'N, 60°48'W, 2,500 m, 28 Apr. 1984, *Otto Huber 9467* (holotype, VEN; isotype, MO).

Herbae perennes humiles 23–35 cm; vaginis 7–10 cm longis 3–3.5 cm latis omnino nervatis ligulatis, auriculis apice rotundatis 10–15 mm longis 17–22 mm latis; laminis coriaceis ligulato-lanceolatis acutis 15–20 cm longis 1.8–2.5 cm latis, costa media haud manifesta subtus tenuiter multinervatis supra nervis obsoletis; pedunculis 17–25 cm longis 2–3.5 mm latis infra capitulum 4–7 mm dilatatis; capitulis compressis 4–6-floris 2–3.5 cm latis; spiculis elliptico-lanceolatis sub fructu 15–18 mm longis; bracteolis oblongo-lanceolatis vel lanceolatis acutis vel acuminatis 4–10 mm longis 1.1–3 mm latis; petalis flabellato-rhomboideis 10 mm longis 7–8 mm latis.

Dwarf perennials 23–35 cm tall. Sheaths membranous, subscarious, 7–10 cm long, 3–3.5 cm wide, venose throughout, the auricles rounded at apex, 10–15 mm long, 17–22 mm wide. Leaf blades coriaceous, ligulate-lanceolate, 15–20 cm long, 1.8–2.5 cm wide, acute, finely nerved on lower side, obsoletely nerved on upper side, the midrib obsolete on both sides. Peduncles compressed, somewhat alate, 3–6-costate, 17–25 cm long, 2–3.5 mm wide except 4–7 mm where dilated below inflorescence. Heads compressed, 4–

6-flowered, 2–3.5 cm wide, 1–1.7 cm high. Spikelets (in fruit) elliptic-lanceolate, 15–18 mm long, 5-seriate. Bracteoles 18–24, oblong-lanceolate or lanceolate, acute to acuminate, lower ones 4–5 mm long, 1.1–1.2 mm wide, the others 7–10 mm long, 2–3 mm wide. Sepals (in fruit) oblanceolate, acute, 13 mm long, 5 mm wide. Petals flabellate-rhomboid, 10 mm long, 7–8 mm wide.

This species is the shortest known in the genus. All the plants seen (Huber, pers. comm.) in a large colony were similarly small. The member of the genus to which it shows closest affinity is *S. ptaritepuiensis* Steyerm., from which it differs in the shorter peduncles and leaves, membranous, striate-nerved sheaths, smaller heads with shorter spikelets, less numerous spikelets, midrib not perceptible on either side, and a longer auricle of the sheath.

Stegolepis humilis Steyermark, sp. nov. TYPE: Venezuela. Bolívar: Camarcaibarai tepui, SW-facing shoulder, 5°52′N, 62°1′W, 1,800–1,825 m, 22–24 May 1986, *Julian A. Steyermark, R. Liesner & B. Holst 132006* (holotype, MO; isotype, VEN). Figure 1.

Herbae perennes humiles 27–52 cm, vaginis manifeste nervatis 12 cm longis ligulatis, auriculis apice rotundatis 5–7 mm longis; laminis linearibus apice acutis 27–45 cm longis 1.3–2.5 cm latis, costa media subtus prominenti, nervis subtus prominentibus supra subtiliter prominentibus; pedunculis 2–3, 5-costatis, 27–52 cm longis, 1–1.5 mm diam. infra capitulum compressis 4–5 mm latis dilatatis; capitulis plerumque 1-floris, interdum 2-floris, compressis; spiculis lanceolatis 15–18 mm longis 7–9 mm latis; bracteolis castaneis infimis suborbiculari-ovatis late acutis 4.5–6 mm longis basi 4–5 mm latis, superioribus lanceolatis acuminatis 12 mm longis basi 5 mm latis; sepalis late lanceolatis acutis 15 mm longis 5–6 mm latis; petalis late flabellatis apice subtruncato-rotundatis 12–13 mm longis 18 mm latis.

Dwarf perennials 27–52 cm tall, the caudex flattened, 11–12 cm long, 7–9 cm wide. Leaf sheaths conduplicate, firmly membranous, conspicuously nerved, 12 cm long, 7 cm wide, ligulate, the auricles rounded, these 5–7 mm long, 12–13 mm wide. Leaf blades silvery green below, linear, symmetrical to slightly subfalcate at the acute apex, 27–45 cm long, 1.3–2.5 cm wide, finely nerved above, prominently nerved below, midrib prominent below, 1 mm wide. Peduncles 2–3, 5-costate with rounded ribs, 27–52 cm long, 1–1.5 mm diam. except below the inflorescence where flattened and dilated to 4–5 mm wide. Heads mainly 1, sometimes 2, compressed. Spikelets lanceolate, fusiform, 15–18 mm long, 7–9 mm wide. Bracteoles dark mahogany or chestnut brown, indurated, 19–21, the lowest suborbicular-ovate, broadly acute, 4.5–6 mm long, 4–5 mm wide at base, the upper ones lanceolate, acuminate, 12 mm long, 5 mm wide at base. Sepals broadly lanceolate, indurated above the middle, sharply slenderly acute, 15 mm long, 5–6 mm wide. Petals with a broadly rhombic-flabellate blade, broadly subtruncate-rounded at apex with a mucronate center, 12–13 mm long, 18 mm wide, unguiculate 11 mm. Anthers 10 mm long; filaments 9.5 mm long. Style subulate, 12 mm long.

Paratypes. VENEZUELA. BOLÍVAR: Murisipán tepui, summit, 5°52′N, 62°3′W, 2,350 m, 26 May 1986, *Holst, Steyermark & Liesner 2921* (MO, VEN); Tereke-yurén tepui, summit, west edge, 5°52′N, 62°2′W, 2,135 m, 26 May 1986, *Liesner, Steyermark & Holst 21075* (MO, VEN).

This taxon is related to *Stegolepis terramarensis* Steyerm. from Cerro Marahuaca, from which it differs in the solitary, or rarely two spikes, acute leaf apex, fewer and more slender peduncles, smaller size, shorter auricles of the nerved, nonindurated ligulate sheath, and more conspicuous midrib and secondary nerves. It differs from the other species with one to few spikelets in size and details of spikelets, bracteoles, leaf nervation, and peduncle.

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PROTEACEAE

PANOPSIS

KEY TO THE SPECIES OF *PANOPSIS*

1a. Leaves sessile or subsessile; reticulation coarsely areolate with areoles 1–5 mm diam.; leaves crowded on the stem, pseudoverticillate; fruit subglobose, 4–5 cm diam. .... *P. sessilifolia*

1b. Leaves petiolate; reticulation generally more minutely areolate with areoles 0.5–1 mm diam.; leaves

scattered on the stem, not pseudoverticillate; fruit fusiform or longer than broad or less than 4 cm in diam. 2
- 2a. Stems, leaf blades, and petioles glabrous or essentially so 3
  - 3a. Leaves abruptly acuminate-cuspidate at apex, 8.5–11.5 cm long; reticulation minute and impressed on both sides; inflorescence 15–17 cm long with axes 0.7–1 cm; below 150 m elev., Terr. Fed. Amazonas ..... *P. cuaensis*
  - 3b. Leaves rounded at apex, 3.5–6 cm long; reticulation elevated and manifest on both sides; inflorescence with a maximum length of 6.5 cm with axes 2–3 cm long; plants at elev. of 1,400–1,600 m, Gran Sabana, Edo. Bolívar ..... *P. ptariana*
- 2b. Young stems, portions of the leaf blades, and petioles pubescent 4
  - 4a. Leaves mainly 8–20 cm long, 3–7 cm wide; inflorescence 15–20 cm long; plants of 125–450 m elev. ..... *P. rubescens*
  - 4b. Leaves 2–15 cm long, 2.5–4 cm wide; inflorescence 5–8 cm long; plants of 1,150–2,250 m elev. 5
    - 5a. Trees 19–22 m tall; leaves 8–15 cm long ..... *P. tepuiana*
    - 5b. Small shrubs 1–1.5 m tall; leaves 2–9 cm long 6
      - 6a. Flowers sessile to 2 mm pedicellate; style glabrous; reticulation of lower leaf surface with larger areoles than on upper surface, subelevated on upper surface; leaves 4.5–9 cm long; plants of the Sierra Parima, Terr. Fed. Amazonas ..... *P. parimensis*
      - 6b. Flowers on pedicels 2.5–7 mm long; style strigillose below the middle and toward the base; reticulation subelevated on lower surface, scarcely evident or obscure on upper surface; leaves 2–7 cm long; plants of sandstone table mountains of eastern Edo. Bolívar ..... *P. ornatinervia*

Panopsis cuaensis Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Río Cuao, Río Orinoco, 125 m, 17 Jan. 1949. *Bassett Maguire & Louis Politi 28409* (holotype, NY).

Arbuscula, ramis glabris; foliis petiolatis, petiolis 5–8 mm longis glabris, laminis discoloribus subtus marronino-brunneis oblongo-ellipticis apice acuminatis vel subcuspidatis basi subacutis vel subobtusis 8.5–11.5 cm longis 3–4 cm latis ubique glabris, nervis lateralibus vix manifestis utroque latere 9, venulis tertiariis ubique tenuiter minuteque subimpresso-reticulatis; floribus non visis; infructescentiae rhachidi terminali 15–17 cm longa adpresso-pubescenti pilis pallidis instructa, axibus tribus vel quattuor 7–10 mm longis; fructu fusiformi extremitatibus rotundatis 2.2–2.5 cm longo 1 cm lato dense brunneo-velutino.

Small tree with glabrous branches. Petioles 5–8 mm long; leaf blades discolored, dull olive green above, maroon brown beneath, oblong-elliptic, abruptly acuminate or subcuspidate at apex, subacute to subobtuse at base, 8.5–11.5 cm long, 3–4 cm wide, glabrous both sides; lateral nerves scarcely evident, ca. 9 each side, divaricate at approximately 10–15°, these and tertiary venation immersed, the tertiary venation finely and minutely reticulate-subimpressed, the midrib elevated below, shallowly depressed above. Flowers not seen. Fruiting rachis terminal, 15–17 cm long, the 3–4 lateral axes 7–10 mm long, the rachis and axes pale appressed-pubescent. Fruit fusiform, rounded at both ends, 2.2–2.5 cm long, 1 cm wide, densely brown velutinous.

This species differs from *Panopsis rubescens* (Pohl) Pittier in its completely glabrous leaves which terminate abruptly in a shortly acuminate or cuspidate apex, fewer and less distinct lateral foliar nerves, glabrous stems, and smaller, shorter fruits rounded at each end.

Panopsis parimensis Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Departamento Atabapo, helechales y formaciones secundarias en la Sierra Parima, 25 km NNE de Parima "B," cabeceras del Río Ocamo, 3°3′N, 64°13′W, 1,150 m, 12 Jun. 1981, *Otto Huber 6136* (holotype, VEN; isotypes, MO, NY).

Frutex 1.5 m, ramis novellis dense ferrugineo-tomentellis; foliis petiolatis, petiolis 2–8 mm longis ferrugineo-tomentellis; foliorum laminis elliptico-obovatis vel elliptico-oblongis apice subacute obtusis basi subacutis vel acutis 4.5–9 cm longis 2–4 cm latis supra minute strigosis costa media dense strigillosa, subtus magis dense pubescentibus praesertim costa media pilis adpressis ferrugineis minutis, nervis lateralibus supra manifestis, venulis tertiariis supra subelevatis tenuiter minuteque reticulatis subtus impressis inflorescentia paniculatim ramosa 4–8 cm longa, ramis dense ferrugineo-tomentosis; floribus sessilibus vel pedicellatis usque 2 mm longis; perianthio 4–4.5 mm longo, tepalis extus dense pubescentibus pilis adpressis instructis; stylo 2.3 mm longo glabro.

Shrub, 1.5 m tall; young leafy stems densely ferruginous tomentose; mature branches dark gray, glabrous. Petioles 2–8 mm long, ferruginous tomentose; leaf blades elliptic-obovate or elliptic-oblong, subacute-obtuse at apex, subacute to acute at base, 4.5–9 cm long, 2–4 cm wide, finely strigose above with pale hairs, more densely strigose along upper midrib, more densely appressed below, especially along the midrib, with shorter ferruginous hairs; lateral nerves ca. 9 each side, not prominent but more manifest than the tertiary venation; tertiary venation of upper surface minutely and finely reticulate, subelevated, impressed on lower surface. Inflorescences terminal, paniculate, densely ferruginous tomentose, 4–8 cm long (including the peduncle), 5–7 cm wide, with 4 divaricately spreading branches up to 4 cm long, and 1 mm diam. Peduncle 8 mm long. Bracts subtending the branches of the inflorescence subulate, 4 mm long, densely ferruginous tomentose. Flowers irregularly crowded on the axes, solitary or 2–3-fasciculate, sessile to 2 mm pedicellate. Perianth 4–4.5 mm long, the segments densely appressed pubescent without. Hypogynous disk slightly angulate. Ovary ferruginous setose. Style 2–3 mm long, glabrous.

This species differs from *Panopsis ornatinervia* Steyerm. of eastern Venezuelan Guayana in the upper leaf surface having a minute subelevated reticulation and the lower surface a larger areolation of impressed veinlets. In *P. ornatinervia,* the upper surface has a pebbly rugulose, but not reticulate, pattern, whereas the lower surface has a subelevated and finer reticulation. Moreover, in *P. ornatinervia* the leaves are rounded at the apex, whereas those of *P. parimensis* are subacutely obtuse and usually larger. Finally, the flowers of *P. parimensis* have shorter pedicels than those of *P. ornatinervia* and have a glabrous style.

ROUPALA

KEY TO SPECIES OF *ROUPALA*

1a. Dwarf shrub less than 2 m tall; leaves 1.3–3 cm long, 0.7–2.5 cm wide; petioles 1–2 mm long; ovary glabrous .... *R. minima*

1b. Shrub or tree 3–20 m tall; leaves 3.5–17 cm long, (2–)2.5–10 cm wide; petioles 10–50 mm long; ovary pubescent 2

2a. Leaves rounded or obtuse at apex 3

3a. Pedicels and rachis of inflorescence glabrous; leaves glabrous below 4

4a. Petioles 3–5 mm long; leaf blades 3.5–7.5 cm long, obtuse at base .... *R. paruensis*

4b. Petioles 12–15(–30) mm long; leaf blades (5–)7–11(–17) cm long, acute at base .... *R. obtusata*

3b. Pedicels tomentose or furfuraceous-puberulent; rachis minutely ferruginous puberulent or castaneous-furfuraceous or puberulent; leaves minutely puberulent or furfuraceous 5

5a. Perianth 7–9 mm long; ovary hirsutulous; leaf blades elliptic or ovate-oblong, obtuse at the base, 2.5–7 cm wide .... *R. sororopana*

5b. Perianth 12–13 mm long; ovary shortly appressed-pubescent; leaf blades ovate to suborbicular-ovate, truncate or broadly rounded at base, 7.5–10 cm wide .... *R. chimantensis*

2b. Leaves acute to acuminate at apex 6

6a. Stems, petioles, and lower surface of leaf blades glabrous or glabrescent; perianth strigillose to glabrescent toward apex .... *R. montana*

6b. Stems, petioles, and lower surface of leaf blades manifestly pubescent; perianth tomentellose to villous 7

7a. Perianth densely pale brown and villous with spreading hairs; rachis of inflorescence brown tomentose; fruit minutely tomentose .... *R. griotii*

7b. Perianth tomentose; rachis of inflorescence yellow tomentose; fruit glabrous .... *R. suaveolens*

Roupala paruensis Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Cerro Parú, cumbre, south to southeast to edge descent to tributary of Caño Asisa, rocky sabanita, open Río Ventuari, 2,000 m, 10 Feb. 1951, *R. S. Cowan & John J. Wurdack 31378* (holotype, NY).

Arbor 7 m, ramis glabris; foliis petiolatis, petiolis 3–5 mm longis glabris, laminis ovato-oblongis apice obtusis vel rotundatis basi obtusis 3.5–7.5 cm longis 2–3.8(–4) cm latis ubique glabris; nervis lateralibus supra haud manifestis vel obsoletis subtus subimpressis vel subelevatis utroque latere 4–5; floribus non visis; infructescentia 18 cm longa glabra, pedicellis fructiferis 2–4 mm longis glabris; fructu oblique obovoideo 1.5–2.5 cm longo 1–1.2 cm lato glabro; seminibus ovatis extremitatibus rotundatis 1.2–1.4 cm longis 0.8–1 cm latis.

Tree 7 m, with glabrous branches. Petioles 3–5 mm long, glabrous; leaf blades alternate, coriaceous, ovate-oblong, obtuse or rounded at apex, obtuse at base, 3.5–7.5 cm long, 2–3.8(–4) cm wide, glabrous both sides, narrowly subrevolute, lateral nerves 4–5 each side, obscure or obsolete above, subimpressed or subelevated below. Inflorescence 18 cm long, rachis glabrous; pedicels 2–4 mm long, glabrous. Fruit obliquely obovoid, 1.5–2.5 cm long, 1–1.2 cm wide, glabrous; seeds brown, ovate, rounded at each end, 1.2–1.4 cm long, 0.8–1 cm wide.

This species is readily distinguished from *Roupala obtusata* Kl., its closest relative, by the smaller, basally obtuse leaf blades with shorter petioles.

NYCTAGINACEAE

The genera *Guapira* and *Neea* are represented in the Venezuelan Guayana by a large number of taxa. Schmidt (1872) treated the known species of these genera at that time as they occurred in Brazil, *Guapira* then included within the genus *Pisonia*. Later, Heimerl (1896) published additions for an account of the West Indian taxa and (1897, 1914, 1932) described various new species from tropical America. Huber (1909) also described several species of these genera from Amazonian Brazil. Standley (1931) took up the family for northwestern South America, recognizing the genus *Torrubia* of Vellozo with a dozen species previously assigned to *Pisonia*. Lundell (1968) transferred the taxa formerly assigned to *Torrubia*, as well as some others which had been placed under *Pisonia*, to the genus *Guapira* Aublet (1775), an earlier legitimate name. Little (1968) transferred eight additional species from *Torrubia* to *Guapira*.

Unfortunately, there has been no recent study published for the taxa occurring in the Venezuelan Guayana. During the many years that have elapsed since the publication of works by Schmidt, Heimerl, and Standley, many unnamed or misidentified collections have accumulated in herbaria. A large number of the taxa represented by these collections are readily separated, while others appear to be closely related and differentiated on characters relating to indument, peduncles, leaf shape, size, venation, branching of inflorescence, and cauliflory. In some cases it is difficult to be certain of the generic distinction where only pistillate flowers are present. In general, however, *Guapira* and *Neea* may be separated using staminate material. Yet Burger (1983) suggested that the two genera may have to be united under *Guapira*. Further studies will be necessary to judge the merits of generic separation.

The present study of the taxa of the Venezuelan Guayana has resulted in the following 26 new taxa, with keys provided for the species of *Guapira* and *Neea*.

GUAPIRA

KEY TO THE SPECIES OF *GUAPIRA* OF THE VENEZUELAN GUAYANA

1a. Leaves 1–4 cm long, 0.8–1.8 cm wide, rounded or manifestly obtuse at apex .... *G. microphylla*
1b. Leaves larger than 4 cm long and 1.8 cm wide, mainly acute to acuminate at apex, or, if rounded or obtuse, the leaves larger 2
  2a. Leaves 25–30 cm long, 15 cm wide .... *G. sipapoana*
  2b. Leaves 5–15 cm long, 2–15 cm wide 3
    3a. Lower and/or upper surface of leaves, or lower midrib, pilosulous with lax, spreading, or divaricate hairs 4
      4a. Upper leaf surface glabrous and shining; inflorescence subglobose or subhemispheric, densely flowered and congested .... *G. davidsei*
      4b. Upper leaf surface, or at least upper midrib, pubescent, and not shining; inflorescence cymosely or widely spreading 5
        5a. Petiole 0.5 cm or less long; peduncle 1.5–2.5 cm long .... *G. pubescens*
        5b. Petiole 1–2 cm long; peduncle (1–)3–9.5 cm long 6
          6a. Peduncle 7–9.5 cm long; petiole densely pubescent with spreading hairs 0.2–0.5 mm long; young stems densely pubescent with spreading hairs 0.2–0.5 mm long .... *G. marcano-bertii*
          6b. Peduncle (1–)3.5–5 cm long; petiole and young stems with hairs less than 0.1 mm long .... *G. rusbyana*
    3b. Lower surface of leaves, including midrib, glabrous or pubescent, but the indument not spreading or divaricate 7
      7a. Lower surface of leaves glabrous or essentially so, the midrib or nerves with scattered microscopic tomentum 8
        8a. Peduncle and petiole densely ferruginous tomentose .... *G. amacurensis*
        8b. Peduncle and petiole glabrous or sparsely pubescent 9
          9a. Peduncle and/or axes of inflorescence sparsely to moderately puberulent 10
            10a. Leaves often broadest above the middle, conspicuously venose; lateral

nerves conspicuous, 9–11 each side, subelevated or impressed on both sides, conspicuously anastomosing with the tertiary veinlets, ascending at an angle of 45° or more; tertiary veinlets forming a prominent network .... *G. fragrans*

10b. Leaves often broadest near the middle, not venose, opaque; lateral nerves inconspicuous, 5–6 each side, impressed, divaricately spreading at an angle of 15–30°; tertiary veinlets obsolete or inconspicuous .... *G. guianensis*

9b. Peduncle and/or axes of inflorescence glabrous 11

11a. Tertiary veinlets prominent and finely reticulate on both sides of leaf blades; eastern Edo. Bolívar .... *G. bolivarensis*

11b. Tertiary veinlets, if present, inconspicuous and subreticulate; southwestern Terr. Fed. Amazonas 12

12a. Leaves oblanceolate to elliptic-lanceolate; staminate perianth cylindric-tubular, 1.8–2 mm wide; stamens 8 .... *G. glabriflora*

12b. Leaves ovate or elliptic-ovate; staminate perianth subinfundibuliform, 3.2 mm wide; stamens 10 .... *G. neblinensis*

7b. Lower surface of leaves, midrib, or nerves with a minute tomentum of nonspreading hairs 13

13a. Tertiary venation on upper and lower leaf surface very conspicuous or elevated .... *G. sancarlosiana*

13b. Tertiary venation either not evident, inconspicuous, or not elevated 14

14a. Principal lateral nerves 8–10 each side; lower leaf surface usually with a persistent rufous tomentum; leaves on fertile branches generally cuspidate at apex; dry fruit 6–7.5 mm long, 3–4 mm wide .... *G. cuspidata*

14b. Principal lateral nerves 6–7 each side; lower leaf surface glabrous except for the sparsely rufous midrib and sometimes sparsely tomentose or glabrescent secondary nerves; leaves on fertile branches rounded, subtruncate, or abruptly shortly acute at apex; dry fruit 8–9 mm long, 5–5.5 mm wide .... *G. ayacuchae*

Guapira amacurensis Steyermark, sp. nov. TYPE: Venezuela. Bolívar: bosque pluvial, E of Río Grande, ENE of El Palmar, near limits of Territorio Federal Delta Amacuro, 12 Jan. 1965, *Luis Marcano-Berti 551* (holotype, VEN; isotypes, MO, NY).

Arbor 15–25 m, ramulis dense-ferrugineo-tomentosis; foliis ovatis, elliptico-ovatis vel lanceolato-ellipticis apice acutis vel acuminatis vel obtuse acutis basi cuneatis plerumque inaequilateralibus 6.5–14 cm longus 3–6.3 cm latis in sicco nigrescentibus vel fuscis, costa media subtus sparsim rufo-tomentello, aliter ubique glabris; inflorescentiis dense ferrugineo-tomentellis, pedunculis ferrugineo-tomentosis pilis 0.2–0.5 mm longis laxis munitis; perianthio masculo infundibuliformi 7 mm longo extus dense ferrugineo-tomentoso; staminibus 7, perianthio foemineo tubuloso extus dense ferrugineo-tomentoso.

Tree 15–25 m tall, the younger branches densely ferruginous tomentose. Petioles 1–3.5 cm long, densely ferruginous tomentose; leaf blades turning black or dark brown, coriaceous, elliptic-ovate, lance-elliptic, or ovate, acute, obtusely acute to acuminate at the apex, acute to cuneate at the generally inequilateral base, 6.5–14 cm long, 3–6.3 cm wide, glabrous both sides except the midrib on lower side sparsely rufous tomentellous or glabrous; lateral nerves 6–11 each side, obsolescent above, slightly more evident below. Inflorescence of staminate plant 2–3 cm high, 4–5 cm wide, ferruginous tomentose; peduncle 1.7–4 cm long, 1–1.5 mm wide, not enlarged at junction with the lowest inflorescence axes, the ferruginous hairs somewhat lax. Staminate flowers sessile to 1 mm pedicellate; bracts 0.5–1 mm long, densely ferruginous tomentose. Staminate perianth infundibuliform, 7 mm long, 3 mm wide above; stamens 7, the filaments exserted 3–5 mm beyond the orifice. Pistillate perianth tubular, up to 7 mm long, densely ferruginous tomentellous without.

Paratype. VENEZUELA. BOLÍVAR: Represa Guri, 55 km NE of Ciudad Piar, 7°35′N, 63°7′W, 200–300 m, 4–5 Apr. 1981, *Liesner & Gonzalez 11174.*

This species differs from *Guapira bolivarensis,* described below, in the larger staminate perianth, generally inequilateral leaf base, and the dark brown to blackish leaves upon drying.

Guapira ayacuchae Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Tobogán de la Selva, 35 km S of Puerto Ayacucho, 85 m, 4 May 1977, *Julian A. Steyermark & Otto Huber 113856* (holotype, VEN; isotype, MO).

Arbuscula 3–4 m, foliis late ovatis ramulorum fertilium apice late rotundatis subtruncatis vel breviter abrupteque acutis basi rotundatis truncatis vel cuneatis 5–15 cm longis 4–9 cm latis, supra costa media nervis lateralibusque ferrugineo-pubescentibus aliter glabris vel glabrescentibus subtus costa nervis lateralibusque minus ferrugineo-pubescentibus inter nervos magis glabrescentibus; nervis lateralibus utroque latere 6–7; inflorescentiis arcte rufo-ferrugineo-tomentellis, pedunculo foemineo 5 cm longo masculo 2 cm longo; perianthio masculo infundibuliformi 3.5–4 mm longo extus modice rufo-ferrugineo-tomentello, perianthio foemineo tubuloso 2.5–3 mm longo extus ferrugineo-tomentello; staminibus 5; fructibus in sicco ellipsoideo-oblongis 8–9 × 5–5.5 mm in vivo ovoideis 10 × 9 mm; pedicellis fructiferis 4–5 mm longis.

Small tree 3–4 m tall. Petioles 1–2 cm long; leaf blades membranous, broadly ovate, on the fertile branches broadly rounded or subtruncate to shortly and abruptly acute at apex, rounded, truncate, or cuneate at base, 5–15 cm long, 4–9 cm wide, the upper surface glabrescent or remotely and minutely puberulent, the midrib and lateral nerves rather densely rufous-ferruginous tomentose, the lower surface more glabrescent, here the midrib less densely rufous tomentose and the secondary nerves only sparsely tomentose to glabrescent; lateral nerves 6–7 each side, impressed and inconspicuous above, scarcely elevated below. Staminate inflorescence umbellately 4-branched, the 4 primary axes 8 mm long; peduncle 2 cm long, 0.9–1 mm wide, this and axes of the inflorescence minutely densely rufous-ferruginous tomentellose. Flowers on pedicels 1–1.8 mm long. Staminate perianth infundibuliform, 3.5–4 mm long, 2–3 mm wide at summit, moderately rufous-ferruginous without. Stamens 5, filaments 6–7 mm long, exserted 2–3 mm. Pistillate inflorescence umbellately 4-branched, the primary axes 10–12 mm long, 1 mm wide; peduncle 5 cm long, this and the axes of the inflorescence closely rufous-ferruginous tomentellose. Flowers on pedicels 1–2 mm long, 4–5 mm long in fruit. Pistillate perianth tubular, 2.5–3 mm long, 1–1.5 mm wide, ferruginous tomentellous without. Fruiting primary axes 1–2.5 cm long, 1–1.5 mm wide, the secondary axes 8–17 mm long. Anthocarp black, broadly ellipsoid-oblong in dried state, ovoid in living state, subsulcate, glabrous, 8–9 mm long, 5–5.5 mm broad in dried state, when fresh 10 mm long, 9 mm wide.

Paratypes. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: alrededores del aeropuerto Puerto Ayacucho, 120 m, *Morillo 3142* (VEN); Tobogán de la Selva, 5°22′N, 67°33′W, 150 m, 14 May 1980, *Steyermark, Davidse & Guanchez 122545* (MO, VEN); 6 km N of Puerto Ayacucho toward El Burro, *Plowman 13752* (F, MO); Estación de Piscicultura, Puerto Ayacucho, 5°37′N, 67°36′W, 75 m, *Huber 618, 662* (VEN); Oripopos, 7 km N of Puerto Ayacucho, *Miller 1618* (MO, VEN). COLOMBIA. DEPARTAMENTO VICHADA: Casuarito, across from Puerto Ayacucho, 5°40′N, 67°40′W, 100 m, *Gentry & Stein 46330* (MO, VEN).

This species has been confused with *Guapira cuspidata* (Heim.) Lundell of northeastern Venezuela. It differs from that species in the larger, glabrous fruit with longer pedicels, 5 instead of 7 stamens in the staminate flowers, generally rounded to subtruncate or abruptly shortly acute apex of the leaves on the fertile branches, fewer and more distantly separated pairs of lateral nerves on the leaf blades, glabrous or glabrescent lower surface of the leaves between the lateral nerves, more sparsely puberulent upper leaf surface with more conspicuously rufous puberulent midrib and lateral nerves, and fewer ultimate axes of the pistillate infructescences.

Guapira bolivarensis Steyermark, sp. nov. TYPE: Venezuela. Bolívar: Departamento Piar, summit of Amaruay-tepui, south side, eastern half, 5°55′N, 62°13′W, 950–1,100 m, 11 May 1986, *Ronald Liesner & Bruce Holst 20800* (holotype, MO; isotype, VEN).

Arbor 6 m, ramulis sparsim puberulis pilis ferrugineo-glanduliferis munitis; foliis ellipticis vel ovatis apice acutis vel acuminatis basi acutis 6–17 cm longis 3–8 cm latis utrinque glabris, nervis lateralibus utroque 8–10 subhorizontalibus vel ad angulum 10–25° adscendentibus, venulis tertiariis utroque reticulatis; inflorescentia masculina 2–2.5 cm longa 2.5–4 cm lata; pedunculo 4–7.8 cm longo glabro; perianthio masculino anguste infundibuliformi 4 mm longo superne 1.5 mm lato extus quasi glabro; staminibus 10; inflorescentiae foemineae pedunculo 1.8–3.3 cm longo; perianthio foemininео cylindrico 3–3.5 mm longo superne 1.1 mm lato extus glabro.

Tree 6 m tall, the young branches sparsely puberulent with appressed-ascending, ferruginous-glandular trichomes. Leaves alternate or opposite. Petiole 0.7–2 cm long, glabrous to sparsely puberulent; leaf blades elliptic to ovate, acute to acuminate at apex, acute at base, minutely dark-dotted beneath, 6–17 cm long, 3–8 cm wide, glabrous both sides; principal lateral nerves 8–10 each side, irregularly spaced, subhorizontal or ascending at an angle of 10–25°; tertiary venation finely reticulate both sides, the veinlets prominulous. Staminate inflorescence somewhat broader than long, 4-flowered, 2–2.5 cm high, 2.5–4 cm wide, subumbellate to broadly paniculate with 3–8 axes, the lower axes larger, glabrate or sparsely puberulent near the apices; peduncle 4–7.8 cm long, 1–1.3 mm broad, glabrous. Staminate perianth narrowly infundibuliform, 4 mm long, 1.5 mm wide at summit, glabrous without except for a few minute hairs at base. Stamens 10, the filaments unequally exserted up to 4 mm above orifice. Pistillate inflorescence terminal, 3–5 × 3.5 cm, sparsely 3–5-flowered, the 2–3 axes sparsely puberulent; peduncle in anthesis 1.8–3.3 cm long, sparsely puberulent. Pistillate perianth tubular-cylindric, 3–3.5 mm long, 1.1 mm near orifice, glabrous without. Fruiting axes 2.5–5 mm long. Young fruit narrowly fusiform, 11–12 mm long, 3 mm wide at middle.

Paratype. VENEZUELA. BOLÍVAR: Amaruay-tepui, steep slopes on W side, 5°55'N, 62°15'W, 550–800 m, 20 May 1986, *Liesner & Holst 20932* (MO, VEN).

This taxon resembles *Guapira glabra* (Heimerl) Steyerm., comb. nov. (*Pisonia glabra* Heimerl, Kew Bull. 1932: 220. 1932) in the glabrity of the leaves and floral parts, prominently reticulate tertiary venation on both leaf surfaces, and subhorizontal to shallowly ascending lateral nerves but differs in having 10 instead of 8 (rarely 9) stamens, short and narrower staminate perianth, and shorter staminate inflorescence with shorter axes.

Guapira davidsei Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Delta Amacuro: Departamento Tucupita, 5–14 km ESE of Los Castillos de Guayana, 8°28–31'N, 62°17–22'W, 50–200 m, 28 Mar.–2 Apr. 1979, *Gerrit Davidse & Angel González 16382* (holotype, VEN; isotype, MO).

Arbor 8 m, foliis oppositis vel ternatis lanceolato-vel oblongo-ellipticis apice basique acutis 6–12 cm longis 2–5 cm latis supra lucidis glabrisque subtus subadpresso-puberulis costa media pilis patentibus 0.1 mm longis munitis, nervis lateralibus utroque latere 7–9; inflorescentia mascula terminali glomerulata vel subhemisphaerica 8–14 mm alta, 10–14 mm lata, pedunculo 1–2.5 cm longo dense ferrugineo-adpresso-pubescenti; floribus 10–35 sessilibus; perianthio masculo infundibuliformi 4–4.5 mm longo supra medium 2.5–2.7 mm lato extus adpresso-pubescenti pilis glanduliferis mixtis munito.

Tree 8 m tall, the younger branches appressed puberulent, the older ones sparsely so. Leaves opposite or 3 at a node. Petioles 3–10 mm long, densely appressed pale puberulent; leaf blades lance-elliptic or oblong-elliptic, acute at apex, acute at base, 6–12 cm long, 2–5 cm wide, glabrous and shining above, minutely subappressed puberulent below with pale hairs 0.1 mm long, the midrib below elevated, with minute, spreading, slightly rigid hairs; lateral nerves 7–9 each side, inconspicuous, impressed. Staminate inflorescence terminal, densely congested, globose or subhemispheric, 8–14 mm high, 10–14 mm broad, the primary axes suppressed. Peduncles 1–3, 1–2.5 cm long, with densely ferruginous, subappressed hairs. Flowers 10–35, sessile. Bracts lanceolate-oblong, subobtuse or rounded, 1 mm long, densely ferruginous pubescent without. Staminate perianth infundibuliform, 4–4.5 mm long, 2.5–2.7 mm above middle, densely ferruginous appressed-pubescent without, mixed with glandular hairs. Stamens 7–8, exserted 2–2.2 mm beyond orifice.

Guapira davidsei is well marked by the congested globose inflorescence with dense ferruginous pubescence. From *G. ferruginea* (Klotzsch ex Choisy) Lundell it is distinguished by having much larger, acutely pointed leaves and numerous glandular hairs intermixed with the pubescence on the outer surface of the staminate perianth.

Guapira glabriflora Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: between San Carlos and El Solano, Departamento Río Negro, 11–17 Mar. 1979, *Luis Marcano-Berti & P. Salcedo 54-979* (holotype, MER).

Arbuscula, ramulis glabris; petiolis 6–10 mm longis; laminis elliptico-lanceolatis vel oblanceolatis apice obtuse acutis basi cuneatim acutis 6.5–12.5 cm longis 2.5–4.7 cm latis utrinque glabris; nervis lateralibus utroque latere 6–9; inflorescentia mascula 10–15-flora, axibus primariis 2–3, 3–15 mm longis sparsim minuteque ferrugineo-puberulis; pedunculo 1.5–4.5 cm longo glabro vel sparsim ferrugineo-puberulo; floribus sessilibus, perianthio tubuloso-subinfundibuliformi 4.5–5 mm longo (in sicco 2.2 mm) apicem versus 1.8–2 mm lato extus prope basim sparsim ferrugineo-puberulo pilis glanduliferis atque apice dense papillato-puberulo aliter glabro; staminibus 8.

Small tree. Petioles 6–10 mm long, glabrous; leaves opposite, the blades drying fuscous, elliptic-lanceolate to oblanceolate, obtusely acute at apex, cuneately acute at base, 6.5–12.5 cm long, 2.5–4.7 cm wide, glabrous both sides, the lateral nerves 6–9 each side, inconspicuous, impressed. Staminate inflorescence 10–15-flowered, the primary axes 2–3, 3–15 mm long, bearing the flowers directly or with short secondary axes up to 5 mm long bearing a few sessile flowers, the axes minutely and sparsely ferruginous puberulent. Peduncle 1.5–4.5 cm long, glabrous or glabrescent or with sparse ferruginous glandular or nonglandular hairs. Bracts minute, ovate-deltoid, subacute, 0.3–0.4 mm long, puberulent. Perianth tubular, slightly and inconspicuously enlarged above the middle, 4.5–5 mm long (2.2 mm dried), 1.8–2 mm wide at summit, 1 mm wide (0.6 mm dried) in lower ⅓, nearly glabrous without except for a few sparse, ferruginous papillate hairs in basal 1 mm and densely papillate-puberulent apically bordering and between lobes. Stamens 8, the filaments exserted 4 mm beyond orifice.

This species is distinguished by its glabrous leaves and nearly glabrous peduncle and staminate perianth. It differs from *Guapira neblinensis* Mag. & Steyerm. in the narrower oblanceolate to elliptic-lanceolate leaves and narrower staminate perianth.

Guapira marcano-bertii Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Delta Amacuro: east of Río Grande, ENE of El Palmar, near limits of Estado Bolívar, 26 May 1964, *Luis Marcano-Berti 209* (holotype, VEN; isotype, MO).

Arbor, ramulis juvenilibus dense pubescentibus pilis patentibus ferrugineis 0.2–0.5 mm longis munitis; petiolis 1–2 cm longis dense pubescentibus pilis patentibus instructis; laminis late elliptico-ovatis apice breviter abrupteque acutis vel acuminatis 7–12.5 cm longis 3–7 cm latis supra costa media incluso villosis pilis patentibus 0.5–0.7 mm longis instructis subtus dense villosis, nervis lateralibus utroque latere 5–8 inconspicuis; infructescencia subumbellata vel subpaniculata, axibus principalibus 2–4, 12–20 mm longis 1.5 mm diam.; pedunculo fructifero 7–9.5 cm longo 2–2.5 mm lato dense tomentoso pilis patentibus 0.2–0.4 mm longis munito; anthocarpio anguste ellipsoideo 9–10 mm longo 3.5–4 mm lato sparsim puberulo 10-costato.

Tree with young stems densely villosulous with spreading ferruginous hairs 0.2–0.5 mm long. Petiole 1–2 cm long, densely ferruginous villosulous with spreading hairs 0.2–0.5 mm long; leaf blades membranous, broadly elliptic-ovate, shortly and abruptly acute to short acuminate at apex, obtuse to acute at base, 7–12.5 cm long, 3–7 cm wide, the midrib above with spreading villous hairs 0.5–0.7 mm long, the upper surface elsewhere with shorter and longer pale hairs 0.5–0.7 mm long, the lower surface densely soft-villosulous with crisp hairs 0.5 mm or more long, the midrib with divaricate hairs up to 1 mm long. Infructescence subumbellate to irregularly paniculately branched, the 2–4 primary axes 12–20 mm long, 1.5 mm diam., densely ferruginous villosulous with spreading hairs to 0.2 mm long. Fruiting peduncle 7–9.5 cm long, 2–2.5 mm diam., densely villosulous with spreading hairs 0.2–0.4 mm long. Fruiting bracts lanceolate, subacute or obtuse, densely tomentose without. Fruiting pedicels 1–3 mm long. Anthocarps narrowly ellipsoid, 9–10 mm long, 3.5–4 mm wide, sparsely puberulent, longitudinally 10-costate.

This taxon differs from *Guapira pubescens* (HBK) Lundell in the much longer petioles and the longer and more abundant pubescence on all parts. From *G. cuspidata* (Heim.) Lundell it differs in the longer peduncles, longer fruits, and the longer spreading pubescence throughout.

Guapira sancarlosiana Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: 4.3 km NNE from San Carlos on Solano Road, IVIC study site, 1°56′N, 67°3′W, 119 m, 8 Jan. 1981, *H. L. Clark & Pedro Maquirino 7794* (holotype, MO). Figure 2.

Arbor 7–12 m, ramulis juvenilibus dense adpresseque rufo-ferrugineo-tomentosis; foliorum laminis coriaceis supra glaucis glabrisque vel modice strigillosis subtus arcte rufo-tomentosis pilis dense adpressis omnino obtectis ovato-ellipticis vel sublanceolato-ellipticis apice breviter abrupteque acutis vel breviter acuminatis interdum rotundatis basi cuneatim acutis 7.5–14.5 cm longis 4.5–7.5 cm latis; nervis lateralibus utroque latere 9–11 subtus elevatis, venulis tertiariis supra subtiliter conspicueque elevatis reticulatis subtus magis grosse reticulatis; petiolis 1.5–3.5 cm longis dense adpresso-rufo-tomentosis; inflorescentia mascula paniculata multiflora 1.5–3.5 cm alta 3–7 cm lata, ramosissima, axibus primariis 0.8–3 cm longis; pedunculo terminali 0.2–3 cm longo 1.5–2 mm diam. dense adpresso-rufo-tomentoso; floribus sessilibus; perianthio breviter infundibuliformi vel subcampanulato 4–4.8 mm longo supra medium 3.8–4 mm lato extus dense rufo-tomentoso; staminibus 5–6.

Tree 7–12 m tall, the young stems densely appressed rufous-ferruginous tomentose. Petiole 1.5–3.5 cm long, densely and minutely appressed rufous tomentose; leaf blades coriaceous, glaucous above, ovate- to sublanceolate-elliptic, shortly abruptly acute to shortly acuminate at apex, sometimes rounded, cuneately acute and often asymmetric at base, 7.5–14.5 cm long, 4.5–7.5 cm wide, glabrous or moderately strigillose above, the lower surface completely covered by a dense, appressed rufous tomentum of short hairs; principal lateral nerves 9–11 each side, subsulcate above, elevated below; tertiary venation above with finely and conspicuously subelevated reticulation, below more coarsely reticulate and elevated. Staminate inflorescence many and closely flowered, much branched, 1.5–3.5 cm high, 3–7 cm wide, the primary axes 0.8–3 cm

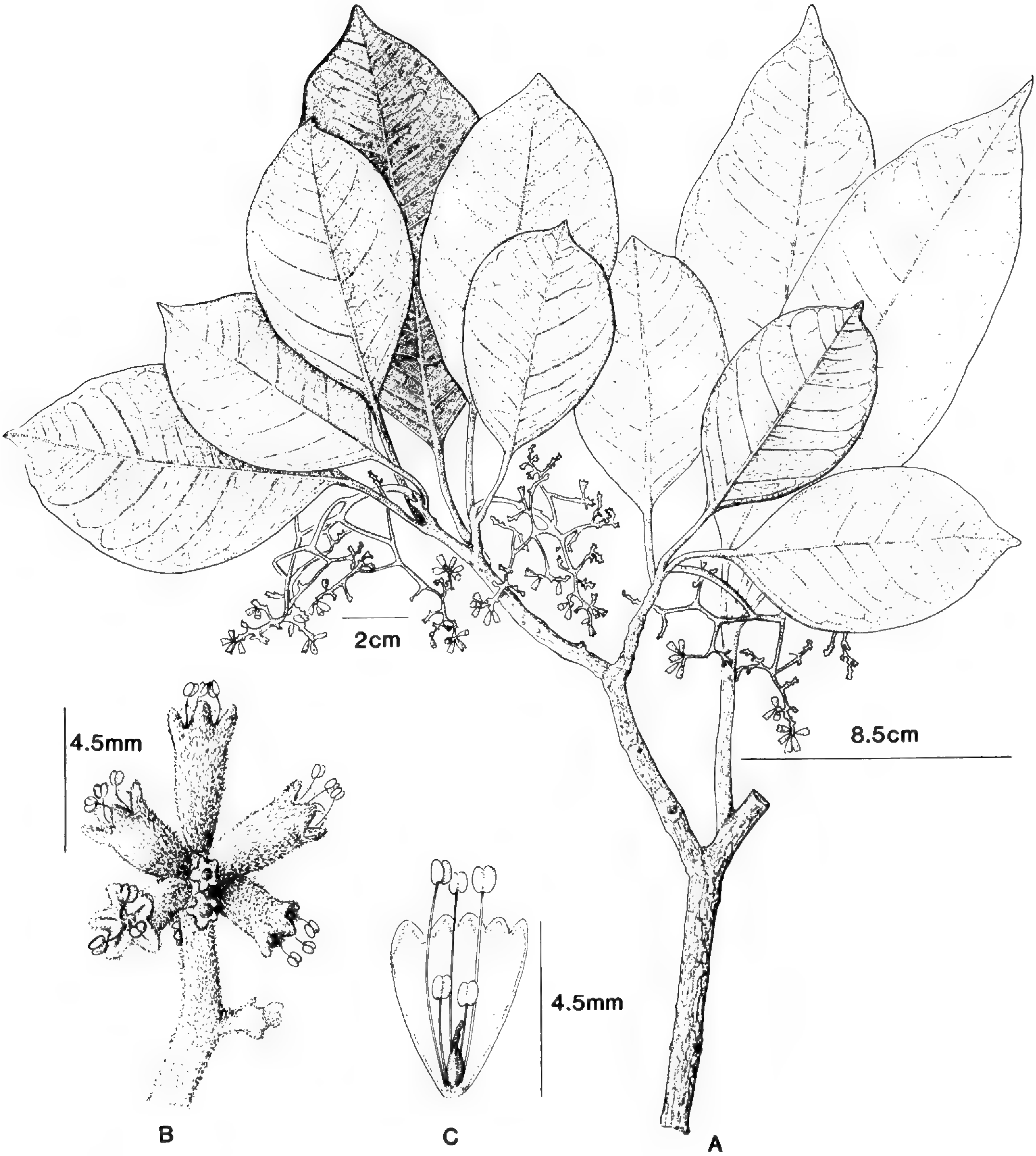

FIGURE 2. *Guapira sancarlosiana.*—A. Flowering branch, staminate plant.—B. Portion of staminate inflorescence.—C. Staminate flower opened. Based on holotype.

long, paniculately branched with 5–6 short axes, bearing small clusters of scattered flowers along the length of the axes. Flowers sessile. Perianth shortly infundibuliform to subcampanulate, 4–4.8 mm long, 3.8–4 mm above middle, densely rufous tomentose without. Stamens 5–6, 3 of the filaments exserted 2.2 mm beyond the perianth.

Paratypes. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: same data as type, *6909* (NY), *7031* (NY), *Clark 7251* (MO); *Clark & Maquirino 7776* (MO); between San Carlos and Solano, *Marcano-Berti & Salcedo 126-979* (MER); supra ostium fluminis Casiquiare, 1854, *Spruce 3751* (NY).

This species is well characterized by the coriaceous leaves which are glaucous above and bear densely appressed rufous puberulence beneath, by the upper and lower leaf surfaces with elevated reticulate tertiary venation, and by the densely branched staminate inflorescences bearing numerous flowers with five stamens, of which three are exserted. *Spruce 3751* was labeled as

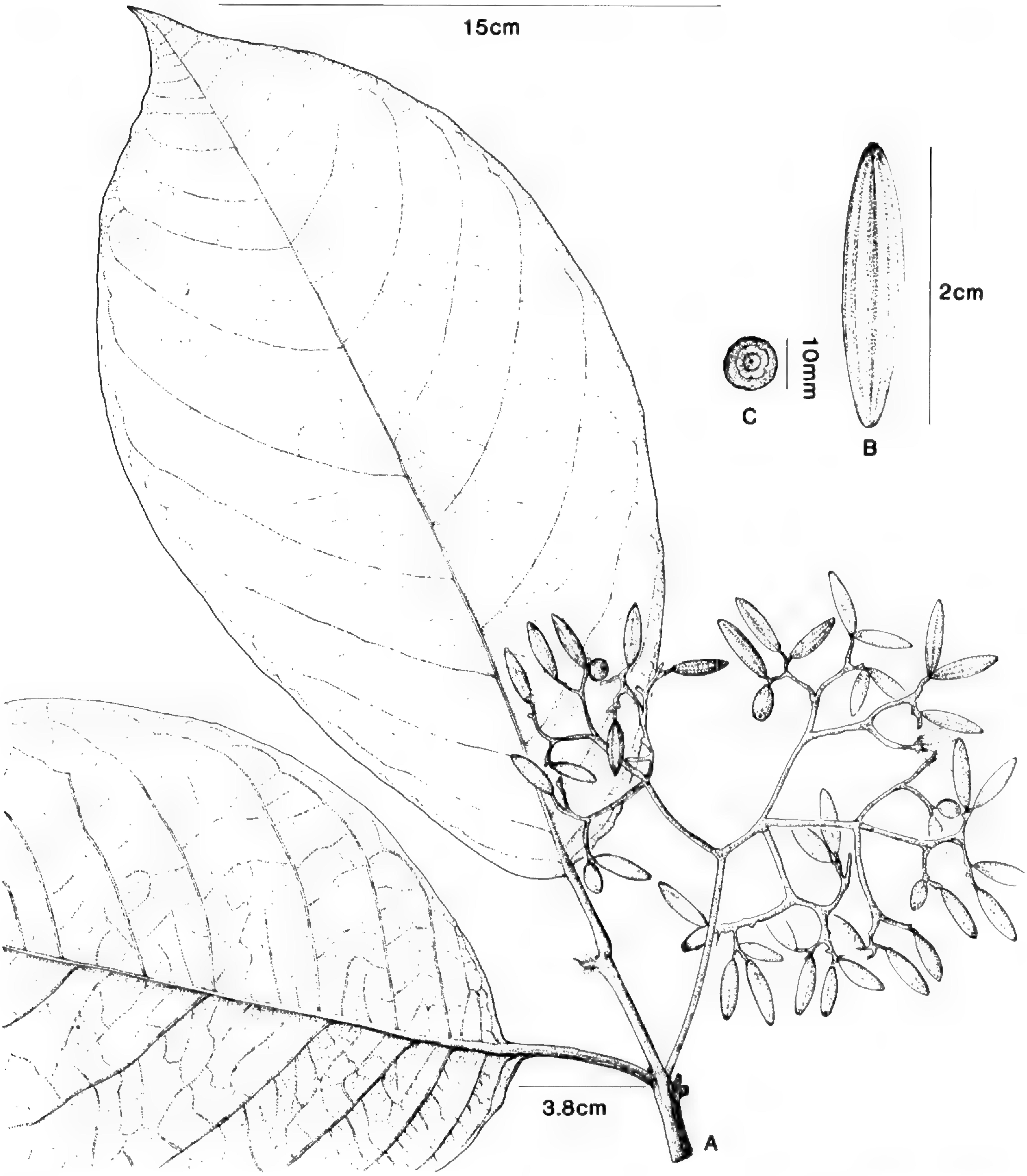

FIGURE 3. *Guapira sipapoana.*—A. Fruiting branch.—B. Fruit.—C. Apical end of fruit. Based on holotype.

an unpublished new species doubtfully referred to *Neea* (as "*Neea*? *rubiginosa*").

Guapira sipapoana Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Reserva Forestal Sipapo, left margin of Río Sipapo, Bloque 1, May 1971, *Carlos Blanco 1158* (holotype, VEN). Figure 3.

Arbuscula, ramulis juvenilibus dense rufo-tomentosis; foliis elliptico-ovatis apice acuminatis basi rotundatis vel obtusis inaequilateralibus 25–29 cm longis 14.5–15 cm latis supra costa media puberula aliter glabris subtus puberulis pilis erectis 0.1–0.2 mm longis praeditis, venulis tertiariis reticulatis subtus prominenter reticulatis; infructescencia axillari, axibus primariis 1.5–2 cm longis; pedunculo 3.8 cm longo 3 mm lato dense rufo-tomentoso; anthocarpio lineari-ellipsoideo 1.5–2 cm longo 4–5 mm lato rufo-tomentoso conspicue 10-costato.

Small tree with young branches densely rufous tomentose. Petiole 3.8 cm long, 3 mm wide, densely rufous tomentose; leaf blades very large, elliptic-ovate, shortly acuminate at apex, rounded or obtuse at the unequal base, 25–29 cm long, 14.5–15 cm wide, upper surface glabrous except for the puberulous midrib; lower surface, including midrib, lateral nerves, and tertiary veinlets, puberulous with erect, slender hairs 0.1–0.2 mm long; tertiary veinlets reticulate, prominently so with large areoles on lower surface. Infructescence in the upper axil, the primary axes 1.5–2 cm long, the secondary axes subumbellate, 2.5–3 cm long, branched above into shorter axes 1.5–2 cm long. Anthocarp linear-ellipsoid, 1.5–2 cm long, 4–5 mm wide, rufous tomentose, 10-costate.

This taxon is distinctive in having very large, prominently reticulate leaves with loose pubescence on the lower surface and in having long, pubescent fruits.

NEEA

KEY TO THE SPECIES OF *NEEA*

1a. Leaves sessile or nearly so, usually obtuse at base, the petiole to 1 mm long; young stem and petiole hirtellous with subspreading rufous-brown hairs; inflorescence both axillary and terminal on the stem .... *N. ignicola*

1b. Leaves petiolate, generally acute to acuminate at base, the petiole 2–35 mm long; young stem and petiole glabrous or pubescent with appressed hairs; inflorescence either cauliflorous on the old stem or terminal on the branches 2

2a. Inflorescence cauliflorous on the old stem 3

3a. Leaves oblanceolate-elliptic or lance-elliptic, 8–12.5(–15) cm long, 2.5–4.5(–5.5)cm wide .... *N. clarkii*

3b. Leaves mainly obovate, oblong, or oblong-ovate, 10–30 cm long, 5–16 cm wide 4

4a. Principal secondary leaf nerves 6–8 each side, slightly elevated on lower surface .... *N. brevipedunculata*

4b. Principal secondary leaf nerves 8–12 each side, conspicuously elevated on lower surface 5

5a. Lower leaf surface and nerves completely glabrous; fruiting peduncle 1–3.5 cm long; flowers sessile; inflorescence dichotomous or with short axes on an elongated rachis .... *N. davidsei*

5b. Lower leaf surface glabrous, but midrib and secondary nerves with minute spreading hairs; flowering peduncle 0.5–0.6 cm long; flowers with pedicels 2–2.5 mm long; inflorescence much branched divaricately .... *N. liesneri*

2b. Inflorescence terminating the stem or its branches 6

6a. Leaves broadly rounded at the apex, obovate or elliptic-obovate .... *N. obovata*

6b. Leaves mainly acute to acuminate at the apex, of other shapes than above 7

7a. Main secondary nerves of leaf blades 15–25 each side, subhorizontal or ascending at an angle less than 20°, relatively close together, 3–4 mm apart .... *N. ovalifolia*

7b. Main secondary nerves of leaf blades generally fewer than 12 each side (fainter intermediate nerves may be present), ascending at an angle usually greater than 30°, or if more than 12 nerves or at a smaller angle, then the nerves more than 4 mm apart 8

8a. Peduncle 6–11 cm long 9

9a. Stem, peduncle, and axes of inflorescence densely ferruginous tomentose; perianth 3 × 1.5 mm, densely ferruginous tomentose .... *N. bernardii*

9b. Stem glabrous; peduncle and axes of inflorescence minutely puberulous or glabrescent; perianth 8–9 × 3 mm, glabrous .... *N. grandis*

8b. Peduncle 1–5 cm long 10

10a. Peduncle and axes of inflorescence glabrous throughout or essentially so 11

11a. Staminate perianth slightly or moderately ferruginous pubescent toward base .... *N. clarkii*

11b. Staminate perianth glabrous or sometimes sparsely puberulous near base, or minutely papillate apically 12

12a. Staminate perianth 6–6.5 × 3.5–4 mm; inflorescence paniculately and irregularly branched, large and conspicuous with elongated rachis and axes, 6–15 cm long, 5–10 cm wide; peduncle 3–5 mm in diameter; principal secondary nerves 9–12 each side; tertiary veinlets conspicuously reticulate and subelevated on upper leaf surface .... *N. robusta*

12b. Staminate perianth 2 × 0.8 mm; inflorescence umbellately or trichotomously branched, 1–2 cm long (or high), 2.5–4 cm wide; peduncle 0.8–1.5 mm in diameter; principal secondary nerves 5–7 each side; tertiary veinlets obsolete on upper surface 13

13a. Upper leaf surface lustrous; lower leaf surface with subelevated, subreticulate tertiary venation more or less manifest; leaves obtuse or rarely rounded at apex; peduncle (pistillate) 1–1.5 mm in diameter; leaves ovate to subovate ..... *N. tepuiensis*

13b. Upper leaf surface dull; lower leaf surface with obsolescent tertiary venation; leaves obtusely acute to acute at apex; peduncle (staminate) 0.8–1 mm in diameter; leaves oblanceolate ..... *N. subglabrata*

10b. Peduncle and axes of inflorescence sparsely to densely ferruginous or puberulent, sometimes with glandular trichomes 14

14a. Junction of lowest axes of inflorescence with summit of peduncle not manifestly enlarged, 0.8–2 mm wide 15

15a. Peduncle usually with paired ferruginous bracts 16

16a. Primary axes of inflorescence 4–7, umbellate; pistillate perianth ferruginous tomentose; main lateral nerves of leaf blades sharply ascending at 50–60° ..... *N. bracteosa*

16b. Primary axes of inflorescence 3, not umbellate; staminate perianth glabrous except for papillate exterior of lobes; main lateral nerves of leaf blades shallowly ascending at 15–25°. ..... *N. amaruayensis*

15b. Peduncle ebracteate 17

17a. Perianth glabrous or glabrescent; bracts mainly glabrous except for the puberulent margins ..... *N. marahuacae*

17b. Perianth variously pubescent; bracts ferruginous dorsally and on margins 18

18a. Ultimate axes of inflorescence racemose with alternately arranged flowers; upper and lower midribs of the leaf blade with minute, ferruginous indument 19

19a. Lower leaf surface covered with an appressed dense indument; perianth (staminate) broadly urceolate; inflorescence much-branched; perianth and inflorescence axes densely ferruginous tomentose with some glandular hairs; peduncle to 1.2 cm long ..... *N. parimensis*

19b. Lower leaf surface glabrous or glabrescent; perianth (pistillate) subinfundibuliform; inflorescence sparsely branched; perianth and inflorescence axes rather sparsely ferruginous tomentose without glandular hairs; peduncle 2–4 cm long ..... *N. tristis*

18b. Ultimate axes of inflorescence cymose or corymbiform, or with fasciculately arranged flowers; upper midrib of leaf blades glabrous, the lower midrib glabrous or the basal part sparsely puberulent 20

20a. Petiole and upper part of stem with pale, minute, spreading papillalike trichomes; perianth with vermiform, short, appressed hairs; lower leaf surface not densely dark-punctate ..... *N. cedenensis*

20b. Petiole glabrous or sometimes minutely glandular; stem glabrous; perianth either minutely appressed puberulent or densely glandular; lower leaf surface densely dark-punctate 21

21a. Tertiary venation scarcely evident on any part of the leaves; axes and peduncle of inflorescence densely ferruginous pubescent; fruit 3.5–5 mm wide ..... *N. clarkii*

21b. Tertiary venation grossly reticulate, subelevated and manifest on both sides of leaves; axes and peduncle of inflorescence sparsely to moderately glandular-pubescent; anthocarp 6–7 mm wide ..... *N. guaiquinimae*

14b. Junction of lowest axes of inflorescences with summit of peduncle enlarged, 2.5–4 mm wide 24

22a. Perianth 3–4.5 mm long, 1.5 mm wide; petiole and young stem sparsely puberulent .... *N. sebastianii*
22b. Perianth 6–8 mm long, 2–3.5 mm wide; petiole and young stem glabrous or glabrescent 23
  23a. Tertiary venation manifest, elevated on lower surface, impressed on upper surface; flowers in small clusters at or near the end of the ultimate axes .... *N. neblinensis*
  23b. Tertiary venation obsolete or scarcely manifest; flowers, if clustered, mainly scattered along the length of the ultimate axes 24
    24a. Pistillate perianth glabrous without; leaves drying blackish; principal secondary nerves 9–12 on each side .... *N. huachamacarae*
    24b. Staminate perianth with minute, sparse to moderate ferruginous indument; leaves drying fuscous brown; principal secondary nerves 6–8 on each side .... *N. mapourioides*

Neea amaruayensis Steyermark, sp. nov. TYPE: Venezuela. Bolívar: Amaruay-tepui, west side, steep slopes, 5°55′N, 62°15′W, 500–740 m, 2 May 1986, *Ronald Liesner & Bruce Holst 20514* (holotype, MO; isotype, VEN).

Frutex vel arbor 2.5–5 m; foliis elliptico-ovatis vel lanceolato-ellipticis apice breviter obtuse acutis 6.5–15 cm longis (2.5–)3.5–7.5 cm latis utroque glabris; nervis lateralibus principalibus utroque 8–10 ad angulum 15–25° adscendentibus, venulis tertiariis reticulatis pagina superiore magis prominulis; inflorescentia masculina 12–21-flora 0.9–1.4 cm longa 1.3–2 cm lata, axibus principalibus tribus 5–8 mm longis 0.5 mm latis sparsim minute ferrugineo-puberulis inaequaliter insertis; pedunculo 1–3 cm longo sparsim vel modice ferrugineo-puberulo pilis subadpressis munito, bibracteato, bracteis oppositis oblongo-ovatis vel oblongis-obtusis 1–2 × 1 mm dense ferrugineo-puberulis 4 mm supra basim dispositis; perianthio masculino cylindrico-subinfundibuliformi 3–3.5 mm longo medio 1.5 mm lato extus glabra; staminibus 8 inclusis.

Shrub or tree 2.5–5 m tall. Leaves mainly opposite; petiole 7–20 mm long, glabrous; leaf blades elliptic-ovate, oblong- or lanceolate-elliptic, abruptly shortly and often subobliquely and obtusely acute, 6.5–15 cm long, (2.5–)3.5–7.5 cm wide, with dark dots beneath, glabrous both sides; principal lateral nerves 8–10 each side with additional shorter intermediate ones, anastomosing 2–5 mm from margin; tertiary venation reticulate, more conspicuous on upper than lower side. Staminate inflorescence relatively small, 0.9–1.4 cm long, 1.3–2 cm wide, 12–21-flowered, the axes unequally inserted, the 3 main ones 5–8 mm long, 0.5 mm wide, sparsely minutely ferruginous puberulent, each axis terminating in 3 shorter axes 0.7–2 mm long, these each supporting 2–3 sessile flowers. Peduncle 1–3 cm long, sparsely to moderately ferruginous puberulent, bibracteate with a pair of oblong-ovate or oblong, obtuse, densely ferruginous bracts 1–2 mm long and 1 mm wide situated 4 mm above base. Staminate perianth subinfundibuliform-cylindric, 3–3.5 mm long, 1.5 mm wide at middle, 1–1.2 mm wide at summit, glabrous without. Stamens 8, included; filaments 0.5–1.5 mm long; anthers suborbicular, 0.6–7 mm long, 0.5–0.6 mm wide.

Paratype. VENEZUELA. BOLÍVAR: Amaruay-tepui, southwest slope, 750–900 m, 24 Apr. 1986, *Holst & Liesner 2702* (MO, VEN).

This taxon possesses paired bracts on the peduncle, as in *Neea bracteata* Steyerm., but differs in the perianth of the staminate flower being completely glabrous except for the papillate margins and exterior surface of the shallow perianth lobes. It differs further in the longer petioles, the unequally inserted lower nonumbellate axes of the staminate inflorescences, and the shallowly ascending lateral nerves of the leaves at an angle of 15–25° instead of the sharply ascending ones of *N. bracteata* arising at 50–60°.

Neea bernardii Steyermark, sp. nov. TYPE: Venezuela. Bolívar: de Santa Elena de Uairen al sur-este, 800–900 m, 23 Apr. 1957, *L. Bernardi 6746* (holotype, MER; isotypes, MO, NY).

Arbuscula vel arbor, ramis dense ferrugineo-tomentosis; foliis in sicco brunneis oppositis late ovatis elliptico-ovatis vel oblanceolato-ellipticis apice obtuse acutis vel breviter acuminatis basi cuneatim acutis 5.5–11.5 cm longis (2.7–)3–6.5 cm latis subtus costa media strigillosa aliter glabris, nervis lateralibus utroque latere 6–10 inconspicuis; petiolis (0.8–)1.5–3 cm longis adpresso-ferrugineo-tomentellis; inflorescentia mascula subcorymbosa 1.5–5 cm alta 2.5–10 cm lata dichotome ramosa dense rufo-ferruginea; axibus primariis duobus, (0.4–)1–3 cm longis 1.5 mm diam. dense adpresso-ferrugineo-tomentosis; pedunculo (2.5–)8–10 cm longo 1.5–2 mm diam. dense adpresso-ferrugineo-tomentoso apice haud manifeste dilatato; perianthio masculino late cylindrico 3–4 mm longo 1.5 mm lato extus dense ferrugineo tomentoso; staminibus 8.

Small or large tree to 40 m tall, with densely ferruginous tomentose branchlets. Leaves opposite; petiole (0.8–)1.5–3 cm long, appressed-ferruginous tomentose; leaf blades drying dull brown to rufous-brown, broadly ovate, elliptic-ovate, or oblanceolate-elliptic, obtusely acute to shortly acuminate at apex, cuneately acute at base, 5.5–11.5 cm long, (2.7–)3–6.5 cm wide, glabrous on both sides except strigose beneath on midrib; lateral nerves 6–10 each side, impressed and inconspicuous above, faintly manifest below; tertiary venation scarcely manifest above, inconspicuously finely reticulate beneath. Staminate inflorescence terminal, subcorymbose, 1.5–5 cm high, 2.5–10 cm broad, dichotomously branched with 2 primary axes (0.4–)1–3 cm long, 1.5 mm diam., these branched into 3 subfasciculate secondary axes (3–)12–16 mm long, each with 2 branches bearing 3–7 clusters of sessile or subsessile flowers, the axes with densely appressed ferruginous tomentum. Peduncle (2.5–)8–10 cm long, 1.5–2 mm diam., densely appressed ferruginous tomentose, its summit 2–3 mm broad, not enlarged at junction with lowest areas. Bracts ovate, acute, 1 mm long, densely ferruginous tomentose. Perianth broadly cylindric or tubular-subinfundibuliform, 3–4 mm long, 1.5 mm wide, densely ferruginous tomentose. Stamens 8, occupying ⅔ of the length of the tube. Fruit oblong, 14 mm long, 7 mm wide, glabrous.

Paratypes. VENEZUELA. BOLÍVAR: El Palmar, forest on margin of Río Grande, 300 m, 20 Feb. 1959, *Bernardi 7156* (VEN); 40 km SE of Tumeremo, near Río Botanamo, 100 m, 7 May 1960, *Little 17597* (US, VEN).

Neea bernardii is distinguished by the greatly elongated peduncle.

Neea bracteosa Steyermark, sp. nov. TYPE: Venezuela. Bolívar: Represa Guri, 55 km NE of Ciudad Piar, 7°35′N, 63°7′W, 250–300 m, 4–5 Apr. 1981, *R. Liesner & A. González 11277* (holotype, VEN; isotype, MO).

Arbor 8 m, ramis juvenilibus ferrugineo-pubescentibus; petiolis 3–10 mm longis; foliorum laminis oppositis vel ad nodos superiores ternatis coriaceis ellipticis vel lanceolato-elliptico apice acutis vel obtuse acutis basi cuneatim acutis 6–9 cm longis 2–3.5 cm latis, nervis lateralibus utroque latere 8–10 inconspicuis; inflorescentia foeminea umbellatim ramosa 1.5–2 cm alta 2–3.5 cm lata, axibus principalibus 4–7 tenuissimis 6–11 mm longis 0.5 mm latis. Pedunculo tenui 1.5–3.2 cm longo modice ferrugineo-hirtello pilis laxis subpatentibus praedito, apice haud dilatato, conspicue bibracteato, bracteis oppositis inaequalibus 2–4 mm longis ferrugineo-pubescentibus; floribus (immaturis) congestis; perianthio (immaturo) modice vel sparsim ferrugineo-adpresso tomentoso.

Tree 8 m with young branchlets ferruginous pubescent. Leaves opposite or sometimes ternate at the upper nodes; petiole 3–10 mm long, glabrous or moderately to sparsely ferruginous pubescent at the base; leaf blades coriaceous, dull brown upon drying, elliptic or lance-elliptic, acute to obtusely acute at apex, cuneately acute at the mainly equilateral base, 6–9 cm long, 2–3.5 cm wide; lateral nerves 8–10, fine and slightly evident below, scarcely evident above, arising at an angle of 50–60°. Pistillate inflorescence 1.5–2 cm high, 2–3.5 cm broad, with 4–7 umbellately branched very slender axes 6–11 mm long, 0.5 mm wide, moderately ferruginous pubescent with lax subspreading hairs 0.1–0.2 mm long; secondary axes 2–5, also umbellate, 3–5 mm long, bearing several clustered flowers at the apices. Peduncle slender, 1.5–3.2 cm long, 1 mm diam., moderately ferruginous with lax subspreading hairs 0.1–0.2 mm long, bibracteate, not enlarged at junction of summit of peduncle with lowest inflorescence axes. Bracts of peduncle paired, unequal, 2–4 mm long, ferruginous pubescent, usually present between ¼–½ the length of the peduncle. Flowers (immature) congested, 85–100. Perianth sparsely to moderately ferruginous pubescent.

This taxon may be differentiated by the bibracteate, very slender peduncles with slender umbellate axes.

Neea brevipedunculata Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: between Paso El Diablo and Caño de Culebra, 25–30 km SE of Puerto Ayacucho, 100 m, 12 May 1980, *Julian A. Steyermark, Gerrit Davidse & Francisco Guanchez 122366* (holotype, pistillate plant, VEN; isotype, MO). Figure 4.

Arbor 6–20 m, ramis glabris, foliis coriaceis opacis obovatis late oblanceolatis vel elliptico-oblongis apice plerumque abrupte obtuseque acutis basi acutis vel obtusis 10–22 cm longis 5–12.5 cm latis omnino glabris, nervis lateralibus utroque latere 6–8; petiolis 1–2.5 cm longis glabris; inflorescentia foeminea multiflora cauliflora 1.5–2 cm alta 2–4 cm lata, ad nodos incrassatos 1–5 inflorescentiis pedunculatis praedita; pedunculis brevibus 1–1.5 cm longis minute puberulis, omnibus ramosis cum 3–4 axibus divaricatis subfasciculatis vel subumbellatis 9–20 mm longis minute adpressoque puberulis; perianthio foemineo infundibuliformi 3.5 mm longo superne 2.5 mm lato extus minute puberulo; perianthio masculo tubuloso 3.7 mm longo 1.5 mm lato extus glabro; staminibus 7 inclusis.

Tree 6–20 m tall, with glabrous branchlets. Petioles 1–2.5 cm long, glabrous; leaf blades coriaceous, opaque, obovate, broadly oblanceolate, or elliptic-oblong, abruptly and obtusely acute to rarely rounded at apex, cuneately acute to obtuse at base, 10–22 cm long, 5–12.5 cm wide; lateral nerves 6–8 each side, slightly elevated below, obsolescent above; tertiary veinlets obscure above, slightly evident below, forming large areoles. Pistillate inflorescence cauliflorous, 1.5–2 cm high, 2–4 cm wide, with 1–5 short, many-flowered, pedunculate inflorescences arising from the old wood at the usually thickened nodes. Peduncles 1–1.5 cm long, minutely puberulent, each branched into 3–4 widely divaricate, subfasciculate or subumbellate primary axes 9–20 mm long, these branched above into short, alternate secondary axes 2–7 mm long bearing the flowers, minutely appressed pale tomentellose. Pistillate perianth infundibuliform, 3.5 mm long, 2.5 mm wide, externally minutely puberulent; pistil 3 mm long (ovary 1 mm long; style 1 mm long with prominently penicillate stigmas 1 mm long); sterile filaments 0.5–1.5 mm long. Staminate flowers in sessile alternately arranged clusters along the short axes of the inflorescence. Staminate perianth tubular, somewhat narrowed at base, 3.7 mm long, 1.5 mm wide, glabrous. Stamens 7, included within perianth; filaments 0.5–2 mm long.

Paratype. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: 3 km NE of San Carlos on Solano Road, at edge of bana (lower Amazon caatinga), 1°56′N, 67°3′W, 119 m, *H. Clark 6605* (staminate plant, MO).

This taxon has been confused with *Neea floribunda* Poeppig & Endl. but differs in the shorter peduncles with more closely crowded, smaller flowers of a different form and in the glabrous staminate perianth.

Neea cedenensis Steyermark, sp. nov. TYPE: Venezuela. Bolívar: Departamento Cedeño: bosque de galería del Caño Chaviripa del drenaje del Escudo Guayanes, carretera Caicara–El Burro, 16 Apr. 1984, *B. Stergios, D. Tephorn, L. Nico & C. Gilbert 8611* (holotype, MO; isotype, PORT).

Frutex, ramulis modice puberulis trichomatibus brevibus patentibus instructis; laminarum foliis lanceolatis vel lanceolato-ellipticis apice anguste subobtusis basi acutis 8.5–11.5 cm longis 2.2–3.5 cm latis utrinque glabris costa media inferiore prope basem trichomatibus ferrugineis praedita excepta, nervis lateralibus utroque ca. 10 inconspicuis, venatione tertiaria inconspicue reticulata; inflorescentia masculina subumbellata ca. 27-flora inaequaliter ramosa, axibus quinque dense ferrugineo-tomentellis; pedunculo 12 mm longo dense ferrugineo-puberulo; perianthio masculino subinfundibuliformi-cylindrico 3–4 mm longo superne 1–1.2 mm lato indumento ferrugineo pilis vermiformibus munito; staminibus 8.

Shrub having stems moderately puberulent with pale, short, spreading trichomes 0.05–0.1 mm long. Petiole with minute, spreading, short papillalike trichomes; leaf blades mainly opposite, lanceolate or lance-elliptic, narrowed to a subobtuse apex, acute at base, 8.5–11.5 cm long, 2.2–3.5 cm wide, 3–3⅓ times longer than broad, glabrous on both sides except for scattered pale-ferruginous trichomes at base of lower midrib, the upper surface punctate; lateral nerves about 10 and inconspicuous both sides; tertiary venation inconspicuously reticulate. Staminate inflorescence terminal, 0.8 cm long, 2 cm wide, ca. 27-flowered, subumbellate with 5 main axes unequally branched 1–2.5 mm above the base, densely ferruginous puberulent, each axis unequally divided into 4 branches 1.5–2 mm long, these 1–2-flowered. Flowers sessile. Bracts subtending flowers lanceolate, acute, 0.8–1 mm long, unequal, densely ferruginous puberulent. Staminate perianth cylindric-subinfundibuliform, 3–4 mm long, 1–1.2 mm wide at summit, abundantly streaked with appressed, ferruginous, vermiform indument without. Stamens 8; filaments 1.5–2 mm long; anthers suborbicular, 0.6 mm long, 0.8 mm wide.

This taxon is characterized by short, spreading trichomes on stems and petioles, vermiform ferruginous indument on the staminate perianth, small inflorescences, and inconspicuous tertiary venation.

Neea clarkii Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: 4.3 km NNE on Solano Road, 1°56′N, 67°3′W, 119 m, *Howard L. Clark 6980* (holotype, NY).

Frutex 3 m, ramulis glabris; petiolis 8–15 mm longis glabris; foliorum laminis coriaceis lanceolato-ellipticis vel oblanceolato-ellipticis apice acutis vel acuminatis basi cuneatim acutis 8–12.5(–15) cm longis 2.5–4.5 (–5.5) cm latis ubique glabris subtus interdum arcte puncticulatis; inflorescentia mascula terminali vel axillari trichotome ramosa, axibus dense ferrugineo to-

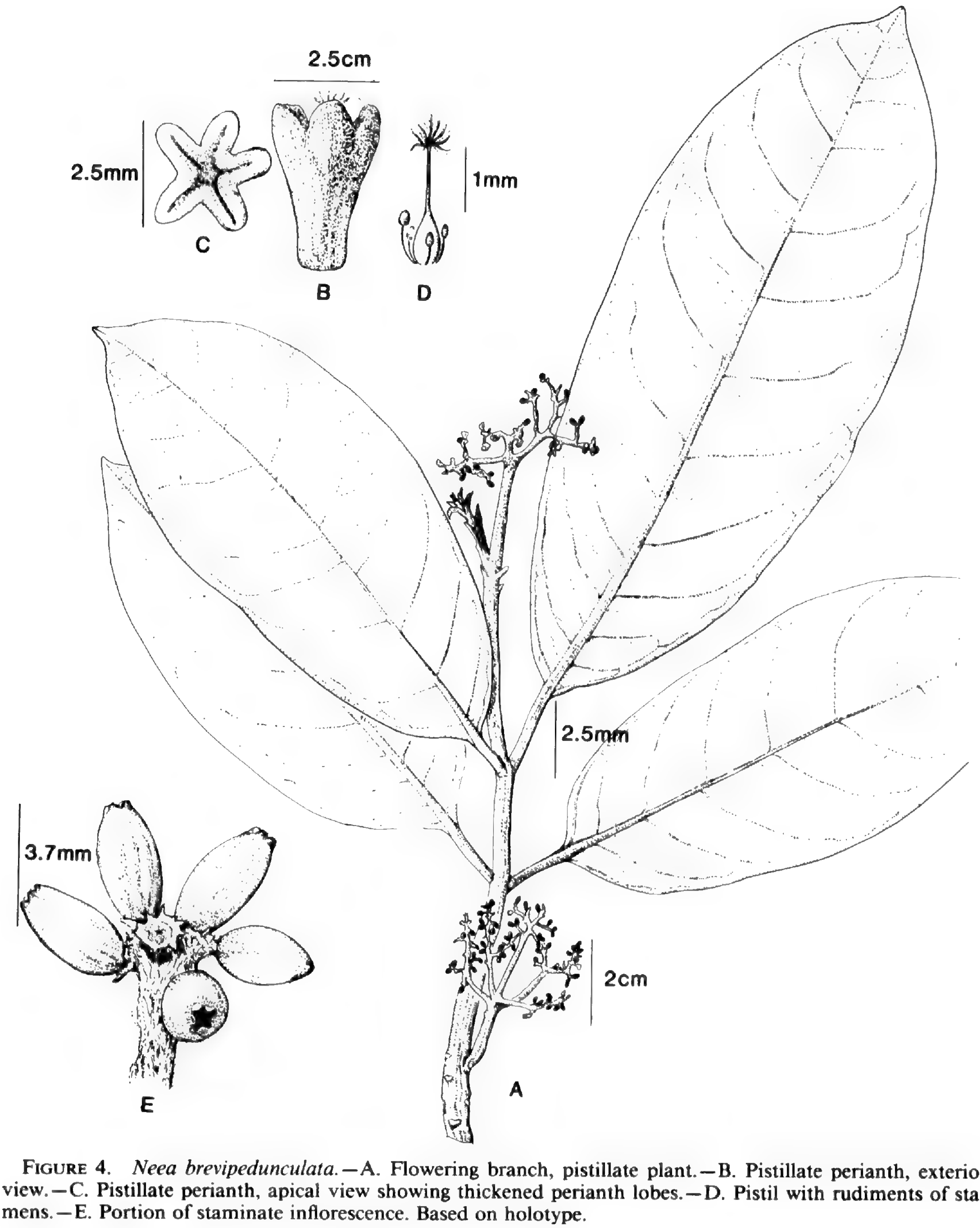

FIGURE 4. *Neea brevipedunculata.*—A. Flowering branch, pistillate plant.—B. Pistillate perianth, exterior view.—C. Pistillate perianth, apical view showing thickened perianth lobes.—D. Pistil with rudiments of stamens.—E. Portion of staminate inflorescence. Based on holotype.

mentosis; pedunculo ferrugineo-tomentoso apice haud dilatato; perianthio masculo subinfundibuliformi 4 mm longo supra medium 1.5 mm lato extus minute sparsimque adpresso-puberulo pilis pallidis munito; staminibus 8, anthocarpio ellipsoideo 8.5–10 mm longo, 3.5–5 mm lato glabro.

Shrub 3 m tall with grayish-white, glabrous branches. Petioles 8–15 mm long, glabrous; leaf blades coriaceous, fuscous, lanceolate-elliptic or oblanceolate-elliptic, acute to shortly acuminate at apex, cuneately acute at the equilateral base, 8–12.5(–15) cm long, 2.5–5.5 cm wide; glabrous both sides, densely dark punctate below; lateral nerves 8–11 each side, finely impressed or obsolescent above, faint or finely elevated below; tertiary venation inconspicuous. Staminate inflorescence terminal or axillary (immature?), trichotomously branched, 10 mm high, 12 mm wide, shortly pedunculate; 3 primary axes 2 mm long (immature), ferruginous tomentose, terminating in groups of 3 or more sessile flowers. Bracts ovate-deltoid, subacute, 0.3–0.4 mm long, densely ferruginous tomentose. Peduncle 4–15 (–30) mm long, 1–1.5 mm wide, ferruginous tomentose, not enlarged at junction of peduncle with lowest axes of inflorescence. Staminate perianth subinfundibuliform, 4 mm long, 1.5 mm wide above the middle, minutely sparsely pubescent with pale hairs without. Stamens 8, included, unequal; filaments 1.3–2.2 mm long. Fruit ellipsoid, 8.5–10 mm long, 3.5–5 mm wide, glabrous.

Paratypes. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: San Carlos, 21 Mar.–17 Apr. 1981, *Delascio, Christensen & Broome 9496* (VEN); 4 km NE of San Carlos, *Liesner 6422* (MO, VEN); prope San Carlos and Río Negro, 1853, *Spruce 3766* (NY); San Carlos de Río Negro, 16 Feb. 1981, *Otto Huber 6067* (VEN).

This species is related to *Neea guaiquinimae,* from which it differs in the absence of glandularity on the peduncles and axes of the inflorescence, the lack of tertiary reticulation on the leaves, and in a denser indument on the peduncle and inflorescence axes.

Huber's specimen matches the photographs of two unpublished names by Heimerl of a *Spruce 3766* collection from "prope San Carlos, ad Río Negro." The photograph from the Vienna herbarium has a note by Heimerl pertaining to a pistillate plant, "Insbesonders durch die Kräftig berandeten Blätter u. wahrscheinlich auch durch Cauliflori ausgezeichnet." This photo shows a cauliflorous, dense, short inflorescence only 10 mm high and 8 mm broad. The other photo from the Berlin herbarium does not show any inflorescence. The specimen of *Huber 6067* also shows a small inflorescence 10 mm high and 8–12 mm broad. Of the three small inflorescences present, one appears at the apex of a leafless short branch, whereas the other two originate 5 mm below the apex of a leafless stem.

The lower leaf surface of the *Huber 6067* collection is densely punctate, but the other collections assigned to *Neea clarkii* do not show punctation.

Neea davidsei Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amacuro: Departamento Tucupita, mountain area, ca. 13 km by road ESE of town of Sierra Imata, 8°23′N, 62°23′W, 400 m, 4–6 Apr. 1979, *Gerrit Davidse & A. González 16558* (holotype, VEN; isotype, VEN).

Arbor 8 m, ramulis glabris; petiolis 1–2 cm longis glabris; foliorum laminis oppositis late obovatis vel late oblongo-ellipticis apice subacute obtusis vel acutis basi cuneatim acutis 11–24(–30) cm longis 6.5–11(–16) cm latis omnino glabris, nervis lateralibus utroque latere 8–10; inflorescentia foeminea cauliflora pedunculata vel epedunculata, axibus minute sparsimque puberulis pilis adpressis fulvis munitis, primariis 3 cm longis superne ramosis usque 5 mm longis; pedunculo vetere fructifero 1–3.5 cm longo 3 mm diam.; bracteis ovatis subacutis 0.5 mm longis extus sparsim adpresso puberulis; floribus sessilibus; anthocarpio 1.2 cm longo 0.8–1 cm lato haud costato.

Tree 8 m, the branches glabrous. Leaves opposite; petiole 1–2 cm long, glabrous; leaf blades broadly obovate or broadly oblong-elliptic, narrowed to a subacutely obtuse or acute apex, cuneately acute at base, 11–24(–30) cm long, 6.5–11(–16) cm wide, wholly glabrous; lateral nerves 8–10 each side, ascending at an angle of 35–45°, indistinctly anastomosing 10–15 mm from margins, elevated and somewhat prominent below, obsolescent or faintly impressed above; tertiary veinlets inconspicuous, grossly reticulate below, obsolescent above. Pistillate inflorescence axillary, cauliflorous on the old wood, pedunculate or epedunculate. Flowers sessile. Old fruiting peduncle 1–3.5 cm long, 3 mm diam. Primary axis on old inflorescence 3 cm long, branched in upper ⅓ with alternate short axes 5 mm long, all axes minutely and sparsely puberulent with pale appressed hairs. Anthocarp 1.2 cm long, 0.8–1 cm wide, not ribbed.

Paratypes. VENEZUELA. BOLÍVAR: between km 11 and 18.5, south of El Dorado, 215 m, 23 July 1960, *Steyermark 86585* (NY, VEN). TERRITORIO FEDERAL DELTA AMACURO: Orocoima, Río Toro, *Bernardi 7573, Buza 3734* (NY).

The axillary, cauliflorous infructescence relates this species to *Neea liesneri* of Cerro de La Neblina, but the former differs in the longer, stouter peduncle, sessile flowers, and completely glabrous lower leaf surface.

The fruiting paratype has the leaves broadly oblong-elliptic and acute, whereas in the holotype the leaf blades are broadly obovate narrowed to a subacutely obtuse apex.

Neea guaiquinimae Steyermark, sp. nov. TYPE: Venezuela. Bolívar: Cerro Guaiquinima, summit, NE sector, 6°00′N, 63°28′W, 1,650 m, 9 Apr. 1979, *Julian A. Steyermark, G.*

C. K. & E. Dunsterville 117971 (holotype, VEN; isotype, MO).

Arbuscula vel frutex 2–3 m, ramis glabris; petiolis 5–20 mm longis minute glanduliferis vel glabris; foliorum laminis elliptico-ovatis apice obtuse acutis basi subacutis vel acutis 5–12.5 cm longis 2–6 cm latis supra glabris subtus glanduloso-punctatis, nervis lateralibus utroque latere venulis tertiariis ubique manifeste grosseque reticulatis; inflorescentia foeminea trichotome ramosa 1 cm alta 1.8 cm lata, axibus principalibus quattuor 4–5 mm longis 0.8 mm diam., modice glanduliferis; pedunculo sub anthesi 2.5 cm longo 1 mm diam. sub fructu 5–7 cm longo 1.5–2 mm lato, sparsim glandulifero; perianthio tubuloso 4 mm longo 1.2 mm lato extus dense glandulifero. Anthocarpio oblongo-ellipsoideo vel ovato-oblongo 12–13 mm longo 6–7 mm lato obtuse 10-costato glabro.

Small tree or shrub 2–3 m tall, the branchlets glabrous. Petioles 5–20 mm long, glanduliferous or the glands deciduous; leaf blades coriaceous, elliptic-ovate, obtusely acute at apex, subacute to cuneately acute at base, 5–12.5 cm long, 2–6 cm wide, glabrous above, densely dark gland-dotted below, slightly revolute on margins; lateral nerves 6–10 each side, slightly impressed or obsolescent above, slightly elevated below; tertiary venation on both sides subelevated, grossly reticulate. Pistillate inflorescence trichotomously branched, 1 cm high, 1.8 cm broad, with 4 primary axes 4–5 mm long, 0.8 mm diam., moderately glanduliferous, the primary axes shortly branched into 4 shorter, moderately glanduliferous secondary axes 1–2 mm long terminating in shortly pedicellate extensions, each bearing 2–3 sessile flowers. Peduncle in anthesis 2.5 cm long, 1 mm diam., sparsely glanduliferous in fruit, 5–7 cm long, 1.5–2 mm wide and glabrous, pendent in fruit, the junction of peduncle with lowest axes not conspicuously enlarged. Bracts narrowly lanceolate, 1 mm long, densely glanduliferous. Pistillate perianth tubular, 4 mm long, 1.2 mm wide, densely glandular without; ovary ellipsoid, 1.3 mm long, sessile; style 1 mm long; stigmas 0.4 mm long, fimbrillate. Anthocarp oblong-ellipsoid to ovate-oblong, 12–13 mm long, 6–7 mm wide, obtusely 10-costate.

Paratype. VENEZUELA. BOLÍVAR: Cerro Guaiquinima, W sector near forested border, 5°45′N, 63°43′W, 1,540 m, *Steyermark, Berry, G. C. K. & E. Dunsterville 117499* (MO, VEN).

This species is distinguished by the sparsely to moderately glandular pubescence of the peduncle and inflorescence axes and by the manifestly subelevated, grossly reticulate tertiary venation on both leaf surfaces.

Neea huachamacarae Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Río Cunucunuma, base of trail to Cerro Huachamacari, 3°39′N, 65°41′W, 220 m, 7 Mar. 1985, *Ronald Liesner 18403* (holotype VEN; isotype, MO).

Arbor 10 m, ramis glabris; petiolis 1–2.5 cm longis glabris; foliorum laminis oppositis oblanceolatis vel oblongo-ellipticis apice acutis obtusis vel rotundatis basi cuneatim acutis 6–15.5 cm longis 3–5.5 cm latis glabris; nervis lateralibus utroque latere 9–12 inconspicuis; inflorescentia foeminea terminali, axibus dense ferrugineo-adpresso-pubescentibus, pedunculo 1–2.5 cm longo 2 mm lato autem 3–4 mm lato ad pedunculi cum apice axibus infimis juncturam inserto; floribus secus longitudinem axis insertis; perianthio subpandurato-tubuloso 7.5–8 mm longo 3–3.5 mm lato extus glabro.

Tree 10 m tall with glabrous branches. Leaves opposite; petiole 1–2.5 cm long, glabrous; leaf blades opaque, drying blackish, oblanceolate or oblong-elliptic, shortly acute, obtuse, or rounded at apex, cuneately acute at base, 6–15.5 cm long, 3–5.5 cm wide; lateral nerves 9–12 each side, not elevated, inconspicuous; tertiary venation inconspicuous. Pistillate inflorescence terminal, the usually 4 primary axes 5–13 mm long, branched into 10–15 secondary axes, the solitary flowers or groups of flowers borne along the length of the axes, not congested in groups at the ends of the axes, the axes densely ferruginous appressed-pubescent. Peduncle 1–2.5 cm long, 2 mm wide except at the junction of the lowest axes of the inflorescence with the top of the peduncle where enlarged to 3–4 mm wide. Perianth subpandurate-tubular, 7.5–8 mm long, 3–3.5 mm wide, glabrous without. Ovary 2–3 mm long; style 5–6 mm long, exserted 2 mm; sterile stamens 6 with filaments 3 mm long.

This species is characterized by having the flowers inserted along the length of the axes of the inflorescence rather than in congested groups at the ends of pedicellate branches. In this respect it resembles *Neea mapourioides* but differs in the glabrous pistillate perianth and the greater number of principal secondary nerves of the leaf blades.

Neea ignicola Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: 11 km N of Puerto Ayacucho toward El Burro, 5°44′N, 67°30′W, 90 m, 26 Jan. 1978, *Otto Huber & Julio Cerda 1456* (holotype, VEN).

Frutex 2–3 m, ramulis dense hirtellis pilis patentibus rufo-brunneis munitis; petiolo vix evoluto usque 1 mm pilis patentibus rufo-brunneis munito; foliorum laminis membranaceis subsessilibus ovato-lanceolatis apice plerumque acuminatis basi obtusis vel rotundatis 3.5–6 cm longis 1.3–2.5 cm latis ubique glabris; nervis lateralibus utroque latere ca. 10; venulis tertiariis ubique conspicue reticulatis; inflorescentia mascula terminali axillarique 5–13 mm alta 7–10 mm lata (immatura?), axibus primariis quattuor alternatim ramosis cum floribus racemose alternatis secus longitudinem insertis autem floribus terminalibus aggregatis; bracteis sub axibus lanceolatis 1–1.5 mm longis; pedunculo filiformi 8–14 mm longo 0.4–0.5 mm lato hirtello pilis rufo-brunneis patentibus munito; perianthio masculo (immaturo) tubuloso extus sparsim hirtello pilis ferrugineis munito; staminibus 6–7.

Shrub 2–3 m tall; branches slender, 1–1.5 mm diam., densely reddish-brown hirtellous with spreading hairs 0.5 mm long. Petiole scarcely developed, up to 1 mm long, hirtellous with lax, subspreading hairs; leaf blades subsessile, membranous, ovate-lanceolate, usually narrowed to an acuminate apex, obtuse or rarely rounded at base, 3.5–6 cm long, 1.3–2.5 cm wide, glabrous both sides; principal lateral nerves 10 or sometimes more on both sides, elevated above, less conspicuous beneath; tertiary venation reticulate both sides, less so beneath. Staminate inflorescence axillary and terminal, 5–13 mm high, 7–10 mm broad, densely hirtellous with rufous-brown spreading hairs; the 4 primary axes alternately and racemosely branched with flowers solitary along the length of the axes, but with terminal flowers in 2s or 3s, the secondary axes scarcely or not developed. Peduncle filiform, 8–14 mm long, 0.4–0.5 mm diam., hirtellous with rufous-brown spreading hairs, not enlarged at apex where joining the lowest axes of the inflorescence. Bracts subtending base of primary axes lanceolate, subacute, 1–1.5 mm long. Staminate perianth (immature) tubular, sparsely hirtellous with ferruginous hairs. Stamens 6–7.

This taxon is readily differentiated by its sessile or subsessile leaves and spreading pubescence.

Neea liesneri Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Departamento Río Negro: Cerro de La Neblina, 0.4 km W of base camp on Río Mawarinuma, 0°50′N, 66°10′W, 140 m, 9 Mar. 1984, *Liesner 16502* (holotype, VEN; isotype, MO). Figure 5.

Arbor 5 m; petiolis 1–2 cm longis; foliorum laminis late obovatis vel lato oblongo-ovatis apice subacutis obtusis vel rotundatis basi acutis majoribus asymmetricis 16–30 cm longis 9–16 cm latis supra glabris subtus costa media nervis lateralibusque elevatis prominentibusque minute puberulis pilis patentibus munitis aliter glabris, nervis lateralibus 9–12 utroque latere distantibus 12–27 mm subtus conspicue elevatis; inflorescentia mascula cauliflora multiramosa multiflora 2.5 cm longa 5 cm lata; axibus dense puberulis pilis adpressis munitis; pedunculo 5–6 mm longo dense puberulo pilis adpressis munito; floribus pedicellatis, pedicellis 2–2.5 mm longis dense puberulis pilis adpressis obtectis; perianthio urceolato 6 mm longo basi 4 mm lato apicem versus 1.5–2 mm lato extus dense puberulo pilis adpressis obtecto; staminibus 7–9; anthocarpio oblongo-ellipsoideo 20 mm longo 8 mm lato minute pubescenti pilis subferrugineis adpressis obtecto.

Tree 5 m tall. Petioles 1–2 cm long; leaf blades broadly obovate or broadly oblong-ovate, subacute to obtuse or rounded at apex, acute at base, the larger leaves conspicuously asymmetrical, the smaller leaves nearly symmetrical, 16–30 cm long, 9–16 cm wide, glabrous above, the midrib and lateral nerves beneath prominent and elevated with minute spreading pubescence, elsewhere glabrous; lateral nerves 9–12 each side, ascending at an angle of 35–45°, anastomosing 5–13 mm from the margin, regularly 12–27 mm equidistant or irregularly spaced, conspicuously elevated below, inconspicuously impressed above; intermediate and tertiary venation below inconspicuously grossly reticulate, inconspicuous above. Staminate inflorescences cauliflorous on the old wood, broader than high, 2.5 cm long, 5 cm broad, much branched, many-flowered, the lateral primary axes divaricate, 1–2 cm long, all parts densely puberulent with pale-fulvous, appressed hairs. Peduncle 5–6 mm long. Staminate flowers on pedicels 2–2.5 mm long and covered with a pale-fulvous, appressed puberulence. Staminate perianth urceolate, 6 mm long, 4 mm wide at base, 1.5–2 mm wide near summit, densely puberulent with pale-fulvous, appressed hairs. Stamens 7–9, the anthers 1.3–2 mm long, apiculate or exapiculate, the shorter filaments 1–2 mm long, the longer ones 3–4 mm long; pistillode 4–5 mm long. Anthocarp oblong-ellipsoid, 20 mm long, 8 mm wide, minutely pubescent with appressed, subferruginous hairs.

Paratype. BRAZIL. AMAZONAS: Between Maloca and Rio Cauaburi, south of Cerro de La Neblina, 50–100 m, *Nilo T. Silva & Umbelino Brazão 60782* (MO, NY).

This remarkably distinct species is characterized by the cauliflorous, many-branched, cymose inflorescence developed on the old wood; large, obovate, conspicuously nerved leaves; and large, pedicellate, urceolate staminate flowers with strongly developed asymmetrical bases.

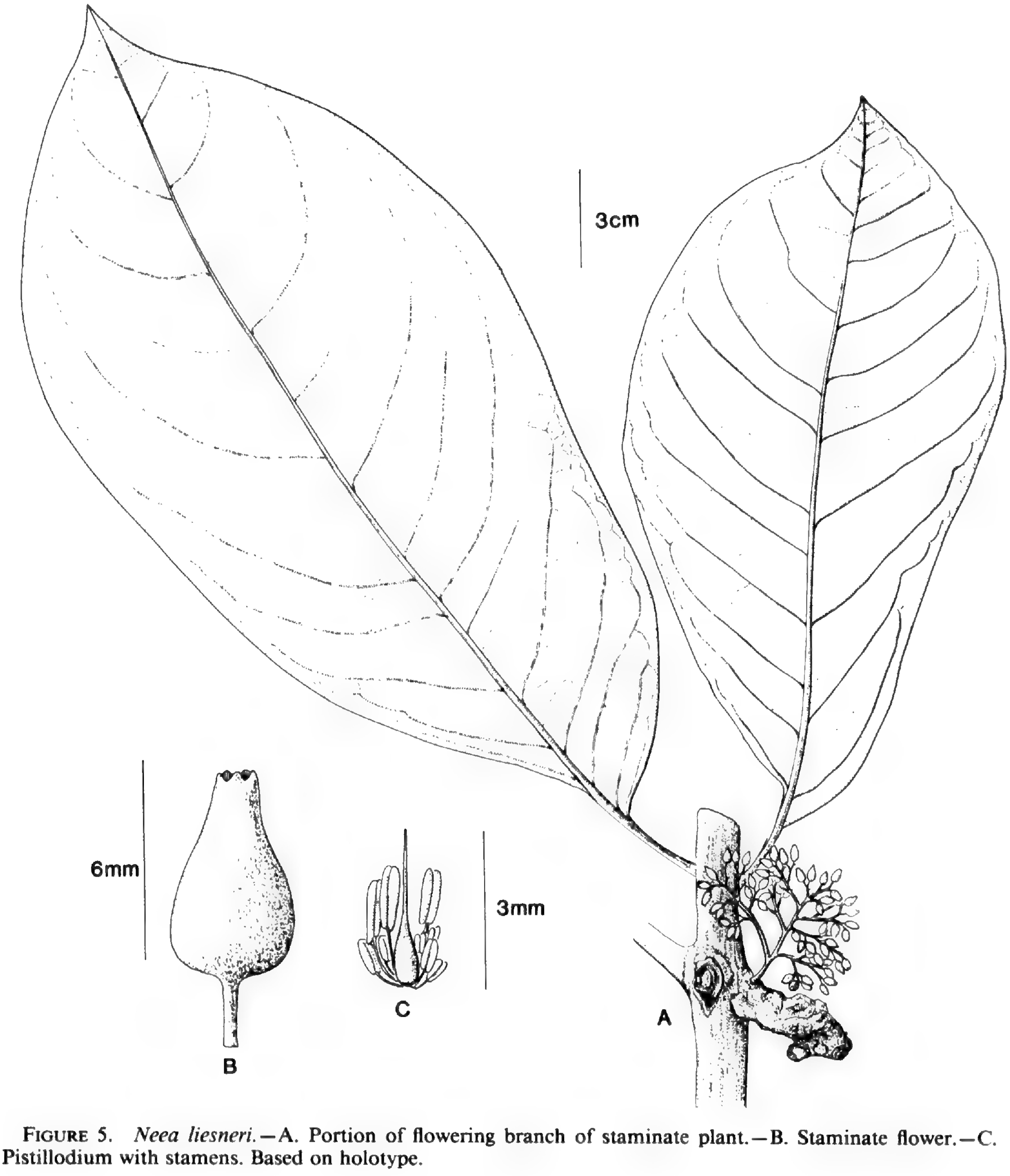

Figure 5. *Neea liesneri.*—A. Portion of flowering branch of staminate plant.—B. Staminate flower.—C. Pistillodium with stamens. Based on holotype.

Neea mapourioides Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: 0.5–1.5 km east of San Carlos, 1°55′N, 67°5′W, 120 m, 1 Dec. 1977, *Ronald Liesner 4096* (holotype, VEN; isotype, MO).

Frutex 3 m, ramulis glabris; petiolis 5–15 mm longis glabris; foliorum laminis oppositis elliptico-obovatis apice abrupte acuminatis basi cuneatim acuminatis 5.5–17.5 cm longis 4–7 cm latis ubique glabris; nervis lateralibus principalibus utroque latere 6–8; inflorescentia mascula terminali 2.5–4.5 cm alta 3.5–7 cm lata, axibus late divaricatis, axibus primariis 3–4, dense ferrugineo-tomentosis, axium ultimorum floribus alternatim dispositis. Pedunculo 1.5–2.5 cm longo 1.5–2 mm lato paullo dilatato usque 2.5 mm lato ad pedunculi cum axibus infimia juncturam inserto minute ferrugineo-tomentoso; bracteis sub floribus ovato-deltoideis subacutis 0.5–0.8 mm longis ferrugineo-tomentosis; perianthio masculo ellipsoideo minute ferrugineo-puberulo 6.5–7 mm longo 2.8–3 mm lato apice angustato; staminibus 7 inaequalibus.

Shrub 3 m tall; branches glabrous. Leaves opposite; petiole 5–15 mm long, glabrous; leaf blades coriaceous, opaque, fuscous, elliptic-obovate, abruptly acuminate at apex, cuneately acuminate at base, 5.5–17.5 cm long, 4–7 cm wide; lateral nerves 6–8 each side, anastomosing 4–6 mm from margin, impressed and slightly manifest below, but essentially obsolescent; tertiary venation obsolete above, scarcely impressed beneath. Staminate inflorescence terminal, 2.5–4.5 cm high, 3.5–7 cm wide, the axes widely spreading, densely ferruginous tomentose, the 3–4 primary axes 1.5–3.5 cm long with the branched part bearing flowers, the ultimate branches bearing sessile flower clusters scattered alternately along the length; peduncle 1.5–2.5 cm long, 1.5–2 mm wide, but at the summit with the lowest axes of the inflorescence enlarged to 2.5 mm wide, sparsely to moderately minutely brown puberulent. Bracts of base of primary axes 1–1.5 mm long, ferruginous tomentose, those subtending the flowers ovate-deltoid, subacute, 0.5–0.8 mm long, ferruginous tomentose. Staminate perianth narrowly ellipsoid, 6.5–7 mm long, 2.8–3 mm wide, narrower at summit, sparsely to moderately minutely ferruginous puberulent. Stamens 7, included within the lower ⅓–½ of the perianth tube, unequal; anthers 1.5 × 0.5–1 mm; filaments 1–3 mm long. Stylopodium 4 mm long.

This species possesses alternately arranged flowers on the axes of the inflorescence as in *Neea huachamacarae* but differs in the fewer lateral nerves, the fuscous-brown instead of blackish leaves when dried, and in having pubescence on the staminate perianth, as opposed to the glabrous pistillate perianth in *N. huachamacarae.*

Neea marahuacae Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Cerro Marahuaca, forested slopes 1–2 km N of Sima Camp, 3°43′N, 65°31′W, 1,100 m, 8–9 Mar. 1985, *Ronald Liesner 18428* (holotype, VEN; isotype, MO).

Frutex 2 m, ramulis glabris; petiolis 7–20 mm longis; foliorum laminis elliptico-oblanceolatis apice acuminatis basi acutis vel acuminatis 7.5–10.5 cm longis 2.5–4.5 cm latis glabris, nervis lateralibus utroque latere 6–8; inflorescentia mascula terminali subumbellatim 5-ramosa 5–8 mm alta 10–15 mm lata, sparsim rufoferrugineo pubescenti; pedunculo tenui 1.5–2 cm longo 0.5–0.7 mm diam. sparsim puberulo pilis adpressis munito; perianthio masculo tubuloso 1.5 mm longo 0.7 mm lato extus glabro vel glabrescenti; staminibus 5–6 inaequalibus inclusis.

Shrub 2 m. Young stems glabrous. Petioles 7–20 mm long; leaf blades opaque, elliptic-oblanceolate, acuminate at apex, acute to acuminate at base, 7.5–10.5 cm long, 2.5–4.5 cm wide, glabrous; lateral nerves 6–8 each side, inconspicuous; tertiary venation obsolete or inconspicuous. Peduncle slender, 1.5–2 cm long, 0.5–0.7 mm diam., simple or forked near base, sparsely appressed-pubescent with reddish-brown pubescence, not enlarged at junction of summit with lowest axes of inflorescence. Staminate inflorescence terminal, subumbellately 5-branched, 5–8 mm high, 10–15 mm wide, sparsely rufous-brown appressed-puberulent; primary axes 2–3 mm long; secondary axes 0.5–1 mm long, each terminating in branched congested clusters, each of these bearing 4–5 flowers. Bracts at base of flower clusters ligulate-lanceolate, acute, 1.2 mm long, 0.3–0.4 mm wide, glabrous except for the minutely puberulous margins near the apex. Staminate perianth tubular, 1.5 mm long, 0.7 mm wide, glabrous or glabrescent without. Stamens 5–6, unequal, included; anthers suborbicular, 0.1 mm long (immature).

Paratype. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Cerro Marahuaca, Sima Camp, S-Central portion of forested slopes along east branch of Caño Negro, 3°43′N, 65°31′W, 1,140 m, 21–22, 24 Feb. 1985, *Steyermark & Holst 130545* (MO).

This montane species of Cerro Marahuaca differs from related species in the glabrous or glabrescent staminate perianth and in the mainly glabrous bracts, except for the apical margins.

The paratype differs from the type collection in having ovate-elliptic to elliptic-obovate leaves, which are larger, indistinctly nerved, and subacutely obtuse at the apex.

Neea parimensis Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Sierra Parima, Simarawochi, Río Matacuni, 3°49′N, 64°36′W, 6–7 km west of Venezuelan–Brazilian frontier, 795–830 m, 18–23 Apr. 1973, *Julian A. Steyermark 106982* (holotype, VEN; isotype, NY).

Arbor 10 m, ramulis dense adpresso-pubescentibus; petiolis 5–8 mm longis dense adpresso-pubescentibus; foliorum laminis membranaceis oblanceolatis apice acutis basi acute attenuatis 4–7 cm longis 1.5–2.5 cm latis supra glabris subtus minute adpresso-puberulis, nervis lateralibus utroque latere ca. 8 vix manifestis; inflorescentia mascula terminali 4 cm alta 5 cm lata multiramosa axibus principalibus 4–8 floribus secus longitudinem alternatim dispositis, axibus dense ferrugineo-tomentosis cum pilis glandulosis interspersis; pedunculo usque 12 mm longis vel nullo dense ferrugineo-tomentoso cum pilis glandulosis interspersis;

bracteis sub floribus quattuor cupulam facientibus late ovatis 0.7 mm longis extus dense ferrugineo-tomentosis; perianthio masculo urceolato 4 mm longo 2.5 mm lato extus dense ferrugineo cum pilis glandulosis interspersis; staminibus 7 inclusis, filamentis 1.2 mm longis.

Tree 10 m tall with densely appressed-pubescent stems. Petioles 5–8 mm long, densely appressed-pubescent; leaf blades membranous, oblanceolate, acute at apex, narrowed to an acute base, 4–7 cm long, 1.5–2.5 cm wide, the upper surface glabrous, the lower surface densely appressed-puberulent with minute scalelike hairs; lateral nerves about 8 each side, scarcely evident. Staminate inflorescence terminal, 4 cm high, 5 cm broad, much branched, the flowers alternately arranged on the numerous axes, the 4–8 principal axes unbranched in the basal 8–13 mm, then forked into alternately or fasciculately disposed secondary axes, densely ferruginous tomentose mixed with glandular hairs. Peduncle none or up to 12 mm long, densely ferruginous tomentose with intermixed glandular hairs. Bracts at base of flowers 4, forming a cupule, broadly ovate, subacute, 0.7 mm long, densely ferruginous tomentose without. Staminate perianth urceolate, 4 mm long, 2.5 mm wide at the middle, constricted below the summit, densely ferruginous tomentose without, mixed with short glandular hairs. Stamens 7, included within the lower half of the perianth tube; filaments 1.2 mm long.

This species is characterized by having a broadly urceolate staminate perianth, much-branched inflorescence, lower leaf surface with a dense appressed indument, and a short peduncle. Glandular hairs are scattered on the perianth, peduncle, and axes of the inflorescence.

Neea robusta Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: third savanna at western base of Cerro Yapacana, 3°40′N, 66°50′W, 100 m, 14–28 Feb. 1978, *Otto Huber 1693* (holotype, VEN).

Arbor 3 m, ramulis glabris; petiolis 1–3.5 cm longis glabris; foliorum laminis obovatis elliptico-lanceolatis elliptico-oblongis vel oblongo-ellipticis apice plerumque breviter obtuseque acutis vel obtusis vel rotundatis basi cuneatim acutis 8–24 cm longis 4.5–9.5 cm latis ubique glabris, nervis lateralibus utroque latere 9–12 supra venulis tertiariis conspicue reticulatis; inflorescentia mascula subpyramidali paniculata ramosa 6–15 cm longa 5–10 cm lata axe superiore magis longiore quam axibus inferioribus, axibus lateralibus 4–8 divaricatis 2–3 mm diam. superioribus brevioribus plerumque alternis, inferioribus longioribus plerumque oppositis vel alternis, axis parte apicali minute adpresso-ferrugineo puberula axibus aliter glabris, floribus sessilibus; perianthio mascula suburceolato 6–6.5 mm longo 3.5–4 mm lato ad apicem magis angustato extus glabro; staminibus 9–10 inclusis; pistillodio 3 mm longo; infructescentia 6–15 cm longo 7–15 cm lato; pedunculo fructifero 1–6 cm longo 3–5 mm lato ad apicem dilatato; anthocarpio in sicco 1.2 × 0.5 cm in vivo 2 × 1 cm.

Tree 3 m tall, the branches glabrous. Petioles 1–3.5 cm long, glabrous; leaf blades coriaceous, obovate, elliptic-lanceolate, elliptic-oblong, or oblong-elliptic, mainly shortly and obtusely acute or obtuse at apex, sometimes rounded, cuneately acute at the base, 8–24 cm long, 4.5–9.5 cm wide, glabrous both sides; lateral nerves 9–12 each side, slightly elevated on upper surface, less conspicuous and impressed on lower surface, anastomosing 5–10 mm from the margin; tertiary venation subelevated and conspicuously reticulate on upper surface, less conspicuously reticulate on lower surface. Staminate inflorescence elongated, subpyramidal, paniculately branched, 6–15 cm long, 5–10 cm wide, the upper axis longer than the lateral ones, 6–9 cm long, 6 mm diam., the 4–8 lateral axes divaricately spreading, 0.3–2 cm long, 2–3 mm diam., the upper ones generally shorter and alternate, the lower axes longer, opposite or alternate, glabrous except minutely appressed ferruginous puberulent apically. Peduncles in anthesis 1–1.2 cm long, in fruiting stage 1–6 cm long, 3–5 mm diam. Flowers sessile and scattered but more congested apically. Bracts subtending flowers deltoid, obtuse, 0.2 mm long. Staminate perianth carnose, suburceolate, narrowed and contracted below summit, rounded at base, 6–6.5 mm long, 3.5–4 mm wide, narrower at summit. Stamens 9–10, included, unequal; anthers broadly rhomboid; filaments 2–4.5 mm long. Pistillode 3 mm long. Infructescence 6–15 cm long, 7–15 cm wide. Anthocarp 1.2 × 0.5 cm in dried state, 2 × 1 cm fresh.

Paratypes. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Caño Yagua at Cucurital de Yagua, 3°36′N, 66°34′W, 120 m, *Davidse et al. 17362* (MO, VEN); Caño Yagua, Chipital, 3°29′N, 66°41′W, 120 m, *Davidse et al. 17320* (MO, VEN); Cucurital de Caname, Caño Caname, 3°40′N, 67°22′W, 100 m, *Davidse et al. 16880* (MO, VEN); 1–2 km SE and E of San Carlos de Río Negro, 1°56′N, 67°3′W, 120 m, *Liesner 6868* (MO, VEN); 10.8 km NE of San Carlos on Solano Road, *Clark 7108* (MO, NY, VEN); 4.3 km NE of San Carlos on Solano Road, *Clark 7038, 7164* (NY); S and SW of San Carlos de Río Negro, *Liesner 6732* (MO, VEN); between San Carlos de Río Negro and El Solano, *Marcano-Berti & Salcedo 131-979* (MER); Caño Yagua N and NE of Cerro Cucurito, 3°36′N, 66°34′W, 120 m, *Huber et al. 3774* (VEN); NE and E base of Cerro

Cucurito, 120 m, *Huber & Tillett 2973* (VEN); 12–15 km NE of San Carlos de Río Negro, road to Solano, 100 m, *Morillo et al. 4170* (VEN). BRAZIL. AMAZONAS: Serra de Neblina, between Maloca and Rio Cauaburi, 50–100 m, *Silva & Brazão 60765* (MO, NY).

This species is characterized by the large, urceolate, glabrous staminate perianth, the irregularly paniculately branched, large inflorescence and general glabrity of parts. The more numerous secondary nerves, thick peduncle, and conspicuously reticulate tertiary venation of the upper leaf surface distinguish it from related species of the Venezuelan Guayana.

Neea sebastianii Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: high rebalsa (seasonally flooded forest), Isla Sebastian, Río Casiquiare above Chapezón, between Boca and Solano, 1°58'N, 67°3'W, 120 m, 31 Jan. 1980, *Ronald Liesner & Howard Clark 8959* (holotype, VEN; isotype, MO).

Arbor 8 m, ramulis juvenilibus dense miniteque adpresso-puberulis pilis ferrugineis munitis; petiolis 3–15 mm longis sparsim puberulis; foliorum laminis ovato-ellipticis apice obtuse acutis vel rotundatis basi cuneatim acutis 7.5–14 cm longis 3.5–6.5 cm latis supra glabris subtus praesertim costa media nervisque minute puberulis aliter pagina inferiore minute puncticulatis atque glandulis sessilibus obtectis; nervis lateralibus utroque latere 10–12; inflorescentia mascula 1–2.5 cm alta 2–2.5 cm lata, axibus 4–5 dense breviter ferrugineo-tomentosis 3–5 mm longis; pedunculo 1.5–2.5 cm longo 1–2 mm diam. ad apicem 2.5–4 mm dilatato dense ferrugineo-tomentoso; perianthio mascula suburceolato 3–4.5 mm longo 1.5 mm lato (immaturo) dense ferrugineo-tomentoso; staminibus 6–8 inclusis.

Tree 8 m, the younger stems with a dense, minutely appressed ferruginous puberulence. Petiole 3–15 mm long, sparsely puberulent; leaf blades subcoriaceous, ovate-elliptic, obtusely acute, or rarely obtuse or rounded at apex, cuneately acute at the slightly asymmetric base, 7.5–14 cm long, 3.5–6.5 cm wide, glabrous above, below minutely puberulent, especially the midrib and nerves, with erect hairs and also with sparse sessile glands on the leaf surface; lateral nerves 10–12 each side, impressed below. Staminate inflorescence terminal, 1–2.5 cm long, 2–2.5 cm wide with 4–5 axes 3–5 mm long, densely ferruginous tomentellose. Bracts subtending flowers ovate, 0.5–1 mm long, densely ferruginous tomentose. Peduncle 1.5–2.5 cm long, 1–2 mm diam., enlarged to 2.5–4 mm wide at the junction above with the lowest primary axes. Perianth suburceolate, 3–4.5 mm long, 1.5 mm wide (immature), densely ferruginous tomentose. Stamens 6–8, included; anthers rhomboid, 0.8–1 mm long.

This species is related to the other newly described species, *Neea neblinensis* Maguire & Steyerm., *N. huachamacarae* Steyerm., and *N. mapourioides* Steyerm., but has smaller perianths and has sparsely puberulent petioles and young stems.

Neea subglabrata Steyermark, sp. nov. TYPE: Venezuela. Bolívar: between Betania and Santa Elena de Uairen, 40 km west of Santa Elena, 4°35'N, 61°28'W, 900 m, 15 Dec. 1978, *Julian A. Steyermark et al. 117615* (holotype, VEN; isotype, NY).

Arbor 15 m, ramulis juvenilibus superne sparsim puberulis pilis laxis 0.1 mm praeditis; petiolis 3–15 mm longis glabris vel sparse puberulis; foliorum laminis oblanceolatis apice acutis vel obtuse acutis basi cuneatim angustatis 4–9.5 cm longis 2.5–4 cm latis ubique glabris, nervis lateralibus utroque latere 6–7 obsolescentibus, venulis tertiariis inconspicuis; inflorescentia mascula subhemisphaerica 1.5–2 cm alta ca. 3 cm lata, axibus primariis 4–6 umbellatim dispositis 5–17 mm longis glabris vel sparsim puberulis, axibus secundariis 2–5 filiformibus umbellatim dispositis 3–5 mm longis plerumque glabris, hic ramosis 1–3 flores ferentibus; pedunculo tenui 2–3.8 cm longo 0.8–1 mm lato apice haud dilatato; bracteis sub floribus lanceolatis 0.8–1.2 mm longis extus parce puberulo-ciliatis; perianthio mascula infundibuliformi 3–3.5 mm longo superne 1–1.6 mm lato basi 0.3 mm lato extus inferne pilis laxis paucis praeditis atque loborum marginibus papillatis aliter glabris; staminibus 6 inclusis.

Tree 15 m, the young branches near tip sparsely laxly pubescent, elsewhere glabrous. Petioles 3–15 mm long, glabrous or with a few sparse, lax hairs; leaf blades opaque, drying dull brown, oblanceolate, acute or abruptly obtusely acute at apex, cuneately narrowed at the equal to slightly asymmetric base, 4–9.5 cm long, 2.5–4 cm wide, glabrous both sides; lateral nerves 6–7 each side, anastomosing 6–8 mm from the margin, the tertiary venation inconspicuous. Staminate inflorescence subhemispherical, 1.5–2 cm high, ca. 3 cm wide, with 4–6 umbellately disposed primary axes 5–17 mm long, glabrous or sparsely laxly pubescent; secondary axes 2–5, filiform, umbellately disposed, 3–5 mm long, glabrous or laxly sparsely pubescent, these branched into pedicellate axes 0.5–2 mm long, each bearing 1–3 flowers subtended by lanceolate, acute bracts 0.8–1.2 mm long, sparsely ciliate-puberulent. Peduncle slender, 2–3.8 cm long, 0.8–1 mm wide, glabrous, not manifestly enlarged at its junction, 1.5 mm wide where united with the lowest primary axes of the inflorescence. Staminate perianth infundibuliform, 3–3.5 mm long, 1–1.6 mm wide at summit, 0.3 mm wide at base, glabrous except for a few sparse hairs near base and papillate-margined lobes. Stamens 6, included; anthers broadly rhomboid, 0.6 × 0.3 mm; filaments 1.5–2 mm long.

Paratype. VENEZUELA. BOLÍVAR: Río Aponguao 2, 151–152 km S of El Dorado, *Gentry et al. 10524* (NY, VEN); Uei-tepui, between Luepa and Cerro Venamo, 1,100–1,300 m, *Steyermark & Nilsson 318* (NY, VEN).

Neea tepuiensis Steyermark, sp. nov. TYPE: Venezuela. Bolívar: Chimantá Massif, Torono tepui, summit, south-facing forested slopes above valley of South Caño, 1,955–2,090 m, 23 Feb. 1955, *Julian A. Steyermark & John Wurdack 1104* (holotype, VEN; isotypes, F, MO, NY).

Arbor 4–5 m praeter gemmas terminales ferrugineas omnino glaberrima; petiolis 2–10 mm longis; foliorum laminis oppositis vel suboppositis plerumque elliptico-ovatis vel obovato-ellipticis vel foliis parvis interdum suborbicularibus apice anguste obtusis vel rotundatis basi praeter folia parva rotundata vulgo subacutis vel anguste acutis (2.7–4.3)7–9.5 cm longis (1.5–3)3.5–5.5 cm latis, nervis lateralibus principalibus utroque latere 5–6; inflorescentia foeminea 1 cm alta 1.7 cm lata (immatura?), axibus primariis quattuor 6–7 mm longis quattuor ramulos parviores 2–3 mm longis gerentibus; perianthio mascula 2 mm longo 0.8 mm lato; infructescentia: axibus primariis 3–4 axes secundarios quattuor subumbellatos 4–7 mm longos gerentibus; pedunculo fructifero terminali 4 cm longo 1–1.5 mm diam. apice haud manifeste dilatato; anthocarpio anguste ellipsoideo-oblongo 9 mm longo 4 mm lato glabro.

Tree 4–5 m tall, glabrous throughout, only the terminal bud glandular-ferruginous pubescent. Leaves opposite or subopposite; petiole 2–10 mm long; leaf blades shining above, elliptic-ovate to obovate-elliptic, or some of the smaller leaves suborbicular, obtuse to rounded at apex, mainly subacute to acutely narrowed at base, or some of the smaller leaves rounded at base, the small leaves 2.7–4.3 cm long and 1.5–4.5 cm wide, but leaves mostly 7–9.5 cm long and 3.5–5.5 cm wide, finely impressed-nerved above, finely and slightly elevated-nerved below, secondary nerves 5–6 each side, faintly anastomosing 5–13 mm from margin, ascending to an angle of 15–20°; tertiary venation slightly evident and reticulate beneath. Pistillate inflorescence 1 cm high, 1.7 cm wide (immature?) with 4 primary axes 6–7 mm long, 0.6 mm wide, each branched into 4 smaller secondary axes 2–3 mm long ending in 3 axes bearing the flowers. Flowers sessile. Pistillate perianth 6 mm long, 2 mm wide. Staminate perianth tubular, glabrous except for the papillate-puberulent lobes at the summit, 2 mm long, 0.8 mm wide. Bracts subtending perianth lanceolate, subacute, 0.8–1 mm long, glandular-pubescent. Infructescence terminal, bearing 3–4 main axes 7–11 mm long and 1 mm wide, these branching into 4 secondary, subumbellate axes 4–7 mm long, these eventually terminating in 4 simple or slightly branched pedicels 1.5–2 mm long bearing the fruits. Anthocarp narrowly ellipsoid-oblong, 9 mm long, 4 mm wide, glabrous, slightly striate.

Paratype. VENEZUELA. BOLÍVAR: Chimantá Massif, Agparamán tepui, forested middle slopes near Río Tirica, 1,365 m, 5 Mar. 1955, *Steyermark & Wurdack 1255* (F, NY, VEN).

This species attains the highest altitude on the sandstone tabular mountains of the Venezuelan Guayana, where it grows at an altitude of 1,365–2,090 m. It is characterized by the glabrity of all parts and is distinguished from *N. robusta* Steyerm. by its smaller flowers and inflorescences and by the obsolete venation of the tertiary veinlets. From *N. subglabrata* Steyerm. it differs in leaf shape, greater diameter of the peduncle, usually subobtuse to rounded leaf apices, lustrous upper surface of leaves, and subelevated, subreticulate tertiary venation of the lower leaf surface.

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BRUNELLIACEAE

BRUNELLIA

Brunellia neblinensis Steyermark & Cuatrecasas, sp. nov. TYPE: Venezuela–Brazil border. Cerro de La Neblina, en bosque alto, 1,500 m, 29 Apr. 1964, *J. Ewel 209* (holotype, NY).

Arbor, foliis oppositis imparipinnatis 6-jugatis; foliolorum laminis haud discoloribus chartaceis elliptico-oblongis apice acutis basi acutis vel subobtusis 15–18.5 cm longis 4.5–6 cm latis crenato-serratis, pagina superiore glabra pagina inferiore praeter costam mediam nervosque minute puberulis, pilis patulis munitis, venulis tertiariis subtus impressis prominulis; nervis lateralibus 16–17 utroque latere distantibus 8–12 mm; foliolis inferioribus 1–2 mm petiolatis; infructescentia dense minuteque tomentosa, calyce 4–5 lobato 3.5–4.2 mm longo, dense tomentoso, lobis triangulari-lanceolatis acutis 1.5–1.8 mm longis 1–1.2 mm latis; folliculis subrotundatis 3 mm longis 2.5 mm latis dense hirtellis basi pilis hispidis munitis; seminibus obconico-subglobosis subcompressis 3 mm longis 2.5 mm latis.

Tree with opposite imparipinnate leaves. Leaf rachis minutely puberulent. Leaflets in 6 pairs, not discolored, chartaceous, elliptic-oblong, acute at apex, asymmetrically acute to subobtuse at base, 15–18.5 cm long, 4.5–6 cm wide, crenate-serrate, the upper leaflets sessile, the lower ones 1–2 mm, shortly petiolate; lower surface glabrous, except minutely puberulent with short spreading hairs on midrib, lateral nerves, and tertiary veinlets; upper surface glabrous. Infructescence densely tomentellose, the branches 1 mm diam. Calyx 4–5-lobed, 3.5–4.2 mm in fruit, densely hirtellous, the lobes triangular-lanceolate, acute, 1.5–1.8 mm long, 1–1.2 mm wide. Follicles subrotund, 3 mm long, 2.5 mm wide, densely hirtellous with additional hispid hairs at base. Seeds shining, obconic-subglobose, narrowed toward one end, 3 mm long, 2.5 mm wide.

This taxon differs from *Brunellia comocladifolia* Humb. & Bonpl. and especially the subsp. *ptariana* (Steyerm.) Cuatrec. in the smaller follicles, shorter calyx with slightly narrower calyx lobes, larger seeds, and the glabrous lower leaf surfaces, except for the minutely tomentellose nerves. From *B. hygrothermica* Cuatrec. it may be distinguished by the concolorous leaves with glabrous lower leaf surface, more numerous pairs of lateral nerves, more depressed and less conspicuous serrations, and shorter calyx. From *B. gentryi* Cuatrec. it is differentiated by the slightly larger calyx diameter, larger calyx lobes, longer and numerous hispid hairs of the follicles, and concolorous leaves not silvery green beneath.

SAPINDACEAE

MATAYBA

Matayba ptariana Steyermark subsp. *guaiquinimae* Steyermark, subsp. nov. TYPE: Venezuela. Bolívar: Departamento Heres, Meseta de Guaiquinima, sector NE de la meseta, cerca de la cumbre, 5°58′N, 63°29′W, 1,400 m, 27 Mar. 1985, *Otto Huber 10388* (holotype, MO; isotypes, NY, VEN).

A subsp. *ptariana* foliolis minoribus apice rotundatis, venulis tertiariis haud elevatis, calycis lobis suborbicularibus dense adpresso-pubescentibus, petalorum squamis interioribus longitudinem petali aequantibus recedit.

Shrub, 2–3 m tall. Leaves bifoliate, glabrous, the leaflets oblong, rounded at the apex, subobtuse or subacute at the base, 2–4 cm long, 1–2.2 cm wide. Inflorescence axillary, 4.5 cm long, the flowering part 2.5 cm long, 6–7 mm wide, subracemose, 23-flowered. Peduncle 2 cm long, 1 mm wide, solitary, minutely appressed-pubescent; bracts ovate-oblong, subacute, 0.7–1 mm long, 0.5 mm wide. Pedicels 2 mm long, densely pubescent with ascending, appressed, pale hairs. Calyx lobes 5, broadly suborbicular-ovate, rounded to obtuse, appressed pubescent without, 1 × 1 mm, sericeous within. Petals pilose-ciliate, suborbicular, broadly rounded above, abruptly short-unguiculate at base, 1.3 mm long, 1.6 mm broad; 2 inner segments oblong, rounded, 1 mm long, 0.8 mm wide, densely pilose both sides. Stamens 8, exserted; anthers suborbicular, 0.8 mm long; filaments 1.7–1.8 mm long, pilose below, glabrous above the middle; disk cupulate, glabrous, 0.5 mm high.

At first, this collection appeared to be distinct from *Matayba ptariana.* However, a second collection (*Huber 10339*), assigned to subsp. *ptariana,* in fruit from a lower altitude at 480 m ("Río Trueno, 35 km west of caserio of Chiguao"), although showing the rounded leaf apices together with inconspicuous impressed veinlets on the lower surface of the new subspecies, has much larger leaflets and longer petioles similar to typical *M. ptariana* subsp. *ptariana.* Until additional material is forthcoming, it seems best to retain a subspecific rank for the Huber collection of the higher altitude.

BOMBACACEAE

NOTES ON *CATOSTEMMA* AND *SCLERONEMA* (BOMBACACEAE)

In the course of preparation of the genus *Catostemma* for the *Flora of the Venezuelan Guayana,* it was found that all the Venezuelan material had been identified either as *C. commune* Sandw. or had remained unidentified. An examination of available material in the herbaria of F, K, MO, NY, US, and VEN indicated that more than one species of *Catostemma* was represented in Venezuela and revealed further the presence of the genus *Scleronema.* The present study includes an attempt to delimit the genus *Catostemma* in Venezuela, together with a description of a new species in *Scleronema.*

Publications by Sandwith (1931, 1948), Ducke (1937), and Paula (1969) have greatly enhanced our knowledge of both genera with the result that the characters differentiating *Catostemma* from *Scleronema* can now be more clearly defined, involving chiefly stamen differences. In *Scleronema* the filaments are dilated and thickened apically with the small, strongly sessile anther appressed across the summit of the filament, whereas in *Catostemma* the uniformly slender filaments bear a larger incumbent anther folded inward over the summit. Additional differences are the longer and more numerous filaments and longer style branches in *Catostemma,* also from available fruiting material, the elongated, ellipsoid, oblong, or obovoid, tardily dehiscent fruit of *Catostemma* as opposed to the globose or subglobose, indehiscent fruit of *Scleronema.*

Sandwith (1931) was able to differentiate two species of *Catostemma* from Guyana, *C. commune* Sandw. and *C. fragrans* Benth., on the basis of vegetative characters found in the seedling leaves and in the venation, especially of the lower leaf surface. In the present study vegetative differences have been noted and employed to distinguish several taxa. Unfortunately, leaves of seedling plants are still unknown from most of the taxa recognized. In addition to the type of tertiary venation of the lower leaf surface, useful characters have been found in the glabrity or stellate tomentum of the buds and petioles. Moreover, the absence or presence of stellate tomentum and its distribution on the style and style branches, and the presence of bracteoles and their position on the pedicels serve to delimit various taxa within the complex. Much of the material in herbaria is sterile or lacks flowers, and this has made delimitation of the taxa difficult.

The author wishes to acknowledge to the curators of F, K, MO, NY, US, and VEN his great appreciation for the loan of herbarium material. Based on the material examined, a description is provided for the taxa of *Catostemma,* together with a citation of specimens, followed by a key to the species.

CATOSTEMMA

KEY TO THE SPECIES OF *CATOSTEMMA*

1a. Adult leaves compound .... *C. digitatum*

1b. Adult leaves simple 2

  2a. Petioles and young stems hirsutulous with spreading to ascending stiffish hairs 0.2–0.4 mm long .... *C. hirsutulum*

  2b. Petioles and young stems glabrous or with minute or closely appressed tomentum 3

   3a. Petioles and young stems stellate-tomentose 4

    4a. Petioles and young stems covered with a minute, gray, stellate tomentum; tertiary venation of lower leaf surface irregular or scarcely evident; lower leaf surface glabrous; bracteoles absent from pedicels; lateral nerves of leaf blades 5–6 each side; style and style branches sparsely stellate-pubescent .... *C. clarkii*

    4b. Petioles and young stems stellate-tomentose with larger, less crowded tomentum; tertiary venation of lower leaf surface more or less regular, subparallel and subhorizontal; lower leaf surface minutely stellate-pubescent to glabrous; bracteoles present on pedicels; lateral nerves of leaf blades 8–12 each side; style glabrous except at base .... *C. fragrans*

   3b. Petioles and young stems glabrous 5

    5a. Tertiary veins of lower leaf surface in more or less subparallel lines obliquely connecting the lateral nerves .... *C. marahuacense*

- 5b. Tertiary veins of lower leaf surface irregularly reticulate and anastomosing, not regularly obliquely parallel 6
  - 6a. Style stellate-pubescent throughout; stylar branches stellate-pubescent; bud scales with minute, appressed, stellate pubescence .... *C. pubistylum*
  - 6b. Style glabrous except at base or lowest ⅓; stylar branches glabrous; bud scales glabrous or the innermost ones pilose 7
    - 7a. Bracteoles absent from pedicels; calyx lobes densely strigose within; innermost bud scales pilose apically .... *C. ebracteolatum*
    - 7b. Bracteoles present, either on the pedicels or immediately subtending the base of the calyx; calyx lobes glabrous within or partly strigose near apex; bud scales glabrous 8
      - 8a. Bracteoles either immediately subtending the calyx or on the uppermost 1–6 mm of the pedicel; leaves without revolute margins 9
        - 9a. Pedicels with congested stellate tomentum, the scales more or less contiguous or overlapping with numerous, relatively elongated rays; leaf base mainly acute to cuneate, more rarely obtuse .... *C. commune*
        - 9b. Pedicels with moderately stellate tomentum, the scales minute, scattered and more separated with fewer and shorter rays; leaf base mainly rounded, or sometimes subcordate .... *C. sclerophyllum*
      - 8b. Bracteoles, at least some of them, toward or below the middle of the pedicel; leaves usually with revolute margins 10
        - 10a. Pedicels 4–10 cm long; principal lateral nerves of the leaves 8–12 each side; leaf blades up to 30 cm long and 11.5 cm wide; petals 17–23 mm long; tree 10–45 m tall .... *C. altsonii*
        - 10b. Pedicels 2.5–3 cm long; principal lateral nerves of the leaves 4–6 each side; leaf blades up to 15 cm long and 4.5 cm wide; petals 15 mm long; shrub 2–4 m tall .... *C. sancarlosiana*

Catostemma altsonii Sandw., Kew Bull. 1928: 366. 1928. TYPE: Guyana. Macreba Falls, Kurupung River, Sept. 1925, *Altson 391* (holotype, K). Figure 6A, a.

Tree, 10–45 m tall, the branchlets glabrous; bud scales glabrous. Seedling leaves 3-foliate. Mature leaves with petioles 0.8–6 cm long, glabrous; leaf blades thick-coriaceous, elliptic-oblong to cuneate-obovate, broadly obtuse or rounded and mucronate at apex, narrowed to a cuneate or obtuse base, 8–30 cm long, 3–11.5 cm wide, glabrous, the margins revolute; primary lateral nerves 8–12 each side, impressed above, slightly elevated below, at irregular angles and not uniformly ascending, branching or anastomosing before reaching the margins, 7–25 mm apart; tertiary venation of the lower leaf surface irregularly reticulate, usually prominulous, usually impressed above on sterile branchlets. Pedicels in anthesis 4–10 cm long, densely stellate-tomentose with brown or pale hairs, with 2–3 bracteoles, these squamiform, 0.5–2 mm long, 1–2 mm wide, ovate, subacute, situated alternately and usually distantly below and above the middle. Calyx densely stellate-tomentose without, 13–15 mm long, the tube 3–5 mm long, the lobes ovate-oblong, obtuse, 10 mm long, glabrous within. Petals obovate-oblong, rounded, 17–23 mm long, 7–8 mm wide. Stamens ca. 35–40; filaments 10–14 mm long; anthers 1–1.3 mm long. Style 10 mm long, glabrous except in lowermost 4–6 mm, there stellulate; style branches 2–3.5 mm long, glabrous. Mature fruit ellipsoid, 15–20 cm long, 3–5 cm diam.; immature fruit obovoid-oblong, ca. 5 cm long, 2 cm diam., minutely ferruginous furfuraceous, fruiting pedicel 5.5–7 cm long.

Distribution. Wallaba forest at 50–125 m elevation; known only from Guyana.

Additional specimens examined. GUYANA: Macreba Falls, Kurupung River, Mazaruni tributary, *Altson 391* (K, type); Essequibo-Mazaruni Divide, about 25 mi. south of Bartica, *Forest Dept. Record No. 2316* (*Field No. D323*) (K); Membaru creek, upper Mazaruni River, *Forest Dept. Record No. P71* (*Field No. 2843*) (K); 107 m Bartica–Potaro road, *Forest Dept. Record No. F1520* (*Field No. 4256*) (K); 1½ mi. Bartica–Potaro road, *Forest Dept. Record No. 6906* (*Field No. CAP149*) (K); near 14th milepost, Bartica–Potaro road, *Sandwith 1124* (K, NY, US); Essequibo–Mazaruni Divide, ca. 25 mi. S of Bartica, *Davis 2315* (K); same locality, *Forest Dept. Record No. 2315* (*Field No. D372*) (K); Potaro River below Tukeit, *Maguire & Fanshawe 23486* (NY); Bartica–Potaro road, 24 mi. south of Bartica at Forest Service's "24 mile Camp," 50–125 m, *Mori et al. 8902* (NY); Membaru Creek, Upper Mazaruni River, *Pinkus 238* (F, NY, US); Bartica–Potaro road, *Forest Dept. No. 107* (*Field No. F 1520, Record No. 4256*) (NY).

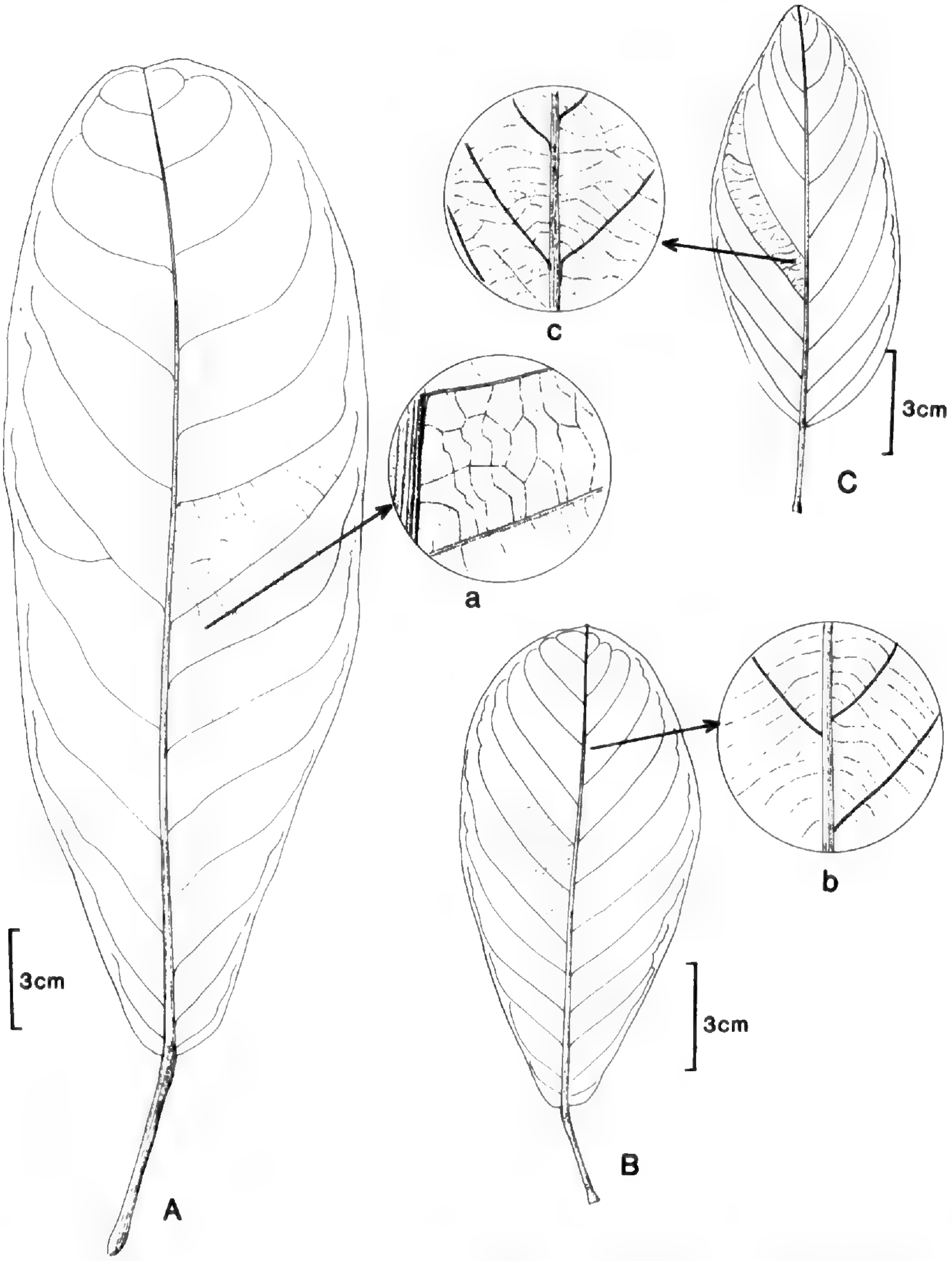

FIGURE 6.—A. *Catostemma altsonii,* leaf. a. Detail of lower leaf surface showing irregularly reticulate tertiary venation.—B. *Catostemma fragrans,* leaf. b. Detail of lower leaf surface showing subparallel, subhorizontal tertiary venation.—C. *Catostemma marahuacense,* leaf. c. Detail of lower leaf surface showing subparallel, subhorizontal tertiary venation. Based on holotype.

Two other species of *Catostemma* are known from Guyana. The present taxon may be distinguished from *C. fragrans* Benth. by the glabrous buds, petioles, and young stems, by the irregularly reticulate tertiary venation on the lower leaf surface, and by the irregular branching of the main lateral nerves. From *C. commune* it can be differentiated by the completely glabrous style and style branches, much smaller bracteoles, longer pedicels, longer petals and calyx lobes, and proportionately longer leaf blades.

Catostemma clarkii Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Mari's bana (low Amazon caatinga), 10.8 km NE of San Carlos on road to Solano, 1°56'N, 67°03'W, 119 m, 19 Aug. 1981, *Howard L. Clark 8126* (holotype, MO).

Arbuscula vel frutex; gemmis ramulis juvenilibusque minute confertimque cano-stellato-tomentellis; petiolis minute cano-stellatis; foliorum laminis subtus praeter costam mediam minute stellatam laminarum juvenilium glabris anguste obovatis, nervis lateralibus utroque latere 5–6; pedicellis minute confertimque cano-stellatis; bracteolis desunt; calyce extus dense stellato-tomentello intus lobis glabris; petalis 20–22 mm longis; stylo sparsim stellato-tomentello ramis 4–5 mm longis leviter stellatis.

Shrub or small tree to 12 m; young stems densely and minutely gray stellate-tomentellose; older branches glabrous. Petioles 4–25 mm long, minutely and densely gray stellate-tomentellose on young leaves, minutely gray stellate to glabrescent on mature leaves; leaf blades narrowly obovate, rounded or retuse at apex, mucronulate in the sinus, narrowed to a rounded or subcordate base; mature leaf blades rigid-coriaceous, 4.5–10.5 cm long, 2–4.5 cm wide, glabrous throughout except for the sparsely stellate basal portion of the lower midrib; young leaves minutely gray stellate-tomentellose on the lower midrib; main lateral nerves 5–6 each side, scarcely manifest, lightly impressed on the upper side, branching before reaching the margins, 8–15 mm distant; tertiary venation beneath inconspicuously anastomosing. Pedicels ebracteolate, ca. 3.2 cm long, densely and minutely gray stellate-tomentellose. Petals ligulate-oblong to subspatulate, 20–22 mm long, 6–9 mm wide. Calyx densely stellate without, the tube campanulate, 4 mm long, the lobes ovate, obtuse, 11 mm long, glabrous within. Stamens numerous, about 40; filaments 12–13 mm long; anthers 0.8–1 mm long. Ovary conic, 7 mm long, 3 mm diam., tapering to an elongate beak 2.7 mm long. Style 9 mm long, sparsely stellate-pubescent from base to apex, the branches 4–5 mm long, lightly stellate-pubescent. Fruit ellipsoid, 6–6.5 cm long, 4.5 cm diam., fruiting pedicel 4.5 cm long.

Paratype. VENEZUELA. Same locality as type, 1 Jan. 1979, *Clark 6919* (MO).

This species is characterized by the minute, pale gray, closely stellate tomentum of the vegetative buds, young petioles, and lower midrib of the early leaves, by the sparsely stellate pubescence on style and branches, and by the scarcely manifest tertiary venation of the lower leaf surface. The stellate tomentum of this species is the most minute of the genus.

Catostemma commune Sandw., Kew Bull. 1931: 51. 1931; Oliver in Hook. Icon. Pl. 1986. 1891, as to flowers and leaf, but not to fruit. TYPE: Guyana. Moraballi Creek, Essequibo River, Aug. 1929, *Sandwith 435* (holotype, K).

Tree to 45 m. Young branches and stems and bud scales glabrous. Seedling leaves usually 3-foliate (rarely 2- or 4–5-foliate), the leaflets oblanceolate, obliquely acuminate at the apex, the acumen triangular-lanceolate, 1–1.8 cm long, 3–6 mm wide above the middle, obtuse, but the midrib excurrent, cuneately attenuate at base except for the rounded lower side of the outer leaflets, 9–32 cm long, 3–8 cm wide, glabrous both sides. Mature leaves with petioles 1–9 cm long, glabrous. Mature leaf blades stiffly chartaceous or subcoriaceous, elliptic or obovate, rounded or retuse at apex, mucronulate with excurrent costa, cuneate to rarely obtuse at base, 4–19 cm long, 2–9 cm wide, glabrous on both sides; main lateral nerves 8–12 each side, impressed above, slightly elevated below, ascending at an angle of 40–50°, branching and anastomosing just before reaching the margins, 8–15 mm distant; tertiary venation faintly impressed-reticulate above, irregularly reticulate with slightly elevated veins below. Pedicels 0.5–2 or 3 cm long, densely stellate-tomentose, bracteolate. Bracteoles paired, approximate, overlapping, alternate, squamiform or rarely conspicuous, situated in the upper part of the pedicel or immediately subtending the calyx, ovate or suborbicular, obtuse to subacute, 1.5–2.8(–6) mm long, 1–1.5(–4.5) mm wide. Calyx densely stellate-tomentose without, the tube campanulate, 4 mm long, 3–4 mm wide; lobes ovate, 7 mm long, 6 mm wide. Petals oblong-spatulate, obtuse, 12 mm long, 4–5 mm wide. Stamens numerous, 40–50; filaments 8–10 mm long; anthers 0.8–0.9 mm long. Style 13 mm long, stellate-tomentose in lower ⅓, elsewhere glabrous; style branches 0.75–1.5 mm long. Fruit oblong-ellipsoid, 7–10 cm long, 3–4 cm diam., densely ferruginous tomentellous.

Common names. Baromalli, common baromalli (Guyana), baramán (Venezuela).

Distribution. In mixed tall forest of greenheart, mora, and morakubea of Guyana, principally in the Essequibo and Cuyuni river basins, and in evergreen mixed forests, often with *Eperua,* in Estado Bolívar and Territorio Federal Delta Amacuro of eastern Venezuelan Guayana, at altitudes of 80–850 m.

Additional specimens examined. WEST INDIES: cultivated in Old Botanic Gardens, St. Vincent, April 1891, *H. Powell* (K). GUYANA: Moraballi Creek, Essequibo River, near Bartica, near sea level, *Sandwith 116* (holotype, K; isotype, NY), *435* (seedling leaves, K, NY); Mazaruni Station, *Forest Dept. Record No. 2398* (*Field No. D402*) (K); Upper Mazaruni River, *Leng 416* (seedling leaves, NY); Matthews Ridge, Barima River, Northwest Territory, 80 m, *Cowan 39361* (F, NY), *39361-A* (fruit, NY); Puruni, 35 m, *Field No. JB 28, Forest Dept. Record No. 7712* (K, NY); Cuyuni River, *Tutin 338* (K, US). VENEZUELA: TERRITORIO FEDERAL DELTA AMACURO: este de Río Grande, este-noreste de

El Palmar cerca de los limites del Estado Bolívar, Nov. 1965, *Carlos Blanco 495* (MO, US, VEN); La Paloma, Río Cuyubini, Sierra Imataca, 100–200 m, *Steyermark 87583* (F, MO, NY, US, VEN); El Morro, Atabuina, Caño Arature, base of Sierra Imataca, 750 m, *Bernardi 7529* (K, NY, VEN); same locality and date, *Buza 329* (K, NY, VEN); near Río Grande, east of Upata, border between Estado Bolívar and Territorio Federal Delta Amacuro, 8°14'N, 61°4'W, 300 m, *de Bruijn 1631* (F, K, MO, NY, US, VEN), *1677* (US, VEN), *1623* (F, MO, NY, US, VEN); same locality, *Breteler 3841* (seedling leaves, NY, US), *4958* (NY, US), *4972* (NY); ENE de El Palmar, cerca de los limites del Estado Bolívar, *Zabala 96* (VEN), *163* (VEN). BOLÍVAR: base of Cerro Pauji, Quebrada 94, km 94 south of El Dorado, 250 m, *Steyermark 86711* (NY, US, VEN), *86712* (VEN), *86715* (F, US, VEN); La Isabel a Río Grande, El Palmar, *Conejos 36* (MO, VEN); Cerro La Reforma, above junction of Río Reforma with Río Toro (Río Grande), Sierra Imataca, 200–250 m, *Steyermark 88113* (NY, VEN); Pica La Lira trail, km 27 S of El Dorado, 220 m, *Steyermark 86640* (K, US, VEN); 5–7 km E of El Cruzero, ESE of Villa Lola, Altiplanicie de Nuria, 315 m, *Steyermark 86049* (seedling leaves, NY, VEN); Río Chirca, *Bernardi 898* (3-foliolate leaves, NY); east of El Palmar, *Marcano-Berti 319* (VEN); Río Caroni, between mouth of Río Aparurén and Urimán, 400 m, *Steyermark 76077* (F, VEN); región de las cabeceras del Río Hacha, 450–850 m, *Bernardi 2897* (NY); Río Caura, arriba del Salto Para, 2–3 km arriba del campamento "Las Pavas," 250–300 m, *J. Steyermark, G. C. K. & E. Dunsterville 112934* (MO, VEN); same locality, *Morillo & Liesner 8944* (MO, VEN); 30 km S of El Dorado, 140 m, *Bernardi 2097* (NY, VEN); Río Venamo, afluente del Ikabarú, *Cardona 1706* (VEN); Río Curutú, upper Paragua, 550 m, *Cardona 2484* (VEN); Salto Ichun, Río Ichun, tributary of Río Paragua, 4°46'N, 63°18'W, 500 m, *Steyermark 90371* (VEN); El Abismo, Río Samay, 4°27'N, 61°34'W, 550–600 m, *Holst & Liesner 2422* (MO, VEN).

In Sandwith's excellent discussion of the baromallis (*Catostemma*) of Guyana (1931), a number of characters were noted by which *C. commune* Sandw., or common baromalli, could be distinguished from *C. fragrans* Benth., or sand baromalli, the latter being the type species of the genus based on a collection by *Robert Schomburgk 280* in 1837 from Berbice, Guyana. One of the differentiating characters mentioned by Sandwith to distinguish *C. commune* was the "large and conspicuous" bracteoles. Sandwith described these as 5–6 mm long and to 4.5 mm wide and noted that they were illustrated in Oliver's figure under the erroneous epithet of *C. fragrans* (plate 1986 of Hook. Icon. Pl., 1891). Bracts conforming to these dimensions are evidenced by a specimen at K which had been sent from the Old Botanic Garden of St. Vincent, collected by H. Powell in April 1891, where it had been cultivated for many years. This specimen was cited by Sandwith as a paratype. However, the actual type specimen at K (*Sandwith 116*) does not have either large or conspicuous bracts. Thus, the only flowering material available to Sandwith was his own collection (the type) and that of Powell from a cultivated specimen.

Three subsequently collected specimens from the wild state show small squamiform bracts only, which do not exceed 2.8 mm in length and 1.5 mm in width. These bracts or bracteoles subtend the very base of the bud, as in *Tutin 338* and *Forest Dept. Record No. 7712* (both at K), or occur on the uppermost 1–6 mm of the pedicel below the base of the calyx, as in *Forest Dept. Record No. 2398, Davis 402* (K). All these specimens were annotated by Sandwith as *C. commune* Sandw. Similarly, flowering collections of this species from adjacent eastern Venezuela show only squamiform bracts situated on the uppermost 1–6 mm of the pedicel.

Thus, the description of the bracts in *C. commune* should be emended as follows: "bracteis squamiformibus late ovatis vel suborbicularibus obtusis vel subacutis 1.5–2.8(5–6) mm longis 1–1.5(–4.5) mm latis binis vel arcte alternantibus."

Catostemma digitatum Shepherd & Alverson, Brittonia 33: 587, fig. 1. 1981. TYPE: Colombia. Antioquia: confluence of Quebrada La Tirana and Río Anori, 3 km upriver (SW) from Planta Providencia, ca. 28 km SW of Zaragota, 7°13'N, 75°3'W, 500 m, 9 Apr. 1977, *W. S. Alverson, S. White & E. J. D. Shepherd 397* (holotype, COL).

Tree to 30 m; young branches or stems glabrous. Buds sericeous-tomentose. Mature leaves 3–5-palmately compound. Petioles 6–21 cm long, glabrous. Leaf blades chartaceous, lanceolate, long-caudate in seedling leaves, subacute or obtuse and mucronulate in mature leaflets, acute at base, mainly glabrous; principal lateral nerves 10–16 each side, arcuately ascending near the margins; tertiary venation below irregularly laxly reticulate, scarcely prominulous. Flowers unknown. Fruit obovoid, 9–12 cm long, 5.5–6 cm diam.; seed 5–7 cm long, 2–4 cm wide.

Distribution. Known only from the departments of Antioquia and Santander, Colombia.

Additional specimens examined. COLOMBIA. ANTIOQUIA: confluence of Quebrada La Tirana and Río Anori, 28 km SW of Zaragota, 7°13'N, 75°3'W, 500 m, *Alverson, White & Shepherd 397* (holotype, COL; isotypes, HUA, MO, NY, WIS); slope facing Río Anori, near Planta Providencia, *Denslow 1404* (seedling, COL, HUA, MO, NY, WIS); confluence of Quebrada

La Tirana and Río Anori, 3 km upriver (SW) from Planta Providencia, ca. 28 km SW of Zaragota, 7°13′N, 75°3′W, 500 m, 9 Apr. 1977, *W. S. Alverson, S. White, & E. J. D. Shepherd 397* (holotype, COL). SANTANDER: Magdalena Valley, Campo 30 km E of Carare, 300 m, *Gentry & Renteria 20065* (COL, MO, UIS), *20106* (COL, MO, UIS).

This is the only species thus far known in the genus with the mature leaves compound.

Catostemma ebracteolatum Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Cerro Sipapo (Paráque), water course above Intermediate Camp, 2 Feb. 1949, *Bassett Maguire & Louis Politi 28741* (holotype, MO; isotype, NY).

Arbor 15–30 m, ramulis juvenilibus glabris; gemmae squamis intimis acuminatis pilosis extimis caudatis; petiolis 3–35 mm longis glabris; foliorum laminis obovatis apice rotundatis retusisque mucronulatis basi acutis vel cuneatis majoribus 6–10 cm longis 2.5–6.5 cm latis ubique glabris, nervis lateralibus utroque latere 7–9 supra impressis subtus leviter elevatis, venatione tertiaria subtus leviter irregulariterque reticulatis; pedicellis 1.5–4 cm longis pilis dimorphis munitis, pilis brunneis minoribus stellato-tomentosis et pallidis longioribus patulis plus minusve serialibus alternantibus ebracteolatis; calyce extus stellato-tomentoso, tubo 4 mm longo, lobis suborbiculari-ovatis obtusis 7–8 mm longis intus dense strigosis; petalis ligulato-oblongis 15 mm longis; filamentis ad 9 mm longis; stylo parte inferiore ⅓ usque ½ stellato-tomentoso ceterum glabro, ramis ad 4 mm longis glabris.

Tree 15–30 m tall, the young stems glabrous; innermost bud scales acuminate, pilosulous, the others glabrous, the outermost caudate. Seedling leaves trifoliolate. Petioles 3–35 mm long, glabrous; leaf blades coriaceous, rich green above, paler below, obovate, rounded and retuse at apex, mucronulate, narrowed to an acute or cuneate base, 6–10 cm long, 2.5–6.5 cm wide, glabrous; lateral nerves 7–9 each side, spreading at first from an angle of 10–20°, then ascending, branching before reaching the margins, impressed above, lightly and narrowly elevated on the lower side; tertiary venation irregularly and inconspicuously reticulate below. Pedicels costate, especially toward apex, 1.5–4 cm long, ebracteolate, with 2-tiered pubescence, the shorter brownish, appressed, stellate-tomentose hairs between paler longer hairs ± prominently spreading from pseudovertical rows. Calyx in pre-anthesis 12.5 mm long, split above the side from one portion, densely stellate without, 4 mm long, 3–5 mm wide above; lobes longer than the tube, 7–8 mm long, suborbicular-ovate, obtuse, densely strigose within. Petals ligulate-oblong, rounded, 15 mm long, 5–6 mm wide. Stamens 25–30; filaments up to 9 mm long; anthers 0.8–0.9 mm long. Style pubescent for 2.5–4.5 mm from the base up to ⅓–½ of the length, glabrous above; style branches up to 4 mm long, glabrous. Fruit orange, rounded at apex, manifestly narrowed to the base, obtusely 3-costate, 7 cm long, 4 cm diam., minutely tomentellose; fruiting pedicel 4 cm long, 5 cm diam.

Paratypes. VENEZUELA. BOLÍVAR: Sierra Ichún, cercanías del Salto María Espuma (Salto Ichún), base of la Sierra Ichún, tributary of Río Paragua, 4°46′N, 68°18′W, 500 m, 28 Dec. 1961, *Steyermark 90371* (F, NY, US, VEN). TERRITORIO FEDERAL AMAZONAS: 4.3 km NNE of San Carlos on Solano road, 1°56′N, 67°3′W, 119 m, *Clark & Maquirino 8081* (MO); Río Cataniapo, 44–45 km SE of Puerto Ayacucho, 5°35′N, 67°15′W, 100–300 m, *Steyermark, Davidse & Guanchez 122136* (MO, VEN), *112386* (MO, VEN), *122402* (MO, VEN); Sierra Parima, headwaters of Río Siapa and Río Padauiri, 1°22′N, 64°38′W, 1,260 m, *Cardona 1507* (US, VEN); Yavita, *Lizot 1972-4* (US, VEN).

This taxon differs from other members of the genus in its two-tiered pubescence on the pedicel, with longer, pale, spreading hairs in more or less separate vertical rows or lines rather prominently differentiated from the more abundant, smaller, brownish, more appressed stellate tomentum in between. In the other species of the genus the stellate tomentum is more uniformly appressed, pale to dark brown, and uninterrupted by longer hairs.

Catostemma fragrans Benth. in Hook. London J. Bot. 2: 365. 1843; Baker in Hook. Icon. Pl. 1793. 1888; Oliver in Hook. Icon. Pl. 1986. 1891, as to fruit. TYPE: Guyana: Berbice, 1837, *Rob. Schomburgk 280* (holotype, K). Figure 6B, b.

Guenetia macrosperma Sagot ex Benoist, Bull. Mus. Hist. Nat. (Paris) 25: 387. 1919. TYPE: French Guiana: Acarouany, *Sagot s.n.* (holotype, P).

Tree (4–)15–30 m tall. Young branches or stem stellate-tomentose. Buds stellate-tomentose. Seedling leaves simple, 12–38 cm long, 3–7 cm wide, obovate-oblong or obovate-elliptic, narrowly elongated, cuspidate at apex, the cuspidate portion linear-subulate, this 1–5 cm long, 0.7–2.5 mm wide, narrowed to a subobtuse to subrotundate base. Mature leaves with petioles 0.5–5 cm long, stellate-tomentose; mature leaf blades coriaceous or subcoriaceous, obovate-oblong, obovate-elliptic, or oblong-elliptic, rounded or retuse, sometimes cuspidate at apex, rounded at base, the larger ones 17–22 cm long, 3–8 cm wide, glabrous above, glabrous to sparsely stellate-puberulent below, sparsely to moderately stellate-pubescent on the lower midrib and main lateral nerves; lateral nerves commonly 8–12 each side, impressed above, elevated below, ± regularly ascending at an angle of 45–60° and subparallel nearly to the margins, 5–20 mm distant; tertiary venation inconspicuous above, below conspicuous and elevated with the veins subparallel and subhorizontal. Pedicels 1.5–4 cm long, densely stellate-tomentose, bracteolate. Bracteoles 2 or 3, situated near the middle or in the lower or upper part of the pedicels, sometimes only 2–3 mm below the base of calyx, paired or usually proximate alternately, ovate, obtuse, 1–2.5 mm long, 1 mm wide. Calyx densely stellate-tomentose without, the tube 3–4 mm long, 4–5 mm wide, the lobes broadly ovate or ovate-oblong, obtuse, 9 mm long, 4–7 mm wide, glabrous within. Petals spathulate-oblong, obtuse, 13–15 mm long, 4–7 mm wide. Stamens about 35–40; filaments 7–8 mm long; anthers 1–1.2 mm long. Style 11–15 mm long, glabrous except stellulate at the very base, the style branches 1.5–2 mm long, glabrous. Fruit oblong-ellipsoid, 4–8 cm long, 3–3.5 cm diam., densely and minutely ferruginous tomentellous; fruiting pedicel 2 cm long.

Common names. Sand baromalli, baromalli or wallaba; baromalli (Guyana); kajoewaballi barmani (Suriname).

Distribution. Sandy soils of wallaba forests at low elevations in Guyana, Suriname, and French Guiana.

Additional specimens examined. GUYANA: near Bartica, Moraballi Creek, Essequibo River, near sea level, *Sandwith 485* (K, NY); Coverden, *Persaud 134* (F, NY); basin of Essequibo River, near mouth of Onoro Creek, 1°35′N, *A. C. Smith 2739* (F, MO, NY, US); Barima River, Northwest District, 8°20′N, 59°50′W, *de la Cruz 3348* (MO, NY, US); Bartica–Potaro road, 24 mi. from Bartica, *Mori et al. 8115* (NY); Bamboo Creek, Rewa River, 35 mi. SSE of mouth, *Forest Dept. Record No. 2087* (*Field No. D96*) (K); lower Demarara River, *Jenman 4336* (K); Mora-mora-bisi Creek, Mapenna River, Corentyne River, *Hohenkerk* in *Forestry Dept. Record No. 794* (K); Kamwatta Creek, Koirimap River, Pomeroon River, *Hohenkerk* in *Forest Dept. Record No. 704-A* (K); Santa, Pokoraro Creek, Kamuni River, Demarara River, *Hohenkerk 704-C* (K). SURINAME: km 6, Wijneweg, "*B.B.S. 174*" (K, MO); Wayombo, *Wood Herbarium 352* (K, NY); Maratakka River, Snake Creek, *Maas 10799* (K, NY, U); Corantynes *B.B.S. 901* (K); Tafelberg, *Maguire 25069*; Foengoe Island, Nat. Park Raleigh Falls, *Roberts 14764* (NY); Christianburg, Demarara River, *Anderson 271* (K); Wilhelmina Gebergte, 2 km below affluence of Oost River, 225 m, *Maguire et al. 54098* (MO, NY). FRENCH GUIANA: south of Crique Gregoire, Sinnamary River, *Oldeman 1600* (NY); *Sagot & Melinon* (photo of *Guenetia macrosperma,* F, MO); Godebert, *Wachenheim s.n.* (K) (as *Guenetia macrosperma*).

This species is the most widely distributed of the species of *Catostemma,* being found in all the Guianas, where it is common, especially in the wallaba forests of Guyana. It differs from the common taller forest species *C. commune* Sandw. in it stellate-pubescent bud scales, petioles, and young stems; simple, long-cuspidate seedling leaves; completely different venation of the lower surface of both seedlings and mature leaves; style glabrous throughout, except at very base; and somewhat shorter, usually alternately arranged bracteoles on the pedicels.

Catostemma hirsutulum Steyermark, sp. nov. TYPE: Venezuela. Bolívar: Chimantá Massif, rich rain forest on northwestern slopes of Abácapa-tepui, vicinity of camp 1 along Río Abácapa, 420 m, 30–31 Mar. 1953, *Julian A. Steyermark 74781* (holotype, MO; isotypes, F, MO, VEN).

Arbor 20–25 m; gemmis petiolis ramulis juvenilibusque dense hirsutulis pilis patulo-adscendentibus munitis; petiolis 3–9 mm longis; foliorum laminis oblongo-obovatis basi subacutis vel subobtusis 3–5(–11) cm longis 0.9–3(–6) cm latis subtus praeter costam mediam hirsutam prope basin glabris; nervis lateralibus utroque 5–7 subtus leviter elevatis; venatione tertiaria leviter irregulariterque reticulata; floribus non visis; fructu obovoideo-oblongo 8–9 cm longo 4 cm lato.

Tree 20–25 m tall. Vegetative buds, petioles, and young stems densely hirsute with spreading-ascending hairs 0.2–0.4 mm long. Petioles 3–9 mm long (on young shoots 35 mm); leaf blades crowded, becoming subverticillate at the ends of branches, 3–5 cm long, 0.9–3 cm wide, coriaceous, shining and deep green above, paler green below, oblong-obovate, rounded and minutely mucronulate at the retuse apex, narrowed to a subacute to subobtuse base, on sterile shoots to 10–11 × 3–6 cm; lateral nerves 5–7 each side, ascending at an angle of 50–60°, branching before reaching the margins, the principal lateral nerves faintly impressed above, slightly elevated below, 2–6 mm distant or on sterile shoots 10–12 mm; tertiary venation beneath faintly to moderately prominent with an irregularly reticulate pattern. Fruit pendent, olive-green, obovoid-oblong, 8–9 cm long, 4 cm diam., minutely stellulate-velutinous.

Paratypes. VENEZUELA. BOLÍVAR: Quebrada Los Brasileros, 4.5 km al SW de Icabarú, 4°20′N, 61°48′W, 480 m, 16 Dec. 1978, *Steyermark, Carreño Espinosa & Dunsterville 117778* (MO, VEN). TERRITORIO FEDERAL AMAZONAS: Cerro Neblina, south of Base Camp, Río Mawarinuma, 0°50′N, 66°11′W, 150–350 m, *Gentry & Stein 47115* (MO).

This taxon differs from other species of the genus in having the pubescence of the buds, petioles, and young stems of elongate, spreading-ascending stiffish, hirsutulous hairs rather than the densely appressed, short-stellate tomentum or glabrity of the other members of the genus. The paratypes differ from the type collection in having larger leaves widest near, instead of above, the middle, but possesses identical elongated, hirsute pubescence.

Catostemma marahuacense Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Departamento Atabapo, Cerro Marahuaca, "Sima Camp," south-central portion of forested slopes along eastern branch of Caño Negro, 3°43′N, 65°31′W, 1,140 m, 28 Feb.–1 Mar. 1985, *Julian A. Steyermark & Bruce Holst 130878* (holotype, MO). Figure 6C, c.

Arbor 20–30 m, ramulis juvenilibus glabris; gemmis glabris; petiolis 0.7–3.2 cm longis glabris; foliorum laminis elliptico-ovatis vel lanceolato-ellipticis ad medium latioribus apice rotundatis obtusis vel subacutis interdum mucronulatis basi obtusis vel subrotundatis 8–14 cm longis 3.5–8 cm latis utrinque glabris, nervis lateralibus utroque latere 9–12 plus minusve fere ad margines uniformiter adscendentibus subparallelisque; venulis tertiariis subtus tenuibus nec elevatis plus minusve subparallelis atque subhorizontalibus; floribus non visis; fructu maturo ellipsoideo 2–3-obtuse costato vel subangulato uniloculare monospermo (raro 2-spermo fide Holst & Liesner) 8–9 cm longo 4–4.5 cm diam. (fructu immaturo magis elongato angustiorique striatulo indumento minute olivaceo-tomentello munito).

Tree 20–30 m tall, the branches glabrous. Bud scales glabrous. Petiole 0.7–3.2 cm long, glabrous; leaf blades chartaceous or subcoriaceous, brittle, elliptic-ovate, oblong- or lanceolate-elliptic, widest at the middle, rounded, obtuse or subacute at the sometimes mucronulate apex, obtuse or subrounded at the base, 8–14 cm long, 3.5–8 cm wide, glabrous both sides, the midrib impressed above, subelevated below; lateral nerves slender, 9–12 each side, impressed above, uniformly ascending at an angle of 45–50°, subparallel and unbranched nearly to the margins, 3–15 mm distant; tertiary venation subimpressed above, faintly subimpressed below and rather inconspicuous, not elevated, forming a ± subparallel and subhorizontal pattern of veinlets. Mature fruit ellipsoid, 2–3-obtusely costate or subangled, unilocular, 1–(2-testa Holst & Liesner)-seeded, 8–9 cm long, 4–4.5 cm diam. (immature fruit longer and narrower after shrinking), striatulate with minute olivaceous indument.

Paratype. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Cerro Marahuaca, same locality as type, 25 Feb. 1985, *Steyermark & Holst 130709* (MO).

The venation of the lower surface in this species resembles that found in *Catostemma fragrans* Benth. of Guyana, but *C. marahuacenses* differs in having glabrous bud scales and less prominent tertiary venation on the lower leaf surface. The tertiary veinlets resemble those found in some species of *Scleronema,* such as *S. neblinense,* but *C. marahuacenses* differs in its elongate ellipsoid, instead of globose, fruit.

Catostemma pubistylum Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: IVIC main study site, 4.3 km NE of San Carlos de Río Negro, 1°56′N, 67°03′W, 119 m, 3 Aug. 1978, *Howard L. Clark & P. Maquirino 6742* (holotype, NY).

Arbor 4–5.5(–8) m; gemmis minute adpressoque stellato-tomentosis; ramulis juvenilibus glabris; petiolis (5–)12–15 mm longis glabris; foliorum laminis obovato-oblongis apice rotundatis retusisque basi rotundatis vel leviter subcordatis majoribus 9–16 cm longis 4.5–6.8 cm latis ubique glabris; nervis lateralibus utroque latere 5–6 subtus elevatis, venatione tertiaria irregulariter reticulatis; pedicellis 2–2.5 cm longis minute sparsimque adpresso-stellato-tomentoso ebracteolatis; calyce extus stellato-tomentoso intus parte apicali strigosa ceterum glabro; stylo 6 mm longo omnino stellato-tomentello, ramis 4 mm longis stellatis.

Tree, 4–5.5(–8) m tall; buds minutely appressed stellate-tomentose; young branchlets glabrous. Petioles (5–)12–15 mm long, glabrous; leaf blades thick-coriaceous with revolute margins, shining above, oblong-obovate, rounded, retuse and mucronulate at apex, narrowed to a rounded or slightly subcordate base, the larger ones 9–16 cm long and 4.5–6.8 cm wide, glabrous both sides; lateral nerves 5–6 each side, ascending at an angle of 30–45°, prominently elevated below, 10–25 mm distant on the larger leaves, branching before reaching the margins, faintly impressed above; tertiary venation irregularly reticulate below with slightly prominulous veinlets. Pedicels 2–2.5 cm long, minutely stellulate-tomentose, ebracteolate. Calyx densely stellate-tomentose without, the tube 4 mm long, 4–5 mm above, the lobes ovate, obtuse, or rounded, 6 mm long, 3.5–4 mm wide, glabrous within except for the strigose apical portion. Petals ligulate-oblong, rounded at apex, 16 mm long, 6.5 mm wide. Stamens 45–55; filaments up to 9 mm long; anthers 0.5–1 mm long. Ovary suborbicular-ovoid, 3 mm long, 3 mm broad at base. Style 6 mm long, stellate-tomentellose throughout; style branches 4 mm long, stellate-pubescent; fruit unknown.

Paratype. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: same locality as type collection, *Clark & Maquirino 8115* (MO).

This species is characterized by a combination of completely stellate style and stylar branches; minutely appressed-stellate bud scales; glabrous petioles, stems, and leaf blades, the latter strongly revolute; and strigose apical inner portion of the calyx lobes.

Catostemma sancarlosianum Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Mari's bana (low Amazon caatinga), 10.8 km NE of San Carlos on Solano Road, 1°56'N, 67°03'W, 119 m, 16 Aug. 1981, *H. L. & K. Clark 8117* (holotype, MO).

Frutex 2–4 m, ramulis praecipue glabris vel partim microscopico stellato-puberulis; gemmis praecipue glabris vel a exudato microscopico interdum munitis; petiolis 2–15 mm longis plerumque glabris vel partim microscopico stellato-puberulis; foliorum laminis maturis supra nitidis crasso-rigido-coriaceis valde revolutis obovatis apice rotundatis retusis breviter mucronulatis basi obtusis rotundatis vel subcordatis 4.5–15 cm longis 2–4.5 cm latis utrinque glabris, nervis lateralibus utroque latere 4–6 supra leviter impressis vel sulcatis subtus praecipue elevatis conspicuisque fere ad margines adscendentibus, venatione tertiaria supra tenuiter impresso-reticulato subtus reticulata venulis tenuiter impressis nonnullis magis oblique transversalibus impressisque; floribus paucis (1–)2–7-fasciculatis; pedicellis 2.5–3 cm longis dense stellato-tomentosis bracteolatis, bracteolis deltoideo-ovatis obtusis 0.8–1 mm longis ad medium vel in dimidio inferiore dispositis; calyce extus dense stellato-tomentoso, tubo 3 mm longo 4 mm lato, lobis late ovato-oblongis obtuse acutis 10–12 mm longis 5–6 mm latis intus glabris; petalis 15 mm longis 6–8 mm latis; stylo 9–11 mm longo glabro, ramis 2 mm longis glabris vel pilis stellatis minutis munitis.

Shrub 2–4 m tall, the branches mainly glabrous or partly stellulate-puberulent with microscopic indument. Buds mainly glabrous or sometimes furnished with a microscopic pale exudate. Petioles 2–15 mm long, mainly glabrous or partly stellate-puberulent with microscopic indument; mature leaves thick, rigid, coriaceous, strongly revolute, obovate, rounded and retuse at the usually mucronulate apex, 4.5–15 cm long, 2–4.5 cm wide, glabrous both sides; main lateral nerves 4–6 each side, scarcely evident and impressed or subsulcate above, usually elevated and conspicuous below, 5–20 mm distant; tertiary venation above with a minutely cellular impressed reticulum surrounded by a slightly more impressed network, reticulate below with mainly finely impressed veinlets, some of these obliquely transverse between the main lateral nerves. Flowers few, (1–)2–7-fasciculate; pedicels 2.5–3 cm long, densely stellate-tomentose, bracteolate, the 2 bracteoles alternately situated at or below the middle, deltoid-ovate, obtuse, 0.8–1 mm long. Calyx densely stellate-tomentose without, 3 mm long, 4 mm wide above, the lobes broadly ovate-oblong, obtusely acute, 10–12 mm long, 5–6 mm wide, glabrous within. Petals ligulate-oblong or ligulate-spatulate, rounded, 15 mm long, 6–8 mm wide. Stamens 35–40; filaments 9–12 mm long; anthers 0.8–0.9 mm long. Style 9–11 mm long, glabrous except stellate in basal 1.5 mm, glabrous or partly minutely stellulate, with style branches 2 mm long.

This species differs from *Catostemma altsonii* in its shrubby habit and low stature and in its thick coriaceous and strongly revolute leaf blades with only 4–6 main lateral nerves on each side.

Catostemma sclerophyllum Ducke, Trop. Woods 50: 39. 1937. TYPE: Brazil. Amazonas: near Manáos, 20 May 1936, *A. Ducke* (holotype, RB no. *29040*).

Medium-sized tree. Bud scales and branches glabrous. Petioles 2–5 cm long, glabrous; leaf blades congested at the apex of the branches, oblong-elliptic, rounded and retuse at apex, subcordate or rounded at the base, 6–10 cm long, 4–7.5 cm wide, glabrous both sides, the main lateral nerves 6–10 each side, branching before reaching the margins; tertiary venation irregularly reticulate between the main secondary lateral nerves, less conspicuously elevated below than the main lateral nerves. Pedicels 2.5–5 cm long, moderately stellate-tomentose, bracteolate; bracteoles alternate, immediately subtending the calyx, 1–1.5 mm long, 1 mm wide, broadly ovate, obtuse. Calyx stellate-tomentose without, 10–12 mm long, the tube 4–5 mm long, the lobes 5–6 mm long, glabrous within. Petals obovate-oblong, 12–15 mm long. Stamens 30–35; filaments 7–9 mm long; anthers 0.5–0.7 mm long. Style 6–7 mm long, glabrous except stellate-tomentose in the basal 2 mm portion; style branches 2–2.5 mm long, glabrous. Fruit ellipsoid, 6–7 cm long.

Distribution. Amazonian Brazil.

Additional specimens examined. BRAZIL. AMAZONAS: circa Manáos, *Ducke 20-5-1936*, Herb. Jard. Bot. Rio de Janeiro 29040 (holotype, RB; isotype, MO); Manáos, Estrada do Aleixo, *Ducke 490* (F, US); Manáos, cataractam altam fluminis Tarumá, *Ducke 749* (F, US); Manáos, Rio Tarumá, *Ducke 1469* (F); same locality, *Steward et al.* (NY). Seen also near Santa Izabel on Rio Negro by Ducke.

This species resembles *C. commune* but differs in having the bracteoles on the pedicels immediately subtending the calyx and alternately arranged; longer, less stellate-tomentose pedicels; somewhat longer petals; and more rigid and thicker leaves, subcordate to rounded at the base. From *C. fragrans* it may be distinguished by having glabrous buds and young stems and by having completely different venation of the lower leaf surface.

SCLERONEMA

The genus *Scleronema* has hitherto been known only from Brazil and Guyana, the most recently described species being *S. guianense* Sandw. (1948). The following species is newly described as the first one known from Venezuela.

Scleronema neblinense Steyermark, sp. nov. TYPE: Brazil. Amazonas: Serra de Neblina, vicinity of Base Camp, Caño Tucano, Rio Cauaburí, 100 m, 15 Nov. 1965, *Bassett Maguire, Julian A. Steyermark & Celia K. Maguire 60181* (holotype, MO; isotype, flowers, NY).

Arbor 20–40 m, ramulis juvenilibus stellato-tomentellis; gemmis dense stellato-tomentosis; petiolis 1–4 cm longis stellato-tomentosis; foliorum laminis plantarum incipientium simplicibus, elliptico-oblongis subito longicuspidatis, cuspide 1.5–3 cm longo, 14–24 cm longis, 5.5–7.5 cm latis utrinque glabris; foliorum laminis maturis late oblongis vel obovatis apice rotundatis basi rotundatis vel subacutis 5.5–14 cm longis, 3.5–7.5 cm latis subtus praeter costam mediam nervis lateralibusque sparsim stellatis glabris, nervis lateralibus utroque latere 7–13 subtus prominentibus elevatis plus minusve fere ad margines uniformiter adscendentibus subparallelisque; venulis tertiariis subtus prominentibus elevatis subparallelis atque subhorizontalibus; pedicellis (1.3–)1.8–2.5 cm longis stellato-tomentosis; calyce extus dense stellato-tomentoso lobis tribus intus moderatim pubescentibus pilis hirsutulo-strigosis praeditis; staminibus 14–16, filamentis apice dilatatis 7–8 mm longis, antheris sessilibus 0.2–0.3 mm longis; stylo 13.5 mm longo, parte basali 4 mm longa stellata, ceterum glabro; fructu globoso 7 × 7 cm subruguloso subglabrescente.

Tree 20–40 m tall, the young branches stellate-tomentose. Buds densely stellate-tomentose. Seedling leaves simple, elliptic-oblong, abruptly long cuspidate, 14–24 cm long, 5.5–7.5 cm wide, the cuspid part 1.5–3 cm long, glabrous both sides. Petioles 1–4 cm long, stellate-tomentose; mature leaf blades chartaceous, oblong or obovate, rounded and sometimes mucronate at apex, rounded to subacute at base, 5.5–14 cm long, 3.5–7.5 cm wide, glabrous above (a few stellate hairs sometimes on midrib), the lower surface glabrous; lateral nerves 7–13 each side, impressed above, prominently elevated below, 5–15 mm distant, ± uniformly ascending at an angle of 45–55°, ± subparallel and unbranched nearly to the margins; tertiary venation prominent and elevated below with the veins ± regularly subparallel and subhorizontal. Pedicels (1.3–)1.8–2.5 cm long, ebracteolate, densely stellate-tomentose with shorter and longer hairs intermixed, the shorter brownish hairs predominating. Calyx minutely densely stellate-tomentose without, tube campanulate, 4 mm long, 4 mm broad at summit, the 3 lobes 4.5 mm long, 4 mm wide, moderately hirsute-strigose within with hairs 1 mm long. Petals lance-oblong, obtuse, 13 mm long, 4 mm wide. Stamens 14–16; filaments 7–8 mm long; anthers 0.2–0.3 mm long. Style 13.5 mm long, stellate-tomentose in the basal 4 mm. Fruit globose, 7 × 7 cm, faintly rugulose, subglabrescent.

Paratype. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Cerro Neblina, Base Camp, Río Mawarinuma, 0°50′N, 66°11′W, 140 m, 4 May 1984, *Gentry & Stein 47148* (fruiting material with one flower present, MO), *47152* (seedling leaves, MO); same locality, 11 Mar. 1984, *Liesner 16539* (MO).

This taxon possesses small sessile anthers terminating the relatively few dilated filaments and indehiscent, globose fruits. The morphologies of the anthers and the dilated filaments are typical of *Scleronema*, and globose fruits are known from other species of the genus, in contrast to the more elongated ellipsoid or oblong fruits of *Catostemma*. Others features of *S. neblinense* shared by the known species of the genus are the relatively few stamens, the relatively few flowers of each axillary fascicle, and the more or less characteristic tertiary venation and subparallel lateral nerves. While the calyx lobes of *Catostemma* are regularly three, those of *Scleronema* vary from three to five. The three calyx lobes of *S. nebli-*

nense are also found in *S. micranthum* Ducke, to which it is most closely related. The former differs in the rounded apex of the perfectly globose fruit and in the greater number of lateral nerves of the leaf blades.

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THEACEAE

BONNETIA

KEY TO RECENTLY DESCRIBED TAXA OF *BONNETIA*

1a. Anthers broader than long or as broad as long, subreniform; ovary incompletely trilocular .... *B. euryanthera*

1b. Anthers longer than broad, oblong or suborbicular; ovary completely trilocular 2

  2a. Style undivided 3

    3a. Lateral nerves elevated on upper surface, impressed on lower surface; leaf blades 2–4 × 1.5–2.5 cm .... *B. tepuiensis* subsp. *tepuiensis*

    3b. Lateral nerves faintly impressed on upper surface, mainly not evident on lower surface; leaf blades 1–2 × 0.8–1.4 cm .... *B. tepuiensis* subsp. *minor*

  2b. Style divided nearly or all its length into 3 branches, or merely shallowly 3-lobed at the apex 4

    4a. Style shallowly 3-lobed .... *B. guaiquinimae*

    4b. Style deeply parted into 3 branches, divided nearly all the way to the base or at least ⅓ from the top 5

      5a. Petals white or pink 6

        6a. Upper leaf surface enervate; sepals subacute or obtusely acute; styles divided ⅔ of their length or 3-parted to the base 7

          7a. Petals 9–9.5 × 4–6 mm; leaves 1.2–2.7 × 0.5–0.8 cm; sepals 9–9.5 mm long .... *B. chimantensis*

          7b. Petals 21–22 × 14–16 mm at the summit; leaves (2–)2.5–5 × 0.8–1.7 cm; sepals 11–12.5 mm long .... *B. bolivarensis*

        6b. Upper leaf surface with impressed nerves above; sepals obtuse or rounded at apex; styles 3-parted ⅓ distance from the top .... *B. toroniensis*

      5b. Petals yellow 8

        8a. Peduncle elongate, 3–6.5 cm long, often surpassing the leaves, ebracteolate 9

          9a. Petals 3.5–4.2 cm long, 2.7–3 cm wide; lateral nerves of both surfaces of the leaves scarcely elevated .... *B. tristyla* subsp. *tristyla*

          9b. Petals smaller; lateral nerves of both leaf surfaces prominently elevated .... *B. tristyla* subsp. *nervosa*

        8b. Peduncle lacking or at most 1.6 cm long, usually concealed by and much shorter than the leaves, verticillate-bracteate 10

          10a. Leaves linear-oblanceolate, 2.5–7 mm wide; petals 8 mm long; peduncles 8–16 mm long .... *B. huberiana*

          10b. Leaves broadly lanceolate, obovate, or oblong-lanceolate, 4–15 mm wide (leaves on vegetative shoots often wider); petals 9–16 mm long; peduncles 3–16 mm long 11

            11a. Leaves lanceolate, acute at the apex, only slightly narrowed at the base, nearly the same width for most of length, 3.5–4.5 × 1–1.5 cm, finely impressed-nerved beneath, not pale punctate there, the stomata not manifest; sepals 12–13 mm long .... *B. ptariensis*

            11b. Leaves oblanceolate or obovate, obtuse, rounded to subacute at the apex, conspicuously narrowed to the base, broadest above the middle, 1–3.5 × 0.4–1(–1.5) cm, mainly enervate beneath, pale punctate there, the stomata manifest; sepals 9–10 mm long .... *B. wurdackii*

In the first installment of the *Flora of the Venezuelan Guayana* (Steyermark, 1984), four new taxa of *Bonnetia* were described. Continued exploration of the summit floras of the Guayana Highland has yielded the following five new bonnetias.

Bonnetia bolivarensis Steyermark, sp. nov. TYPE: Venezuela. Bolívar; Ptari-tepui, cumbre, 5°47′N, 61°47′W, 2,400 m, 19 Nov. 1984, *Otto Huber 9818* (holotype, VEN; isotype, MO).

Frutex 1 m; foliorum laminis dense rosulatis subsessilibus oblongo-lanceolatis apice obtuse acutis basi obtusis (2–)2.5–5 × 0.8–1.7 cm; sepalis 11–12.5 × 4–5 mm; petalis 21–22 × 14–16 mm; stylis tribus 3–3.5 mm longis fere usque ad basem divisis.

Shrub 1 m tall. Leaves crowded at summit of branches, oblong-lanceolate, subsessile, narrowed to an obtusely acute apex, obtuse at base, (2–)2.5–5 × 0.8–1.7 cm, faintly impressed-nerved both sides (the midrib slightly elevated below) or the lateral nerves not evident. Flowers solitary, sessile or subsessile; bracts immediately subtending flower oblong-lanceolate, acute to obtuse, 11–12 × 4.5 mm, dorsally carinate, setulose marginally with dark setae 1 mm long. Sepals lance-oblong, subacute, 11–12.5 × 4.5 mm, obtusely dorsally keeled basally and apically; petals white, subcuneately obovate, subtruncate apically with unequally rounded sides, narrowed to the base, 21–22 mm long, 14–16 mm wide at summit, 4 mm wide at base. Stamens numerous, multiseriate; filaments 5 mm or less long; anthers 0.5–0.8 × 0.6 mm. Pistil 9 mm long, the styles 3, 3–3.5 mm long, divided about ⅔ of their length.

The larger flowers and larger subacute leaves differentiate this taxon from *B. chimantensis* Steyerm., *B. tepuiensis* Kobuski & Steyerm., and *B. toronoensis* Steyerm. In its deeply 3-parted style it further differs from *B. tepuiensis.*

Bonnetia euryanthera Steyermark, sp. nov. TYPE: Venezuela. Bolívar: meseta de Jaua, cumbre, sección oriental-central, afloramientos de piedra arenisca en sitios expuestos con vegetación herbácea y arbustos achaparrados, 4°35′N, 64°15′W, 2,020 m, 14 Feb. 1981, *Julian A. Steyermark, Charles Brewer-Carias & Ron Liesner 124311* (holotype, NY; isotypes, MO, VEN). Figure 7.

Subfrutex 1 m, ramulis parum ramosis; cicatricibus valde confertis; foliis alternis ad apicem confertis oblongis vel obovata-oblongis apice rotundatis vel obtusis sessilibus vel subsessilibus 3–4.5 cm longis 1–2 cm latis, nervis lateralibus vix manifestis; inflorescentia terminali conferta dense cymosa, 12–15 flora, axibus duobus vel tribus 3–5 mm longis; bracteolis sub floribus oblongo-ligulatis vel obovato-oblongis rotundatis 3–4.5 mm longis 1.5–2 mm latis marginibus versus basem praesertim minute setosis; floribus sessilibus vel subsessilibus; sepalis 5, inaequalibus exterioribus ovalibus vel suboblongis rotundatis 5–6 mm longis 3–4 mm latis, interioribus majoribus ovatis obtusis 6–7 mm longis 4 mm latis dorsalibus carinatis; petalis 5 suborbiculari-obovatis apice rotundato-subtruncatis 10–11 mm longis apicem versus 6–8 mm latis; filamentis numerosis 2-seriatis; antheris subreniformibus latioribus quam longioribus 0.5 mm altis 0.6–0.7 mm latis 4-thecatis; ovario uniloculari imperfecte 3-loculari placentatione parietali placentis valde intrusis; stylis trifidis, ramis 1–1.25 mm longis.

Dwarf shrub 1 m tall, sparsely branched with the leaf scars closely crowded, about 2 mm distant. Leaves alternate, closely crowded near the summit, coriaceous, oblong to obovate-oblong, rounded or obtuse at apex, sessile or subsessile, 3–4.5 cm long, 1–2 cm wide; lateral nerves scarcely evident on either side. Inflorescence terminal, compact, densely cymosely subpaniculate, 2 cm high, 2.5 cm wide with 2–3 short axes 3–5 mm long, 1.5 mm wide, 12–15-flowered, on a short peduncle 2 mm long, 1.5 mm wide. Bracteoles ligulate-oblong, rounded, 3–4.5 mm long 1.5–2 mm wide, with minutely setulose margins especially manifest in lower half. Flowers sessile, crowded. Sepals 5, unequal, the outer oval or oblong, rounded, 5–6 mm long, 3–4 mm wide, the inner larger, ovate, obtuse, 6–7 mm long, 4 mm wide, dorsally carinate. Petals 5, pink, rose and white, suborbicular-obovate, subtruncate-rounded at apex, 10–11 mm long, 6–8 mm wide near apex, 2 mm wide at base. Stamens numerous; filaments filiform, 3–5 mm long, 2-seriate, attached at base to a thickened tissue; anthers 4-celled, subreniform, broader than long, 0.5 mm high, 0.6–0.7 mm wide, the thecae oblong or subelliptic. Pistil 5.5 mm long; ovary 3.5 mm long, 1-celled (incompletely 3-celled), the placentae parietal and conspicuously intruding toward center; ovules numerous. Style 1 mm long, trifid, the style branches 1–1.25 mm long; stigmas terminal.

Paratype. VENEZUELA. Same locality and date as type, *Steyermark, Brewer-Carias & Liesner 124322* (NY, VEN).

This species is remarkably distinct in the shape of the anthers, which are broader than long or

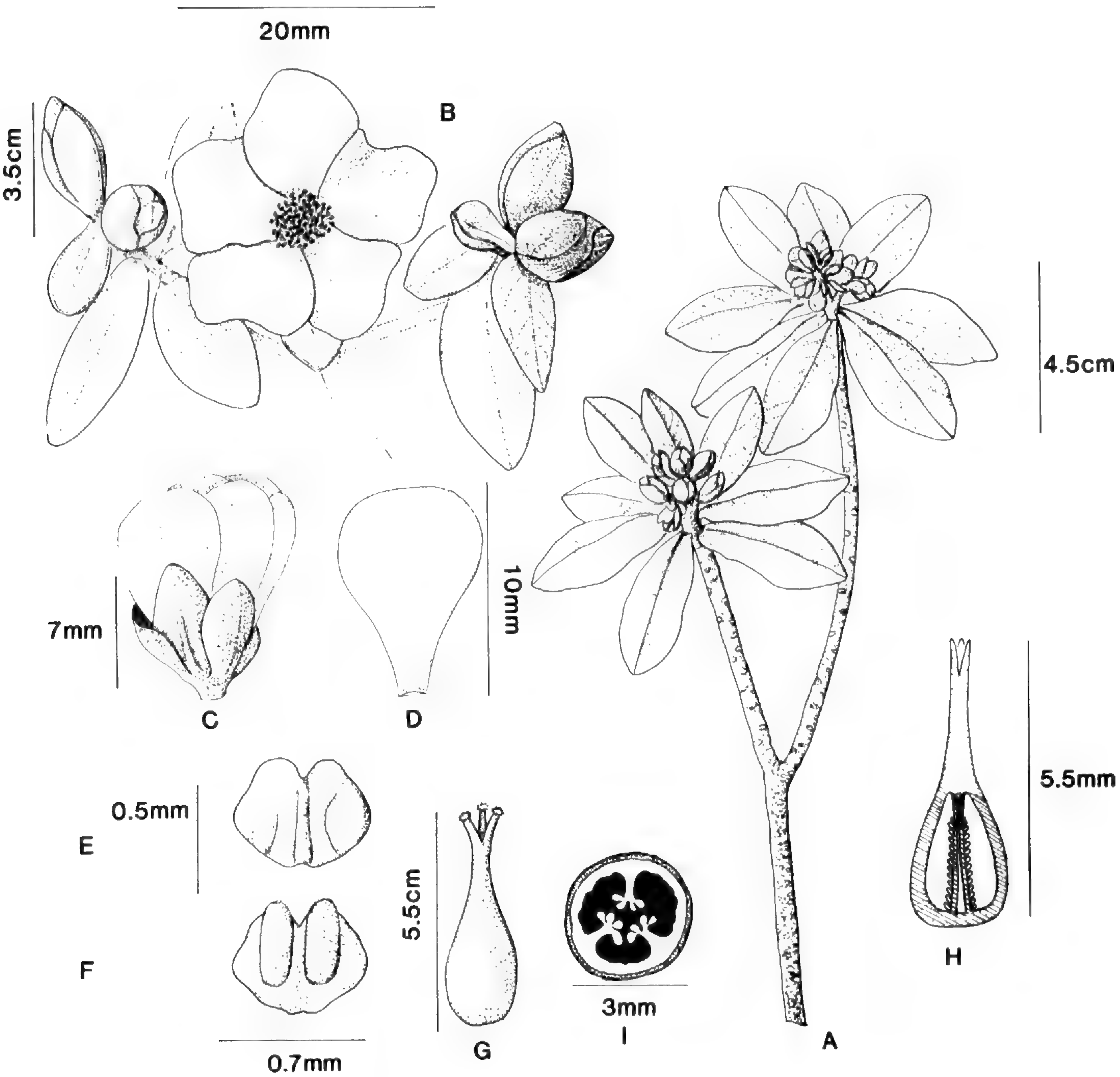

FIGURE 7. *Bonnetia euryanthera.* — A. Fertile branch in bud stage. — B. Portion of flowering branch enlarged. — C. Flower, lateral view. — D. Petal. — E. Anther, ventral view. — F. Anther, dorsal view. — G. Pistil. — H. Longitudinal section through pistil showing placentae and ovules. — I. Cross section through ovary showing single locule occupied by intruding parietal placentae with ovules. Based on holotype.

as broad as long and subreniform to suborbicular. Other distinctive features are found in the incompletely trilocular ovary with parietal placentae extending toward and almost fusing at the center, their ovules crowded and touching the ends of the placenta dissepiment, in this respect simulating the drawing of the ovary of *Bonnetia celiae* Maguire (Maguire, 1972, fig. 22k), which is quite different from the completely trilocular ovary of *B. neblinae* Maguire (Maguire, 1972, fig. 23g). Several dissections of the ovary verify observations which were also confirmed by botanical colleagues at the Missouri Botanical Garden. A longitudinal section of the ovary shows that the placental partitions are not united. They nearly come together, but a slight space develops between them without tearing any vascular tissue. The broad anthers are more nearly like those shown in figure 19 (Maguire, 1972) for *Archytaea angustifolia* Maguire (A, b–c), *Ploiarium alternifolium* (B, b–c), *Bonnetia neblinensis* Maguire (D, b–c), and *B. steyermarkii* Kobuski (F, b–c). In this respect they differ from the linear-oblong anthers of *Bonnetia jauaensis* Maguire (Maguire, 1976) collected on another part of the summit of Cerro Jaua of the Meseta de Jaua.

Cronquist (1981) stated that the gynoecium of all four subfamilies of the Theaceae has axile placentation, "(2–)3–5(–10) carpels," and forms a compound ovary with equal ovule and carpel number, except for *Piquetia,* which has the carpels united only at the base. In his treatment of the Bonnetiaceae, Maguire (1972) stated that the ovary is "5–3-locular" and that the placentation is "axial or a permutation thereof." In our species, it would be more accurate to state that the ovary is incompletely trilocular, or actually unilocular with three parietal placentae extending inward but not fusing or united.

Bonnetia guaiquinimae Steyerm., sp. nov. TYPE: Venezuela. Bolívar: Cerro Guaiquinima, cumbre, sector SE, 5°40'N, 63°26'W, 1,250 m, 26 May 1978, *Julian A. Steyermark, Paul Berry, G. C. K. & E. Dunsterville 117421* (holotype, MO).

Frutex 1.5 m; foliorum laminis subpetiolatis oblongo-lanceolatis vel oblanceolatis apice acutis basi subacutis vel subobtusis 5–6.5 × 1.3–1.6 cm subtus enervatis integerrimis; sepalis minute mucronatis 10–12 × 6–8 mm; petalis 20 × 15–20 mm; filamentis 3.5–7 mm longis; stylo subulato apice leviter 3-lobato.

Shrub 1.5 m tall. Petiole 1–2 mm long; leaves coriaceous, entire, oblong-lanceolate to oblanceolate, acute at apex, gradually narrowed to a subacute or subobtuse base, 5–6.5 × 1.3–1.6 cm, enervate below, the midrib subimpressed below, the lateral nerves elevated above. Sepals coriaceous, suborbicular-obovate, rounded at a shortly cuspidate apex, 10–12 mm long, 6–8 mm wide above the middle, 3–4 mm wide at base. Petals white, obovate, narrowed to a subunguiculate base, 20 mm long, 15–20 mm wide at the summit, 2–3 mm wide at base. Filaments distinct, 3.5–7 mm long; anthers 1.5–1.8 × 0.7 mm. Pistil 9 mm long; style united, merely 3-lobed at apex.

This taxon is characterized by the shallowly 3-lobed style and the entire, oblong-lanceolate, acute leaves, which are enervate beneath. It may be distinguished from *B. chimantensis* Steyerm. by the larger petals, shallowly trilobed style, and larger leaves enervate beneath. It differs from *B. toronoensis* Steyerm. in the larger sepals and petals, and larger, entire leaves enervate below, while it is differentiated from *B. tepuiensis* and subsp. *minor* Steyerm. by the larger, minutely mucronate sepals, longer filaments, and completely entire leaves.

Bonnetia ptariensis Steyerm., sp. nov. TYPE: Venezuela. Bolívar: Ptari-tepui, cumbre, 5°45'N, 61°45'W, 2,360–2,420 m, 23 Feb. 1978, *Julian Steyermark, V. Carreño E., R. McDiarmid & C. Brewer-Carias 115645* (holotype, MO).

Frutex 2.5 m; foliis sessilibus lanceolatis apice acutis majoribus 3.5–4.5 × 1–1.5 cm minute obscureque serrulatis; floribus solitariis minute breviter pedunculatis, pedunculis teretibus vel subteretibus 4–6 cm longis; sepalis lanceolatis vel suboblanceolatis acutis 12–13 × 3–5 mm; petalis luteis obovatis apice rotundatis 16–18 × 12 mm; antheris 0.8 × 0.7 mm; stylis tribus 6 mm longis fere usque ad basim divisis.

Subshrubs 2.5 m tall. Leaves coriaceous, lanceolate, acute at apex, slightly narrowed to the base, the larger ones 3.5–4.5 × 1–1.5 cm and obsoletely pinnately nerved, the midrib slightly elevated below, microscopically and obscurely serrulate. Flowers solitary on (sub-)terete peduncle 4–6 mm long; bracts immediately subtending flower narrowly oblanceolate, acute, 12–13 × 3–4 mm. Sepals subconvex, lanceolate or sublanceolate, acute, 12–13 × 3–5 mm, 10-striate, minutely ciliolate, obtusely carinate; petals yellow, obovate, rounded above, 16–18 mm long (pre-anthesis), 12 mm wide near apex, 2 mm wide at base; filaments 1.5–3.5 mm long (pre-anthesis); anthers 0.8 × 0.7 mm long. Pistil 10 mm long; styles 3, 6 mm long, free nearly to the base.

This species differs from the yellow-flowered *B. wurdackii* Maguire in the larger, lanceolate, and acute leaves, longer sepals, larger petals (even in bud), longer filaments, and longer style branches. Furthermore, the leaves do not show the pale-punctate stomata, which are clearly visible in *B. wurdackii.* It is easily distinguished from *B. tristyla* by the short pedicels, smaller floral parts, and smaller leaves, and is well differentiated from *B. huberiana* by the larger lanceolate leaves, shorter pedicels, and larger floral parts.

Bonnetia tristyla Gleason subsp. **nervosa** Steyermark subsp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Cerro Yapacana, 2 Jan. 1951, *Maguire, Cowan & Wurdack 30632* (holotype, VEN; isotype, NY).

A subsp. *B. tristyla* foliis supra costa media necnon nervis lateralibus nonnullis (6–8) conspicue manifesteque elevatis, nervis lateralibus supra inaequaliter prominentibus; petalis minoribus 25–38 mm longis recedit.

Petiole absent or 1–2 mm long. Leaves suboblong, oblong-oblanceolate, or oblong-obovate, obtuse to rounded at apex, narrowed to a subobtuse or subacute base, 4–8 cm long, 1.5–3.5 cm wide, the midrib on upper surface and 6–8 pairs of lateral nerves conspicuous and elevated, the other intermediate pairs of lateral nerves less conspicuously and lightly impressed, nerves on lower surface subequal and lightly impressed. Peduncle 3–4.5(–6.5) cm long. Sepals 12–20 mm long, the outer 12–15 mm long, the inner ones 15–20 mm long. Petals 25–38 × 15–22 mm.

Paratypes. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Cerro Avispa, Río Siapa, summit, 1°30′N, 65°51′W, 1,510 m, *Dunsterville* (*G. C. K. & E.*); Yapacana, summit, 3°45′N, 66°45′W, 1,000–2,000 m, *Steyermark & Bunting 103103*; Yapacana, 1,200 m, *Maguire et al. 30665*; Cerro Avispa, Río Siapa, summit, 1°30′N, 65°51′W, 1,510 m, *Cardona 3098*; Neblina, summit, Cañon Grande slopes E of summit camp, "1,200–2,200" m, *Maguire et al. 42179*; Neblina, Cañon Grande SSW of summit camp, 1,050–1,100 m, *Maguire et al. 42498*; Yapacana, *Maguire et al. 30632*; Neblina, Cañon Grande, slopes E of summit camp, 1,200–1,300 m, *Maguire et al. 42235*; vicinity of Cerro Vinilla, 30 km SSW of Ocamo, caños affluent to Río Orinoco, 2°31′N, 65°23′W, 440–600 m, *Steyermark et al. 130405*; Serranía del Vinilla, 20 km SW of Ocamo, 2°20′N, 65°22′W, 760 m, *Huber 6168*; altiplanicie de arenisca, E side of Río Siapa or Matapire, slightly above leaving the Macizo of Aracumuni, 1°36′N, 65°41′W, 600 m, *Huber 6006.*

This taxon differs from typical *Bonnetia tristyla* in having smaller petals, prominently elevated upper midrib, and unequally prominent lateral nerves on the upper surface of the leaf, with 6–8 conspicuously elevated pairs alternating with fine, lightly impressed alternate nerves. There is also a tendency for the base of the leaf blade in subsp. *tristyla* to be cuneately narrowed, whereas in subsp. *nervosa,* the base of the leaf blade is usually slightly obtusely curved or rounded above its junction with the petiole.

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NOTES ON *LAPLACEA*

The last revision of the genus *Laplacea,* by Kobuski (1950), recognized nine species. Two of these, *L. acutifolia* (Wawra) Kobuski and *L. obovata* (Wawra) Kobuski, were considered by Wawra (1886) as varieties of *Laplacea semiserrata,* or of *Wikstroemia fruticosa* by Blake (1918).

Kobuski noted that great variation existed in size of the flowers and fruits, even within a single species, and that the keys to the species had been "based almost entirely on leaf characters and pubescence."

The species of *Laplacea* can be divided into two groups, those with asymmetrical leaves and those with symmetrical leaves, both of which occur in the Venezuelan Guayana, the common asymmetrical type represented by *L. fruticosa* (Schrader) Kobuski, the symmetrical type by *L. pubescens* Planchon & Linden. Variations occur in each species (Fig. 8B, b, 8C, c). Specimens from the Territorio Federal Amazonas (Maroa, Duida, Huachamacari, Yutaje, and Cerro de La Neblina), as well as a specimen from Cerro Sarisariñama of the state of Bolívar (*Cardona 380*) (Fig. 8A, a) may be referred to typical *L. fruticosa.* However, two specimens from the summit of the Chimantá Massif (*Steyermark & Wurdack 879* and *1126*) (Fig. 8D, d) from the state of Bolívar, differ conspicuously from other Guayanan material, as well as from specimens outside the Venezuelan Guayana conforming to *L. fruticosa.* These specimens have stouter branches with larger leaf scars; thicker, larger leaves, enervate beneath, broader at the subsessile base as to appear nonpetiolate; rather conspicuous hairy tufts along the leaf margins in the sinuses of the marginal teeth; longer, stouter pedicels; and larger sepals and petals. The isolation of the Chimantá specimens from the upper slopes of this sandstone mountain, well known for its endemic flora, may help explain the evolutionary trend here noted toward the segregation of morphological characters at variance from typical *L. fruticosa.* A specific or subspecific category for this population might be envisioned. However, in view of the degree of variation shown by other taxa of this species, varietal rank is here proposed.

Laplacea fruticosa (Schrader) Kobuski var. **chimantae** Steyermark, var. nov. TYPE: Venezuela. Bolívar: Chimantá Massif, central section, along west branch of headwaters of Río Tirica above Upper Falls, 2,090 m, 17 Feb. 1955, *Julian A. Steyermark & John J. Wurdack 879* (holotype, VEN; isotypes, F, NY). Figure 8D, d.

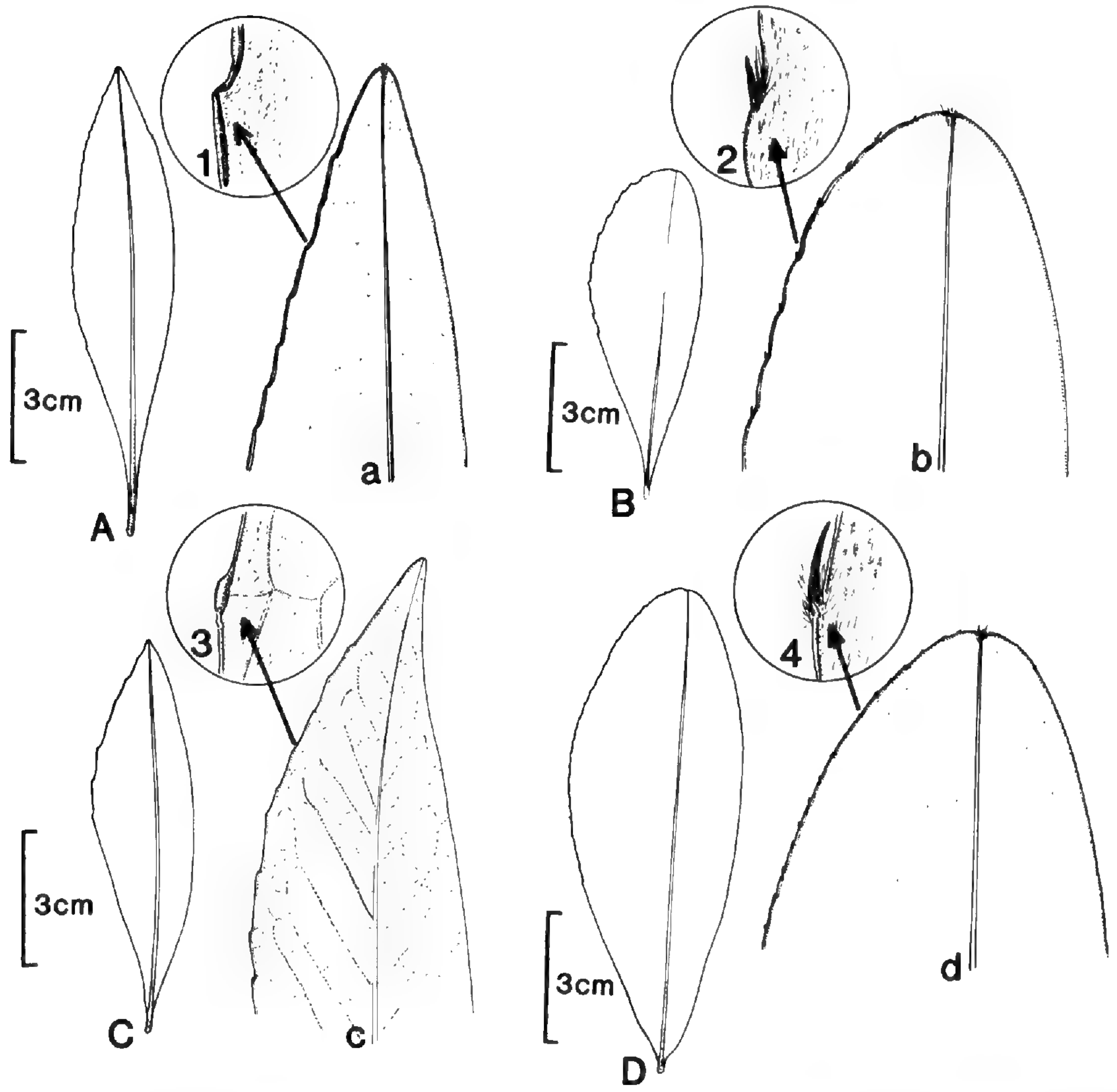

FIGURE 8. A–C. *Laplacea fruticosa* var. *fruticosa.*—A. Leaf of *Cardona 380.* a. portion of margin with detail of a sinus (1).—B. Leaf of *Maguire et al. 37153.* b. portion of margin with detail of a sinus (2).—C. Leaf of *Steyermark et al. 120086.* c. portion of margin with detail of a sinus (3).—D. *Laplacea fruticosa* var. *chimantae,* leaf of *Steyermark & Wurdack 879.* d. portion of margin with detail of a sinus showing tufts of hairs (4).

A var. *fruticosa* foliis sessilibus vel subsessilibus apice late rotundatis in petiolum nihil angustatis basi 5–9 mm latis, dentibus marginalibus pilis caespitosis gerentibus, pedunculis robustis 2–3 cm longis 2.5–3 mm crassis, sepalis petalisque majoribus recedit.

Tree 5–20 m tall, the leafy branches 5–10 mm thick, the leaf scars conspicuous, orbicular, 2.5–4 mm wide. Leaves sessile to subsessile, abruptly contracted into a petiolar portion 1–2 mm long; leaf blades thick-subcoriaceous, asymmetric, oblanceolate-oblong, rounded at the slightly emarginate apex, gradually narrowed to a broad base, 9.5–12.5 cm long, 3–4.8 cm wide, 5–7 mm wide at base, the midrib bordered on one side by foliar tissue 3–4 mm wide, on other side 2–3 mm wide, the lower surface enervate, mainly glabrous but with scattered, pale, minute, appressed, simple hairs over a pustulate surface, inconspicuously appressed-subserrulate from about $^{3}/_{8}$ distance from base to apex with dark acicular teeth 1 mm long, these bearing at their base a tuft of silky hairs 1 mm long (seen best from lower margin); upper surface enervate, glabrous. Peduncle 2–3 cm long, 2.5–3 mm thick, glabrous. Flower bud just before anthesis 2–2.5 cm long, 1.5–2.5 cm wide. Sepals broadly suborbicular, the two outermost 20 mm long, 15 mm wide, the others 17–25 mm long, 13–22 mm wide, minutely gray sericeous most of the length without, glabrous within. Petals broadly oblong-obovate, broadly rounded and emarginate at apex, 25 mm long, 15–22 mm wide, minutely gray sericeous without in the central 5–9 mm portion, glabrous on the marginal 4–5 mm, glabrous within. Filaments 5–6 mm long, glabrous; anthers broadly oblong, broadly rounded at the extremities, 2.5 mm long, 1.5 mm wide. Ovary barrel-shaped, 8 mm long, 5 mm wide, densely sericeous.

Paratype. VENEZUELA. BOLÍVAR: Chimantá Massif, Agparamán tepui, southeast-facing forested slopes below escarpment, 1,880–1,955 m, 26 Feb. 1955, *Steyermark & Wurdack 1126* (F, NY, VEN).

The broad, nonpetiolate leaf bases of var. *chi-*

mantae differ markedly from the generally narrowed, subpetiolar ones of typical *Laplacea fruticosa,* in which the leaf base is conspicuously narrowed toward the base into a subpetiolar portion 5–8 mm long and 1–2 mm wide with the midrib bordered on either side by a very narrow strip of tissue only 0.5–1 mm wide on each side. In *L. fruticosa* var. *pulcherrima* (Melchior) Kobuski, the leaf base is broader than in typical *L. fruticosa,* but the apex is gradually obtusely narrowed and is not broadly rounded as in var. *chimantae.* The tufts of hairs at the base of the marginal teeth are absent from most specimens examined but are present to a lesser degree in *Dusen 15451* from Brazil and *Maguire et al. 37259* from Cerro de La Neblina in Venezuela. The enervate lower leaf surface may also occur in other specimens of *L. fruticosa,* but more frequently the lower surface shows venation.

The second species of *Laplacea* in the Guayana Highland, *L. pubescens* Planchon & Linden ex Triana & Planchon, is represented by two collections, *Maguire, Wurdack & Bunting 37272* from the summit of Cerro de La Neblina, and *Maguire, Cowan & Wurdack 30285* from the summit of Cerro Huachamacari, both from Territorio Federal Amazonas. Elsewhere, the species ranges in the Andes from Venezuela south to Peru and Bolivia. On Cerro de La Neblina it varies slightly from typical *L. pubescens* of the Andes, whereas on Cerro Huachamacari it has developed more reduced leaves, and in both Guayanan collections the lower surface of the leaves is enervate, as contrasted with the more evident venation shown in most of the specimens of *L. pubescens. Laplacea fruticosa,* the more common species, also occurs on Cerro Huachamacari, but at a lower altitude of 1,100 m of forested talus slopes, as well as on Cerro de La Neblina.

Laplacea pubescens Planchon & Linden ex Triana & Planchon var. **minor** Steyermark, var. nov. TYPE: Venezuela. Territorio Federal Amazonas: between Summit Camp and Southwest Escarpment, Cerro Huachamacari, 1,850 m, 17 Dec. 1959, *Bassett Maguire, R. Cowan & J. Wurdack 30285* (holotype, NY).

A var. *pubescens* foliorum laminis minoribus recedit; laminis symmetricis oblanceolatis apice anguste obtusis basi valde angustatis supra medium conferte crenulatis 2.5–4.5(–9) cm longis 1–2(–3) cm latis subtus enervatis; pedicellis 6–8 mm longis; sepalis 5–11 mm longis; petalis cuneiformi-obovatis 16–21 mm longis supra medium 14–15 mm latis.

Leaf blades symmetrical, oblanceolate, narrowly obtuse at the apex, strongly narrowed at the base, 2.5–4.5(–9) cm long, 1–2(–3) cm wide, closely crenulate above the middle, enervate beneath. Pedicels 6–8 mm long. Sepals 5–11 mm long. Petals cuneiform-obovate, 16–21 mm long, 14–15 mm wide above the middle.

Paratype. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Cerro de La Neblina, savanna edge, 3 km N of Cumbre Camp, 1,800 m, 12 Jan. 1953, *Maguire, Wurdack & Bunting 37272* (NY).

Both collections have the leaf surface enervate beneath. However, the paratype (*Maguire et al. 37272*) has the larger leaves typical of *L. pubescens* var. *pubescens.* In both collections the indument of the lower surface is sparse compared with specimens from the Andean portion of the range of the species.

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THYMELEACEAE

DAPHNOPSIS

Daphnopsis guaiquinimae Steyermark, sp. nov. TYPE: Venezuela. Bolívar: Cerro Guaiquinima, cumbre, la extensión más septentrional del cerro en el sector noreste, la parte pedregosa, abierta y plana con vegetación baja, 6°0'N, 63°28'W, 1,650 m, 9 Apr. 1979, *Julian A. Steyermark, G. C. K. & E. Dunsterville 117977* (holotype, VEN; isotype, MO). Figure 9.

Frutex 1.5 m; ramulis juvenilibus sericeo-strigosis; foliorum laminis elliptico-oblongis vel lanceolato-ellipticis apice plerumque obtusis vel rotundatis basi obtusis vel subacutis 3–6 cm longis 1–3 cm latis supra glabris subtus minute strigillosis costa media subtus dense strigillosis venulis tertiariis pagina superiori irregulariter contortis; pedunculis filiformibus 10–20 mm longis sericeo-strigillosis; calyce 7 mm longo supra medium 2 mm lato extus antrorse sericeo, lobis ligulato-oblongis subobtusis utrinque sericeo-hirtellis, orificio glabro; staminibus 8, 2-seriatis; squamis hypogynis 7–8 subulatis glabris fere liberis 1.7–2 mm longis.

Shrub 1.5 m tall; juvenile stems 2–3 mm diam., sericeous-strigose. Petiole 2–3 mm long, strigillose, leaf blades subcoriaceous, gray-white below, elliptic-oblong or lance-elliptic, mostly obtuse to rounded at apex, rarely subacute, obtuse to subacute at base, 3–6 cm long, 1–3 cm wide, glabrous above, minutely strigillose below, slightly more densely on the lower midrib; principal lateral nerves 7–10 each side; tertiary venation above irregularly contorted and twisted, below more regularly reticulate. Inflorescence terminal or axillary, the peduncles filiform, 10–20 mm long, 0.5 mm wide, sericeous-strigillose. Calyx subcylindric-obovoid, 7 mm long, 2 mm wide at and above middle, 1 mm wide at base, antrorsely sericeous without, densely antrorsely sericeous within in the lower 4 mm; lobes 4, unequal, the outer ligulate-oblong, obtuse, 1.2–1.5 × 0.5 mm, the inner 1 × 0.08 mm, sericeous-hirtellous on both surfaces, the orifice glabrous. Stamens 8 in 2 series; anthers sessile, suborbicular-oblong, 0.6 mm long, the upper 4 opposite the calyx lobes, the lower 4 alternate with the calyx lobes; style terminal, 0.3 mm long; stigma clavate, 0.3 mm long. Hypogynous scales 7–8, subulate, glabrous, 1.7–2 mm long, cleft nearly or all the way to the base, free or nearly so.

The type and only specimen of this species was indicated by Nevling (1967) as a new species of *Daphnopsis* related to *D. longipedunculata* Gilg ex Domke, described originally from Mount Roraima. The chief differences possessed by the new taxon are the greater number of hypogynous scales (8 vs. 4 as in the Roraima specimen), peduncles 1–2 cm long contrasted with 2.5–9 cm on the Roraima specimen, and the shorter style. Domke (1935) stated that the umbels in *D. longipedunculata* were on axillary peduncles but added ("atque terminali?"), apparently suspecting that they may also be terminal, as is the case in the Guaiquinima specimens. He also stated that staminate as well as pistillate flowers occur. This indicates that the specimen *Ule 8739* from Roraima studied by Domke was monoecious. In the Guaiquinima specimens, there is also an indication of monoecism, since the anthers are well developed and suborbicular-oblong on some flowers but poorly developed and linear-oblong on others, even on the same plant.

The hypogynous scales in the Guaiquinima plant are regularly disposed as eight filiform appendages. Although they appear to be free, as in *Funifera utilis* Leandro, they are connected at their very base by a slight membrane on the disk, which appears to be adnate to the actual base of the calyx tube, thus showing the relationship with *Daphnopsis*. Conversely, they could be interpreted as completely free as in the genus *Funifera*. Nevling (1967) at first interpreted the style to be lateral (eccentric) in *Daphnopsis longipedunculata*, but later (pers. comm., 1986) confirmed my observation that the style is terminal.

Daphnopsis nevlingiana Steyermark, sp. nov. TYPE: Venezuela. Bolívar: Cerro Sarisariñama, Meseta de Jáua, summit, 4°41′40″N, 64°13′20″W, 1,400 m, 16–18 Feb. 1974, *Julian A. Steyermark, V. Carreño E. & Charles Brewer-Carias 109199* (holotype, VEN; isotype, MO).

A *Daphnopsis longipedunculata* Gilg ex Domke foliorum paginis superioribus venatione tertiaria irregulariter contorta, perianthio rubescenti cum apice albo, calycis tubo intus praeter infra medium sparse pubescentem glabro, squamis hypogynis quattuor incrassatis prope apice obtusum lutescentibus rubescentibusque recedit.

Slender tree 3 m tall with bark difficult to tear, the young branches strigose. Petiole 3–4 mm long, moderately strigose. Leaf blades elliptic-oblong or ovate-oblong, rounded at apex, acute at base, 4–7.5 cm long, 2–4.5 cm wide; upper surface mainly glabrous except strigose along the depressed midrib; lower surface uniformly short-strigose with the lower midrib more densely strigose with longer hairs; lateral nerves 7–9 each side, faint above, slender and slightly manifest below; tertiary veins of upper surface irregularly contorted, loosely and inconspicuously reticulate. Pistillate calyx dull red with whitish tips, cylindric, 5 mm long, 4-lobed; lobes unequal, puberulous in upper half, glabrous below, the larger ones 1 mm long, 0.8 mm wide, pubescent over a larger area with longer hairs toward the base; the smaller lobes 0.7 mm long, 0.7 mm wide, ovate-oblong; calyx tube glabrous within except for small sericeous patches below the middle. Hypogynous scales 4, linear-lanceolate, 1.5–2 mm long, 0.2 mm wide in lower part, dull yellow, dull reddish near the tip. Pistil 4 mm long; ovary ellipsoid, 2.4 mm long, densely sericeous; style 1.5 mm long, glabrous; stigma subglobose, 0.5 mm long.

This species differs from *Daphnopsis longipedunculata* Gilg ex Domke by having peculiarly contorted, irregular tertiary venation on the upper leaf surface; the calyx reddish white with white tips and with glabrous interior except for sparse

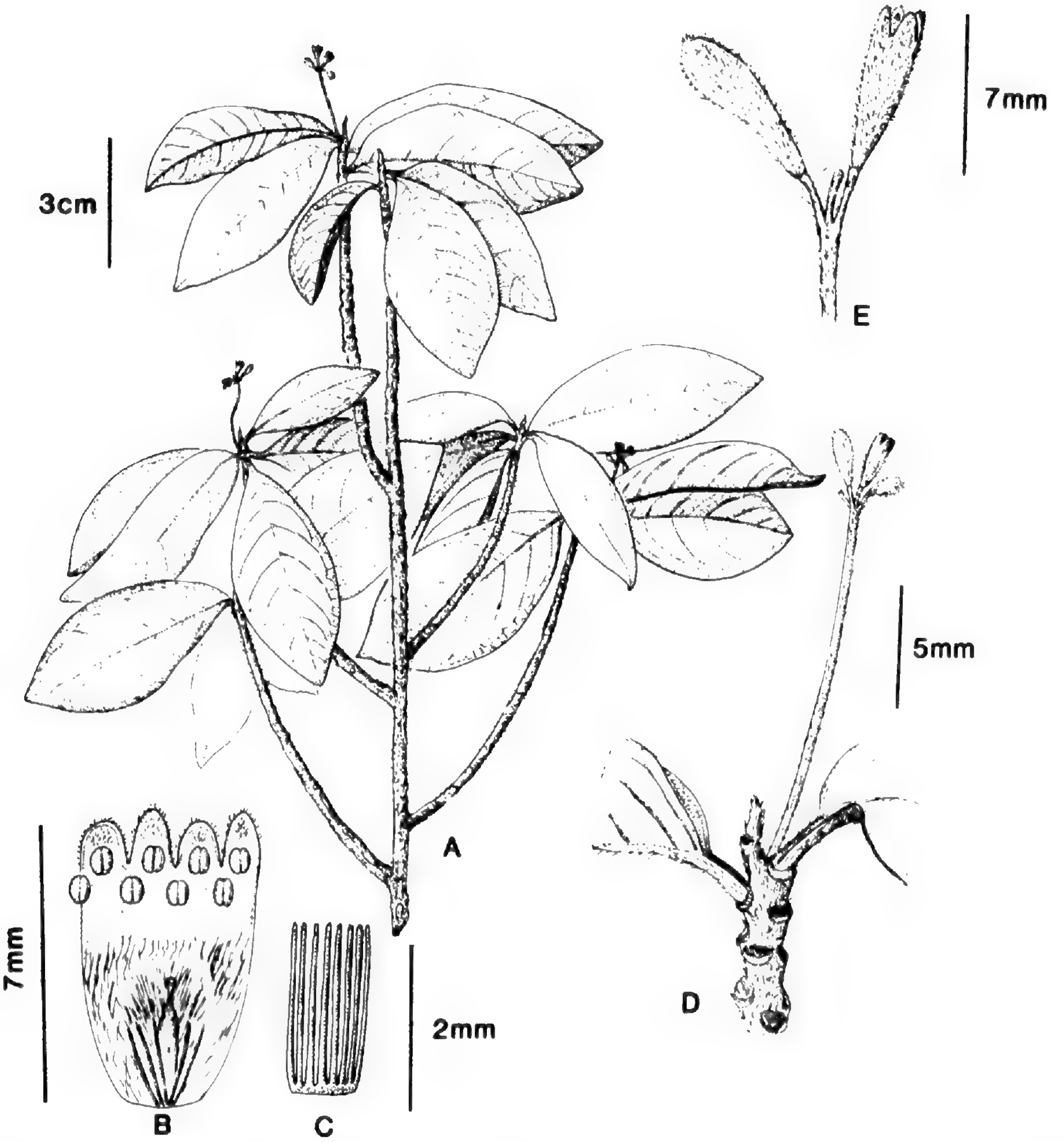

FIGURE 9. *Daphnopsis guaiquinimae.*—A. Flowering branch.—B. Flower, interior view.—C. Hypogynous scales.—D. Peduncle with flowers.—E. Group of flowers.

pubescence below the middle; and hypogynous scales thickened and dull yellow with reddish near the obtuse tips.

SCHOENOBIBLUS

Schoenobiblus amazonicus Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: 25 km S of Puerto Ayacucho, 5°30′N, 67°35′W, 5 Aug. 1967, *Wessels-Boer 1953* (holotype, MER; isotype, MY). Figure 10.

Arbor 6 m; foliorum laminis oblanceolato-obovatis apice acuminatis base acutis 36 cm longis 12.5–14 cm latis subtus praesertim costa media necnon nervis lateralibus puberulis; petiolis subtus dense strigillosis; pedunculo principali 5.5–11.5 cm longo; inflorescentia umbellata, 10–20-flora; pedicellis 10–18 mm longis; calycis tubo lineari 17–18 mm longo 0.6–0.8 mm lato extus sericeo intus supra medium retrorse sparsimque strigoso ceterum glabro, lobis quattuor linearibus apice rotundatis 6 mm longis 1.5 mm latis extus sericeo-lanuginosis intus villosis; stylo filiformi 18 mm longo.

Tree 6 m tall; buds fusiform, subobtuse, 6.5 mm long, 2.5 mm wide. Petiole 6–9 mm long, 2.5–3 mm wide, strigillose beneath; leaf blades oblanceolate-obovate, acutely acuminate at apex, acute at base, 36 cm long, 12.5–14 cm wide, glabrous above, moderately strigillose on midrib and lateral nerves below, these sparsely puberulous on leaf surface, with the midrib elevated, this impressed above; main lateral nerves 8–12 each side, anastomosing near margin; tertiary veinlets reticulate with large areoles. Main peduncle(s) solitary or 2, terminal or axillary, branching at the summit into 2 secondary sericeous axes, one of them solitary, the other forking into 2–3 shorter secondary axes 2–4 cm long. Flowers 10–20-umbellate; pedicels 10–18 mm

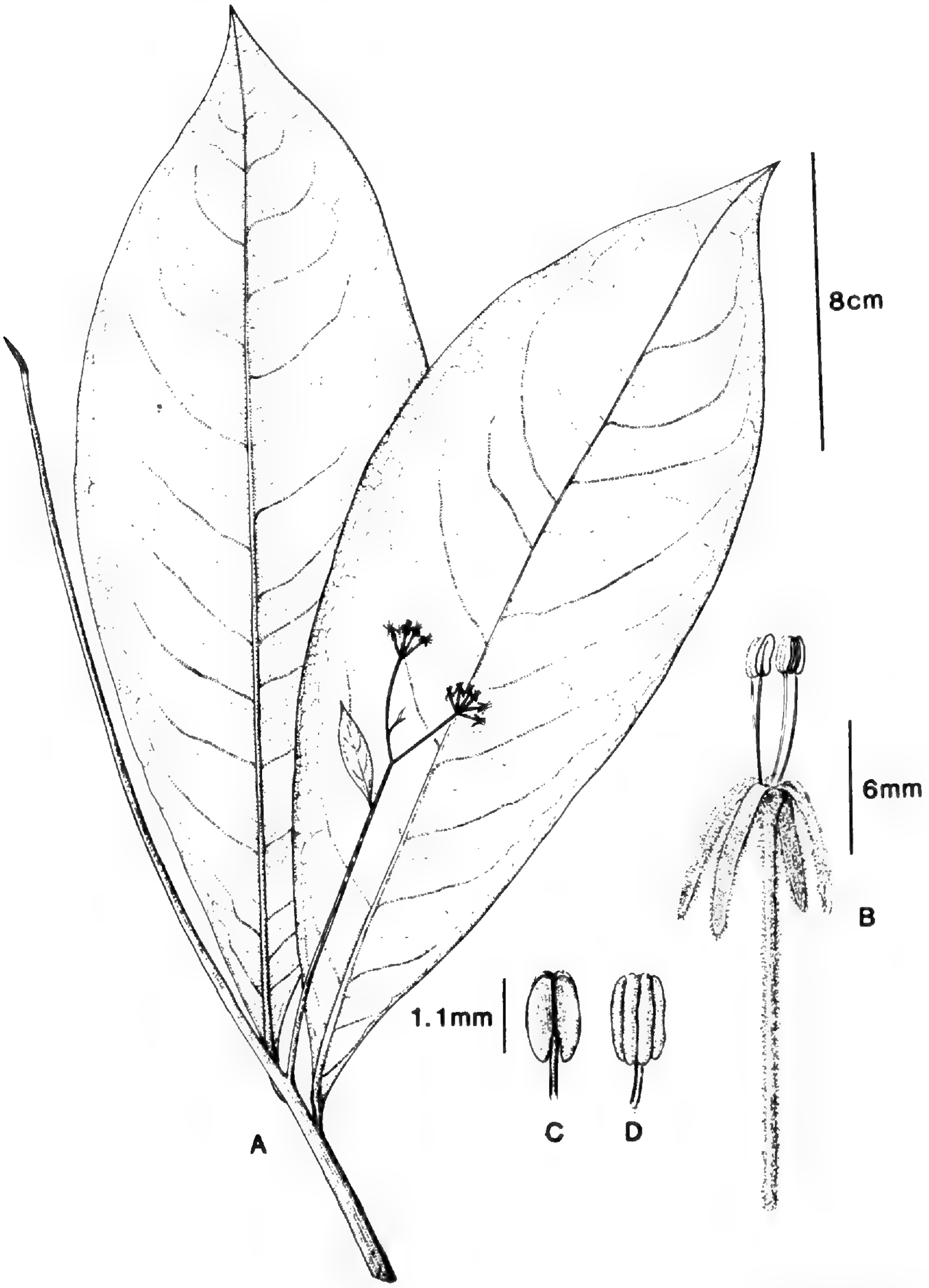

FIGURE 10. *Schoenobiblus amazonicus.*—A. Flowering branch.—B. Flower.—C. Stamen, dorsal view.—D. Stamen, ventral view.

long. Calyx tube linear, 17–18 mm long, 0.6–0.8 mm wide, short-sericeous without, retrorsely sparsely strigose within in the upper half, glabrous in the lower half; lobes 4, spreading, revolute at margins and at apex, linear, rounded at apex, 6 mm long, 1.5 mm wide, sericeous-lanuginose without, villosulous within. Stamens 4; anthers suborbicular or broadly oblong, 1.1 mm long, 0.7–0.9 mm broad; filaments long exserted, erect-ascending, 5–5.5 mm long, glabrous. Style filiform, 18 mm long, glabrous, attaining the orifice; stigma ellipsoid, 1.2 mm long.

The new taxon differs from *Schoenobiblus daphnoides* Martius of Brazil in the much broader leaves and less-branched inflorescence, while from other Venezuelan material identified as *S. daphnoides* it is differentiated by the longer, more slender calyx tube, narrower calyx lobes with shorter, gray sericeous pubescence, and much longer peduncle.

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SYMPLOCACEAE

SYMPLOCOS

KEY TO THE SPECIES OF *SYMPLOCOS* OF THE VENEZUELAN GUAYANA

1a. Ovary 4-celled; pubescence of lax or spreading hairs at least on the upper part of the branchlets, petioles, and lower leaf surface, and/or on the lower nerves .... *S. ulei*

1b. Ovary 3- or 5-celled; pubescence absent or of appressed or sericeous hairs 2

  2a. Calyx lobes acute to acuminate at apex; style pubescent 3

    3a. Inflorescence shorter than the petiole, sessile or nearly so, 2–3-flowered; calyx lobes 1.8–2 mm long; corolla 7 mm long; leaves minutely and distantly crenulate .... *S. acananensis*

    3b. Inflorescence equaling or longer than the petiole, shortly pedunculate, 5–8-flowered; calyx lobes 2.5–3 mm long; corolla 8–9 mm long; leaves entire to subentire .... *S. schomburgkii*

  2b. Calyx lobes obtuse to rounded at apex; style glabrous 4

    4a. Ovary 5-celled 5

      5a. Leaves glabrous beneath, acuminate at apex, acute at base; petiole glabrous throughout .... *S. martinicensis*

      5b. Leaves sparsely pubescent beneath on the nerves, obtuse at apex, rounded or obtuse at base; petiole strigillose adaxially .... *S. chimantensis*

    4b. Ovary 3-celled 6

      6a. Calyx glabrous without, except for the ciliate lobes; filaments not connate, free or nearly so to the base; leaves completely glabrous beneath; petioles glabrous .... *S. pycnophylla*

      6b. Calyx appressed-pubescent, strigillose, or sericeous without, at least on the lobes; filaments free above, connate below; leaves with at least the lower midrib appressed-pubescent; petioles appressed-pubescent or sericeous 7

        7a. Calyx lobes longer than the calyx tube; leaves rounded to obtuse at apex, rounded or obtuse at base, 3.5–6 cm long .... *S. jauensis*

        7b. Calyx lobes shorter than or equaling the calyx tube; leaves acuminate at apex, acute at base, 7–10 cm long 8

          8a. Fruit densely strigillose, 5 mm long; stamens 25–40; lower leaf surface sparsely appressed-pubescent to glabrescent; bracts suborbicular, rounded or obtuse; corolla 3 mm long .... *S. yapacanensis*

          8b. Fruit glabrate, 6–8 mm long; stamens 20–25; lower leaf surface glabrous; bracts acute; corolla 4–4.5 mm long .... *S. neblinae*

Symplocos acananensis Steyermark, sp. nov. TYPE: Venezuela. Bolívar: gallery forest bordering savanna, vicinity of Guadequen, Río Acanán, affluent of Río Carrao, west of Cerro Las Hermanas, 5°56′N, 62°17′W, 470 m, 1–3, 20 May 1986, *Julian A. Steyermark, R. Liesner & B. Holst 131868* (holotype, VEN; isotype, MO).

Frutex 1.5 m, ramis plerumque glabris; foliis petiolatis, petiolis 1.2–5 mm longis glabris; foliorum laminis elliptico-oblongis apice breviter acuminatis basi obtusis vel parum rotundatis 4.5–8 cm longis 2.5–3.5 cm latis glabris, marginibus minute obtuseque serrulatis, nervis lateralibus utroque latere 4–5; inflorescentiis axillaribus sessilibus vel fere 2–3 floris; bracteis sub floribus extus adpresso-pubescentibus arcte ciliatis; calycis tubo cupulato 1.2–1.5 mm longo glabro, lobis 5 late lanceolatis acuminatis 2 mm longis 0.8–0.9 mm latis praeter margines ciliatos glabris; corolla 7 mm longo, tubo 2.5 mm longo, lobis 5 oblongis apice rotundatis 4.5 mm longis; staminibus ca. 20, filamentis superne libris inferne in tubum 3.5 mm longum coalescentibus glabris 1.5–3.5 mm longis; stylo 5 mm longo in dimidio inferiore piloso.

Shrub 1.5 m tall with mainly glabrous branches. Petioles 1.2–5 mm long, glabrous; leaf blades chartaceous, elliptic-oblong, abruptly short-acuminate at apex, obtuse to slightly rounded at base, 4.5–8 cm long, 2.5–3.5 cm wide, glabrous both sides, appearing subentire but the margins with microscopically obtuse serrulations 0.1–0.2 mm long, 2–4 of these dispersed in 1 cm of margin; lateral nerves 4–5 each side, faintly anastomosing with the tertiary veinlets 4–8 mm from the margin, obsolete above, slightly manifest below; tertiary veinlets slightly reticulate below, scarcely or not manifest above. Inflorescence axillary, 2–3-flowered, sessile or nearly so, shorter than the petioles; flowers fasciculate, sessile. Bracts subtending flowers lanceolate, subacute, 1 × 1 mm, pubescent without, strongly ciliate, with caducous black glands. Corolla 7 mm long, the tube 2.5 mm long, 1.5 mm wide; lobes 5, oblong, rounded at summit, 4.5 mm long, 2.1 mm wide. Calyx tube cupulate, 1.2–1.5 mm long, 1.5–2 mm wide above, glabrous; calyx lobes 5, broadly lanceolate, acuminate, 2 mm long, 0.8–0.9 mm wide, glabrous except for the ciliate margins. Corolla 7 mm long, the tube 2.5 mm long, the 5 lobes oblong, rounded at the apex, 4.5 mm long. Stamens about 20, ca. 4-seriate; filaments free above, forming a tube 3.5 mm long, the longer filaments 1.5–3.5 mm long, the shorter ones 1 mm long, all glabrous; anthers broadly oblong, 0.2 mm long. Style 5 mm long, pilose in the lower half. Fruit not seen.

This species is closely related to the group of *Symplocos schomburgkii* Klotzsch ex Schomb., *S. guianensis* (Aublet) Gürke, and *S. pilosiuscula* Brand. It is distinguished from *S. guianensis* by the glabrous branches, from *S. schomburgkii* by the sessile or nearly sessile inflorescence which is fewer-flowered and shorter than the petiole, the shorter corolla and calyx lobes, and minutely crenulate leaf margins. The new species differs from *S. pilosiuscula* in the acute to acuminate calyx lobes.

RUBIACEAE

Chomelia glabricalyx Steyermark, sp. nov. TYPE: Venezuela. Bolívar: primary forest and river edge, Río Caura, 5–10 km S of Las Pavas (Salto Para), 6°12'N, 64°28'W, 240 m, May 1982, *Gilberto Morillo 6811* (holotype, VEN).

Frutex 1 m, ramis glabris spinosis; foliorum laminis ovato- vel lanceolato-ellipticis apice acutis vel subacuminatis basi cuneatim acutis 4.5–9.5 cm longis 1.5–4 cm latis praeter axillas inferiores barbellatas nervorum atque interdum folia basi sparsim ciliatis aliter glabris; inflorescentia 6-flora, pedunculo filiformi 14–20 mm longo glabro; floribus sub anthesi sessilibus sub fructu 0.5–1 mm pedicellatis basi sine involucro; calyce hypanthioque glabro, hypanthio 1.5 mm longo 1 mm lato, lobis inaequalibus ligulato-oblongis obtusis 0.5–1 mm longis glabris; corolla 4 mm longa tubo extus glabro, lobis subtus glabris apicem versus sparsim strigillosis; fructu anguste cylindrico 10 mm longo 3.5 mm lato 0.5–1 mm pedicellato.

Shrub 1 m tall; branches glabrous, spinose. Leaves petiolate, petioles 2–5 mm long, ciliate on upper margins; leaf blades ovate to lanceolate-elliptic, acute to subacuminate at apex, cuneately acute at base, 4.5–9.5 cm long, 1.5–4 cm wide, glabrous both sides except for barbellate lower axils of the lateral nerves and sometimes with few sparse ciliate hairs at the base; lateral nerves 5–6 each side, scarcely evident above, slightly impressed below. Stipules subulate, projecting 0.5 mm long. Inflorescence 6-flowered; peduncle filiform, 14–20 mm long, glabrous; flowers not involucrate at base, sessile, or in fruit 0.5–1 mm pedicellate. Calyx and hypanthium glabrous; hypanthium tubular, 1.5 mm long, 1 mm wide, glabrous; calyx lobes unequal, ligulate-oblong, obtuse, 0.5–1 mm long, 0.5–0.7 mm wide, glabrous. Corolla subcylindric, 4 mm long, 1.2 mm wide; tube 2.5–3 mm long, glabrous without; lobes oblong, obtuse, 1.5 mm long, glabrous below, sparsely strigillose upward. Fruit narrow-cylindric, 10 mm long, 3.5 mm wide, 0.5–1 mm long pedicellate.

This taxon is related to the recently described *Chomelia delascioi* Steyerm. and *C. stergiosii* Steyerm. The present taxon differs from *C. delascioi* in the larger, barbellate leaves, shorter corollas, and more numerously flowered inflorescence, and from *C. stergoisii* in the shorter corolla and calyx lobes and the completely glabrous hypanthium and calyx lobes.

Coccocypselum huberi Steyermark, sp. nov. TYPE: Venezuela. Bolívar: Distrito Roscio, Serranía del Caco, 25 km NW of San Ignacio de Yuruani, 2.5 km ESE of Wanarú, 5°12'N, 61°15'W, 1,150–1,200 m, 1 Mar. 1984, *Otto Huber 9123* (holotype, VEN; isotype, MO).

Herba radicans, caulibus repentibus 0.8–1 mm diam. modice strigillosis; stipulis lineari-setaceis 1.2 mm longis sparsim strigillosis; foliis petiolatis, petiolis 3–13 mm longis dense strigosis; foliorum laminis ellipticis anguste oblongo-ovatis vel elliptico-ovatis apice subacutis vel subobtusis basi acutis vel obtusis 2–2.8 cm longis 1–1.5 cm latis utrinque breviter strigillosis, nervis lateralibus utroque latere 5–7; inflorescentia 1-flora, pedunculo sub anthesi 1.5 mm longo sub fructu 4–5 mm longo dense strigilloso; hypanthio dense strigoso; calycis lobis inaequalibus lanceolatis acutis 1.8–2.5 mm longis 0.4–0.5 mm latis ubique sparsim strigillosis ad basim inter lobos glandula solitaria interposita munitis; corolla albida 4.8–5 mm longo extus sparsim strigillosa; bacca (immatura) in statu vivo 1–1.5 cm diam., in sicco 5 mm longo 4.5 mm lato modice strigilloso.

Creeping herb with moderately strigillose stems 0.8–1 mm diam.; stipules linear-setaceous, 1.2 mm long, sparsely strigillose. Petioles of the larger leaves 10–13 mm long, of the smaller ones 3–5 mm long, densely strigose; leaf blades elliptic, narrowly oblong-ovate, or elliptic-ovate, subacute to subobtuse at apex, acute to obtuse at base, moderately short-strigillose both sides, more abundantly on nerves beneath, 2–2.8 cm long, 1–1.5 cm wide; lateral nerves 5–7 each side, faint on lower side. Flowers solitary, the peduncle 1.5 mm long in anthesis, 4–5 mm long in fruit, densely strigillose. Calyx 3.5 mm long, the tube subglobose, 1.3 × 1.3 mm, densely strigose, the lobes unequal, lanceolate, acute, 1.8–2.5 mm long, 0.4–0.5 mm wide, sparsely strigillose on both sides, at base within setose with erect hairs, each sinus at the base furnished with 1 squamella. Corolla white, infundibuliform, 4.8–5 mm long, sparsely strigillose without, the tube 2.8–3 mm long, the lobes broadly lanceolate, 2 mm long, 0.8 mm wide. Stamens not exserted, attached ½ distance of the tube length; anthers oblong, obtuse, 1.1 mm long. Style 3 mm long, glabrous. Immature fruit urceolate-globose, 5 mm long, 4.5 mm wide (dried), 1–1.5 cm diam. (living).

The present taxon approaches the endemic Jamaican species, *Coccocypselum pseudotontanea* Griseb. Both possess white corollas and small leaf blades, but the Venezuelan species differs in having shorter stipules, shorter calyx lobes and corolla, shorter and 1-flowered peduncles, one squamella at the base of each side of the inner part of the calyx lobe, larger fruits with appressed pubescence, and the freely rooting habit.

Perama dichotoma Poepp. & Endl. var. **monocephala** Steyerm., var. nov. TYPE: Venezuela. Territorio Federal Amazonas: Departamento Atabapo, Cerro Huachamacari, ladera sur-este 175–180 m, 12–14 Oct. 1984, *Francisco Delascio 12358*; hierba pilosa; hojas arrosadas verde oscura por el haz, verde pálido por el envés; pedúnculo floral erecto, violaceo-morado en su base; flores blancas con el apice de los pétalos lila) (holotype, VEN; isotype, MO).

A *P. dichotoma* var. *dichotoma* et var. *scaposa* caulibus simplicibus monocephalis recedit; capitulis solitariis depressis 2–4 mm altis 5–6 mm latis.

Herb, 4–5 cm tall. Leaves rosulate, ovate or elliptic, 7–10 mm long, 3–6 mm wide, densely pilose above, pilose on main nerves below. Heads solitary, ca. 10-flowered, depressed-hemispheric, 2–4 mm high, 5–6 mm wide. Corolla lavender.

Perama dichotoma has the inflorescence usually consisting of several to numerous heads on filiform forking branches. The new variety has only a solitary head of flowers terminating a simple peduncle.

NOTES

NEW COMBINATIONS IN CENTRAL AMERICAN ARACEAE

Work in recent years with the Araceae of Central America necessitates new combinations involving species in the genera *Monstera* and *Philodendron* which were erroneously published as belonging to *Rhodospatha* and *Syngonium* respectively.

Monstera costaricensis (Engl. & Krause) Croat & Grayum, comb. nov. *Rhodospatha costaricensis* Engl. & Krause, Das Pflanzenr. 4. 23B (Heft 37): 95. 1908. TYPE: Costa Rica. Limón: Ferme de Boston, Atlantic watershed, 30 m elev. 10°01′N, 83°15′30″W, *Tonduz 14628* (holotype, B).

We had concluded that this distinctive species of *Monstera,* occurring in primary forest at Finca La Selva, was undescribed and had provisionally assigned it the name "*Monstera undulata.*" It now turns out that this species was previously described by Engler & Krause (1908) in the genus *Rhodospatha*; the transfer to *Monstera* is herewith effected. *Monstera costaricensis* is distinguished from other species by its strongly undulate petiole sheaths, tuberculate petiole bases and pistils shaped like bowling pins. The lamina may be either entire (as on the holotype) or perforate. *Monstera costaricensis* is now known in the Atlantic lowlands of Costa Rica from La Selva to Punta Mona. It probably occurs in Nicaragua and Panama as well.

Monstera dissecta (Schott) Croat & Grayum, comb. nov. *Tornelia dissecta* Schott, Oesterr. Bot. Z. 8: 179. 1858. TYPE: Costa Rica. Cartago: Volcán de Turrialba, *Wendland 500* (holotype, GOET).

Although the name *Monstera dilacerata* is well known and firmly entrenched in both taxonomic and horticultural aroid literature, it has been applied in a highly indiscriminate manner and, indeed, may be impossible to confidently assign to any real biological entity. As described by Madison (1977), "the type of *M. dilacerata* is an inferior specimen consisting of a few leaves from an immature cultivated plant of uncertain geographic origin." Such a specimen, even if it could be located, would be virtually impossible to identify with any biological species in a genus as phenotypically plastic as *Monstera*; but the type of *Monstera dilacerata* is apparently not extant, having been destroyed in the Berlin herbarium during World War II, and we know it only from photos.

Madison (1977), determined to salvage this well-known name by any means, adopted the concept of Engler & Krause (1908). Although the latter authors applied the name *M. dilacerata* rather consistently (i.e., to the species here treated as *M. dissecta*), their concept would appear to be completely irrelevant; what matters is the interpretation of the type material. It could be argued that Engler & Krause might have seen living (perhaps even fertile) material from the original collection, but they give no such indication and the point is moot.

Madison (1977) himself made matters significantly worse by applying the name *Monstera dilacerata* with reckless abandon. Based on his specimen citations, herbarium annotations, and the use of his keys, Madison has employed the name *M. dilacerata* for no fewer than four distinctly different species in Costa Rica alone (Croat & Grayum, unpubl. data). Given the expansive geographic distribution of *Monstera dilacerata* sensu Madison (from Guatemala to Amazonian Brazil), the application of the latter name to any one of the four Costa Rican species would have to be entirely arbitrary. Indeed, the type might just as well have come from Brazil, and may represent a different species altogether.

The only alternative seems to be the relegation of the much-abused name *Monstera dilacerata* Schott to the limbo of nomen dubium status, where it will probably lie forever unless someone can come up with a way (epidermal anatomy?) to unequivocally interpret the type specimen, in the unlikely event that it ever turns up. Three of the four Costa Rican species in the *Monstera dilacerata* complex have apparently never been described (they will be described elsewhere). The fourth clearly corresponds to *Tornelia dissecta* Schott, the type of which is extant at GOET and has been studied by the present authors (Madison was apparently unaware of its existence). The specimen is a good one and agrees in all details with a species we know well from throughout Costa Rica (but mostly from the Atlantic slope)

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at elevations of ca. 100–1,800 m. Contemporary collections from the general vicinity of the type locality include: *Grayum & Sleeper 3304* (CR, MO); *Grayum et al. 3490* (CR, MO); and *Grayum & Hammel 5739* (MO). The appropriate new combination in *Monstera* is made above.

Philodendron rothschuhianum (Engl. & Krause) Croat & Grayum, comb. nov. *Syngonium rothschuhianum* Engl. & Krause, Das Pflanzenr. 4. 23E (Heft 71): 124. 1920. TYPE: Nicaragua. Matagalpa: Matagalpa, 1,000 m, *Rothschuh 229* (holotype, B).

This species has long been excluded from *Syngonium,* perhaps having been first so treated by Birdsey (1955) in an unpublished thesis. Croat (1981) erroneously placed the species with *P. anisotomum* Schott. There is no longer any doubt that it is a distinct species, distinguished from the latter by having the posterior lobes more broadly confluent with the anterior lobe and by details of the inflorescence. The species ranges from Nicaragua to western Panama (Veraguas) from sea level to 1,000 m.

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TWO CUBAN NOVELTIES IN *XYRIS*

Among the *Xyris* kindly loaned by the curators of F, NY, MO, and US for a study of North American Xyridaceae were materials of two species of undescribed *Xyris,* both from the Isle of Pines. From descriptions of the white sand savannas of that island, once so frequently visited by such collectors as N. L. Britton, E. P. Killip, and P. Wilson, it is easily seen that it is ideal *Xyris* habitat, having nearly all of the *Xyris* species endemic to Cuba as well as most of those found both in southern Florida and along the Mosquito Coast and Belize. It is seen that western Cuba is perhaps the most significant floristic connector between the Florida peninsula and Mesoamerica for not only Xyridaceae but for Eriocaulaceae and many genera of sedges as well. Thus these two novelties are presented as but a small part of what promises to be a considerable updating as the new *Flora de Cuba* progresses and as Cuban-based botanists continue the work.

Xyris curassavica Kral & Urquiola, sp. nov. TYPE: Cuba. Isle of Pines: vicinity of Los Indios, 13 Feb. 1916, *N. L. Britton, E. G. Britton & P. Wilson 14219* (holotype, NY; isotypes, CM, F, MO, US). Figure 1.

Planta perennis, densicespitosa, laxa, 1.5–4 dm alta, caulibus contractis, radicibus gracilibus fibrosis. Folia vulgo erecta vel leviter expansa, torta, (5–)10–20(–25) cm longa; vaginae integrae, laminis 4–5-plo breviores, lampro-glandaceae vel roseolae, marginibus in laminas gradatim convergentibus, ad apicem breviligulam (usque ad 2 mm longam) fascientibus, raro eligulatis; laminae valde compressae, anguste lineares, pallide luteovirides, 0.5–2 mm latae, ad apicem subulatae, raro paucitrichomatiferae, marginibus integris, leviter incrassatis, raro distante papillosis, paginis glabris, longitudine valde 1–3-nervatis. Vaginae scaporum proximale lampro-glandaceae, folia principalia superantia, brevilaminatae. Scapi lineari-filiformes, flexuosi, torti, apicem versus in sectione transversali teretes vel ovati, 1–3(–4)-costati, ca. 0.5 mm crassi, costis glabris vel remote scabropapillosis. Spicae late ovoideae vel subglobosae, 5–7(–10) mm longae, pauciflorae, laxe spiraliter imbricatae, pallide lampro-ferrugineae, rotundatae, ecostatae, integrae; area dorsali distincta vel indistincta, ovata, pallide viridia; bracteae steriles 2–3, fertilibus breviores; bracteae fertiles vulgo ovatae, 4.5–5 mm longae, anguste rotundatae, ad marginem tenues, integri, tum erosae. Sepala lateralia libera, subaequilatera, elliptica, curvata, 4–4.5 mm longa; ala carinalis lata et firma, a basi ad apicem scabrido-papillosa. Laminae petalorum late obovatae, luteolae, ca. 4.5 mm longae, apice anguste rotundatae, erosae. Antherae lanceolato-oblongae, ca. 1.5 mm longae, valde bifidae et sagittatae, filamentis ca. 0.5 mm longis. Staminodia bibrachiata, brachiis apice sparsim penicillatis. Capsula ellipsoidea, ca. 3 mm longa; placenta marginalis. Semina anguste ovoidea vel curtocylindracea, 0.5–0.7 mm longa, succinea, translucida, apiculata, longitudine valde et irregulariter anastomosocostata.

Densely cespitose, soft-based perennial 1.5–4 dm high, the stems contracted, the roots slender-fibrous. Leaves mostly erect to slightly spreading, twisted, (5–)10–20(–25) cm long; sheaths ¼–⅕ as long as blades, entire, a lustrous tan or red-brown, tapering gradually from the clasping base, multicostate and carinate to the blade, there with a scarious, rounded ligule to 2 mm long; blades strongly flattened, narrowly linear, pale yellow-green, 0.5–2 mm wide, apically subulate and sometimes with a few coarse trichomes, the edges entire and slightly thickened, sometimes remotely papillate, the surfaces longitudinally strongly 1–3-nerved, often papillate or rugulose-papillate proximally. Scape sheaths lustrous tan proximally, open and short-bladed distally, shorter than principal leaves. Scapes linear-filiform, flexuous, twisted, distally subterete or oval in cross section, 1–3(–4)-costate, ca. 0.5 mm thick, the costas smooth or distantly scabro-papillose. Spikes broadly ovoid to subglobose, 5–7(–10) mm long, the bracts few, loosely spirally imbricate, lustrous pale red-brown with distinct or indistinct ovate pale green (when young) dorsal areas, the backs convex, toward apex low-carinate; sterile bracts 2–3, smaller than the fertile bracts and grading into them, the lowest oblong, strongly carinate; fertile bracts mostly ovate, 4.5–5 mm long, the apex narrowly rounded, the margins thin, entire or aging erose. Lateral sepals free, subequilateral, elliptic, curvate, 4–4.5 mm long, the broad keel firm, scabro-papillate from near base to acute apex. Petal blades broadly obovate, yellow, ca. 4.5 mm long, the narrowly rounded apex erose. Anthers lance-oblong, ca. 1.5 mm long, deeply bifid and sagittate, on stout filaments ca. 0.5 mm long. Staminodia bibrachiate, the flat, narrow branches sparsely penicillate. Capsule ellipsoid, ca. 3 mm long, the placentation marginal with placentas extending from base to near summit. Seeds lance-ovoid to short-cylindric, 0.5–0.7 mm long, apiculate, pale red-brown, translucent, longitudinally distinctly but irregularly anastomosing-ribbed.

Frequent in sand savannas, Isle of Pines, Cuba.

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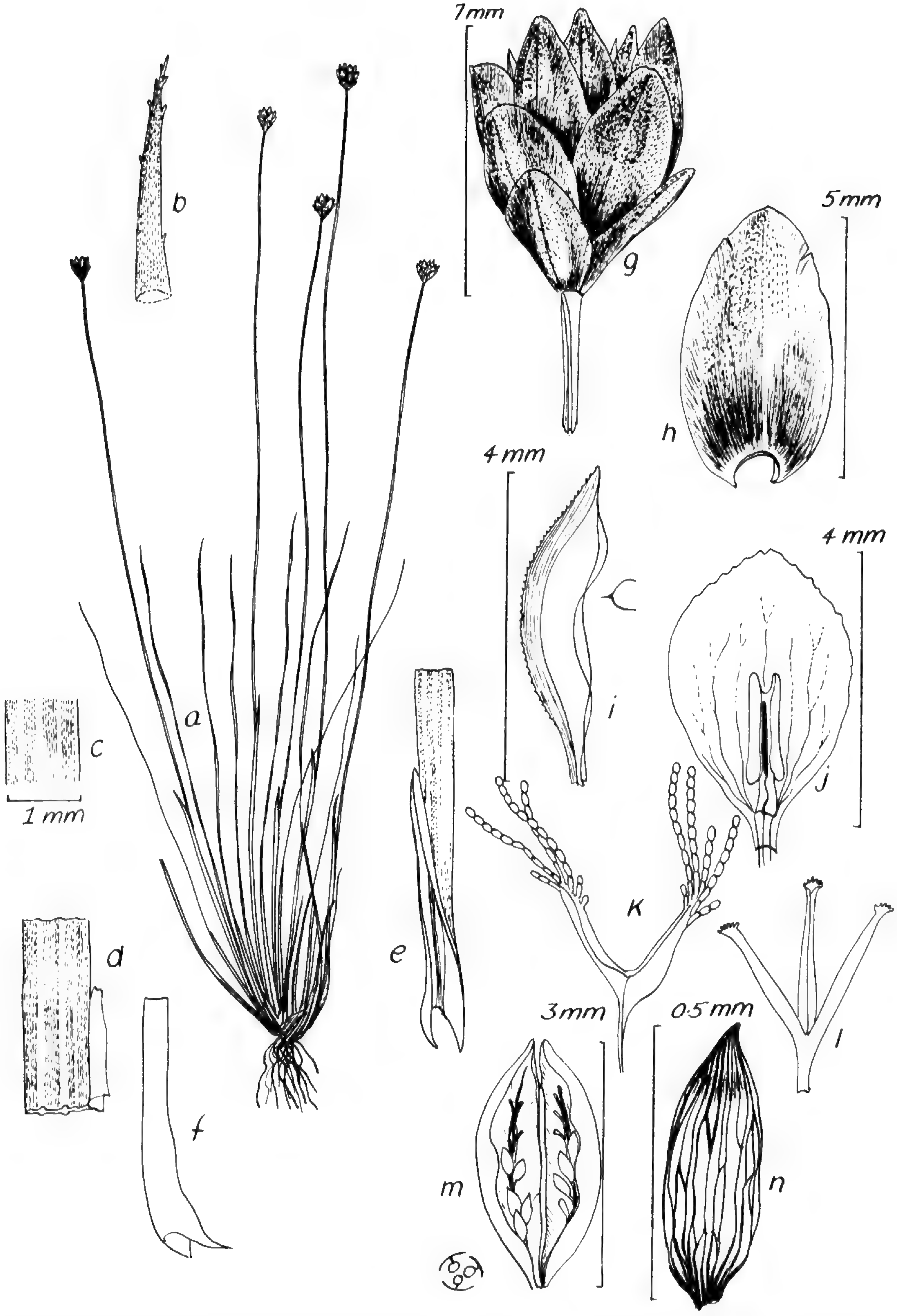

FIGURE 1. *Xyris curassavica* (*Alain & Killip 2194*).—a. Habit sketch.—b. Leaf apex.—c. Sector of mid-blade.—d. Leaf blade–sheath junction.—e. Apex of leaf sheath.—f. Leaf base.—g. Spike.—h. Fertile bract.—i. Lateral sepal.—j. Petal blade and stamen.—k. Staminode.—l. Stylar apex.—m. Capsule, one valve removed, showing placentation.—n. Seed.

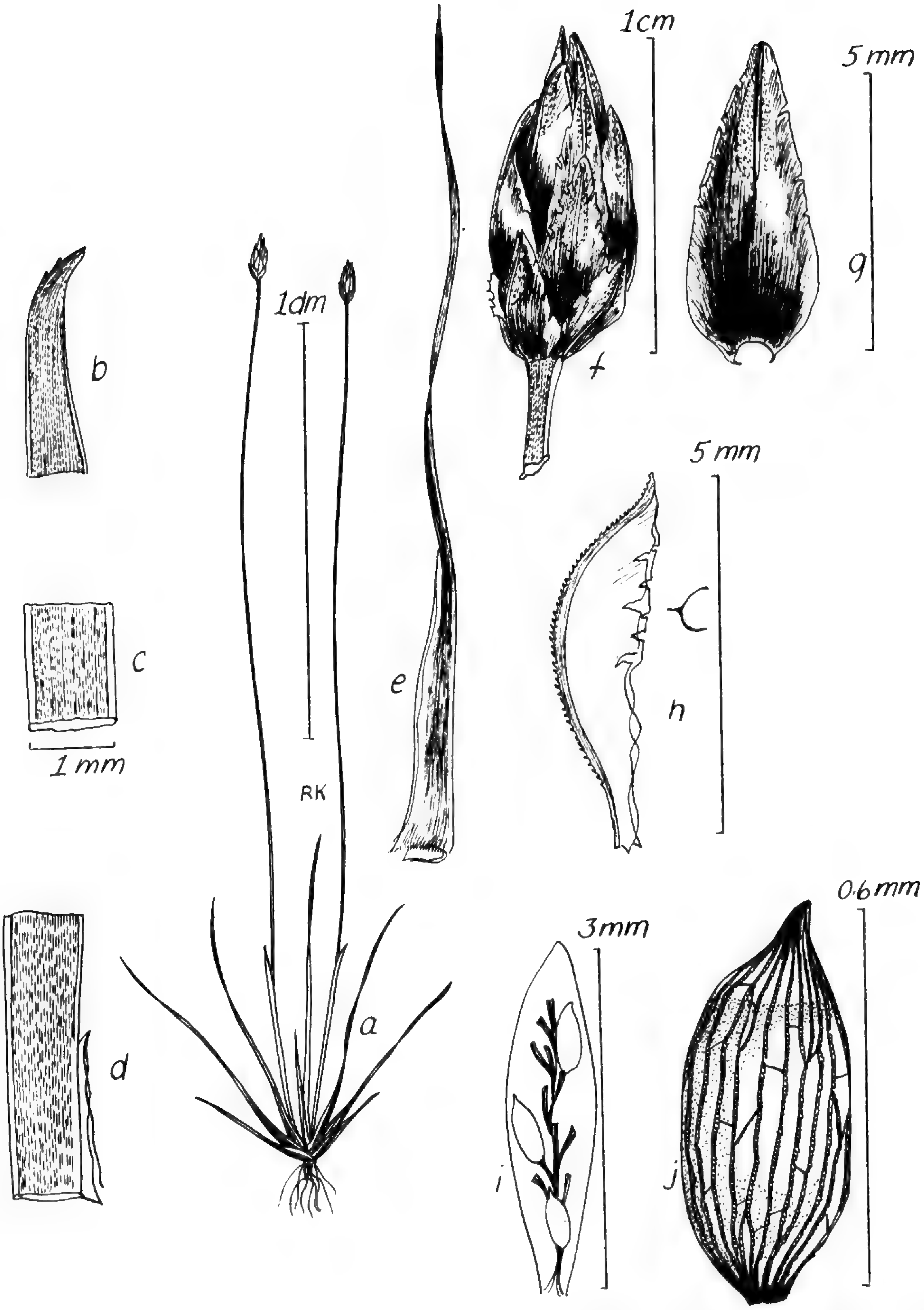

FIGURE 2. *Xyris paleacea* (*Leon & Victorin 17823*).—a. Habit sketch.—b. Leaf apex.—c. Sector of leaf at mid-blade.—d. Leaf blade–sheath junction.—e. Leaf.—f. Spike.—g. Fertile bract.—h. Lateral sepal.—i. Capsule valve with placenta.—j. Seed.

Additional specimens examined. CUBA. ISLE OF PINES: Los Indios, white sand sabanas, 27 Dec. 1951, *Alain & Killip 2194* (US); Los Indios, sabanas, 4 Feb. 1953, *Killip 42612* (US); Los Indios, sabanas, 22 Feb. 1953, *Killip 42868* (GH, NY); Los Indios, savannas, 22 Feb. 1953, *Killip 42873* (CAS, F, GH, NY, U, US).

This species most resembles *X. bicarinata* Griseb., another Cuban endemic, in general habit and somewhat in leaf but has thinner, paler leaf bases; flatter leaf blades; more slender scapes; and broader spikes with thinner fertile bracts less tending to spread and recurve. The aspect is less robust and smoother.

Xyris paleacea Kral & Urquiola, sp. nov. TYPE: Cuba. Pinar del Río: Laguna de Sta. Maria, W of Sn. Luis, May 1940, *H. Leon & M. Victorin 17823* (holotype, US). Figure 2.

Planta solitaria vel parum cespitosa, annua vel perennis,usque ad 3 dm alta, caulibus contractis, radicibus gracilibus fibrosis. Folia leviter flabellate expansa, 4–6 cm longa; vaginae integrae, laminis 2–3-plo breviores, carinatae, lampro-ferrugineae, marginibus in laminas gradatim convergentibus, ad apicem breviligulam rotundatum fascientibus, aut eligulatis; laminae compressae, leviter tortae, 0.5–1.5 mm latae, ad apicem anguste acutae, leviter incrassatae, marginibus pallidis incrassatis, papillatis vel leviter tuberculatis, paginis glabris, longitudine leviter striatis. Vaginae scaporum brunneolae, nitidae, multicostatae, folia principalia superantes, brevilaminae. Scapi filiformes, apicem versus leviter compressi, ca. 0.5 mm lati, distincte bicostales, costis pallidis glabris aut papillosis. Spicae lanceolato-ovatae, pauciflorae, ca. 1 cm longae, acutae; bracteae spiraliter laxe imbricatae, rufo-brunneolae, laceratae; area dorsalis lanceolata, pallide viridis; bracteae steriles vulgo 2, fertilibus breviores; bracteae fertiles lanceolato-ovatae, 5–6 mm longae, apicem versus anguste cucullato-incurvatae, valde carinatae. Sepala lateralia libera, subaequilatera, pallide fusca, valde curvata, 4.5–5 mm longa, acuta; ala carinalis firma, angusta, a basi ad apicem scabridula. Petala et stamina non visa. Capsula ellipsoidea, ca. 3 mm longa; placenta marginalis. Semina ellipsoidea, ca. 0.6 mm longa, succinea, apiculata, translucida, longitudine valde et irregulariter anastomoso-costata.

Solitary or in small tufts, annual or short-lived perennial to 3 dm high, the stems contracted, the roots filiform-fibrous. Leaves flabellately spreading-ascending, 4–6 cm long; sheaths entire, ⅓–½ as long as the blades, carinate, lustrous red-brown, narrowing gradually from the dilated, clasping base to the blade, there either with a short, scarious, rounded ligule or merging with blade base; blades green-brown or maroon, flattened, slightly twisted, 0.5–1.5 mm wide, the apex incurved, narrowly acute, slightly thickened, papillate or tuberculate-edged, the margins pale, incrassate, smooth or papillose, the surfaces smooth, longitudinally striate-nerved. Scape sheaths shorter than principal leaves, at base tubular, lustrous brown, multicostate, opening distally, short-bladed. Scapes filiform, distally slightly compressed, ca. 0.5 mm wide, distinctly bicostate, the costas pale, smooth or papillate. Spikes lance-ovoid, ca. 1 cm long, acute, of a few, loosely spirally imbricate, red-brown, lacerate bracts with pale green, papillose, subapical, lanceolate dorsal areas; sterile bracts usually 2, oblong, strongly carinate, 3.5–4 mm long; fertile bracts lance-ovate, 5–6 mm long, toward the narrow, subcucullate tip strongly carinate, the borders thin, becoming strongly lacerate. Lateral sepals 4.5–5 mm long, free, subequilateral, strongly curved, acute, the thick, narrow keel scabrid from near base to tip. Flowers and stamens not seen. Capsule ellipsoid, ca. 3 mm long, the placentation marginal, the placentas extending from base to near tip. Seeds ellipsoid, ca. 0.6 mm long, amber, apiculate, longitudinally strongly but irregularly anastomosing-ribbed.

Endemic to pine savanna, Pinar del Río, Cuba.

This species, thus far known only from the type specimen, appears allied to *X. brevifolia* Michaux and *X. flabelliformis* Chapman and is distinguished from them by a combination of (often) longer, pale-incrassate-bordered leaves; overall narrower spike outline with narrower, lacerate-bordered fertile bracts; and slightly longer and differently sculptured seeds.

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A NEW "VIORNA" *CLEMATIS* FROM NORTHERN ALABAMA

In 1983, while examining specimens from the Huntsville, Alabama, area donated to VDB by the collector, Mr. James D. Morefield, I was particularly interested in a distinctive "Viorna" that he had collected previously from the lower western slopes of Round Top Mountain (summit elevation ca. 1,600 feet). This mountain is a distinctive westward lobe of Huntsville Mountain and is south-southwest of Monte Sano Mountain in the same trend, the whole massif a part of the Cumberland Plateau. The *Viornae* subsection of *Clematis* is distinguished primarily by the thickened, bevelled-edged sepals which in the live flower form (usually) an urceolate design, the flowers themselves being arranged singly or in few-flowered cymes in leaf axils with the primary peduncle short to elongated but always having leafy bracts. The subsection is confined to North America and centers in the southeastern United States; it is notable for its narrow endemics.

I visited the locality and, thanks to the accuracy of Morefield's label information, was able to locate the population quickly and to find an abundance of plants in flower and early fruit. Further exploration on the same mountain trend resulted in discovery of yet another thriving population of this new *Clematis*. Named in honor of its perceptive first collector, it is described as follows:

Clematis morefieldii Kral, sp. nov. TYPE: United States. Alabama: Madison Co., SE Huntsville, along upslope side of eastward unpaved extension of Deborah Avenue, 0.65 mi. SSW of Round Top Mtn., limerocky face of slope, clay soil, in *Cotinus–Quercus.* Vines 2–5 m, sprawling on boulders or shrubs and forest reproduction; calyx greenish with rose tints, 17 June 1983, *R. Kral 70176* (fruiting material from same locality, 27 June 1986, *R. Kral* with *J. R. Carter 73540*) (holotype, MO; isotypes, ALU, AUA, BM, CM, DOV, DUR, EKY, F, FLAS, FSU, GA, GH, ILL, ISC, K, LAF, MICH, MISSA, MO, NCU, NY, OS, PAC, RSA, SMU, TENN, TEX, UC, US, VDB, VSC, WAT, WILLI). Figures 1, 2.

Planta perennis, scandens, usque ad 5 m longa, cirrhos efferens. Caules valde flexuosi, subteretes, 2–3 mm crassi, valde costati, rufobrunnei, parce vel copiose albovillosi vel pilosi vel araneosi. Foliola principalia remota, expansa, imparipinnata, usque ad 2 dm longa, rhachidi breviter pilosa vel villosa, flexuosa; foliola binatim, 9–11, expansa, ad apicem rhachidis gradatim redacta, superiora cirrhosa, inferiora anguste vel late ovata, 5–10 cm longa, acuta vel acuminata, brevimucronata, tenuia, integra vel bi- vel-triloba, petiolulis pilosis, 4–15 mm longis; pagina superior glabra flavovirens; pagina inferior sericea aut pilosa. Flores axillares, solitares aut pauci in cyma dispositi sessiles, pedunculis ad anthesin dense albovillosis, erectis vel expansis, 15–25 mm longis, ad basim bibracteolis. Sepala oblongo-lanceolata, 20–25 mm longa, acuminata, ad apicem margine anguste albomarginato, erecta tum ad apicem leviter expansa vel breviter reflexa, dorsaliter albosericea, subrosea aut pallide viridia et rubentia, margine incrassata, albotomentulosa, ventraliter glabra, inconspicue paucinervosa. Stamina linearia, 12–20 mm longa, filamentis compressis, supra medium pilosis, antheris cum apiculo 3.0–3.5 mm longis, pilosis. Achenium rhomboideo-ovatum, ca. 7–9 mm longum, acuminatum, compressum, sericeum, margine incrassato, stylo 30–35 mm longo, brunneoplumoso.

Perennial scandent vine to 5 m long. Stems flexuous, copiously villous and/or arachnoid with white hairs. Principal leaves imparipinnate, to 2 dm long, spreading, the rachis base shorter than the lowest leaflets, the rachis axis flexuous, pilosulous or villous; leaflets paired, 9–11, spreading or erect, reduced distally on rachis, the upper 1–3 forming tendrils, the lowest broadly to narrowly ovate, 5–10 cm long, acute to acuminate, mucronulate, thin, entire to 2- or 3-lobate, on pilose petiolules 4–15 mm long; upper surface smooth, yellow-green; lower surface sericeous or pilose. Flowers axillary, solitary or (more often) 1–3(–5) in sessile cymes, the peduncles at anthesis densely white-villous, erect or spreading, 15–25 mm long, with 2 bracteoles at base. Sepals oblong-lanceolate, 20–25 mm long, erect, the tips acuminate, with narrow white borders, slightly spreading to short-reflexed, the backs pink or pale green-and-red, albosericeous, the edges thick, white-tomentulose, the inner surface smooth, longitudinally inconspicuously few-nerved. Stamens linear, 12–20 mm long, the filaments flattened, pilose from middle to apex, the anthers including apiculus 3–3.5 mm long, pilose. Fruit body rhomboidal-ovate, 7–9 mm long, acuminate, compressed, marginally thickened, sericeous, the style 30–35 mm long, with a brown, plumose coma.

Additional specimens examined. UNITED STATES. ALABAMA: Madison Co., SE Huntsville, along upslope

ANN. MISSOURI BOT. GARD. 74: 665–669. 1987.

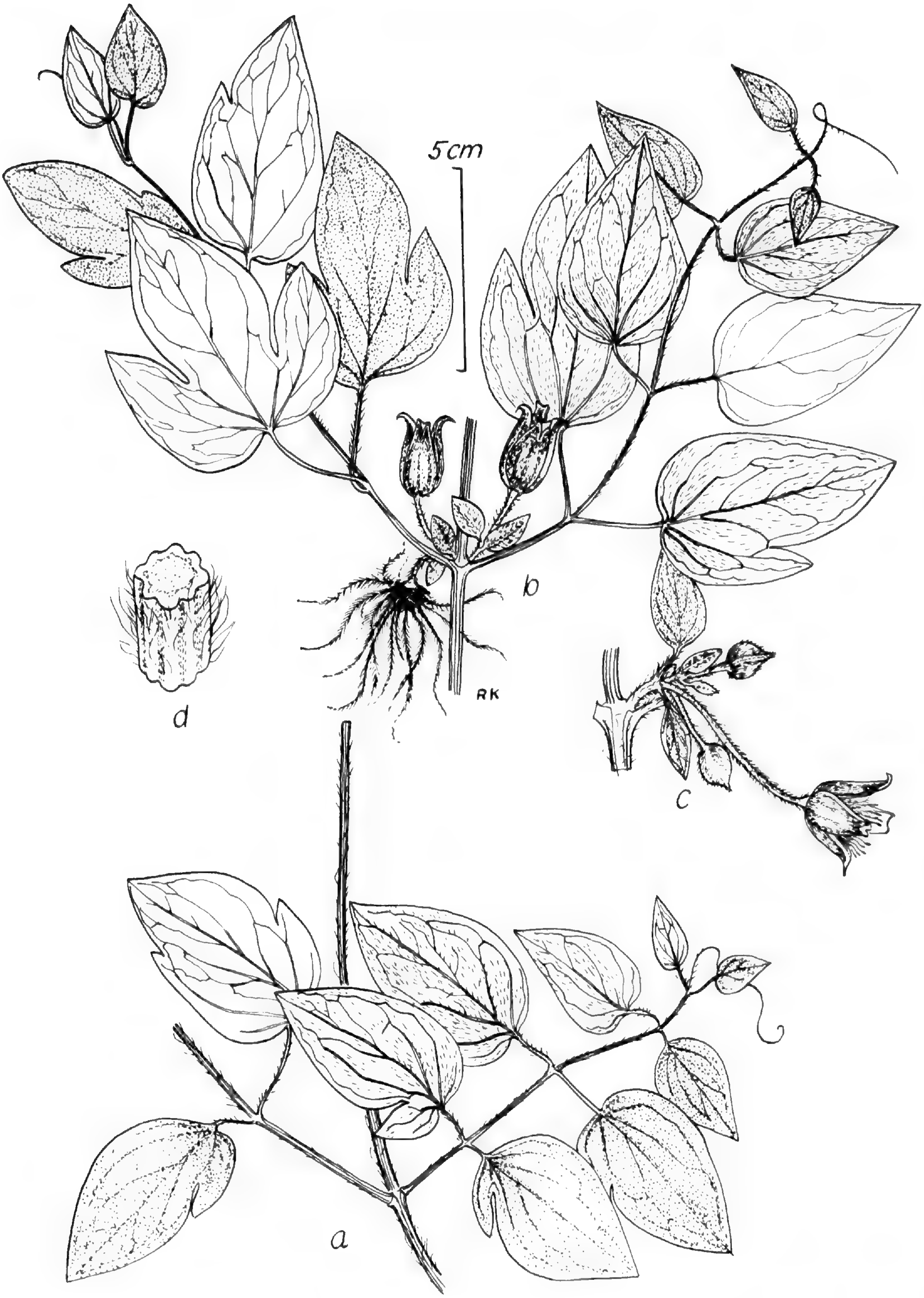

FIGURE 1. *Clematis morefieldii*.—a. Habit sketch, lower node.—b. Sketch of node from mid-vine.—c. Flowering node, largest leaves removed.—d. Sector of mid-stem. (Drawn from *Kral 70176*.)

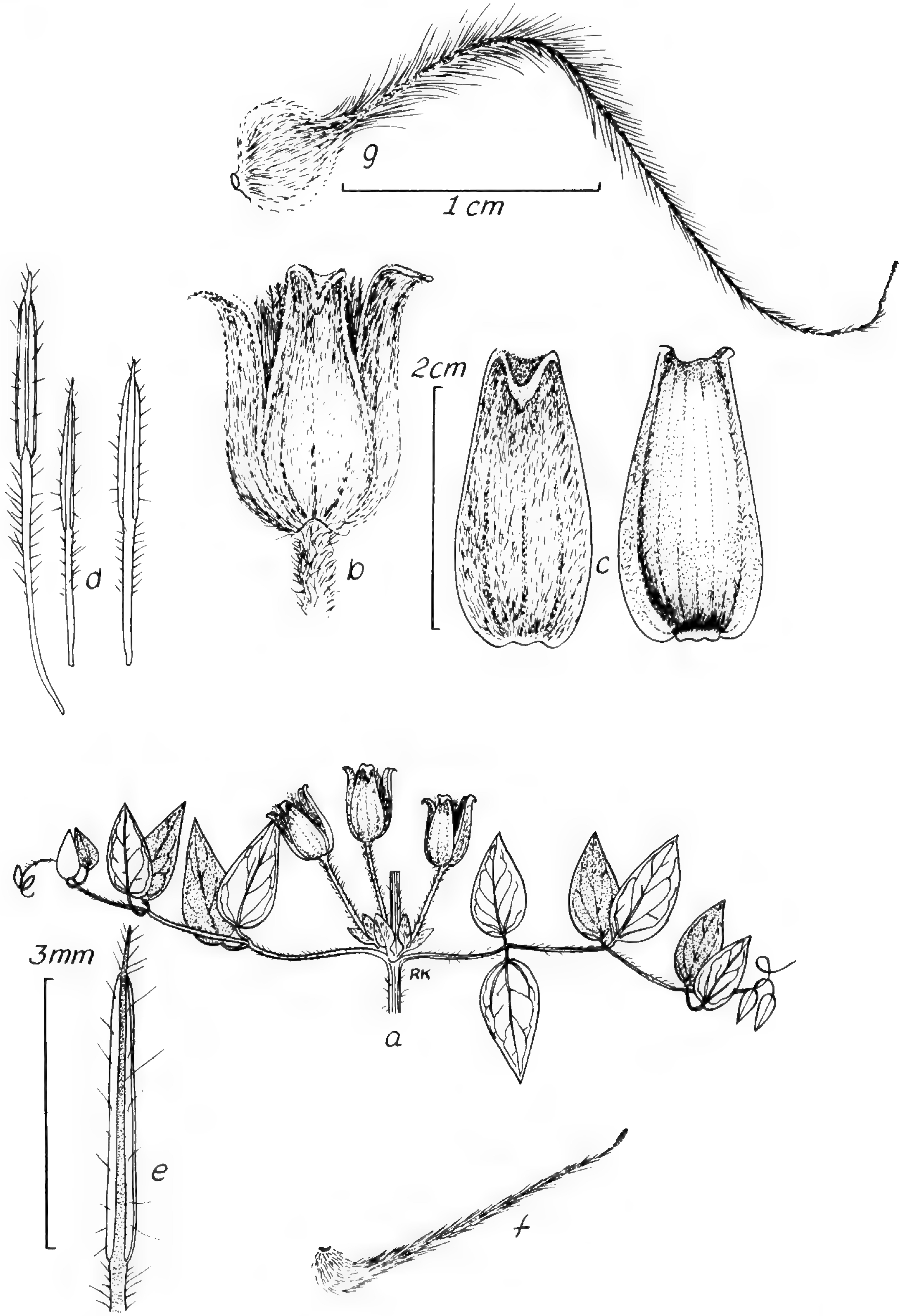

FIGURE 2. *Clematis morefieldii.*—a. Upper flowering node.—b. Flower.—c. Dorsal (left) and ventral (right) sides of sepal.—d. Three stamens.—e. Anther, enlarged.—f. Carpel.—g. Fruit with long persistent style. (Drawn from *Kral 73540.*)

side of eastward dirt extension of Deborah Avenue, 0.65 mi. SSW of Round Top Mtn., margin of mixed woods on rocky limestone slope, locally common, elev. 920 ft., 31 May 1982, *J. D. Morefield 629* [JDM (Morefield Herbarium), VDB]; vine of loam pockets in juniper–*Cotinus*–mixed hardwood, rather dry area, upper end of Drake Avenue, W face of mountian at E side of Huntsville; calyx pinkish, 17 June 1983, *R. Kral 70216* (VDB, and to be distributed).

This viorna, so far found only in the limestone uplands around Huntsville, Alabama, is closely related to the variable *Clematis viorna* L. Dr. Carl S. Keener (1975: 45), an authority on the genus, considers such variants as *C. gattingeri* Small, *C. flaccida* Small, and *C. beadlei* (Small) Erickson as part of that species, an opinion supported by the biosystematic study of the complex by Dr. W. M. Dennis (1976). However, Keener suggested (loc. cit.), "Nevertheless, critical population studies of *C. viorna*, especially in central Tennessee and adjacent Kentucky, would be instructive and might reveal more precise taxonomically definable topogamodemes."

It seems that this species, nested well inside an area of much of the diversity in *C. viorna*, is indeed distinctive. Of particular interest is the character combination of villous and arachnoid tomentum on the shoot, velvety lower leaflet surface, and stouter, usually shorter, peduncles which bear bracts only at the very base (this of particular significance as a character state in the viornas). The inflorescence is curious,the lower flowering nodes often producing sessile dichasia in the axils, or the bracteoles of these dichasia supporting more flower buds in their axils. The upper nodes are unifoliar and frequently display a wandlike length of progressively reduced leaves with the flowers paired in the axils, while the ultimate and penultimate nodes are often single-flowered; thus the overall effect is one of a narrow raceme with well-spaced nodes.

The plants are found in consistent habitat, namely the limestone measures that outcrop below the sandstone caprock of the Huntsville Mountain chain of the Cumberland Plateau which borders the Highland Rim on the east side of Huntsville. The vines root in a basic clay-loam amongst boulders of massive limestone, often sprawling over the rock itself. The forest type is an open to dense mixture of *Juniperus* with hardwoods typical of basic substrate, the more dominant being *Carya carolinae-septentrionalis, C. ovata, Quercus shumardii, Q. muehlenbergii, Q. alba, Q. stellata, Ulmus, Celtis, Acer saccharum,* and *Fraxinus americana.* However, the most notable indicator is the Smoketree, *Cotinus obovatus.* The shrub layer is marked particularly by *Rhus aromatica, Symphoricarpos, Hypericum frondosum, Forestiera ligustrina,* and *Viburnum rufidulum.* Associated and prevalent herbaceous markers include *Anemone virginiana, Delphinium carolinianum, Euphorbia corollata* (var.), *Tragia urticifolia, Hypericum sphaerocarpon, Zizia aptera, Thaspium pinnatifidum, Spigelia marilandica, Scutellaria ovata, Pycnanthemum incanum* (complex), *Blephilia hirsuta, Dasystoma macrophylla, Hedyotis purpurea,* and many composites—particularly *Aster, Solidago,* and the handsome white-liguled *Polymnia canadensis* var. *ligulata.* Most notable here are, however, *Silphium brachiatum* and *Solidago auriculata,* these always in close association with *Cotinus* and the new *Clematis.* The only other *Clematis* so far found in the same area is *C. virginiana,* which is part of a different section. Plants of this entire assemblage grow well on the clays and cherts derived from surrounding limestones and are markedly and abruptly different from the associations of the overlying shales and sandstones of this region.

Further field exploration of the same geologic and floristic system is being conducted with an eye toward occurrence of the *Cotinus* association, this now known to extend north into Franklin and Marion counties in Tennessee and south into Morgan County in Alabama. Where this tree occurs there is likely habitat for *Clematis morefieldii.*

Mr. J. D. Morefield, a careful and perceptive student of botany, is gratefully acknowledged. During the few years of his adult residence in Huntsville he developed an excellent personal herbarium which adds much to our information about the flora of northern Alabama, his *Clematis* being but one of many interesting discoveries. Today he is a graduate resident at the Rancho Santa Ana Botanic Garden and is involved in revisional and floristic studies centering in the Basin and Range physiography. The *Clematis* is therefore named in his honor and as a reminder that he is missed back east.

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TWO NEW SPECIES OF *CORDIA* (BORAGINACEAE) FROM CENTRAL AMERICA

Increased collecting efforts in Central America associated with various floristic projects have provided a wealth of new material. A large number of new species have been reported, and many others, previously poorly known, are now represented by a sufficient number of collections to be understood more adequately. Since 1970, efforts in southern Central America have rendered earlier works incomplete in terms of taxa included and distributional data. Recent studies of *Cordia* in Mexico and Central America (Miller, 1985), and preparations of treatments for floras of Nicaragua (Miller, in press) and Panama (Miller, in press) have uncovered two new species from Central America.

Cordia liesneri James S. Miller, sp. nov. TYPE: Costa Rica. Puntarenas: ridge north of airport, Rincón de Osa, 10 Feb. 1974, *Ronald L. Liesner 1976* (holotype, MO 2664908; isotypes, AAU, US). Figure 1.

Frutex vel arbor parva 3–6(–8) m alta, ramunculis glabris. Folia persistentia, petiolis 6–11(–18) mm longis; laminae anguste elliptico-ovate, (11–)14.5–30(–40) cm longae, (3.8–)6.5–9.5(–13.5) cm latae, glabrae, apice longi-acuminatis, basi rotundatis ad obtusis. Inflorescentiae axillaris, (2.5–)6–8.5 cm latis. Flores sessiles, bisexualis; calyx tubulari-campanulatus, 5–6.8 mm longus, 3-lobatus; corolla alba, tubularis, 8.4–11 mm longa, 5-lobata, lobis oblongis, reflexis; stamina 5, filis 7.6–10 mm longis, puberulis, antheris oblongis, 1.3–2 mm longis. Fructus drupaceus, putamine inaequilateraliter ovoideo, 9–18 mm longo, 9–12 mm lato, rostrato ad apiceum.

Shrub or small, slender-trunked tree 3–6(–8) m tall, the twigs glabrous. Leaves persistent, coriaceous; petioles 6–11(–18) mm long, broadly canaliculate adaxially, glabrous or nearly so; blades narrowly elliptic-ovate, (11–)14.5–30(–40) cm long, (3.8–)6.5–9.5(–13.5) cm wide, the apex long-acuminate, the acumen (2.3–)2.8–3.5(–4.6) cm long, the base rounded to obtuse or rarely acute, the margin entire, the adaxial surface glabrous or rarely minutely strigillose, the abaxial surface glabrous or minutely strigillose. Inflorescence axillary or sometimes internodal, pendulous, cymose, (2.5–)6–8.5 cm broad, the branches shortly brown-canescent. Flowers sessile, bisexual, monomorphic; calyx tubular-campanulate, 5–6.8 mm long, 3–4.7 mm wide at the mouth, lacking ribs, sparsely and minutely brown-strigillose, 3-lobed, the lobes often somewhat unequal, deltate to ovate, 0.6–1.1 mm long; corolla white, tubular with reflexed lobes, 8.4–11 mm long, 5-merous, the lobes oblong, 2.4–4 mm long, 1.8–2.5 mm wide, the tube 4.4–7.2 mm long; stamens 5, the filaments 7.6–10 mm long, the upper 2.1–3.2 mm free, pubescent on the lower free portion and at the point of insertion, the anthers oblong, 1.3–2 mm long; ovary ovoid to broadly ovoid, 1.3–2 mm long, 1–1.3 mm broad; disc crateriform, 0.6–0.7 mm tall, 1–1.1 mm broad, glabrous; style 5.4–9 mm long, the stylar branches 2–3(–6) mm long, the stigma lobes clavate to nearly discoid. Fruits borne in the cup-shaped calyx, red or orange at maturity, drupaceous, the stone inequilaterally ovoid, rostrate at the apex, 9–18 mm long, 9–12 mm broad, the surface with low ridges, the endocarp bony.

Distribution. *Cordia liesneri* is known only from the Golfo Dulce region of Puntarenas, Costa Rica, where it occurs in wet forests below 200 m in elevation.

Among the Central American members of sect. *Myxa* (Endl.) DC., *Cordia liesneri* is distinctive in its oblong-ovate leaves longer than those of related species, axillary inflorescences, and bright red fruits containing large and prominently rostrate stones. This species is perhaps most closely related to *Cordia lucidula* I. M. Johnston with which it shares a similar habit of growth, relatively large, glabrous leaves, a 3-lobed calyx, and red drupacous fruits. However, it differs from *C. lucidula* by having axillary inflorescences and rostrate endocarps.

Collections of *Cordia liesneri* have existed since Skutch and Allen collected in the Golfo Dulce region in 1947 and 1951 respectively. However, they have been identified incorrectly as *Cordia protracta* I. M. Johnston, which differs by its terminal inflorescences and pentamerous calyx, and as *Cordia eriostigma* Pittier, which differs in having terminal inflorescences and a campanulate corolla. Allen (1956) briefly described *C. liesneri* under the name *C. protracta* and stated that flowering occurs in December and that fruits mature in January.

Additional specimens examined. COSTA RICA. PUNTARENAS: region between Esquinas and Palmar Sur

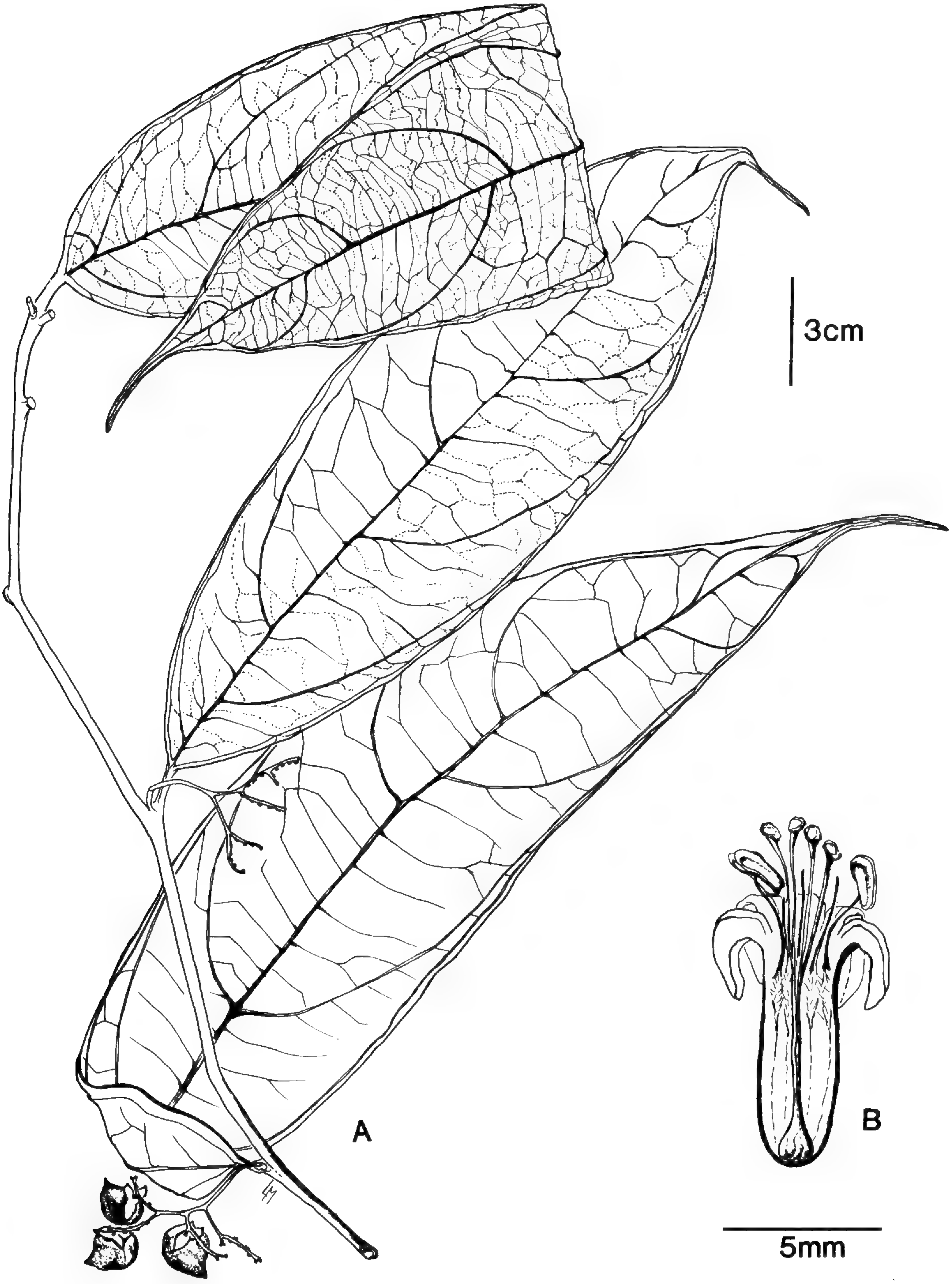

FIGURE 1. *Cordia liesneri.*—A. Fruiting branch, after *Liesner 1976* (MO).—B. Open corolla, after *Burger & Liesner 7224* (NY).

de Osa, elev. 30 m, *Allen 5772* [DS, F (2), GH, US]; region between Equinas and Palmar Sur de Osa, elev. 75 m, *Allen 5827* (DS, F); about 5 km W of Rincón de Osa, Osa Peninsula, elev. 50–200 m, *Burger & Liesner 7224* (CR, F, NY); slopes adjacent to airport, Rincón de Osa, *Liesner 1858* (AAU, CR, MO, US); Golfo Dulce and Río Terraba, elev. 30 m, *Skutch 5303* (F, MICH).

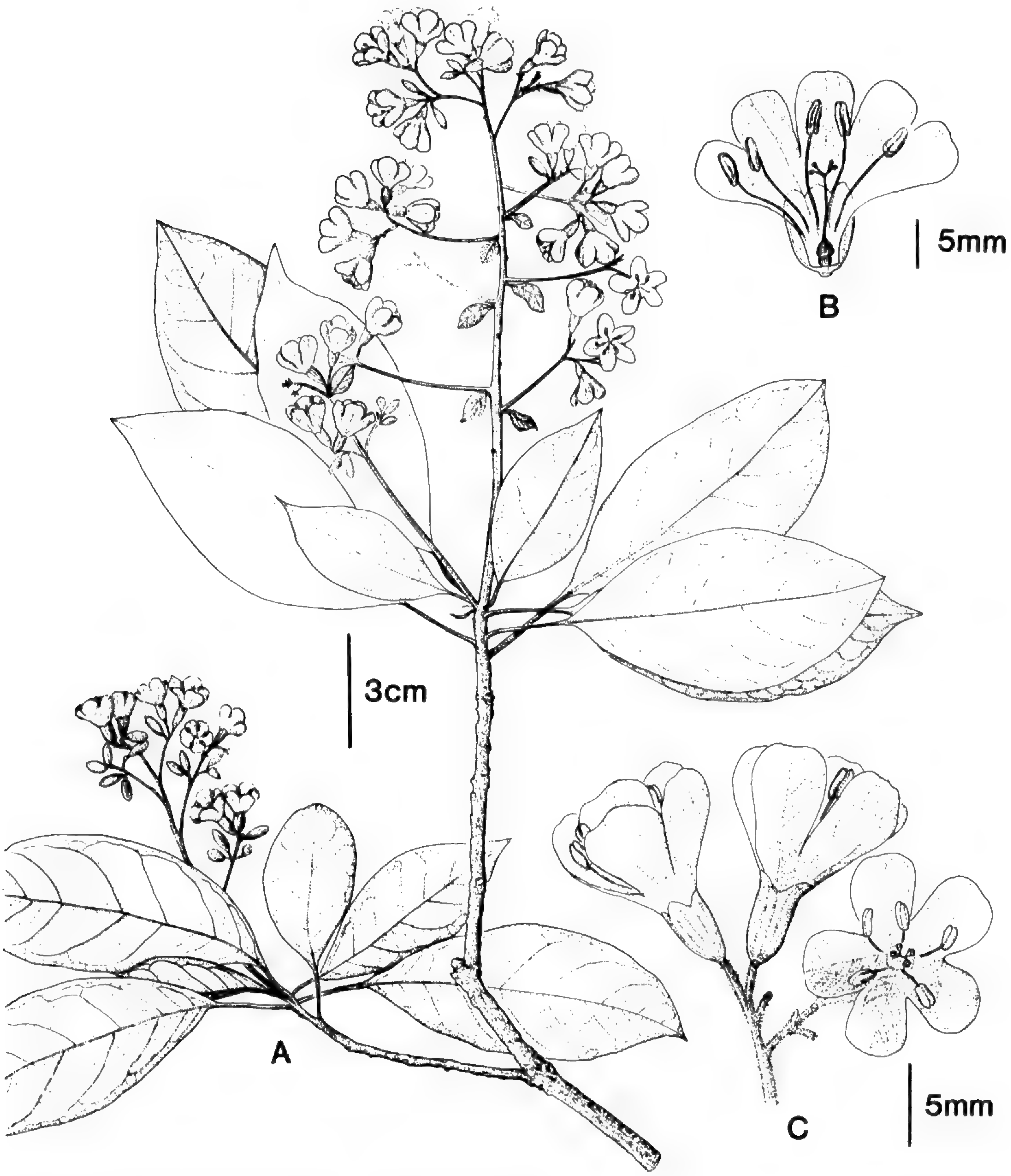

FIGURE 2. *Cordia cardenasiana*.—A. Flowering branch.—B. Open flower.—C. Apex of a flowering branch showing intact striate calyx. All after *Contreras 6835* (holotype).

Cordia cardenasiana James S. Miller, sp. nov. TYPE: Guatemala. Petén: Cardenas, on rocky hill, 24 Mar. 1967, *Elias Contreras 6835* (holotype, LL 279752; isotypes, DS, F, LL, US). Figure 2.

Arbor ad 15 m, ramunculis glabris. Folia deciduis, laminis ellipticis, 4.4–11.4 cm longis, 2.4–4.5 cm latis, glabris. Inflorescentia cymo-paniculatis. Flores heterostyli; calyx tubularis, 5–6 mm longus; corolla tubularis 14.2–16.8 mm longa, lobis 5, oblongis, 5.2–6.2 mm longis; stamina 5, filis glabris; ovarium obloidum, 1.2–1.4 mm longum; discus annularis. Fructus non visi.

Tree 15 m tall, the twigs glabrous. Leaves deciduous; petioles 8–30 mm long, canaliculate adaxially, glabrous; blades elliptic, 4.4–11.4 cm long, 2.4–4.5 cm wide, the apex acute to acuminate, the base acute, the margin entire, the adaxial surface glabrous but evenly papillose, the abaxial surface glabrous. Flowers on short pedicels to 1.5 mm long, distylous, borne with the leaves; calyx tubular, 5–6 mm long, 3–3.8 mm wide at the mouth, unequally lobed and tearing upon dehiscence or dehiscing circumscissily, striate or faintly costate, inconspicuously short-puberulent; corolla white, tubular with somewhat spreading lobes, 14.2–16.8 mm long, 5-merous, the lobes oblong, 5.2–6.2 mm long, 4.8–6 mm wide, the tube 4.7–5 mm long; stamens 5, the filaments 9.8–11.5 mm long, the upper 7–7.6 mm free, glabrous, the anthers oblong, 2.3–3 mm long; ovary obloid, 1.2–1.4 mm long, 1.3–2.5 mm broad; disc annular, 1.4 mm tall, 1.3 mm broad, glabrous; style 6.8–7 mm long, the stylar branches 1.4–1.6 mm long, the stigma lobes clavate. Fruits unknown.

Distribution. *Cordia cardenasiana* is known only from the type collection made in Petén, Guatemala.

Cordia cardenasiana is a small tree that must be quite attractive in flower. Like related species, it presumably produces all of its flowers in a short period during the dry sesaon. It is assigned provisionally to sect. *Gerascanthus* (P. Br.) G. Don, but a definite sectional placement cannot be made until fruits are known. Members of sect. *Gerascanthus* have ellipsoid fruits with a fibrous wall, and the base of the style remains attached. Members of sect. *Rhabdocalyx* A. DC. have fruits with a bony endocarp; some species are otherwise indistinguishable from sect. *Gerascanthus*. Although *Cordia* is diverse in pollen morphology, the two sections share pollen grains of the same type (Nowicke & Ridgway, 1973), and this character cannot resolve the sectional placement of *C. cardenasiana*.

Cordia cardenasiana is probably most closely related to *C. gerascanthus* L., with which it shares glabrous leaves and a terminal, cymose-paniculate inflorescence. Although most populations of *C. gerascanthus* have pubescent staminal filaments, populations with glabrous filaments are known from southeastern Mexico (Johnston, 1950; Miller, 1985); filaments of *C. cardenasiana* are glabrous. Among the Mexican and Central American species of *Cordia*, *C. cardenasiana* is distinctive in having parallel-sided corolla lobes, a character that it shares only with *C. alliodora* (Ruiz & Pavón) Oken, *C. gerascanthus*, and *C. globulifera* I. M. Johnston. A key is provided below, and a key to the remaining species of the section from this region is in Miller (1986).

1a. Plants with ant domatia; indument of stellate hairs .... *C. alliodora*
1b. Plants lacking ant domatia; indument of simple hairs.
    2a. Inflorescence cymose-paniculate.
        3a. Calyx striate or faintly costate, glabrous; corolla less than 18 mm long .... *C. cardenasiana*
        3b. Calyx costate, pubescent; corolla more than 20 cm long .... *C. gerascanthus*
    2b. Inflorescence condensed, nearly umbellate .... *C. globulifera*

I thank the curators of the following herbaria for lending collections: AAU, CR, DS, F, GH, LL, MICH, MO, US. I also thank my wife, Leslie Miller, for support and the illustration of *Cordia liesneri*, John Myers for the illustration of *Cordia cardenasiana*, and G. Schatz for helpful comments on the manuscript.

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SARACHA SPINOSA—A NEW COMBINATION IN PERUVIAN SOLANACEAE

The name *Saracha* R. & P. was long misapplied to the group of herbaceous neotropical plants now correctly known as *Jaltomata* Schldl. (Gentry, 1973). With reestablishment of the name *Jaltomata* for the herbaceous plants, the need for reinstatement of *Saracha* to the group of shrubs of upland South America that had long been erroneously known as *Poecilochroma* Miers became evident. The redefinition of *Jaltomata* was followed by D'Arcy (1973: 626, 1986: 28), Gentry & Standley (1974: 42), Hunziker (1979: 53), and Nee (1986: 76) and the reinstatement of *Saracha* by Hunziker (1979: 56). Both genera are in need of revision, and not all combinations have been made to recognize the restored generic names. However, determination of a collection made in the course of preparing a flora for Huascarán National Park in the uplands of the Cordillera Blanca in northcentral Peru (Smith, in prep.) requires the following new combination:

Saracha spinosa (Dammer) D'Arcy & D. N. Smith, comb. nov. *Poecilochroma spinosa* Dammer, Bot. Jahrb. Syst. 37: 637. 1906. TYPE: Peru. *Weberbauer 2907* (B, not seen, destroyed; photo, MO).

Copiously armed shrub with long, trailing or weeping branches; twigs glabrate, sometimes with minute simple trichomes; leaves of many short shoots caducous and leaving behind sturdy, grayish, acicular spines 8–25 mm long. Leaves entire, elliptical, obtuse or rounded at each end, mostly 12–20 mm long, coriaceous, glabrous or with minute simple trichomes, shiny above, the margins subrevolute; petioles 2–5 mm long. Inflorescences consisting of solitary terminal or axillary flowers; peduncles wanting; pedicels slender but broadening upwards, 10–15 mm long. Flowers pendant, the calyx cupular, ribbed, dentate, sometimes irregular, 6–8 mm long, sometimes splitting; corolla apically plicate in bud, narrowly campanulate, ca. 20–25 mm long, ca. 15 mm wide at the mouth, the apex truncate with 5 deltoid teeth 2 mm long; yellow and evenly minutely puberulent outside, inside basally uniformly dark violet, this reduced upwards to a field of lobes and spots and pure yellow at the apex; filaments ca. 15 mm long, inserted at the base of corolla tube, glabrous and unappendaged, the anthers oblong, apiculate, basally cordate, 4–5 mm long, yellow, included; ovary obconical, 4 mm long, the basal third enveloped in nectary, glabrous, the style glabrous, exserted beyond the anthers and nearly equalling the corolla. Fruit (not preserved) a leathery berry about the size of a gooseberry, perhaps 7 mm across.

Saracha spinosa is a weak, clambering shrub that assumes a down-curving, weeping habit when it lacks support. The branches can reach several meters in length. The corollas are not so broadly campanulate as in other members of the genus. The plicate folds in the corolla in bud were not found by Hunziker (1979: 58) in the species he discussed. *Saracha spinosa* is further distinct from other members of the genus in having formidable slender spines which apparently derive from short leafy shoots in the manner of *Dunalia spinosa, Iochroma horrida,* and some other related Solanaceae. The spines on the specimen at hand are copious, ascending, 8–25 mm long, and needlelike. Fruit was not available for dissection to ascertain the details referred to by Hunziker (1979: 58) in his notes on three other species of *Saracha.*

In his discussion under *Poecilochroma* in the *Flora of Peru,* Macbride (1962: 58) suggested that this species is similar to *P. lindeniana* Miers and to *P. lobbiana* Miers, but both of these are unarmed and have more open campanulate corollas, as is to be seen in the type illustration and photos examined of these two species.

The collection made in this study bears a remarkable similarity to a specimen of *Dunalia* collected by López & Sagástegui which we tentatively refer to *D. spinosa* (Meyen) Dammer. The leaves of the López & Sagástegui collection are small and elliptical like those of our collection of *Saracha* and unlike the larger oblanceolate leaves of other specimens of *D. spinosa,* including the type collection (*Meyer,* BM, destroyed, photo MO). The flowers, too, are superficially similar but narrower, and of course the filaments have the basal appendages characteristic of the genus *Dunalia* (Hunziker, 1959–60: 212). Had we not examined the interior of the flowers, we would have thought these the same species, not different genera.

The great similarity between *Saracha spinosa* and the neighboring *Dunalia* within adjacent parts of Peru argues a need for unusual care in determining specimens of these plants and caution in accepting past determinations. Under his treatment of *Saracha* (*Poecilochroma*) *spinosa* Macbride cited the following four specimens, which appear to be at least geographically consistent: Dept. La Libertad: Prov. Bolivar, *Ferreyra 1254*; Prov. Santiago de Chuco, toward Angasmarca, *West 8162*. Dept. Ancash: Prov. Huari, 3,600 m, *Weberbauer 7014*. Dept. Ayacucho: Prov. Huamanga, above Quinua, *Weberbauer 5542*.

Saracha spinosa is apparently restricted to interandean valleys of the western and central chains of the Peruvian Andes. It has an extended range of about 700 km, within which, at least according to Weberbauer (1945: 420), the species is sometimes locally common. Collection sites known to us show that it occurs in shrubland ranging from about 78°05′W to 74°08′W and from about 7°22′S to 8°05′S. The species has an apparent elevation range from 3,300 to 3,700 m. The type locality, which was imprecise, is near or within Huascarán National Park.

The Park is in the Ancash Department of central Peru, 300 km (air distance) north of Lima. The reserve occupies nearly all the Cordillera Blanca, which is the world's highest tropical mountain range. The cordillera is located between 8°50′S and 10°00′S latitude and between 77°05′W and 77°49′W longitude with a north–south length of 158 km and an area of 340,000 ha (131 sq. mi.). The elevation range is from 3,240 m to the 6,770 m summit of Nevado Huascarán Sur, the bulk of the Park above 3,500 m. The outcrop is a mixture of igneous and sedimentary rocks. The cordillera was extensively glaciated and still has many glaciers and icefields. Its topography is complex and supports a mosaic of vegetation types. The most diverse and densest shrub communities are found in the valleys reaching lower elevations (3,500–3,800 m), where the microclimate is warmer and moister. Although valleys with these conditions are found on both sides of the cordillera, the greatest number are on the eastern side.

In over a year of field collecting throughout the entire park, *Saracha spinosa* was located only once, in Quebrada Rurichinchay near the valley bottom in a community dominated by *Miconia salicifolia* and with *Alnus acuminata, Myrica pubescens, Vallea stipularis,* and *Weinmannia* aff. *laxiflora.*

SPECIMENS EXAMINED

Saracha spinosa. PERU. DEPT. ANCASH: Prov. Huarí, Huascarán National Park, Quebrada Rurichinchay between boundary and Quebrada Pachachaca. 3,600–3,700 m, *D. N. Smith 12475* (CPUN, HUT, MO, USM, dupla). DEPT. AYACUCHO: Prov. Huamanga, road from La Quinua to Abra Apacheta de Tambo, 12,000 ft., *Plowman & Davis 4651.*

Dunalia aff. *spinosa.* PERU. DEPT. LA LIBERTAD: Prov. Bolívar, Laguna de Los Ichus, al pié de rocas, 3,600 m, *López & Sagástequi 3241* (MO).

This study was supported by National Science Foundation Grant BSR-8305425.

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YUTAJEA, ANOTHER NEW GENUS OF RUBIACEAE FROM THE GUAYANA HIGHLAND

Of the genera of Rubiaceae endemic to the region of the Guayana Highland, none had previously been described from the Serranía de Yutaje in the Territorio Federal Amazonas of Venezuela. A recent expedition to this region collected material of a rubiaceous tree, here described as a new genus. It is fitting to name the genus for Yutaje, a sandstone mountainous area where numerous endemic species are already known.

Yutajea Steyermark, gen. nov. TYPE: *Y. liesneri* Steyermark. Tribe Isertieae.

Arbor. Stipulae interpetiolares persistentes late lanceolatae acutae. Inflorescentia thyrsiformi-paniculata seriebus verticillatis dispositis, axibus in dichasia desinentibus. Calyx truncatus tandem in lobes 3–4 irregulariter rumpens. Corolla late cylindrica vel subinfundibuliformis rosea, lobis 6 in aestivatione imbricatis paullo inaequalibus, tubo intus dense pubescenti, orificio barbato. Stamina 6 prope basim tubi corollae affixae. Antherae sub-basifixae transverse rugulosae inclusae. Ovarium 6-loculare, ovulis numerosis.

Yutajea liesneri Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Depto. Atures, 5–8 km NW of Yutaje settlement, along stream flowing south from east side of unnamed peak, 3 km west of Río Coro Coro, west of Serranía de Yutaje, 05°40′N, 66°9′W, 700–1,000 m, 10 Mar. 1987, *Ronald Liesner & Bruce Holst 21826* (holotype, MO; isotype, VEN).

Arbor 6-metralis, ramulis superioribus adpresso-pubescentibus; stipulis late lanceolatis acutis 8 mm longis 4 mm latis; foliis oblanceolatis vel lanceolato-ellipticis apice acuminatis basi acutis 13.5–20 cm longis 5.5–8.5 cm latis; inflorescentia thyrsiformi-paniculata late ovoidea multiflora pedunculato, axibus principalibus 12–16 modice vel dense hirtellis in verticillos 3–5 ordinatos atque in dichasia composita desinentibus; calyce hypanthioque 4–6 mm longo subadpresso-pubescenti; calyce ante anthesin truncato vel paullo undulato sub anthesi in lobos 3–4 irregulariter rumpenti, lobis suborbicularibus vel suborbiculari-ovatis apice rotundatis, marginibus minute ciliolatis; corolla rosea late cylindrica vel subinfundibuliformi 8–9 mm longa 4–7 mm lata, tubo extus glabro intus praeter partem basilarem 1.5 mm glabrum adpresso-pubescenti atque prope orificium barbato pilis longioribus instructo; lobis 6 paullo inaequalibus suborbiculari-ovatis vel obovato-oblongis apice obtusis vel rotundatis ubique glabris marginibus minute papillatis; staminibus 6, antheris linearibus.

ANN. MISSOURI BOT. GARD. 74: 676–678. 1987.

Tree 6 m tall, the twigs appressed-pubescent distally. Stipules broadly lanceolate, acute, 8 mm long, 4 mm wide, strigose. Leaves oblanceolate to lance-elliptic, acuminate at apex, acute at base, 13.5–20 cm long, 5.5–8.5 cm wide, the upper surface glabrous, the lower surface pilosulous on midrib and lateral nerves, sparsely pubescent on some tertiary veins, glabrous on surface between the tertiary veins; lateral nerves 12–17 each side, anastomosing near margin, elevated below; midrib sulcate above and elevated below; tertiary veinlets inconspicuous above, finely reticulate and impressed below. Inflorescence thyrsiform-paniculate, broadly ovoid, 35–50-flowered, 6–11 cm long excluding the peduncle, 4.5–7 cm wide, the main axes 12–16 in 3–5 verticils ending in often compound dichasia, moderately to densely hirtellous; lowest axes 12–25 mm long, the others 7–15 mm long. Bracts subtending axes ovate, acute, 2.5–4 mm long, 1.5 mm wide, minutely hirtellous. Peduncle terminal, 8–12 cm long, 2.5–3 mm diam., moderately pubescent. Calyx and hypanthium 4–6 mm long, subappressed-pubescent; hypanthium obconic, 3–5 × 3–5 mm. Calyx truncate or slightly undulate before anthesis, splitting irregularly during anthesis into 3–4 thickened, suborbicular or suborbicular-ovate lobes, these rounded at apex, 3–3.5 mm long, 4–8 mm wide, minutely ciliolate at the margins. Corolla pink or roseate, fleshy-thickened, broadly cylindric or subinfundibuliform, 8–9 mm long, 4–7 mm wide, the tube 5 mm long, 4–7 mm wide, glabrous without, within densely appressed-pubescent except for the glabrous basal 1.5 mm, and with longer barbate pubescence at the orifice; lobes 6, slightly unequal, suborbicular-ovate or obovate-oblong, obtuse or rounded at apex, 4–5 mm long, 2.5–3 mm wide, glabrous both sides, the margins minutely papillate. Stamens 6; anthers linear, 3.5–5 mm long, 0.8–1.5 mm wide, the thecae transversely rugulose, terminating in an oblong, rounded connective 0.5–1 mm long, 0.5 mm wide; filaments ligulate-linear, thickened, 1.5 mm long, 0.7 mm wide, inserted 1.5–2.5 mm above the base of the corolla tube, broader than the base of the thecae. Style 4–6 mm long, papillate-verrucose; stigmas 4–6, ligulate, 0.5 mm long. Disk annular, the margin undulate, 1 mm long, 4 mm diam. Ovary 6-celled, ovules ca. 8 in each cell.

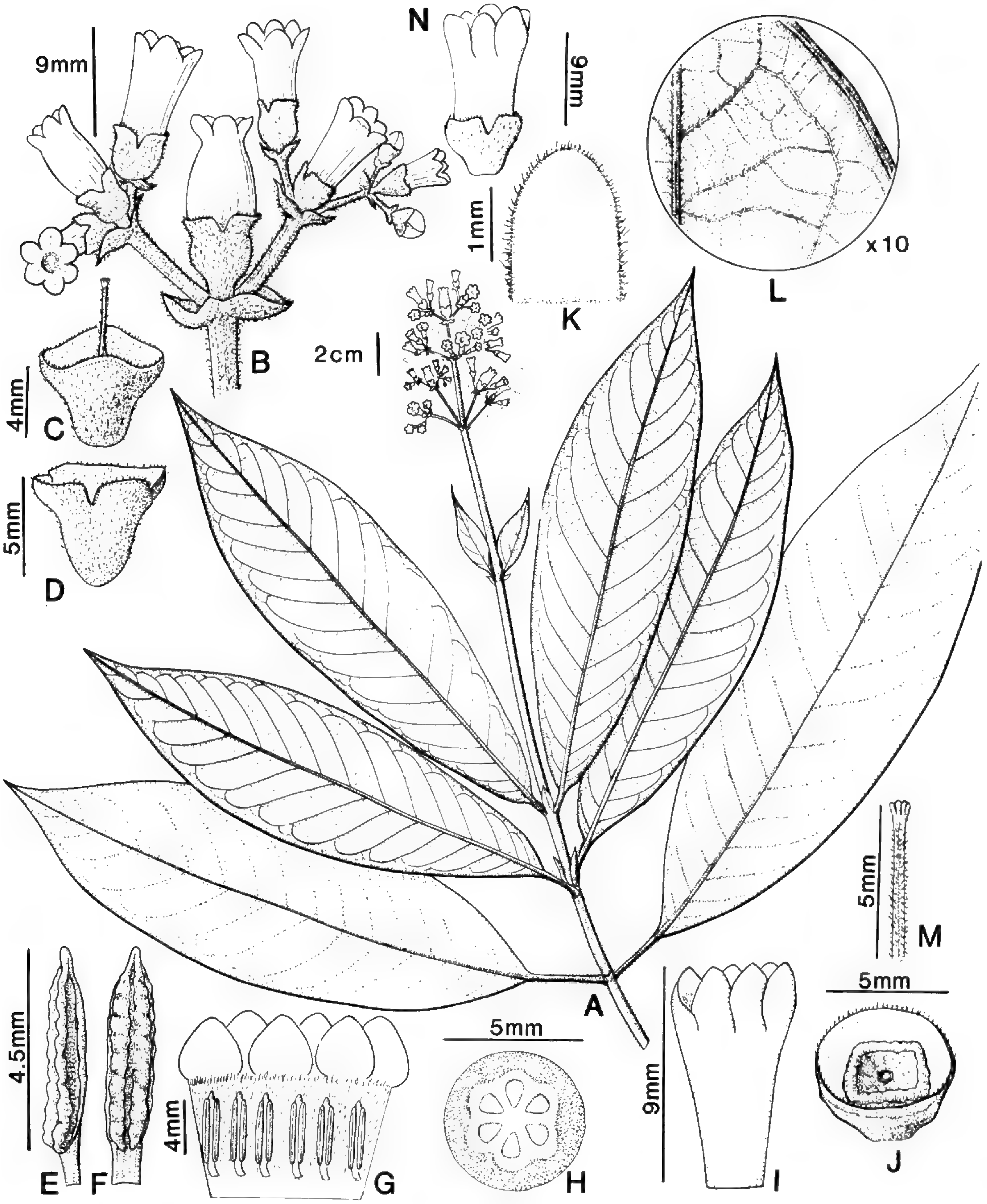

FIGURE 1. *Yutajea liesneri.*—A. Habit.—B. Portion of inflorescence.—C. Calyx and hypanthium before anthesis.—D. Calyx and hypanthium during anthesis.—E. Stamen (lateral view).—F. Stamen (ventral view).—G. Corolla, interior view.—H. Transverse section through ovary, semidiagrammatic.—I. Corolla, subinfundibuliform type.—J. Disk, from above, in depression at base of calyx tube.—K. Floral bract, exterior view.—L. Detail of lower leaf surface.—M. Style and stigmas.—N. Flower with broadly cylindrical corolla type with slightly unequal lobes.

Yutajea is a member of the tribe Isertieae as circumscribed by Kirkbride (1979) and may be placed next to its closest related genus, *Isertia.* From *Isertia* it differs especially in having the stamens inserted near the base of the corolla tube and in having sub-basifixed anthers. The slightly unequal corolla lobes and the uniformly pubescent interior of the corolla tube are additional characers at variance with *Isertia*. The corolla of *Yutajea* is short-cylindric or subinfundibuliform with imbricate lobes. Boom (1984) described the corolla tube in *Isertia* as "cylindrical, short or elongate" and the lobes as "valvate or imbricate in bud." In her abstract of characters delimiting the tribe Isertieae, Kirkbride (1979) characterized the aestivation of the corolla as "valvate" but later (p. 315) gave the aestivation as "valvate or valvate-imbricate." As Boom indicated, *Isertia* may have either valvate or imbricate aestivation. In *Isertia* the stamens are inserted near the mouth of the corolla tube, the anthers are dorsifixed, and the orifice of the corolla is usually villous or barbate, except in *I. scorpioides* Boom, while the remainder of the interior of the corolla tube is glabrous in all the species with the exception of *I. longifolia* (Hoffsg. ex Roemer & Schultes) Schumann.

Yutajea adds another endemic genus of the Rubiaceae to the list of twelve previously described from the Guayana Highland (Steyermark, 1986).

The collections cited in this paper were made under Grant No. 3264-86 of The National Geographic Society.

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—*Julian A. Steyermark, Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166, U.S.A.*

BOOK REVIEW

Duke, James A. 1986. *Isthmian Ethnobotanical Dictionary,* Third edition. Pawan Kumar Scientific Publishers, Jodhpur, India. ISBN 81-85046-35-2. Price $60.

The Isthmian Ethnobotanical Dictionary, concerned with useful plants of Panama, is 205 pages in length, each page measuring approximately 8½ × 11 inches. It is in its third edition, the first appearing in 1972, the second in 1978. The latest contains 325 black-and-white line drawings of flowering plants and a few ferns.

The author explains that the *Dictionary* "... contains herbal folklore in tropical plants which complements the voluminous folklore on temperate plants." In his introduction he indexes "some frequent ailments and the more common herbs used to treat them." Actually, many of the plants listed are trees and shrubs. The diseases range from abscesses to yellow fever. For example, under "indigestion" he lists by common name more than 50 herbs used therapeutically in Panama. In the body of the text, in an alphabetical and composite fashion, he lists the common names of the plants without discussing them; secondly, the diseases themselves (in full capitals), including a brief layman's definition of the disease and the genera of plants used therapeutically; lastly, the binomial name (in full capitals) and a discussion of how the plants are used by the natives. While emphasis is placed on medicinal plants, the discussion may include such uses of the plants as food, in construction, in the fashioning of fishhooks, etc. Occasionally, the treatments extend extra Panama, e.g., under bamboo there is an elaborate discussion of about 1,500 words, a goodly segment of which refers to the uses of the grass in India and Benegal.

By the use of abbreviations in parenthesis, Duke indicates how common names are used in Panama and in adjacent countries, e.g., in Costa Rica, "Costa Rican Spanish (CR)"; in Darién, Panama, "Darien Spanish (D)"; "English (E)"; etc.

In the eyes of a botanist, apart from the wealth of ethnobotanical data, the three most striking features of the *Dictionary* are: 1) the completeness of the list of ethnobotanical plants; 2) the accuracy in the spelling of binomial names and the authorities; and 3) how easily one familiar with the vegetation of Panama can recognize the individual species from the line drawings.

There are several items which I find disturbing, the prime being a lack of discussion in the Introduction concerning the various ethnic groups in Panama, plus the lack of a map of their locations in the Republic. The author sometimes leaves the impression that the Kuna Indians are the only aboriginals in Panama worth considering ethnobotanically. Why not more consideration of the Chocó Indians, granted that they are not as sedentary in Panama as are the Kunas? After all, Duke tells us (p. 26): "I am called 'Borojo' among the Darién Chocó because, for a while I was distributing 'borojo' seedlings like Johnny Appleseed." The Guyami Indians of western Panama are hardly given a nod. The obvious answer is that Duke spent a considerable portion of his early scientific life among the Kunas.

From the viewpoint of a print job, the book leaves something to be desired, considering that the price of the book is $60.00 (U.S.). The paper is of questionable quality, occasionally the ink is smudged; all too often one encounters a blank space in a sentence, a word or words having been deleted; occasionally the alignment of words in a column or sentence is poor.

An important point: books whose titles contain the word "dictionary" are usually segregated on library shelves under "for reference only." Such a restriction may limit the uses of the book and have an impact on its popularity.

I suggest that in the next edition a small superscript number be appended after each binomial to indicate the plant family; this could be checked against a list of numbered families in an appendix.

In the introduction, Duke in a cursory, but delightful, somewhat droll, style leaves no doubt considering his love for Panama, its people, and its vegetation. His concern for the future disappearance of the magnificent jungles of Darién strikes a familiar note; his defense of folklore medicine is convincing: "... I could spend a month with the herbals and modern medical texts and come up with hundreds of examples of folk medicine that have been vindicated or justified by subsequent scientific research." As far as Panama's herb lore is concerned, he has already done the basic spadework in admirable fashion. One must not forget that James Duke collected more than 6,000 "numbers" (herbarium specimens, each number usually in duplicate or triplicate) in the Republic of Panama (cf. Dwyer, in the Botany and Natural History of Panama, Missouri Botanical Garden, 1985), a memorial to his assiduity and a base for his ethnobotany.—*John D. Dwyer, Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166, U.S.A.*

ERRATUM

The incorrect author citation was used in the introduction to the paper titled "Notes on the Breeding Systems of *Sacoila lanceolata* (Aublet) Garay (Orchidaceae)," by Paul M. Catling [74(1): 58–68. 1987]. Instead of "var. *paludicola* Luer" it should be "var. *paludicola* (Luer) Sauleda, Wunderlin, et Hansen, Phytologia 56: 308. 1984."

Volume 74, No. 2, pp. 183–462 of the ANNALS OF THE MISSOURI BOTANICAL GARDEN was published on 29 September 1987.

THE GENERA OF EUPATORIEAE (ASTERACEAE)

R. M. King & H. Robinson
Smithsonian Institution

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Cover illustration. *Peperomia gentryi* Steyermark.

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The Annals, published quarterly, contains papers, primarily in systematic botany, contributed from the Missouri Botanical Garden, St. Louis. Papers originating outside the Garden will also be accepted. Authors should write the Editor for information concerning arrangements for publishing in the ANNALS. Instructions to Authors are printed on the inside back cover of the last issue of each volume.

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CONTRIBUTIONS TO A SYMPOSIUM ON THE EVOLUTION OF THE MODERN FLORA OF THE NORTHERN ROCKY MOUNTAINS: INTRODUCTORY REMARKS

The following nine papers represent contributions from a symposium presented on June 11, 1985, at the University of Montana. The symposium was sponsored jointly by the Paleobotanical Section and the Pacific Section of the Botanical Society of America and was held during the annual meetings of the Pacific Division of the American Association for the Advancement of Science.

The main purpose of the symposium was to bring together current information about the evolution of the present-day vegetation of the northern Rocky Mountains. While much of this information is paleobotanical, the participants anticipate that their syntheses will prove useful to people in a wide variety of disciplines of the life and earth sciences, and they have constructed their written reports accordingly.

A frequent problem for nonpaleobotanists interested in learning about the past vegetation in a given region is that it is difficult to locate this information. Reports about past vegetation are by no means rare, but they are scattered, and we have lacked good syntheses. The following papers attempt to solve that problem for the northern Rocky Mountain region. Each is a succinct yet authoritative summary of a particular body of information authored by leading specialists in that field. A number of authors have gone beyond presenting reviews and have included information and ideas in their treatments that have not been published elsewhere. Thus, each report is intended to be a definitive work on a particular duration of geologic time.

Readers will note what may appear to be two major inconsistencies from paper to paper. One has to do with geologic time and the application of epoch names, while the other is the use of the terms "flora" and "vegetation."

Paleobotanists generally agree on the absolute ages of the various plant-bearing strata, but they may disagree on the absolute age of the boundary between epochs. Thus, the same deposit may be regarded as latest Eocene by one worker and earliest Oligocene by another. Where this might cause confusion in this series of papers, authors have been asked to provide the absolute age as well as the epoch.

Workers dealing with modern plants and with those from the not too distant past use the term "flora" to indicate a list of taxa present and "vegetation" to include all aspects of those plants. Historically, fossil "floras" were little more than lists of species identified from a deposit. Later, such lists expanded to include taxonomic descriptions, comparisons, and, more recently, in-

Ann. Missouri Bot. Gard. 74: 681–682. 1987.

formation about frequency of occurrence of remains and environment of deposition. Interpretations of community structure, mean annual temperature, mean annual range of temperature, seasonality, and amount and seasonal distribution of rainfall are often included in modern treatments as well. While these are clearly aspects of "vegetation," the term "flora" has persisted and is often used instead. Thus, those working with ancient plants may not distinguish between these two terms and may use "flora" when "vegetation" is appropriate.

A second purpose of the symposium was to honor four workers who pioneered the study of the past vegetation of the northern Rocky Mountain region. These are: Herman F. Becker, Roland W. Brown, Erling Dorf, and Harry D. MacGinitie. Their contributions have been summarized by Jack Wolfe, and the summary is included as part of this publication. Drs. Becker and MacGinitie passed away after the symposium was held and their bibliographies are included here. The accomplishments of these scientists provided a solid foundation on which modern work rests. Even more importantly, they provided leadership and encouragement to the current generation of paleobotanists, and the papers published as a part of this symposium owe much to their efforts.

—*Charles N. Miller, Jr., Department of Botany, University of Montana, Missoula, Montana 59812, U.S.A.*

DEDICATION

This symposium is dedicated to four colleagues, all unfortunately deceased, who have contributed significantly to the paleobotany of the northern Rocky Mountains: Herman F. Becker, Roland W. Brown, Erling Dorf, and Harry D. MacGinitie. The work of all four men has provided a foundation of collections and knowledge on which this symposium is partially based. Two of these valued colleagues were, in fact, alive at the time (June 1985) the symposium was held. We had intended to honor Herman Becker during the course of the meetings at which the symposium was held, but he was at that time in the throes of his terminal illness and was unable to attend. Also regrettable is the death in January 1987 of Harry MacGinitie. Early in his paleobotanical career, Becker solicited and received much advice from Brown, Dorf, and MacGinitie, colleagues whom Becker greatly respected; thus, dedication of this symposium to all four men is particularly appropriate.

As Dilcher (1987) notes, Herman F. Becker (1907–1985) entered paleobotany late in life, and thus his paleobotanical career, mostly on the staff of the New York Botanical Garden, covered less than two decades. In that time, however, Becker monographed several latest Eocene (Oligocene in some chronologies) floras from southwestern Montana and discussed in shorter contributions some enigmatic plant fossils. The Montana floras contain early records of many microthermal taxa, and Becker's extensive collections of these floras have been a major basis for expanding knowledge of the development of microthermal vegetation and the evolution of microthermal taxa.

Roland W. Brown (1893–1961) was for 30 years the Mesozoic and Cenozoic paleobotanist of the U.S. Geological Survey (see Mamay, 1963) and was particularly concerned with the Cretaceous and Tertiary floras of the Rocky Mountains and adjacent High Plains. His contributions included numerous short, largely taxonomic papers; Brown's sharp eye for details kept his contemporaries "on their toes" in regard to determinations. However, Brown's major contribution was the monograph "Paleocene floras of the Rocky Mountains and Great Plains," which represents the accumulation of a massive amount of data. Discussions of the Cretaceous–Tertiary boundary in the Rocky Mountains, the development of the flora and vegetation in this region, or the general distribution of Paleocene vegetation rely on Brown's monograph.

For many years, Erling Dorf (1905–1985) was a highly respected professor in Geology at Princeton University. His paleobotanical contributions ranged from studies of Devonian plants from Beartooth Butte, Wyoming, to studies of the Pliocene–Pleistocene floras of California to taphonomic observations following the eruption of Paricutin in Mexico. Dorf was also concerned with general patterns of climatic change as evidenced by land floras. Of particular relevance to this symposium, however, is Dorf's fieldwork on rocks and their floras near the Cretaceous–Tertiary boundary in the northern Rocky Mountain region and particularly his monographic treatment of the latest Cretaceous Lance and Medicine Bow floras; this monograph remains the most recent and significant treatment of latest Cretaceous plants in the northern Rockies.

Harry D. MacGinitie (1896–1987) was a source of encouragement and advice to all concerned with the Tertiary floras of western North America (Wolfe, 1987). His published contributions span 42 years (1933–1974) and include several major monographs of both Paleogene and Neogene floras, including those of the Rocky Mountains. MacGinitie's systematic work was always of high quality. The areas of historical plant geography, paleoecological analyses of fossil plant assemblages, and climatic change were, however, of major concern to him, and embedded in his floral monographs are thoughtful and extensive discussions of the development of the vegetation and flora of western North America. Many now generally accepted concepts regarding the floristic and vegetational history of western North America during the Tertiary have their origins in MacGinitie's work.

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Harry D. MacGinitie

MEMORIAL TO HARRY D. MACGINITIE (1896–1987)

Back in the early 1950s, a bus trip from Portland, Oregon, to Boston would have been a long one, especially for a kid just entering college. But not for this freshman, because I had along Harry D. MacGinitie's recently published "Fossil Plants of the Florissant Beds, Colorado." The copy is now well worn, the binding tattered. Why a budding paleobotanist could and should have read this book is part of the story that follows.

In December 1952, I visited Berkeley—then the Mecca of Tertiary paleobotany—and met with R. W. Chaney, the widely accepted leader of this field. Chaney assigned Marie Pabst the task of entertaining this possible novitiate. Among the many questions asked of Pabst were: who produced good work, who was a model? Unhesitatingly, Pabst reached for the bookshelf and pulled out MacGinitie's (1941) "A Middle Eocene Flora from the Central Sierra Nevada." "This is the best work that has been done in western Tertiary paleobotany," she declared. "This is *the* work to emulate."

Mac MacGinitie was a paleobotanist's paleobotanist to Pabst, as well as to his other colleagues. He considered all evidence that bore on a scientific problem, and his conclusions and hypotheses were written logically and clearly, eschewing jargon whenever possible. He considered all reasonable alternatives and stated basic assumptions. If he changed his mind on a subject, he clearly stated this and the evidence that resulted in the change. His knowledge of leaf architecture of the angiosperms was immense, and the great bulk of his determinations of fossils are still valid. Most importantly, Mac shared his knowledge continually by discussions with his colleagues and would even spend his time in the herbarium helping with identifications. In both personal contact and his publications, Mac has had a profound influence in Tertiary paleobotany in North America.

By modern "publish or perish" standards, Mac's publications were few. Each, however, contains a few to several essays that could have readily been extracted as separate papers. And, each typically contains new approaches to Tertiary paleobotany.

Mac's first publication in 1933 was the first comprehensive account of an upland Miocene flora from the Columbia Plateaus. In this paper, Mac's discussion of the climatic implications of the flora is the first to attempt to assign numbers to climatic parameters and clearly reveals his interest in, above all, paleoclimate. I recall one discussion with Mac in which he stated that he entered paleobotany largely because he thought that fossil plants were the best indicators of paleoclimates. He was well aware of the significance of altitude, and his assignment of about 2,500 feet to the Trout Creek has not been significantly altered by newer (and supposedly more reliable) techniques.

The Weaverville flora, published in 1937, was Mac's Ph.D. thesis, which was completed under R. W. Chaney in 1935. This year also saw another major event in Mac's life; Beatrice MacGinitie (nee Hess), who became his wife on February 2, 1935, was a constant source of encouragement and emotional support to Mac for the rest of his life.

The Weaverville flora reveals Mac's increasing involvement with both the detailed climatic implications of fossil-plant assemblages and the possible causes of climatic change. Further, the detailed discussion of the geologic occurrence of the fossils and of basinal geology placed the Weaverville flora in a taphonomic context. Mac attributed the Weaverville flora to the early Oligocene, recognizing that the flora contained elements that indicated an age younger than the Goshen flora.

The monograph of the Eocene Chalk Bluffs flora, published in 1941, shows a maturation of many concepts. As in his earlier works, Mac considered the paleoecological significance of the fossil taxa in a depositional framework. He presented solid evidence for the co-occurrence of taxa whose modern counterparts have markedly different climatic tolerances and suggested that at least some tolerances have changed through time. Mac documented that the neotropical element in the Chalk Bluffs was today largely found in the Mexican uplands and that the flora also contained a large paleotropical element. This monograph also contains the first significant discussion of the plant biogeography of the North American Eocene. Mac laid the cornerstones for future discussions of the historical biogeography of the western North American Tertiary.

The taxonomy in the Chalk Bluffs paper has largely withstood the test of time. Mac, using solid leaf-architectural criteria, demonstrated that the many leaves of "*Aralia,*" a major element in western American Paleogene floras, represented a platanaceous genus. He referred the leaves to *Platanophyllum* and discussed the phyletic relationships of the species; recently they have been reassigned to the new genus *Macginitiea,* named in his honor. One of the major reasons that most of Mac's taxonomic determinations and paleoclimatic inferences still remain valid is revealed in the Chalk Bluffs monograph: "In no case were ecological considerations given weight in the choice between two living forms as modern representatives of fossil plants. . . . If identifications are based on ecology, and then ecology is deduced from identified species, the result is a kind of cyclic reasoning which may lead to considerable error" (MacGinitie, 1941: 96).

While teaching briefly at the University of Colorado, Mac was associated with T. D. A. Cockerell, the paleoentomologist who had worked extensively with insects from the famous lake beds at Florissant, Colorado. No comprehensive treatment—systematic or ecologic—existed of the Florissant flora, and, at the urging of Cockerell and the vertebrate paleontologist Childs Frick, Mac began work on the Florissant flora in 1936, work that culminated in his 1953 monograph of the flora.

Mac's research was, however, interrupted by World War II. Although Mac was 45 when the United States entered the war, he still decided to serve. Because of Mac's expertise in the theoretical aspects of climatology and meteorology, he enrolled as an instructor in the U.S. Army Air Corps. Lt. MacGinitie's primary responsibility was teaching crewmen the significance of, and to recognize, different cloud formations. After the war, Mac returned to Humboldt State and to his work on the Florissant.

Above all, the Florissant work involved carefully detailed taxonomic work. Mac reduced the 258 species previously attributed to the flora to less than half that number, but still the Florissant is the largest flora yet described from the Tertiary of western North America. One common practice in Tertiary paleobotany was the erection of a "fossil" species for fossils that resembled a given living species. Mac, however, challenged that practice: "Fossil plants in two different floras may be likened to the same *living* species without in any way implying identity of the two fossil forms. Their differences may be great enough in opposite directions to place them in different species . . ." (MacGinitie, 1953: 79). As Mac noted, the usual practice led to erroneous concepts of age and floristic relationships.

In the Florissant monograph, Mac introduced and elaborated on a number of new ideas and observations that have subsequently been well substantiated. Particularly significant is the idea that given lineages may persist in a region by adapting to changing environmental conditions; he was led to this conclusion because of the sharing of numerous lineages between the older Green River flora and the Florissant. Mac also clearly stated (p. 46) that fossil leaf assemblages typically are biased towards streamside or lakeside vegetation and, hence, may not adequately reflect the regional flora and vegetation; this point has been increasingly made apparent by many taphonomic studies. In discussing the paleoclimatic significance of floras then placed in the Oligocene, Mac noted: "The point emphasized by this discussion is that if we accept a Middle Oligocene age for the Goshen flora, the remainder of that period must have witnessed an almost complete revolution in the flora of the region, and more critical events must be crowded into the Upper Oligocene than paleontologists have hitherto been willing to concede" (MacGinitie, 1953: 67); Mac was the first to recognize the major and rapid climatic change that is now placed near the end of the Eocene.

Mac completed the Florissant study in 1951. Probably because of administrative duties as Chairman of Natural Sciences at Humboldt State, Mac did not immediately start on a new project. In 1954, James Bump sent Mac some leaves from a new site in Nebraska, and encouragement from Bump and Harold J. Cook enticed Mac to start fieldwork on the Kilgore flora, which was completed in 1958. Following his retirement from teaching in 1960, Mac finished the systematics of this assemblage. He had become increasingly aware of the value of palynology in paleoecological interpretations, and, despite no prior palynological experience, he became knowledgeable of basic pollen morphology with the help of Estella Leopold. The Kilgore paper was the first in North American Tertiary paleobotany to illustrate both megafossils and microfossils and extract from both types of fossils paleoecological data. The climatic discussion in the Kilgore paper was based on a wide range of data (paleobotanical, sedimentological, vertebrate, and molluscan) and probably remains the most comprehensive discussion of Neogene climates in the Plains region of North America.

The Kilgore paper also contains an expansion of the thesis, first expounded in the Florissant paper, that many plant lineages can persist in a given region despite significant climatic change. If, as Mac demonstrated, the bulk of the Kilgore species were derived from older species in the same region, then ". . . it should be questioned whether any flora, as a unit, migrated during the Tertiary . . . . The terms 'Arcto-Tertiary,' 'Madro-Tertiary,' and the like imply extremely useful concepts if we do not think of these terms as representing areas or centers from which mass migrations occurred. They picture to us in a general way the vegetation occupying an area, although the particular type of vegetation was slowly changing" (MacGinitie, 1962: 87). This statement by Mac represented a clear-cut departure from the geofloral hypotheses then so widely accepted in North American Tertiary paleobotany and historical plant geography. However, as originally submitted to the Board of Editors of the University of California Publications in Geological Sciences, Mac's manuscript was uncharacteristically vague about this point. Clyde Wahrhaftig, one of the editors, asked me what Mac meant. From numerous discussions with Mac, I knew what he was attempting to state, and at Wahrhaftig's request, Mac rewrote his manuscript to the statement quoted above.

On retiring from Humboldt State, the MacGinities moved from Arcata to Napa, a move that was beneficial to Mac and especially to many students and colleagues. He was made a Research Associate at the University of California Museum of Paleontology and had ready access to extensive paleobotanical collections (many of which he had made) and the University of California Herbarium and libraries. He was in an area active in the geological and botanical sciences, and Mac was often to be found in deep discussions with students and colleagues, to whom he freely gave of his time. Every thesis in paleobotany completed at Berkeley from the 1960s through the 1980s acknowledges Mac's assistance.

With typical enthusiasm, Mac then began work on the Eocene floras of the Rocky Mountains to understand better the floras and vegetation that preceded the Florissant. The first of these floras, that of the upper part of the Green River Formation in Utah and adjacent Colorado, was, like the Florissant, a classic flora. The last significant descriptive work, that by Roland Brown, was more than 30 years old, and the paleoecological significance of the Green River flora had never been thoroughly investigated. At the same time, Mac also began collecting from early and middle Eocene localities in Wyoming. In 1968 he completed work on the Green River flora (MacGinitie, 1969) and in early 1972 on the Kisinger Lakes flora (MacGinitie, 1974). He continued work on other Wyoming Eocene floras, but, unfortunately, none were completed for publication. A major hindrance to completion of these works was a deterioration of leg joints, which required surgery and made fieldwork difficult and painful.

In Mac's last two works on the Green River and Kisinger Lakes floras are the same type of careful and detailed discussions of paleoecology and paleoclimatology that are present in his earlier publications. Certain parts of these monographs should be carefully read by any paleobotanist or student in paleobotany, e.g., the chapters "Certain Aspects of Floristic Evolution" and "Paleobotanical and Botanical Species" (MacGinitie, 1969: 68–70, 81–86), and "Distribution of Correlative Living Species" (MacGinitie, 1974: 29–34). Indeed, Tom Taylor and Edie Smoot selected the second-listed chapter as one of eight papers on Tertiary paleobotany in the "Benchmark Papers in Systematic and Evolutionary Biology Series" (MacGinitie, 1984). Mac's discussions of systematic determinations also had become more sophisticated; he continually discussed the exact reasons certain generic determinations were made (not that a fossil taxon simply "looked like" an extant taxon) and illustrated much of the material in detail. Written with Estella Leopold, who also contributed a chapter to the Kisinger Lakes paper, the summary of floristic and vegetational development in the Tertiary of the Rocky Mountains (Leopold & MacGinitie, 1972) remains a most useful and concise summary on that topic.

The symposium held in honor of MacGinitie at the 1983 annual meeting of the American Association of Stratigraphic Palynologists was a well-deserved tribute. Palynologists recognized both the wide scope of Mac's contributions throughout his career and his bringing together of palynology and megafossil research in the Kilgore and later papers. During a tribute listing his many accomplishments, Mac, sitting in the front row, nudged Estella Leopold and whispered, "I never realized that I was that good." Mac had generally lived in the shadow of R. W. Chaney, and even when disagreeing with Chaney or other colleagues, was careful not to cite by name the originators of hypotheses; instead, Mac would simply and clearly, through data and logic, refute the hypotheses. One of the rare instances when Mac named names was, in fact, at the 1983 AASP symposium when he stated of a colleague, "He was a nice man but a terrible paleobotanist," much to the amusement of the audience.

One of Mac's major attributes was his ability to grow intellectually, to accept new concepts and weld them into his already considerable framework of floristic evolution and vegetational/climatic change in the Tertiary of western North America. If new and/or refined techniques of analysis (e.g., palynology and leaf architecture) appeared, he was among the first to use these techniques. Mac kept up with advances in paleobotany even after he was no longer an active researcher in the mid 1980s. Above all, Mac was always ready to discuss with colleagues any problem of mutual interest and to share with them his vast wealth of knowledge and experience. Fortunately, part of Mac's legacy to us—his enquiring mind and thoughtful statements—will endure in his publications. When Mac ceased being an active researcher, he, in typical generosity, brought down to Berkeley his entire professional library, leaving for present and future students an additional legacy.

Thanks are due to Beatrice Ann Minkler (nee MacGinitie) for supplying much pertinent biographical material. Howard E. Schorn supplied the accompanying photograph and contributed to some of the content of this memorial. Patrick F. Fields supplied the list of MacGinitie's publications.

Biographical Data

Harry Dunlap MacGinitie was born in Lynch, Nebraska, on March 29, 1896. After graduating from high school in Sturgis, South Dakota, he moved to California. He attended and received an A.B. from Fresno State College in 1926, after which he attended Stanford University for a year. In 1926–1928, MacGinitie taught high school before obtaining a position in 1928 at Humboldt State College (now University) in Arcata, California, where he taught until 1960, except for a year (1932–1933) when he attended Berkeley full time, a year (1936–1937) when he taught at the University of Colorado (Boulder), and two years (1943–1945) when he taught meteorology in the U.S. Army Air Corps; he was chairman of the Division of Natural Sciences from 1947 to 1960. MacGinitie did his graduate work in geology and paleontology at the University of California (Berkeley), receiving a Ph.D. in Paleontology in 1935. His research in the 1930s and 1940s was done as a Research Associate of the Carnegie Institution of Washington. Following retirement from formal teaching in 1960, MacGinitie was appointed a Research Associate of the University of California Museum of Paleontology. He was a Fellow of the California Academy of Sciences and the Geological Society of America and a member of the Paleontological Society. He died on January 31, 1987, in Napa, California.

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HERMAN F. BECKER

MEMORIAL TO HERMAN F. BECKER (1907–1985)

Herman F. Becker was born in Duesseldorf, Germany, on January 10, 1907. After completing his initial education at the Realgymnasium in Neunkirchen (1923), he undertook the study of botany in Dahlem (Berlin) at the Botanical Gardens with the encouragement of his father and grandfather. There he completed studies as a horticulturist. He met his wife, Ruth, in Berlin and they were married in Frankfurt, Germany in 1928.

He saw no possibility of continuing his study of botany in Germany so he decided to go to the United States and arrived in New York in March 1930. His wife and young son followed about one year later after he had obtained work as a Horticultural Assistant (1930–1939) at the Brooklyn Botanical Garden. Twin sons were born in New York.

Beginning in 1939 he taught at Brooklyn College as a Lecturer in Geology while he undertook his B.A. degree, which he completed in 1947. He continued to teach at Brooklyn College while earning an M.A. degree from Columbia University in 1952.

During this time he took part in a geology field trip to the West with several geology students. While on this trip he was told, "Becker, you look for plant fossils," because everyone knew of his interest in plants. He came back to New York excited about a shoe box full of fossil plants that he had collected.

Becker wanted to continue in research but had little opportunity to do so while teaching a heavy course load as a Lecturer and later Instructor at Brooklyn College (1939–1955). However, in the summer of 1947 he began field studies under the direction of Professor A. J. Eardley, director of geologic work at the Rocky Mountain Field Station of the University of Michigan. Soon he was directed to Professor Chester Arnold. He continued to maintain contact with Arnold and collected fossils in the Ruby River Basin area of southwestern Montana during the summer of 1949. He then enrolled in a Ph.D. program at the University of Michigan to work in Paleobotany with Professor Arnold. At first he worked on his degree in the summers. But, after completing additional fieldwork on the paper shales

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of the Ruby River Basin in the summer of 1955, he remained at Michigan, completing his Ph.D. degree in 1956. He was awarded the Ermine Cowles Case Award in Geology for his outstanding Ph.D. dissertation.

Herman Becker attempted to teach again at Brooklyn College, but the heavy course load gave him no time for his research on the fossil plants of the Ruby River Basin to which he was by this time very committed. Thus, in 1958 he joined the New York Botanical Garden, first as a Research Associate and later as a Curator of Paleobotany. Between 1957 and 1968 he made seven more major collecting trips to southwestern Montana, which provided him with the research material that formed the basis of many of his publications.

The first two major floristic papers he published were on the paper shale beds of the Ruby River Basin flora (middle Late Oligocene) (1961a) and the Mormon Creek flora (upper Middle Oligocene) (1960c). With continued extensive summer fieldwork in southwestern Montana, he published monographic papers on the Beaverhead Basin (lower Middle Paleocene) (1969c), the Metzel Ranch flora in the Ruby River Basin (lower Late Oligocene) (1972b), and the York Ranch flora of the Ruby River Basin (Upper Oligocene–Lower Miocene) (1973b). In these floristic papers he not only presented the fossil flora from the specific fossil beds he collected, but he applied the resulting data to questions of the correlation of their floristic elements to other North American Tertiary floras, taxonomic age relationships of the specific floras, and the phytogeographical distribution of modern equivalents for the fossil plants described.

Herman Becker worked at a time when the questions being asked in the field of paleobotany were concerned primarily with paleoecological and phytogeographical issues. However, perhaps because of his strong botanical background, he developed a special interest in the relationship between fossil and extant plants and the evolution of plants through time. In his paper on the Beaverhead flora he wrote: "The writer does not agree to calling Tertiary fossil species 'identical' with any extant species, and applying to it the modern specific epithet, especially where Miocene–Oligocene, or older plants are concerned . . . . In a strict sense, no individual of a modern species is morphologically or genetically identical with another, a fact expressed in major or minor variability as a phenotype. Genetic, physiological, and many morphological characters are usually not available to the paleobotanist to pronounce a specimen identical or unquestionably equivalent to a modern form" (1969c: 10).

The importance of his research was recognized by several honors he received after his retirement. In 1977 he was awarded a special Distinguished Service Award for his research in paleobotany by the Paleobotany Section of the Botanical Society of America, and in June 1985 a special symposium was held in his honor. This symposium was sponsored by the Pacific Sections of the American Association for the Advancement of Science and the Botanical Society of America and was titled "Evolution of the Modern Vegetation of the Northern Rocky Mountains." Several well-known scientists presented papers at this symposium and a special plaque was presented to Dr. Becker. In 1981 he received a Distinguished Achievement Award from the Brooklyn College Alumni Association.

Becker was always characterized by an outgoing friendly nature, an interest in people, and an enthusiasm for plants, living and fossil. His extensive research papers, which students of paleobotany continue to study and cite, stand as a record of his persistent hard work in the field and the laboratory. His research collections provide an exceptional documentation of the history of ancient plants that once lived in the area of present-day southwestern Montana. To paleobotanists of now and of the future, Herman Becker showed pages of new chapters in plant history when he dug out and pried open the "books of paper shale" at the Ruby River Basin. He will be remembered as a friend, a good colleague, and a research scholar.

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—David Dilcher, Department of Biology, Indiana University, Bloomington, Indiana 47405, U.S.A.

LAND PLANTS OF THE NORTHERN ROCKY MOUNTAINS BEFORE THE APPEARANCE OF FLOWERING PLANTS

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Abstract

Evidence of land plants before the appearance of flowering plants near the end of the Early Cretaceous is spotty. Seas covered much of the land during the Paleozoic and early Mesozoic, but certain areas were exposed, perhaps as islands. Evidence of Devonian vegetation from Beartooth Butte, Wyoming includes rhyniophytes, trimerophytes, zosterophylls, and lycopsids. Fossils from several different deposits show Late Mississippian to Pennsylvanian age vegetation like that of coal swamps to the east. The floras include lepidodendrids, calamites, ferns, seed ferns, and cordaites, with conifers present at some localities. Triassic and Early Jurassic land vegetation is poorly known in the region, as most strata are marine; but Late Jurassic sediments reflect the general emergence of the land concurrent with uplift along the Nevadan orogenic zone at the western edge of the present northern Rocky Mountains. The interior basin supported bryophytes, horsetails, cycads, caytonialeans, ginkgoes, and conifers, with bennettitaleans and ferns dominating. This was followed in the Early Cretaceous by similar flora but with the swamp vegetation dominated by conifers. These plants apparently grew under a generally arid but seasonally wet frost-free climate. It was into this environment that the first flowering plants of the region migrated.

The object of this paper is to give an overview of the types of vegetation that occurred in the northern Rocky Mountain region before the appearance of flowering plants there. This region extends along the Rocky Mountains from central Colorado and Utah north into southern Alberta and British Columbia. The time span involved extends from the Early Devonian Siegenian, about 385 million years ago, to the Early Cretaceous Aptian, about 110 million years ago (Fig. 1). During the intervening 275 million years both the vegetation and the land it occupied changed radically, keeping pace with similar vegetational and land mass changes elsewhere in the world.

In fact, evidence of vegetation within the present northern Rocky Mountain region is spotty (Fig. 2). The best records of Paleozoic vegetation come from deposits in Europe and eastern and midwestern North America. Similarly, early Mesozoic, i.e., Triassic and Jurassic, floras are more abundant and better preserved in Europe and the southwestern United States than in the northern Rocky Mountains. It isn't until the Late Jurassic and Early Cretaceous that records within the region are as good as those found elsewhere. The Paleozoic and Mesozoic sites that are known in the northern Rocky Mountains, however spotty, show that the types of plants in the region are similar to those elsewhere and that they probably were organized in similar communities which occupied similar habitats. Thus, while the deposits within the region fail to provide conclusive evidence, they nonetheless permit inference based on our knowledge of nearby vegetation outside the area.

DEVONIAN

During the Early Devonian, the only part of the period for which we have evidence, the present northern Rocky Mountains was an area of lowlands and shallow seas along the western margin of the early land mass Laurussia (Bambach et al., 1980). This continent lay across the equator, extending from about 10° south latitude to about 40° north latitude, with the present northern Rocky Mountains situated at about 12° north latitude (Ziegler et al., 1981, fig. 7.5). Because of its position, the area had a tropical climate with warm temperatures and abundant rainfall throughout the year. This, combined with the location of the northern Rocky Mountains in the Devonian along the western coast of the continent where sharp changes in climate were moderated by ocean currents, resulted in what must have been ideal growing conditions.

Two deposits of Early Devonian plant fossils have been recorded in the Beartooth Butte Formation in the northern Rocky Mountains. The classic site at Beartooth Butte, Wyoming (Fig. 1A) has been known for over 50 years. Five taxa were described by Dorf (1933, 1934a, 1934b)

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FIGURE 1. Index map and geologic time column showing the approximate locations and ages of the localities mentioned in the text.—A. Beartooth Butte, Early Devonian.—B. Cottonwood Gulch, Early Devonian.—C. Deseret Limestone, Utah, Early Mississippian.—D. Uinta Mountains, Late Mississippian.—E. Daggett County, Utah, palynoflora, Late Mississippian.—F. Bear Gulch Palynoflora, Late Mississippian.—G. Manning Canyon Shale, Early Pennsylvanian.—H. Weber Formation, Early Pennsylvanian.—I. McCoy Formation, Late Pennsylvanian.—J. Spotted Ridge Flora, Pennsylvanian.—K. Cutler Formation, Permian.—L. Wyoming Red Beds, Triassic.—M. Morrison Flora, Utah, Late Jurassic.—N. Morrison Flora, Wyoming, Late Jurassic.—O. Morrison Flora, Montana; Late Jurassic.—P. Kootenay Formation, Late Jurassic.—Q. Douglas County, Oregon, Late Jurassic.—R. Kootenai Formation, Early Cretaceous.—S. Lower Blairmore, Early Cretaceous.—T. Shasta Flora, Early Cretaceous.—U. Burro Canyon Formation and Cedar Mountain Formation, Early Cretaceous.

based on imprints of plant fragments. More recently, Hueber (1972) and Tanner (1982, 1983) described additional remains from the locality. The deposit is regarded as Emsian in age, about 375 million years old.

Tanner (1982, 1983) described fossils from the new Beartooth Butte Formation locality near Cottonwood Gulch (Fig. 1B) in northcentral Wyoming, about 50 km east of the original site (Fig. 1A). It is believed to be Siegenian in age, about 385 million years old, and thus somewhat older than the Beartooth Butte locality. Locating a second deposit in the region raises hope that these are not isolated occurrences and that further search will turn up more deposits.

Five taxa were originally described by Dorf (1933) from the Beartooth Butte locality. These include *Psilophyton wyomingense* Dorf for flattened branch systems bearing numerous spines (Fig. 2A, B), (?) *Psilophyton* sp. for an elongated presumed sporangium, *Bucheria ovata* Dorf (see note on change in name below) for narrow axes bearing numerous lateral sporangia (Fig. 2C, D), *Hostimella* sp. for flattened branch systems lacking spines, and (?) *Broggeria strobiformis* for a cylindrical strobiluslike structure. Hueber (1970)

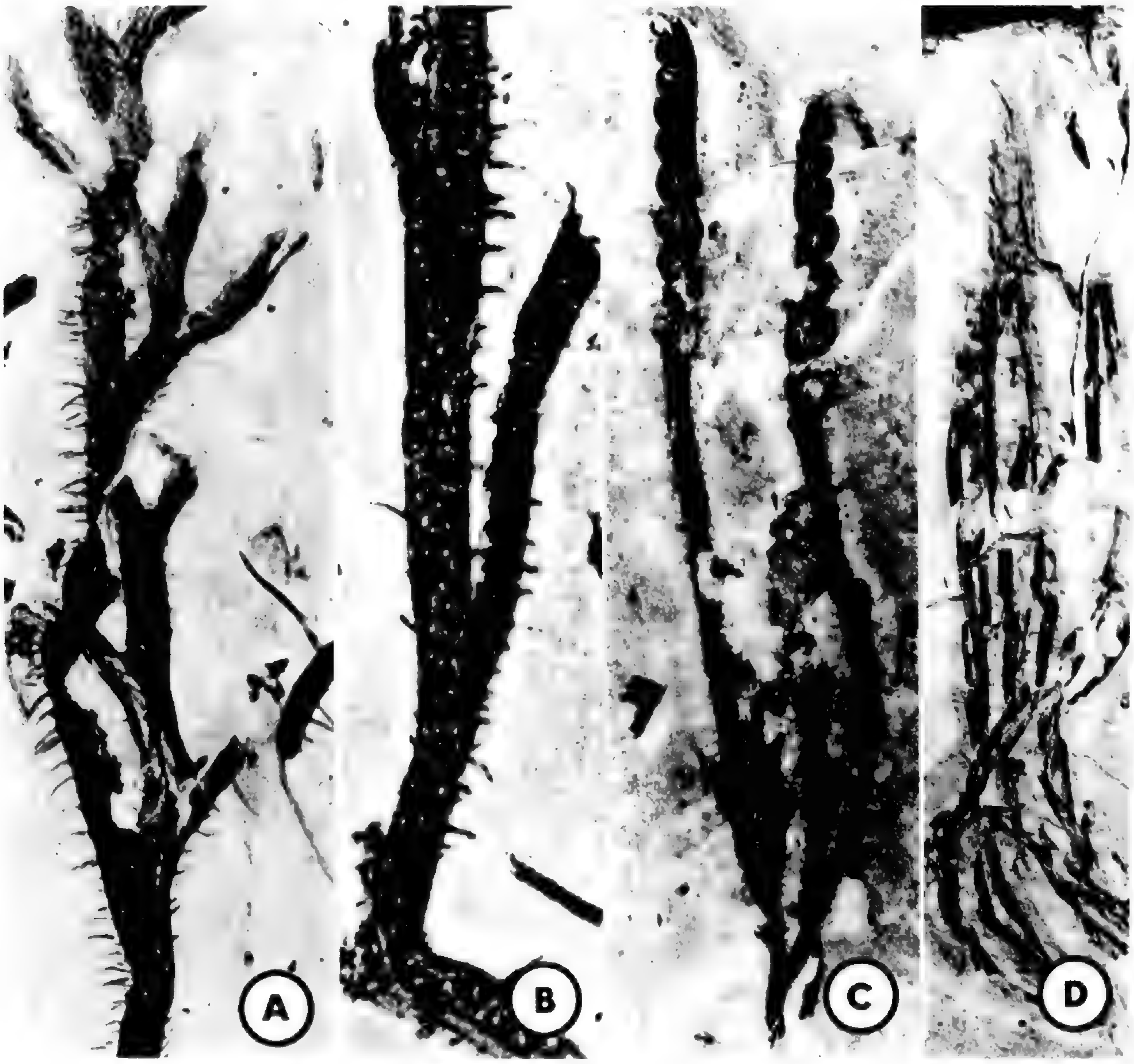

FIGURE 2. Examples of plant fossils from the Early Devonian Beartooth Butte Formation. A, B. *Psilophyton wyomingense* Dorf.—A. Holotype, from Dorf (1933, plate V, fig. 3), ×2.5.—B. from Dorf (1933, plate V, fig. 5), ×2.5.—C. *Rebuchia ovata* (Dorf) Hueber, USNM 168991B counterpart, ×1.3.—D. *Rebuchia ovata* (Dorf) Hueber, USNM 168992, ×1.3. (Figs. A, B reproduced by permission of the University of Chicago Press; Figs. C, D from photographs courtesy of F. M. Hueber.)

changed the name of *Bucheria ovata* to *Rebuchia ovata* and later (1972) described its vegetative axes linked with the fertile stems (Fig. 2C, D). These clearly show the affinity of the plant with the Zosterophyllophytina.

More recently Tanner (1982, 1983) described additional taxa from both sites of the Beartooth Butte Formation, bringing the total known to 14. Six of these are based on vegetative axes with attached fertile parts, five are known from vegetative axes alone, while one taxon is based on a sporangial pair. Present are rhyniophytes, trimerophytes, zosterophylls, and the early lycopsids *Drepanophycus* and *Leclercquia* (Tanner, 1983). There are also two taxa of undetermined botanical affinities.

Discussion. Even though the two localities occur in the same formation, palynological evidence indicates that they may be separated by as much as 20 million years. Such a gap is not apparent in the megafossils or the fish fauna preserved at both, although the Cottonwood Creek assemblage lacks definitive marker species (Tanner, 1983).

In comparison with other Early Devonian assemblages in North America and Europe, the Wyoming flora shows a surprising lack of trimerophytes and a richness in zosterophylls and early lycopsids. The new information about the floristic diversity of the Beartooth Butte Formation does not support the floristic zones proposed by Gierlowski (Ziegler et al., 1981) in which the western North America zone is characterized by relatively low generic diversity of two to six taxa per assemblage and a lack or restriction of zosterophylls. Including the unnamed sporangial pair and two morphotypes of sterile axes, the Wyoming assemblage has ten genera, three of which belong to the Zosterophyllaceae.

Early Devonian plants share an architectural plan that with few exceptions consists of relatively naked aerial branches up to a meter tall, which branch from rhizomes that bear adventitious roots or rhizoids (Gensel & Andrews, 1984). This is often interpreted as implying that these plants grew in marshy habitat. Since many of the known Early Devonian plant assemblages, and particularly the Wyoming sites, are from near equatorial paleolatitudes with equable temperatures and moisture, transpiration stress may not have been enough to require actual growth in standing water or even saturated soil as would be found in coastal marshes. Occurrence at more inland and upland sites may have been possible.

MISSISSIPPIAN

While movement of other continental plates between the Early Devonian and Mississippian was significant, the position of Laurussia, and thus the present northern Rocky Mountains, was relatively unchanged. There was an apparent increase in mountain building activity west of Laurussia and an increase in the amount of shallow seas and evaporite formation (Bambach et al., 1980, fig. 11). Much of the northern Rocky Mountains was an evaporitic basin in which limestone was deposited. However, some land was exposed within this zone of shallow seas, for plant remains are recorded as petrifactions in northwestern Utah (Fig. 1C; Tidwell & Jennings, 1986), as impressions and as pollen and spores in northwestern Utah (Fig. 1D, E; Arnold & Sadlick, 1962; Schemel, 1950), and as pollen and spores associated with exceptionally well-preserved fish and invertebrates at Bear Gulch (Fig. 1F) near Lewistown, Montana (Cox, 1986).

Deseret Limestone petrifactions. Tidwell & Jennings (1986) described a new lycopod, *Stansburya,* from the Early Mississippian Deseret Limestone near Grantsville, Utah, south of Great Salt Lake. Six stem specimens were included in a single carbonate concretion. The stems are about 1.4 cm in diameter and are dichotomously branched. Scalelike leaves are tightly appressed helically around the stems. None of the axes contain secondary tissues, and this led the authors to interpret the fossils as representing an herbaceous plant. Much remains to be learned about this new genus, but discovery of these fossils in the Deseret Limestone suggests that further search may be rewarding.

Daggett County, Utah, Palynoflora. Schemel (1950) reported several different types of pollen and spores isolated from a coal sample from Late Mississippian sediments in northwestern Utah (Fig. 1E). Over 90% of the palynomorphs belong to *Densosporites.* Similar spores have been found in Pennsylvanian age sediments both dispersed and in strobili of presumed arborescent lycopods (Taylor, 1981). Several other types of spores occur in the Utah coal in small amounts and suggest that sphenopsids, ferns, pteridosperms, and cordaitaleans grew in the vicinity.

Uinta Mountains Flora. The megafossil assemblage reported from a locality in the Uinta Mountains in northeastern Utah (Fig. 1D) is a small one based on poorly preserved imprints of vegetative remains (Arnold & Sadlick, 1962). *Archaeocalamites* was identified from pith casts. These show ribs continuous across the nodes rather than alternate as in *Calamites.* The occurrence of *Lepidodendron* is documented by imprints of characteristic stems, leafy twigs, and detached leaves. Defoliated axes, probably of seed fern fronds, identified as *Caulopsis,* are present, as are detached fern or seed fern pinnules of *Fryopsis* (formerly *Cardiopteris*). Lastly, *Rhodea,* frond portions of a seed fern characteristic of the Late Mississippian and Early Pennsylvanian, has also been identified.

Arnold & Sadlick (1962) interpreted the plant remains as representing streamside vegetation with fragments washed into an estuary or bay by river currents. The plant fragments are small and are imprints with occasional flecks of carbon. However, the siltstone matrix contains numerous flecks of black material that presumably represent macerated plant debris (Arnold & Sadlick, 1962).

The assemblage is regarded as Chesterian in age based on associated invertebrates (Arnold & Sadlick, 1962) and is correlated with the Late Visean or Early Namurian stages in Europe. The plant assemblage compares well with floras of similar age in the Appalachian trough.

Bear Gulch palynoflora. Palynomorphs are also preserved in rocks that have given up exceptionally well-preserved vertebrate and invertebrate fossils at Bear Gulch, near Lewistown, Montana (Fig. 1F; Melton, 1971). The palynomorphs (Cox, 1986) include: *Acanthotriletes, Anapiculatisporites, Chaetosphaerites, Convolutispora, Cyclogranulatisporites, Denosporites,* *Endosporites, Lycospora, Procoronospora, Punctatisporites, Raistrickia, Rotaspora, Savitrisporites, Tripartites,* and *Verrucosisporites.* The assemblage indicates a Chesterian age for the deposit and correlates with the Namurian A stage of Europe.

Furthermore, the palynoflora indicates that a diverse assemblage of ancient vascular plants inhabited the land that then surrounded the bay in which the Bear Gulch sediments were deposited. Although the correlation of the pollen and spore species found here with the plants that produced them remains uncertain, other species of some of these genera have been found in sporangia. By analogy the following megafossil forms may have been present: lepidodendrids (*Denosporites* and *Lycospora*), zygopterid ferns (*Convolutispora*), progymnosperms (*Cyclogranisporites*), cordaitaleans (*Endosporites*), filicalean ferns (*Raistrickia*), marattialean ferns (*Verrucosisporites*), and seed ferns (*Punctatisporites* and *Schulzospora*) (Kosanke, 1950; Millay & Taylor, 1979; Taylor, 1981).

Discussion. The two palynofloras and the Uinta Mountain megaflora combine to give solid evidence that vegetation similar to that occurring in eastern North America and Europe was present in the northern Rocky Mountains during the Late Mississippian.

PENNSYLVANIAN

By Pennsylvanian time Laurussia was connected to Gondwana in the process of forming Pangaea, but the present northern Rocky Mountains remained at about 10° north latitude (Bambach et al., 1980; Ziegler et al., 1981). More of the present land surface was covered by shallow seas than earlier, but sufficient land was exposed to support vegetation characteristic of the period.

Early Pennsylvanian vegetation is well in evidence in the Manning Canyon Shale flora from northern Utah (Fig. 1G). Similar remains, though not as extensive, are known from the Weber Formation in central Colorado (Fig. 1H). Late Pennsylvanian plant remains are known from the McCoy Formation in central and northern Colorado (Fig. 1I), and additional fossils have been reported from a locality in central Oregon (Fig. 1J) of uncertain stratigraphic placement within the Pennsylvanian.

Manning Canyon Shale. Plant fossils recovered from the Manning Canyon Shale in northern Utah (Fig. 1G) are well-preserved imprints that show considerable variety of plant form (Tidwell, 1962, 1967; Tidwell et al., 1974). While the strata were once thought to straddle the Mississippian–Pennsylvanian boundary, the flora best correlates with Early Pennsylvanian Namurian B or possibly late Namurian A stages of Europe.

The plants are like those of coal swamps to the east. Arborescent lycopods were numerous (Tidwell et al., 1974). *Lepidodendron* (Fig. 3D), *Lepidophloios,* and *Sigillaria* are known to have been present based on stem imprints. In addition, remains of the presumed reproductive organs of these plants are represented by *Lepidostrobus, Lepidocarpon,* and *Sigillariostrobus,* with *Stigmaria* (Fig. 3C) representing the underground parts and *Lepidophyllum* and *Cyperites* the foliage.

Both *Archaeocalamites* and *Calamites* (Fig. 3A) were present, as were three species of calamitalean foliage of the *Asterophyllites* type (Fig. 3B). A poorly preserved *Calamostachys* has been found, but details of its construction and the type of spores it produced remain unknown.

Ferns and seed ferns are represented by 11 species of foliage assigned to the genera *Adiantites, Cornypteris, Crossopteris* (Fig. 3F), *Diplothmema, Mariopteris, Neuropteris, Rhodea, Sphenopteridium, Sphenopteris* (Fig. 3E), and *Zeilleria* (Fig. 3G). In addition, the pollen organs *Aulacotheca* and *Telangium* are present, as well as seeds of *Cornucarpus, Holcospermum, Lagenospermum, Rigbycarpus,* and *Trigonocarpus.*

Cordaitales are represented by three species of foliage, a *Cordaianthus* (Fig. 3H), and six species of seeds.

Thus, the Manning Canyon Shale flora represents vegetation similar to that of coal swamps in the midwestern and eastern United States. The setting is interpreted as a coastal swamp community at the margin of a fresh or brackish water embayment that underwent several transgressive–regressive cycles (Tidwell, 1967). Some of the taxa have stratigraphic ranges suggesting a Mississippian age for the flora, but most indicate a Pennsylvanian age correlating with the Namurian B stage in Europe.

Weber Formation, Colorado. Scattered plant remains are known from the Weber Formation in Colorado (Fig. 1H), which Read & Mamay (1964) treated as Early Pennsylvanian Zone 6. *Lepidodendron johnsonii* Arnold (1940) represents the westward extension of typical coal swamp vegetation into central Colorado. The

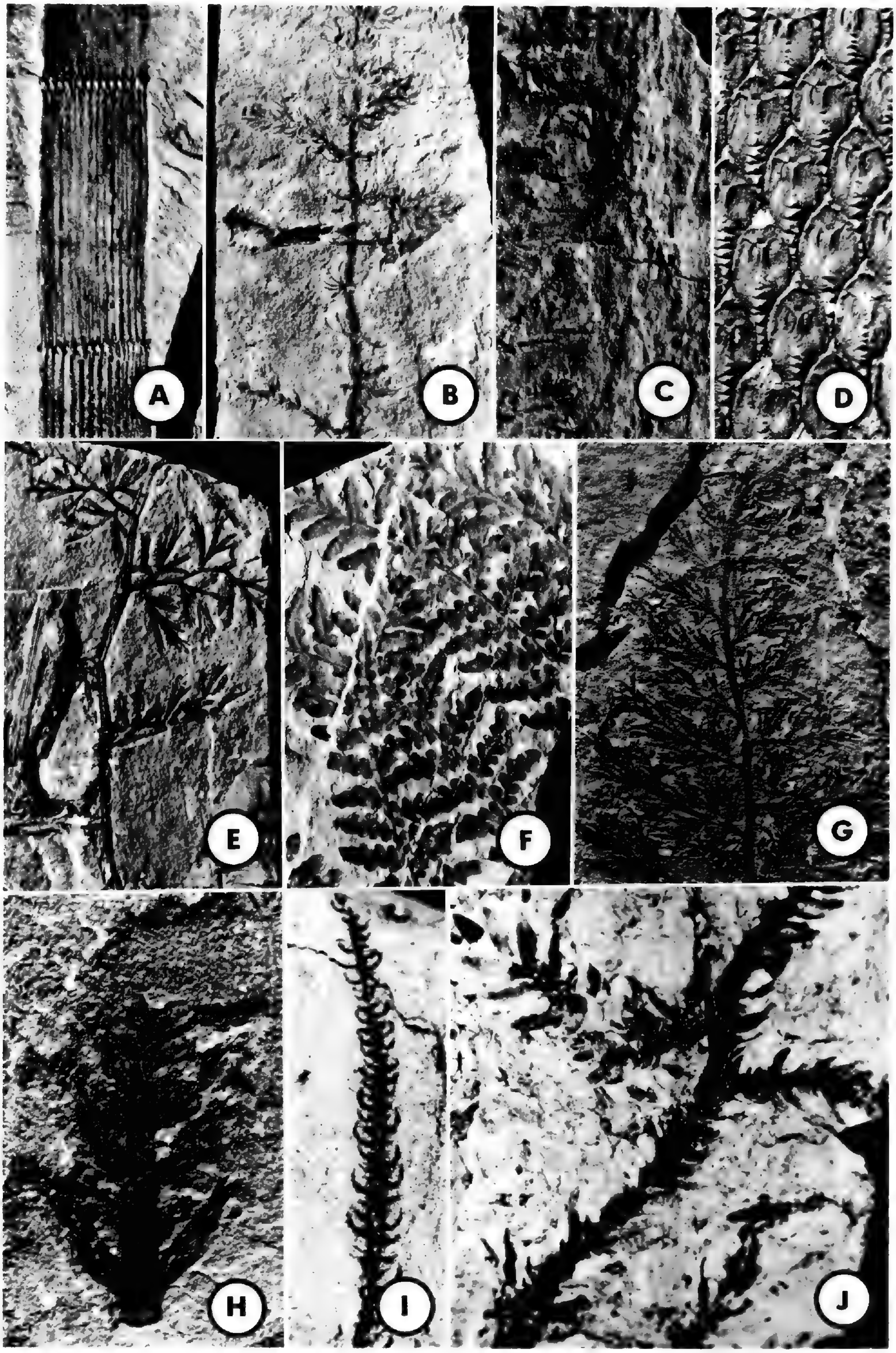

FIGURE 3. Example Pennsylvanian plant fossils from the northern Rocky Mountains.—A. *Calamites*, ×0.6.—B. *Asterophyllites*, ×1.0.—C. *Stigmaria*, ×0.5.—D. *Lepidodendron*, ×0.95.—E. *Sphenopteris*, ×0.7.—F. *Crossopteris*, ×0.6.—G. *Zeilleria*, ×1.1.—H. *Cordaianthus*, ×0.9.—I. *Walchia* sp., UMMP 22131, ×1.0.—J. *Lecrosia gouldii* Arnold, UMMP 21005, ×1.0. (Figs. A–H from photographs courtesy of W. D. Tidwell.)

small amount of coal in the Weber Formation suggests, however, that the coal swamp was of limited development and of short duration (Arnold, 1940). Read (1933) reported imprints of *Trichopitys whitei* from the Weber Formation and in 1934 added *Lepidostrobus, Stigmaria, Calamites, Asterophyllites, Adiantites, Dactylophyllum, Neuropteris, Sphenopteris, Diplomema, Cordaites,* and *Cordaianthus.*

McCoy Formation. Several localities within the McCoy Formation in Colorado (Fig. 1I) have yielded imprints of plant remains (Arnold, 1941). Examples are: *Calamites gigas* Brongn., *Odontopteris mccoyensis* Arnold, *Cordaites angulosostriatus* Grand'Eury, *Samaropsis hesperius* Arnold, *Lecrosia gouldii* Arnold (Fig. 3J), *Walchia stricta* Florin, and *Walchia* sp. (Fig. 3I; Arnold, 1941). Arnold commented on the arid environment evidenced by the plants and by desiccation features in the rocks. Thus, the fossils may represent forms that grew on drier sites than the coal swamp represented by the plants from the Weber Formation. The McCoy Formation is regarded as Late Pennsylvanian Zone 10 by Read & Mamay (1964), and the drier setting may correlate with similar events in coal swamps to the east (Phillips et al., 1985) or may reflect some early uplift of the ancestral Rocky Mountains (Pfefferkorn & Gillespie, 1980).

Spotted Ridge flora, Oregon. The position of this plant megafossil assemblage (Fig. 1J) within the Pennsylvanian has not been determined; none of the fossils found to date in this flora are reliable stratigraphic indicators. The flora has the distinction of being the westernmost deposit of Paleozoic plants in the conterminous United States and is thought to have grown on an island arc or microcontinent that was some distance west of the North American craton (Pfefferkorn & Gillespie, 1980). The following taxa have been reported: an unnamed lepidodendrid branchlet, *Mesocalamites hesperius* (Arnold) Mamay & Read, *M. crookensis* Mamay & Read, *Mesocalamites* sp., *Phyllotheca paulinensis* Mamay & Read, cf. *Asterophyllites equisetiformis* (Schlotheim) Brongn., *Pecopteris oregonensis* Arnold, *Dicranophyllum rigidum* Mamay & Read, cf. *Cordaianthus longibracteatus* Florin, and cf. *Schizopteris trichomanoides* Goeppert (Arnold, 1953; Mamay & Read, 1956; Read & Merriam, 1940). Of these, *Mesocalamites hesperius, Phyllotheca paulinensis, Pecopteris oregonensis,* and *Dicranophyllum rigidum* are the most common, with the others represented in the collection by one to a very few specimens (Mamay & Read, 1956). The large size of the collection rules out sampling bias, and the numbers of specimens are thought to reflect plant abundances with reasonable accuracy (Mamay & Read, 1956).

Mamay & Read (1956) commented that the plant remains occur in sandstone and mudstone and show little evidence of transport. In fact, some *Calamites* stems appear to have been preserved in growth position. Most of the sediments are terrestrial in origin or some possibly originated in a marine or brackish water estuary. Thus, the vegetation represented does not appear to be directly comparable with any of the coal swamp communities of the eastern and midwestern United States. While the plants probably grew in a moist habitat, the latter was not a coal swamp.

Discussion. In addition to the fossil assemblages described above, fragmentary plant remains are known from subsurface samples in Montana (Pfefferkorn & Gillespie, 1980), and a small collection of fossils has been reported from Pennsylvanian sediments in Wyoming (Sando et al., 1975). These indicate that the type of vegetation present in eastern North America during the Pennsylvanian also occurred on exposed land surfaces in the present northern Rocky Mountain region. Nonetheless, Pfefferkorn & Gillespie (1980) recognized the vegetation of the region as belonging to a distinct floral province, the Cordilleran, of which *Crossopteris* (Fig. 3F) is a characteristic endemic.

PERMIAN

The Permian was a pivotal period of geologic time from the standpoint of plant evolution and from the types of vegetation that occurred. Toward the end of the Pennsylvanian, eastern and midwestern coal swamps reflect a change in community structure from domination by arborescent lycopods to domination by marattiaceous tree ferns (Phillips et al., 1985). This perhaps foretells of changes to come with breakup of Pangaea and the movement of continents poleward during the early Mesozoic.

Deposits of Permian age plant remains in the region are few, and none that are known provide the quantity of well-preserved fossils typical of earlier periods. One occurrence of Permian age plant remains has been reported by Mamay & Breed (1970) from the southern periphery of the present northern Rocky Mountains. They reported eight specimens from the Cutler Formation in southern Utah (Fig. 1K). From these are identified *Taeniopteris* sp., *Supaia rigida* White, *Protoblechnum bradyi* Mamay & Breed, and *Callipteris* sp. This represents the northernmost occurrence of *Supaia. Protoblechnum bradyi* is most similar to a species from eastern Asia and suggests the possible affinities of the Utah assemblage with the Asian flora (Mamay & Breed, 1970).

Similar remains are found in deposits in Texas, New Mexico, and Arizona, and we can only speculate that exposed land surfaces in the present northern Rocky Mountains supported similar plants.

TRIASSIC

The only plant fossils reported from the Triassic in our region are an *Equisetum,* two species of *Pterophyllum,* two of *Zamites* and one *Podozamites* (Berry, 1924). These come from the so-called "red beds" in westcentral Wyoming (Fig. 1L). These fossils are similar to those found in the Chinle Formation in the Southwest (Ash, 1972; Daugherty, 1941) and suggest that a similar vegetation occurred in the northern Rocky Mountains.

JURASSIC

During the Early and Middle Jurassic, the present northern Rocky Mountain region was covered by an inland sea in which marine limestone and sandstones were deposited (Imlay, 1984; Silverman & Harris, 1967). Uplift in the Nevadan orogenic belt south and west of the present northern Rocky Mountains resulted in a broad interior basin of low relief that was poorly drained by rivers northward and received sediments from highlands to the southwest and from the Canadian shield to the east (Brenner, 1983; Walker, 1974). The large size of the interior basin is reflected by the widespread deposition of shales and sands of the Late Jurassic Morrison Formation and its equivalents, which are recognized from southern Utah and Colorado north into southern Canada (Walker, 1974).

Geologic studies suggest that a somewhat arid but seasonally wet climate prevailed during the Late Jurassic (Walker, 1974), supporting a savannalike vegetation with many shallow lakes and swamps. There were probably dry periods during which water tables dropped and exposed accumulated debris to oxidation and decay. This may explain why plant fossils are not more abundant in the region (Walker, 1974).

Plant fossils are known from scattered localities throughout the region (Delevoryas, 1969; Tidwell, 1975), but large assemblages of remains that reflect vegetation are known only from central Montana (Fig. 1O) and southern Canada (Fig. 1P). South of the northern Rocky Mountain region are a number of occurrences of silicified remains from the Late Jurassic Morrison Formation (Fig. 1M). Some noteworthy examples are: *Hermanophyton kirkbyorum* Arnold (1962), a *Rhexoxylon*-like log, *Osmundacaulis wadei* Tidwell & Rushforth (1970), the only species of petrified osmundaceous rhizome known from the Jurassic of North America, as well as several different coniferous woods (Medlyn & Tidwell, 1975, 1979).

Within the region there are reports of foliage imprints of the two cycadophytes *Nilssonia nigricollensis* Wieland and *Zamites arcticus* Goeppert (Knowlton, 1916) and of petrified cycadeoid trunks (Delevoryas, 1960; Ward, 1905), both from Wyoming (Fig. 1N).

The most extensive Late Jurassic flora (Table 1) in the northern Rocky Mountains is that preserved in shales of the Morrison Formation in central Montana (Silverman & Harris, 1967; Brown, 1972). Plant remains have been found at six localities, one near Lewistown and the rest south of Great Falls near the town of Belt (Fig. 1O).

While three of the six localities in central Montana are close to one another, the most distant sites are over 170 km apart. *Zamites arcticus* (Fig. 4A), *Nilssonia* cf. *compacta* (Fig. 4D), *Podozamites lanceolatus* (Fig. 4G), and *Pityophyllum lindstromii* (Fig. 4F) occur at all six localities; and these taxa probably represent the dominants of the regional vegetation. *Pagiophyllum* sp. (Fig. 4F) and *Cladophlebis virginiensis* (Fig. 4C) occur at five of the sites and were thus also widespread. *Sagenopteris elliptica* (Fig. 4E), leaflets of a caytonialean seed fern, and *Coniopteris hymenophylloides* (Fig. 4B), foliage of a dicksoniaceous fern, are locally abundant at certain localities. Nowhere are remains of conifers as abundant as those of cycadophytes. Ginkgophytes (Brown, 1975) are present but rare. Thus, the vegetation appears to have been a relatively open one with scattered conifers, more closely spaced cycadophytes and tree ferns, occasional ginkgophytes, and an understory of ferns.

One of the localities clearly represents material

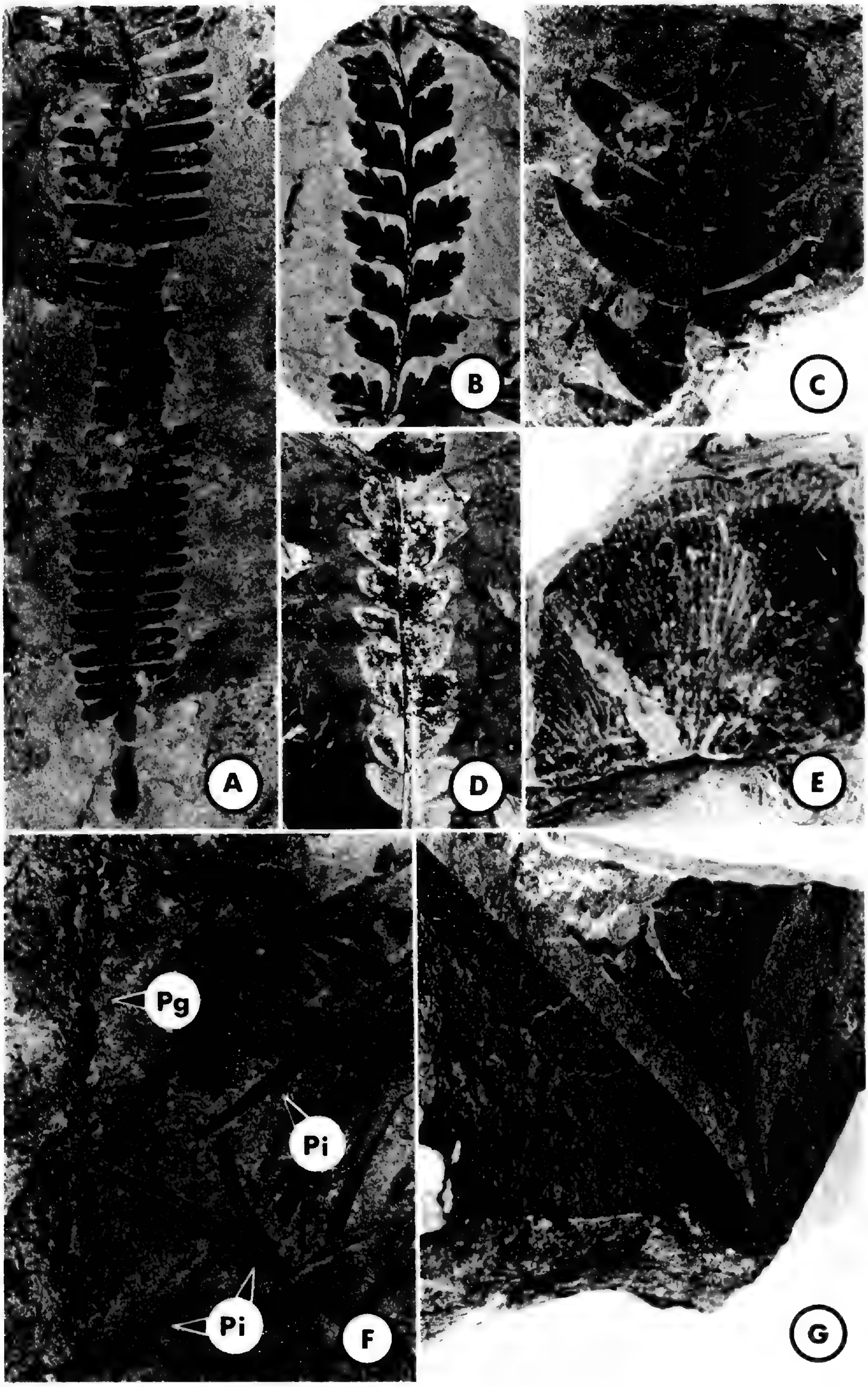

FIGURE 4. Typical plant fossils from the Late Jurassic Morrison Formation, Montana.—A. *Zamites arcticus* Goeppert, UMPM 1091, ×1.2.—B. *Coniopteris hymenophylloides* (Brongn.) Seward, UMPM 1092, ×1.5.—C. *Cladophlebis virginiensis* Fontaine, UMPM 1094, ×1.4.—D. *Nilssonia* cf. *compacta* (Phill.) Bronn., UMPM

washed in from surrounding areas, and others provide evidence of an extensive swamp and swamp margin community stable enough to result in a thin but mineable seam of low grade coal (Silverman & Harris, 1967). While coal formation indicates deposition of plant debris in water having oxygen low enough to retard degradation of remains by aerobic bacteria, some areas of the swamp were above water level and supported growth of marchantioid liverworts.

A similar vegetation extended northward into Canada (Fig. 1P) where megafossils are preserved in sediments of the Kootenay Formation (Bell, 1956), and microfossils are known from the Upper Vanguard Formation (Pocock, 1962). However, there is no reason to assume that a given swamp extended over that distance. Rather, there were probably many swamps that formed and disappeared over the several million years represented by the Late Morrison Formation and the Kootenay and Upper Vanguard formations in Canada. Thus, it is doubtful that direct correlation of these strata is possible.

Furthermore, the Canadian flora appears more diverse than that in Montana (Bell, 1956). While some of this apparent diversity is simply more species of the same genera and is probably due to taxonomic splitting, several genera occur in the Canadian flora that are absent in Montana. These are the fern *Klukia,* the seed fern *Czekanowskia,* the cycadophytes *Ctenis, Pseudoctenis,* and *Ptilophyllum,* and the ginkgophyte *Baieria* (Bell, 1956).

There is another Late Jurassic flora close to but outside the northern Rocky Mountain region (Fig. 1Q). Over 60 taxa have been reported from 20 localities in Douglas County, Oregon (Ward, 1905), and essentially no research has been done on this assemblage since it was treated in the *Status of the Mesozoic floras of the United States, 2nd paper* over 80 years ago. A modern study of these fossils has great potential to advance substantially our knowledge of Jurassic vegetation.

TABLE 1. Fossil plants from the Morrison Formation of central Montana.

Bryophytes
Marchantiolites sp.
Ferns and fern allies
Equisetum laterale Phillips
Hausmannia fisheri (Knowlton) Oishi & Yamasita
Coniopteris hymenophylloides (Brongn.) Seward
Adiantites montanensis (Knowlton) Brown
Cladophlebis alberta (Dawson) Bell
C. heterophylla Fontaine
C. virginiensis Fontaine
Cycadophytes
Nilssonia cf. *compacta* (Phillips) Bronn.
Zamites arcticus Goeppert
Cycadolepis spp.
Weltrichia sp.
Anomozamites sp.
Sagenopteris elliptica Fontaine
Ginkgophytes
Ginkgoites cascadensis Brown
G. pluripartita (Schimper) Seward
Conifers
Pagiophyllum sp.
Podozamites lanceolatus (Lindley & Hutton) Braun
Pityophyllum lindstromii (Heer) Nathorst
Pityocladus sp.
Schizolepis sp.

EARLY CRETACEOUS

The broad interior basin in which sediments of the Late Jurassic Morrison Formation were deposited persisted into the Early Cretaceous. Sedimentation was not continuous, however. It ceased for a time and then resumed. This cessation resulted in a disconformity overlain by a layer of coarse sandstone which occurs throughout the region (Walker, 1974). The disconformity is regarded as the boundary between the Jurassic and the Cretaceous (Brown, 1956).

Sometime after the resumption of deposition, plant remains were deposited. In central Montana this was not until what is believed to be the Aptian stage of the Early Cretaceous (LaPasha & Miller, 1984) even though invertebrates in the basal sandstone of the Kootenai Formation indicate a Neocomian age for those strata (Walker, 1974).

The plant-bearing layers of the Kootenai For-

←

1093, ×1.7.—E. *Sagenopteris elliptica* Fontaine, UMPM 1095, ×2.7.—F. *Pagiophyllum* sp. (Pg) and *Pityophyllum lindstromii* (Heer) Nathorst (Pi), UMPM 1096, ×1.5.—G. *Podozamites lanceolatus* (Lindley & Hutton) Braun, UMPM 1097, ×1.4.

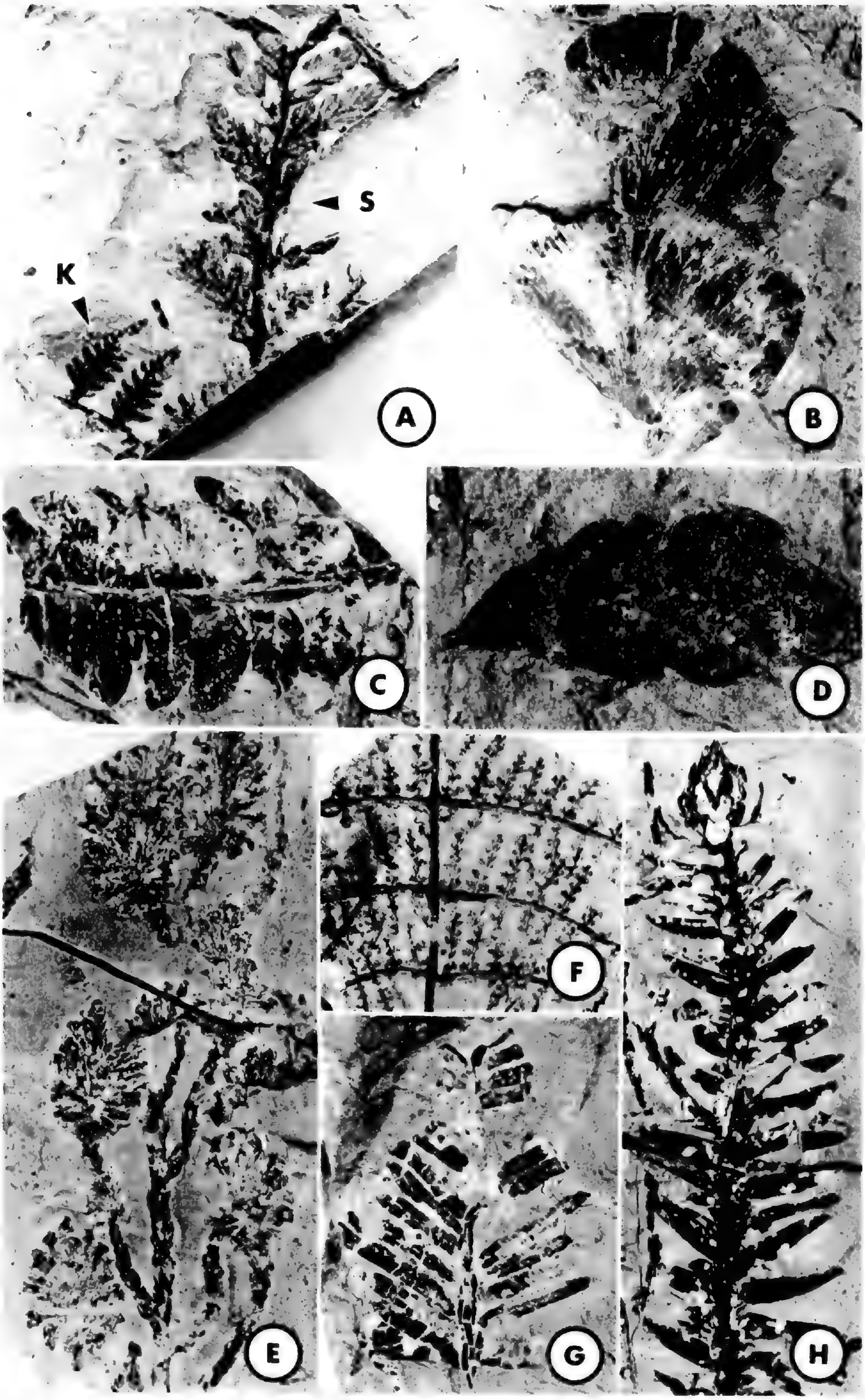

FIGURE 5. Typical plant fossils from the Early Cretaceous Kootenai Formation.—A. *Klukia canadensis* Bell (K) and *Sphenopteris latiloba* Fontaine (S), UMPM 1098, ×1.6.—B. *Sagenopteris williamsii* (Newberry) Bell, UMPM 1099, ×1.3.—C. *Cladophlebis oblongifolia* Fontaine, UMPM 1100, ×3.5.—D. *Sagenopteris mclearnii*

mation represent deposition of sediments and plant remains in poorly drained swamps that formed from infilling of lakes. Evidence suggests that the swamps contained standing water throughout the year. Some areas were above water level as indicated by the occurrence of liverworts, which were probably preserved in place (Brown & Robison, 1974, 1976; LaPasha & Miller, 1984, 1985). However, the water table at these sites was high enough to keep the soil saturated.

Certain plants (Table 2) probably grew in the swamps in which their remains were deposited. This is indicated by the occurrence of large, locally abundant remains in low diversity assemblages in a wide variety of sediment size classes (LaPasha & Miller, 1984). Fossils that fit this category are *Marchantiolites, Diettertia, Coniopteris simplex* (Fig. 5F), *Acrostichum, Sagenopteris williamsii* (Fig. 5B), and *Athrotaxites berryi* (Fig. 5E). Remains of other plants are generally found as abundant, small fossils occurring in high diversity assemblages and in narrow ranges of sediment size classes, particularly coarse sediments suggesting slight transport. Examples of these are *Coniopteris, Cladophlebis* (Fig. 5C), *Sphenopteris* (Fig. 5A), *Sagenopteris elliptica, S. mclearnii* (Fig. 5D), *Ginkgo* (Brown, 1975), *Elatides* (Fig. 5H), and *Elatocladus* (Fig. 5G). The same reasoning, combined with the relative scarcity of fossils, suggests that remains of *Equisetum, Klukia* (Fig. 5A), *Hausmannia, Zamites,* and other bennettitaleans were transported some distance, but exactly how far is unknown.

While certain species are common to both the Morrison flora and the Kootenai flora (Tables 1, 2), the two represent different types of vegetation. The Kootenai flora appears to have been dominated by conifers, especially *Athrotaxites,* with bennettitaleans relatively rare (Miller & LaPasha, 1983, 1984). Ferns formed the understory; and although *Sagenopteris* is abundant at certain localities, the stratum of vegetation it occupied remains unknown.

The Kootenai Formation is widespread in Montana and has equivalents in adjacent states, but plant fossils are known in abundance only near Great Falls. Permineralized cycadeoid trunks have been reported from the Burro Canyon For-

TABLE 2. Fossil plants from the Kootenai Formation of central Montana.

Bryophytes
  Marchantiolites blairmorensis (Berry) Brown & Robison
  Megzgeriites montanensis LaPasha & Miller
  Diettertia montanensis Brown & Robison

Sphenopsids
  Equisetum montanensis LaPasha & Miller
  E. cascadensis LaPasha & Miller

Lycopsids
  Minerisporites sp. A
  Minerisporites sp. B

Pteropsids
  Coniopteris hymenophylloides (Brong.) Seward
  C. simplex (Lindley & Hutton) Harris
  Klukia canadensis Bell
  Hausmannia montanensis LaPasha & Miller
  Acrostichum longipennis Fontaine
  Cladophlebis constricta Fontaine
  C. inclinata Fontaine
  C. oblongifolia Fontaine
  C. oerstedii (Heer) Seward
  C. virginiensis Fontaine
  Sphenopteris brulensis Bell
  S. latiloba Fontaine
  S. mclearnii Bell
  S. goeppertii Dunker
  Arcellites sp.
  Parazollopsis cascadensis LaPasha & Miller

Cycadophytes
  Sagenopteris elliptica Fontaine
  S. mclearnii Berry
  S. williamsii (Newberry) Bell
  Zamites arcticus Goeppert
  Pseudocycas douglasii LaPasha & Miller

Ginkgophytes
  Ginkgo pluripartita (Schimper) Heer

Conifers
  Athrotaxites berryi Bell
  Elatides curvifolia (Dunker) Nathorst
  Elatocladus dunnii Miller & LaPasha
  E. montanensis Miller & LaPasha
  Masculostrobus montanensis Miller & LaPasha
  Conites sp.

←

Berry, UMPM 1101, ×2.3.—E. *Athrotaxites berryi* Bell, UMPM 894a, ×1.8.—F. *Coniopteris simplex* (Lindley & Hutton) Harris, UMPM 1102, ×1.3.—G. *Elatocladus montanensis* Miller & LaPasha, holotype UMPM 914, ×1.7.—H. *Elatides curvifolia* (Dunker) Nathorst, UMPM 907, ×1.4.

mation (Fig. 1U) in Colorado (Brown, 1950). *Frenelopsis varians* and *Tempskya* are known from the Cedar Mountain Formation (Fig. 1U) in Utah (Tidwell et al., 1976), although the upper parts of both of these formations are regarded by some as younger than the Kootenai Formation (Ash & Read, 1976; Tschudy et al., 1984).

An extensive assemblage of plant remains (Fig. 1S) is known from the Lower Blairmore Formation of Alberta (Bell, 1956), and the Kootenai flora compares best with this assemblage. The Lower Blairmore flora is of special interest because it contains the earliest convincing flowering plant megafossils in the region, leaf imprints identified as *Sapindopsis angusta* (Heer) Seward & Conway (Bell, 1956). While it is possible that the sites these leaves come from are in fact somewhat younger than the Kootenai flora, it is also possible that the leaves indeed represent some of the earliest flowering plant migrants into the region.

Another extensive Early Cretaceous assemblage is known from outside the northern Rocky Mountain region, but it is nonetheless of special interest. Like the Jurassic plants from Douglas County, Oregon, those from the Shasta Series in northern California (Fig. 1T) represent a large and diverse assemblage that has received no further work since the flora was described over 80 years ago (Ward, 1905). These fossils should be the subject of a modern study.

SUMMARY

This report deals with the record of terrestrial vegetation in the northern Rocky Mountains prior to the appearance of flowering plants. The span of time involved covers the Early Devonian 385 million years ago to the Early Cretaceous about 110 million years ago. Before the Late Jurassic the evidence, with few exceptions, is discontinuous and spotty. At best, it permits inferences about the type of vegetation present in the region.

Recent work on plant remains from the original and a second collecting site in the Early Devonian Beartooth Butte Formation of northern Wyoming has added considerably to the forms known. Represented are rhyniophytes, trimerophytes, zosterophylls, and early lycopsids. These compare well with plants of similar age known from eastern North America and western Europe, making the Beartooth Butte assemblage one of the better known Early Devonian floras of the world.

Several deposits of Late Mississippian and Early Pennsylvanian fossils show that vegetation like that of coal swamps of Appalachia and the North American interior occurred in the northern Rocky Mountain region as well. The latter vegetation was composed of arborescent lycopsids, arborescent sphenopsids, tree ferns, seed ferns, and cordaites like that of the Interior-Appalachian Province to the east, but the presence of unique forms is grounds for treating the western vegetation in the distinct Cordilleran Province. Similarly, because of species unique to it, the Spotted Ridge flora of Oregon is treated as representing the Oregonian Province.

Our record of vegetation is spotty in sediments of the Permian, Triassic, and Early and Middle Jurassic in the northern Rocky Mountains. By comparison, evidence of Late Jurassic and Early Cretaceous vegetation is relatively abundant and informative. Much of the present northern Rocky Mountains was then a broad interior basin of low relief that supported an open savanna type of vegetation interspersed with shallow lakes, swamps, and rivers. During the Late Jurassic conifers appear to have been widely scattered, cycadophytes and ferns were more closely spaced, and ginkgophytes and caytonialean seed ferns were more rare and occasional. This vegetation presumably grew under somewhat arid conditions with seasonal wet periods. Temperatures were equable, and there is no evidence of freezing conditions.

While the interior basin persisted into the Early Cretaceous and was the site of deposition of plant fossils, the vegetation represented had an entirely different aspect. Conifers were abundant and dominated the vegetation, with cycadophytes rare and widely scattered. Ferns formed the understory and caytonialean seed ferns were locally abundant. Rainfall and temperatures were like those of the Late Jurassic.

There is no evidence of flowering plants in the flora of the Early Cretaceous Kootenai Formation in Montana, which is regarded as Aptian in age. However, imprints of flowering plant leaves are present but rare in sediments of presumably equivalent age in adjacent Canada. Whether or not the sediments containing the leaves are somewhat younger than Aptian, as some believe, these imprints represent some of the first flowering plants in the northern Rocky Mountain region.

Thus, angiosperms made their first appearance in the northern Rocky Mountains toward the end of the Early Cretaceous, and it is important to know about the vegetation that occurred on the land as they migrated into the region. Unlike problems confronting the first land plants in the Early Devonian that colonized relatively barren land, the establishment of flowering plants required their successful competition with vegetation that was already in place. This is indeed a remarkable feat; however, this survey shows that replacement of one form of vegetation by another has been the rule throughout the 275 million years discussed in this paper.

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ANGIOSPERMS OF THE NORTHERN ROCKY MOUNTAINS: ALBIAN TO CAMPANIAN (CRETACEOUS) MEGAFOSSIL FLORAS[1]

DAVID R. CRABTREE[2]

ABSTRACT

Synchronous first occurrences of pollen and leaves indicate that angiosperms entered the Northern Rocky Mountain (NRM) region during the Middle Albian, approximately 8 Ma later than such shifts in floras from southern Laurasia. The earliest angiosperm pollen and leaf flora corresponds to the Potomac sub-Zone IIB in that it exhibits a pretricolporate palynoflora and a comparable grade of evolution based on leaf rank. The Albian megaflora is characterized by abundant leaves of the Platanophyll, Protophyll, and Pentalobaphyll morphotypes. Sapindophylls are common and diverse. The flora contains early North American occurrences of the widespread Upper Cretaceous leaf form genera *Trochodendroides* and *Cinnamomoides.* Pentalobaphylls (Araliaephylls) appear early and assume a more important position in the lowland vegetation of the NRM region than in other regions. Magnoliidae, Hamamelididae, and Rosidae are represented in the Albian flora. The Albian megaflora is a regional variation of a largely cosmopolitan Laurasian flora. Latest Albian and Cenomanian megafloras suggest the development of north–south provincialism within the region. Post-Cenomanian to Campanian floras show gradual diversification with various Platanaceae and Hamamelidaceae as numerical dominants. Pinnate palms are present by the early Campanian. Higher-level taxa present in the region in the Early Campanian include Magnoliales, Laurales, Chloranthales, Nymphaeales, Menispermaceae, Trochodendrales, Platanaceae, Hamamelidaceae, Cercidiphyllales, Fagales, Rosidae, and palmate Dilleniidae.

In 1874 Leo Lesquereux stated:

> The plants of the Dakota group, as known mostly by detached leaves, are stiking by their beauty, the elegance, the variety of their forms, and their size . . . it suffices to say that, at first sight, they forcibly recall those of the most admired species of our time . . . and the evident likeness of their facies . . . strikes the paleontologist and may lead him into error . . . for, really, when we enter into a more detailed analysis of these Cretaceous leaves, we are by and by forcibly impressed by the strangeness of the characters . . . which seem at variance with any of those recognized anywhere in the floras of our time . . . . Hence, this flora does not leave any satisfaction, any rest, to my mind.

In this paper I summarize and evaluate the evidence relevant to the paleoecology and evolution of early angiosperms in the Northern Rocky Mountain (NRM) region based on the megafloral record. The refinement of descriptive terminology for leaf architecture (Hickey, 1973, 1979; Dilcher, 1974) and elucidation of the phylogenetic significance of leaf morphology (Hickey & Wolfe, 1975), along with the U.S. National Cleared Leaf Collection and the U.S. Geological Survey Cleared Leaf Collection, have provided the framework for the present study.

The rich Cretaceous leaf fossil deposits of the western interior of North America have long been recognized for their importance to angiosperm paleobotany. Early treatments of these floras (during the late 1800s and early 1900s) mistakenly placed many leaf species into Recent genera. Even investigators who realized their predicament (see Lesquereux quote above) were ham-

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pered in their attempts to interpret these leaves by the absence of appropriate operational paradigms. Throughout this report, genera of doubtful occurrence in the Cretaceous are marked with quotation marks. Where possible I have provided reappraisals of the affinities of these leaves in my discussions of Cretaceous leaf morphotypes and individual floras.

I cover the period of about 30 million years from the apparent advent of angiosperms during the Middle Albian to the middle of the Campanian. This includes the latter part of stage one of angiosperm evolution (Vakhrameyev, 1982), during which the group became established in restricted areas of a predominantly gymnosperm-dominated vegetation; and it includes most of stage two, in which angiosperms radiated explosively and displaced gymnosperms from many parts of the world.

The floras reported here come from British Columbia, Washington, Alberta, Montana, Wyoming, and Idaho (Figs. 1, 2).

Coniferous communities were the dominant form of vegetation in the world, at least through the Early Cretaceous (Hughes, 1969, 1976; Krassilov, 1981; Miller, 1977; Penny, 1969). Lower Cretaceous conifers from the NRM region are regarded as belonging to the Taxodiaceae, Araucariaceae, Podocarpaceae, Pinaceae, and Cheirolepidiaceae (Bell, 1956; Miller & LaPasha, 1984; Singh, 1964, 1971). With the exception of the Cheirolepidiaceae, which declined during the Albian, and the addition of the Cupressaceae which appear to have diversified during the middle and Late Cretaceous, these groups form the nucleus for the development in the Late Cretaceous of the North Pacific refugium (Vakhrameyev, 1982). Compressions and impressions of foliage and cones of Taxodiaceae, Cupressaceae, and Araucariaceae occur abundantly in coarser sediments throughout the region in the Upper Cretaceous (Berry, 1929a; Knowlton, 1905).

Ginkgophytes decrease in the region during the Albian, the latest flora in which they form an important component being the Lower Blairmore (Dawson, 1886; Bell, 1956), although foliage is reported from the Cenomanian Dunvegan Formation in northern Alberta (Bell, 1963), and *Salisburia* (cf. *Ginkgo*) seeds are reported as late as the Campanian Belly River flora (Dawson, 1886). The Ginkgophyte decline is delayed in the extreme northern latitudes. Although northslope Alaskan floras exhibit a notable decline in the Late Albian (Scott & Smiley, 1979), the group remains important at least into the early Senonian in the Atane beds of Greenland (Seward & Conway, 1935), and into the Campanian in the Chignik Formation of central Alaska (Hollick & Martin, 1930). *Ginkgo* persists into the Paleogene in the Ft. Union Formation of Montana and the Willwood Formation of Wyoming (pers. obs.).

Fern communities of the Recent families Gleicheniaceae, Schizaeaceae, Dicksoniaceae, and Osmundaceae, and the extinct family Tempskyaceae occur abundantly in certain facies, a characteristic feature of the middle Cretaceous that Krassilov (1981) interpreted as evidence for extensive fern marshes. Pteridophytic communities colonized the widespread upper Albian and Cenomanian volcanic ash flats, occasionally being preserved in situ as in the Albino Member of the Mowry Shale in southwestern Montana (Crabtree, 1983; Vuke, 1982). Ferns such as *Gleichenia, Anemia, Sphenopteris, Cladophlebis, Tempskya, Coniopteris,* and *Onychiopsis* (but see Skog, 1985) are found throughout the region in the Albian and Cenomanian (Andrews, 1948; Andrews & Kern, 1947; Andrews & Pearsall, 1941; Ash & Read, 1976; Bell, 1956; Knowlton, 1917; Read & Brown, 1937; Seward, 1924). Post-Cenomanian floras show a decreasing representation of these genera, concomitant with increasing Polypodiaceae s.l. (pers. obs.).

Cycadophytes such as *Nilssonia, Zamites, Pseudoctenis, Ctenis,* and *Otozamites* decline rapidly after the Aptian. However, certain species persist in the Cenomanian Dunvegan flora (Bell, 1963) and the Turonian upper Frontier flora (Berry, 1929d), and *Zamites albertensis* Berry is abundant in the Campanian Allison flora of Alberta (Berry, 1929a). Cycadophytes also persist in the Late Cretaceous of Alaska (J. Wolfe, pers. comm.).

Sagenopteris, foliage of pteridosperms of the Caytoniales, is abundant during the Aptian and early Albian in the region (Bell, 1956; LaPasha & Miller, 1985) but is only rarely reported from the later Albian or from the Upper Cretaceous (see Winthrop flora in this report).

The relative abundance of major plant groups, and the entry of angiosperms into the region during the Middle and Upper Albian, can be seen in the histograms depicting the changing composition of the flora during the Middle and Upper Albian (Fig. 3). One histogram (Fig. 3A) is based on published megafossil floras and my own observations of unpublished floras. The other

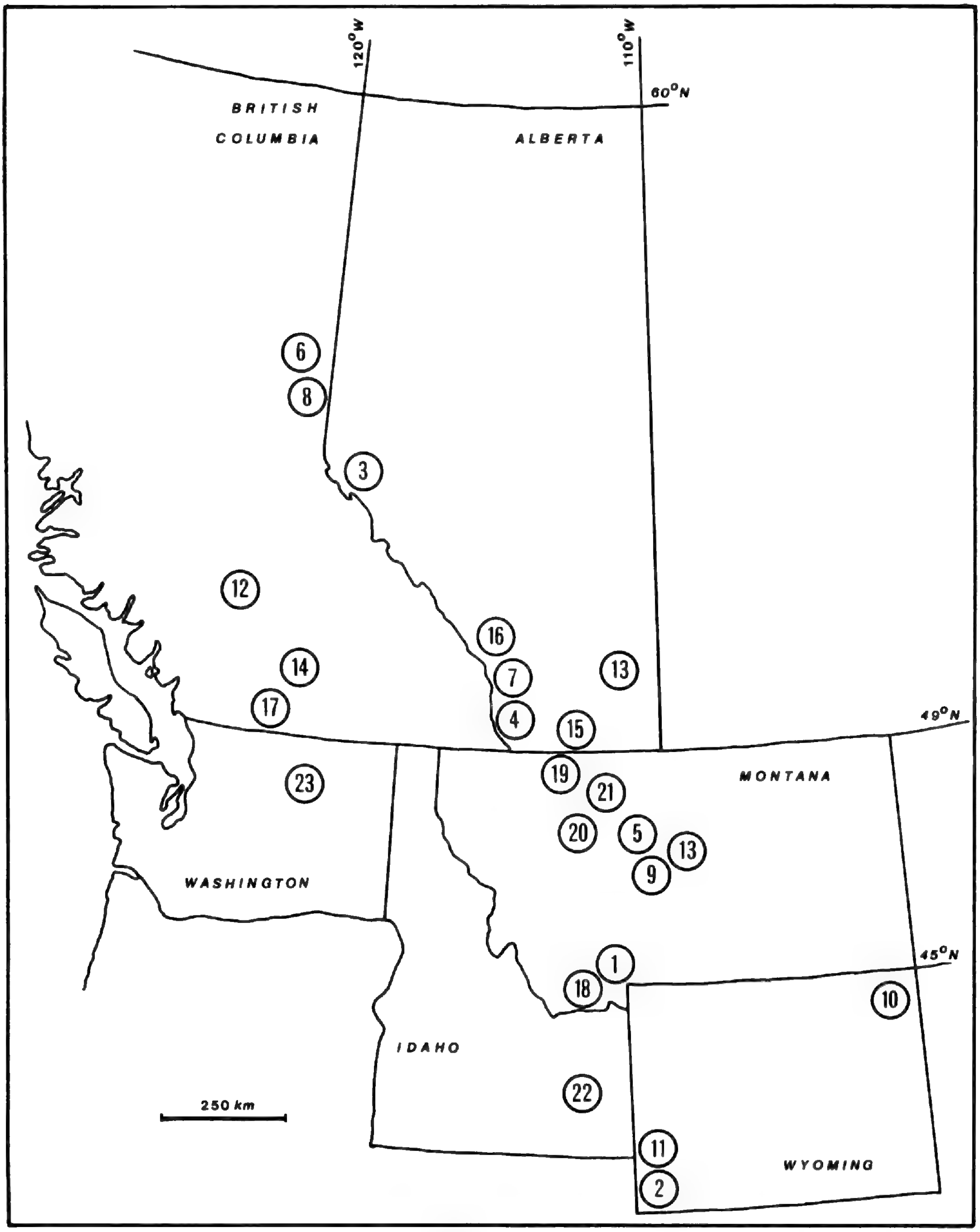

FIGURE 1. Geographic locations of plant megafossil collections in the northern Rocky Mountain region. Collection sites are numbered in alphabetical sequence. Names of sites appear in Figure 2. Appendix I contains additional information on locations.

(Fig. 3B) is based on published palynofloras. Percentages shown in the histograms were calculated by counting species of each major plant group within individual floras. These raw count totals were summed and a percentage calculated for each chronostratigraphic subdivision of the Albian. Megafossil floras show a bias towards preservation of vegetation adjacent to the deposi-

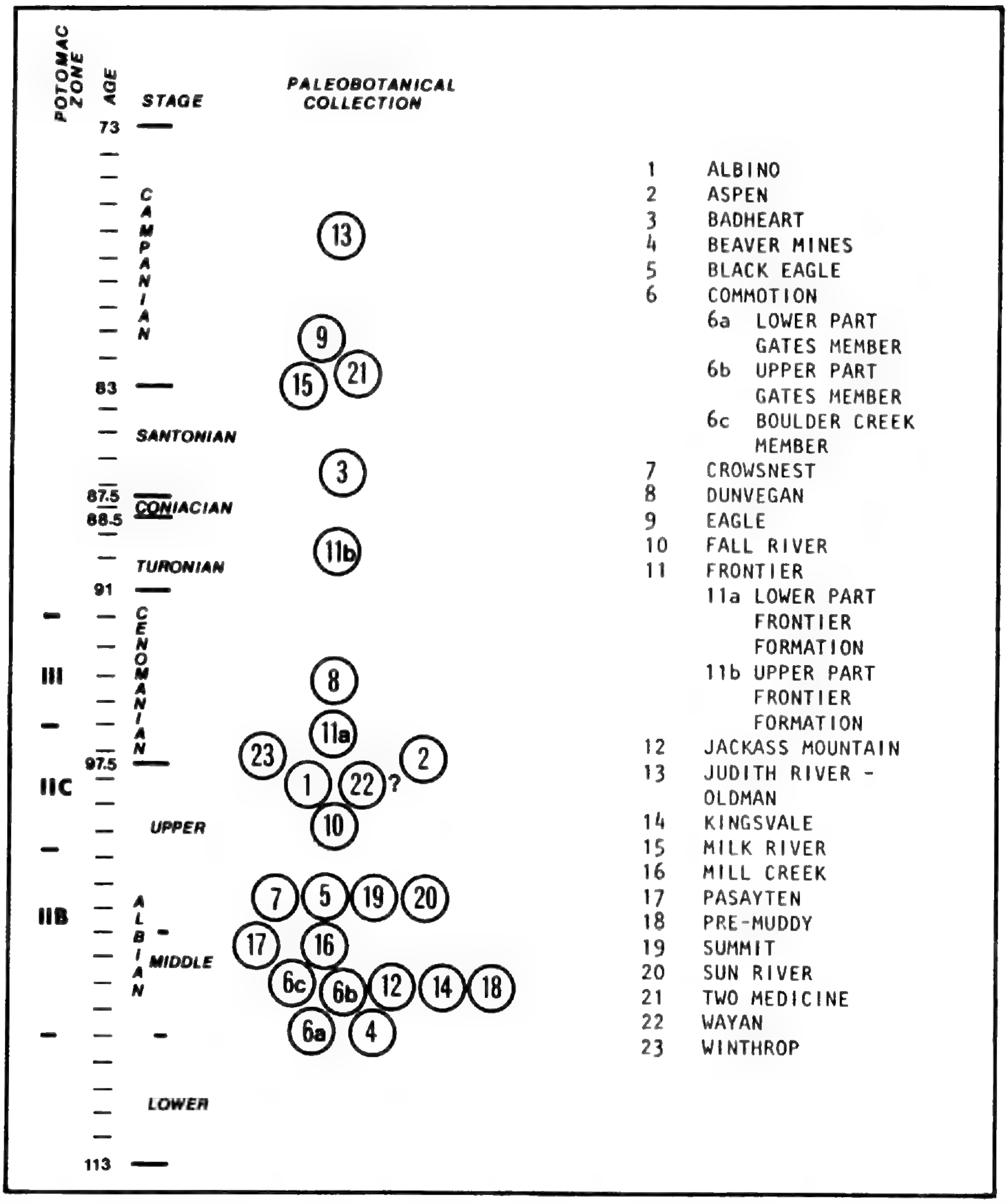

Figure 2. Chronostratigraphic positions of plant megafossil collections in the northern Rocky Mountain region. Stage boundary dates according to Harland et al. (1982). Ages are in million years. Potomac Zones from Hickey & Doyle (1977). Stratigraphic placement of collections is based on my interpretation of the literature. Substage boundaries are based on my interpretation of western North American chronostratigraphy. Collections of uncertain age are indicated with question marks (see text and Appendix I for discussion).

tional environment; thus Figure 3A approximates the components of the lowland vegetation. Palynofloras used in Figure 3B were recovered mostly from marine and marginal marine environments, and thus more closely reflect the regional flora. From Figure 3A it is apparent that dramatic changes occurred in the lowland flora during the Middle and Upper Albian. In these environments angiosperms increased at the expense of ferns. Because this trend is not evident in Figure 3B, it is apparent that this early angiosperm radiation had its greatest impact on lowland vegetation.

Paleogeographic and Geologic Setting

The northern Rocky Mountain region during most of the Cretaceous occupied a strip of land some several hundred kilometers wide, situated between the Pacific geosyncline/island arc to the west and the mid-continent epeiric sea to the east (McGookey et al., 1972; Williams & Stelck, 1975). Paleolatitudes may have varied up to ten degrees from the present range of 41°N in southern Wyoming to 60°N in northern Alberta and British Colombia. The paleocontinent positions of Smith et al. (1981) indicate that northern Alberta has rotated 8–10° to the south since the Cretaceous, and southern parts of the region are presently approximately 2–5° farther south.

The first major expansion of the Cretaceous epeiric sea began in the Late Aptian and continued into the Albian, attaining its maximum extent in the late Middle Albian when it reached unbroken from the Arctic Ocean to the Gulf of Mexico (McGookey et al., 1972; Vuke, 1984; Williams & Stelck, 1975). The fluctuations of the sea initiated a famous series of transgressive–regressive clastic cycles of deposition that continued until the end of the Cretaceous (Waage, 1975). Geological formations in the region tend to parallel the north–south trending western shoreline of the seaway. Cretaceous sediments accumulated in terrestrial and marine environments to great thicknesses: up to 3,500 m in southwest Wyoming (Rubey et al., 1975) and 2,134 m in northwest Montana (Rice & Cobban, 1977). The source areas in present British Columbia, western Alberta, Idaho, Washington, Oregon, western Montana, and western Wyoming are inferred to have had considerable relief in order to account for the great thickness of accumulated sediments. Orogenic activity in the region was of long duration beginning in the Late Jurassic and Early Cretaceous with the uplift of the Nevadan Orogeny. The main thrusting of the Sevier Orogeny occurred throughout the Cretaceous, and the uplift of the Laramide Orogeny took place during and subsequent to the Campanian (Gilluly, 1963; Nichols et al., 1985).

PALEOCLIMATE

Generalized interpretations of paleoclimate, which include the North American Cretaceous, have been published by Frakes (1979), Habicht (1979), Lamb (1977), Schwarzbach (1974), and Vakhrameyev (1978). They recognized a general humidification in Laurasian climate from the Jurassic into the Cretaceous. This can be correlated with the widespread inundation of continental crust, a worldwide phenomenon in the Cretaceous, and the opening of the Atlantic Ocean.

Assessment of precipitation patterns and amounts during the Cretaceous in the NRM region is difficult with our present knowledge. Parrish et al. (1982) mapped the Cretaceous precipitation in the region as low to moderately low largely on account of the presumed orographic effect of the Rocky Mountains. However, they noted that the presence of important high latitude coals in the region, especially in the Late Cretaceous, may argue for heavy seasonal precipitation, perhaps a monsoonal effect.

Growth rings in fossil wood can be used to assess environmental influences on plant development (Creber, 1977; Creber & Chaloner, 1984, 1985; Fritts, 1976). Presence and degree of development of latewood and growth rings is generally correlated with available moisture. However, there are many examples of growth rings in trees living in regions of high rainfall. For instance, *Agathis* from Fiji, where annual rainfall is 2,000–6,000 mm, have well-developed growth rings (Ash, 1985). Nonetheless, I know of no exception to the formation of growth rings in the wood of trees growing in seasonal climates, and conversely, the absence of growth rings always indicates a nonseasonal climate (except perhaps in certain warm-climate swamp communities).

I examined 27 specimens of six species of coniferous woods from the Late Albian Vaughn Member of the Blackleaf Formation in northwest Montana in thin section for the presence and configuration of growth rings. Transverse sections could be grouped into three broad categories:

Category A.	Woods exhibiting no growth rings.
Category B.	Woods exhibiting broad (3–5 mm) and consistent growth rings with considerable latewood.
Category C.	Woods exhibiting rings of variable width, including broad rings (up to 5 mm), pseudorings, and considerable latewood.

The Vaughn Member has been interpreted as a deltaic swamp deposit (Cannon, 1966) and was situated at about 55°N paleolatitude (Couillard & Irving, 1975). Cold-seasonality did not exist during the Albian at this paleolatitude. Seasonality as the result of low light during winter months may be a factor at 50°N, although I know of no literature on the subject. Broad-leaved evergreen forests are known to have extended to 65°N during the Cretaceous (Wolfe & Upchurch, 1986). Incomplete seasonal leaf-drop, formation of latewood, and cambial quiescence might well be associated with the northern extensions of this forest. Among several possible explanations for the mixed assemblage of woods, the following is suggested as the most plausible: the trees were growing in a warm, seasonally dry climate, with some species (Category A) living in areas of year-round groundwater. The pronounced develop-

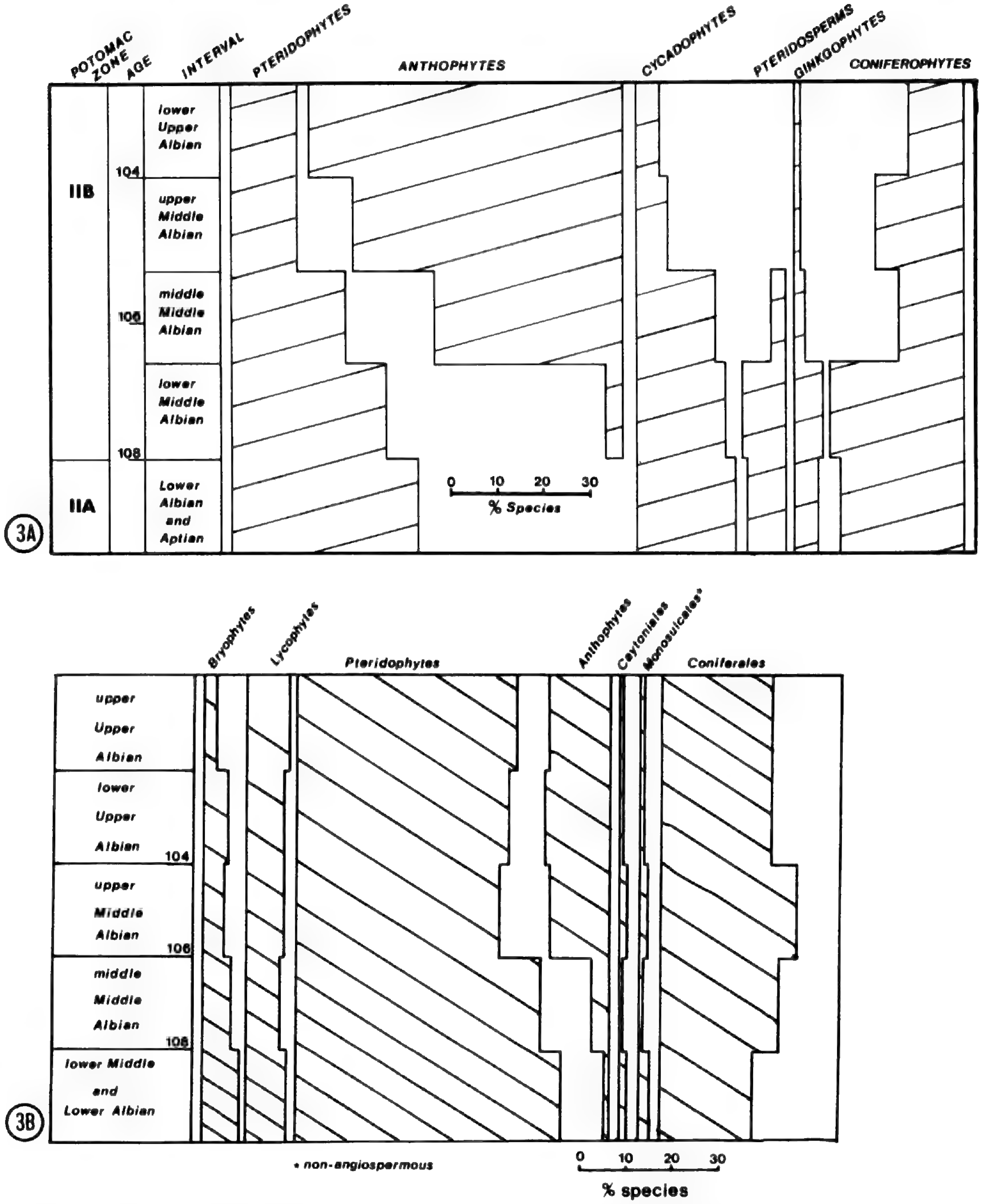

FIGURE 3. Relative abundance of major plant groups during the Albian of the northern Rocky Mountain region. Ages are in million years before present. A. Percentage occurrence of major plant groups based on megafossils. Occurrences of species for each plant group were tabulated for individual floras. These counts were then summed and a percentage calculated for each time interval as listed below. Total species counted for each interval are indicated in parentheses. Aptian and Lower Albian (119): Kootenai (Miller & LaPasha, 1984; LaPasha & Miller, 1985); Bullhead, Gething, and Luscar (Bell, 1956). Lower Middle Albian (150): Beaver Mines (Berry, 1929b; Bell, 1956; Mellon, 1967); Lower Gates Member (Stott, 1963). Middle Middle Albian (130): Upper Gates Member (Mellon et al., 1963); Pasayten (Penhallow, 1907; Bell, 1956); Kingsvale and Jackass Mountain (Bell, 1956); Fall River and Pre-Muddy (pers. obs.); Boulder Creek (Bell, 1956; Stott, 1963). Upper Middle Albian (150): Mill Creek (Dawson, 1886; Berry, 1929c; Bell, 1956; Mellon, 1967). Lower Upper Albian (89): Crowsnest (Bell, 1956; Mellon, 1967); Summit, Sun River, and Black Eagle (pers. obs.). B. Percentage occurrence of major plant groups based on microfossils. Percentages calculated as above. Assignment of spores

ment of latewood in Categories B and C suggests seasonality in precipitation. An alternative explanation is that low light availability in winter induced latewood formation in some species but not others.

Late Albian or Cenomanian woods of *Cupressinoxylon* sp. (Andrews & Kern, 1947) and *Paraphyllanthroxylon idahoense* Spackman (1948) from the Wayan Formation in southeastern Idaho have no prominent growth rings and can be seen as evidence for equable year-round temperatures. These woods suggest either the absence of seasonality in precipitation or that the trees grew in swampy or other well-watered habitats.

Later in the Cretaceous there is further evidence for seasonal or low precipitation in the region, possibly related to the mountain building of the Laramide Orogeny. The Campanian Two Medicine Formation in northwestern Montana includes caliches, desiccated carbonate nodules, and sandstone bodies of episodic rivers that indicate a seasonal wet–dry climate, with the dry season longer (Lorenz, 1981). The abundance of large (mesophyll and megaphyll size), apparently deciduous leaves in the Two Medicine flora supports such a climatic seasonality, although the leaves can be interpreted alternatively as indicative of successional communities. Low or seasonal precipitation is further indicated by a substantial notophyllous evergreen component of coriaceous leaves typically without drip tips. Coniferous woods from the lower Two Medicine exhibit pronounced growth rings of highly variable thickness (Crabtree, pers. obs).

Oxygen isotope ratios are used most accurately to estimate maximum paleotemperature and to establish temperature trends of ocean waters (Frakes, 1979). Oceanic temperatures can be used to estimate temperatures on nearby land masses. Since the NRM region during much of the Cretaceous was a relatively narrow land mass positioned between the Pacific Ocean on the west and the epeiric seaway on the east, it is likely that oceanic temperatures are significant for approximation of the land temperatures.

Isotopic ratios from the continental platform off the Soviet Union (Douglas & Savin, 1975) indicate a Cretaceous temperature maximum in the Albian, followed by cooling in the Late Albian and Cenomanian. Subsequently, a rewarming occurred in the early Senonian before a Maastrichtian cooling (but see also Boersma, 1984). The Albian maximum is probably the warmest period that the world has experienced since Paleozoic time (Frakes, 1979). Latitudinal gradients in surface water temperatures were less steep during the Cretaceous, and the average temperatures of deep water appear to have been significantly higher than at present (Schopf, 1980). Mid and Late Jurassic oxygen isotope ratios from Montana and Wyoming indicate that the surface water had a maximum of 20°C (Donn & Shaw, 1977). Polar ice was unknown during the Cretaceous, and Frakes (1979) hypothesized that north polar surface water was no cooler than 7–19°C and may have been at the high end of this range based on isotopic paleotemperatures of about 15°C for putative North Pacific Deep Water from the equatorial Pacific (Stevens, 1971). A computerized model of surface water temperatures for an ice-free Arctic predicts a temperature increase of 7–10°C over the present 0–5°C temperature range (Sellers, 1969).

Hermatypic coral reefs occur in tropical and subtropical oceans. Because modern reefs form only when minimum water temperatures exceed 18°C, their fossil distribution can be used to estimate minimum oceanic paleotemperatures. The Mesozoic distributions of reefs (Newell, 1971; Beauvais, 1973) indicate that oceanic currents in temperate latitudes were significantly warmer than at present. A reef from the Jurassic of Wyoming (Beauvais, 1973) indicates that they formed as far north as 50°N paleolatitude, but there is doubt that the Wyoming reef is hermatypic (G. Stanley, pers. comm.). Nonetheless, bona fide hermatypic reefs are present during the Jurassic and Cretaceous at latitudes 10–20° north of their present distribution.

Several papers discuss paleofloristic climatic zonation during the Cretaceous based on the composition of eastern Asian megafloras (Krassilov, 1973a, 1975, 1978) and microfloras

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and pollen to major plant groups follows the interpretations of Singh (1971) and Norris (1967). Numbers in parentheses after age below indicate total number of species counted for that interval. Lower Albian and lower Middle Albian (179): McMurray-Clearwater (Vagvolgyi & Hills, 1969); Loon River (Singh, 1971). Middle Middle Albian (206): Harmon (Singh, 1971); Upper Grand Rapids (Norris, 1967). Upper Middle Albian (200): Cadotte (Singh, 1971); Joli Fou (Norris, 1967). Lower Upper Albian (184): Paddy (Singh, 1971); Viking (Norris, 1967). Upper Upper Albian (213): Shaftsbury (Singh, 1971); Upper shale (Norris, 1967).

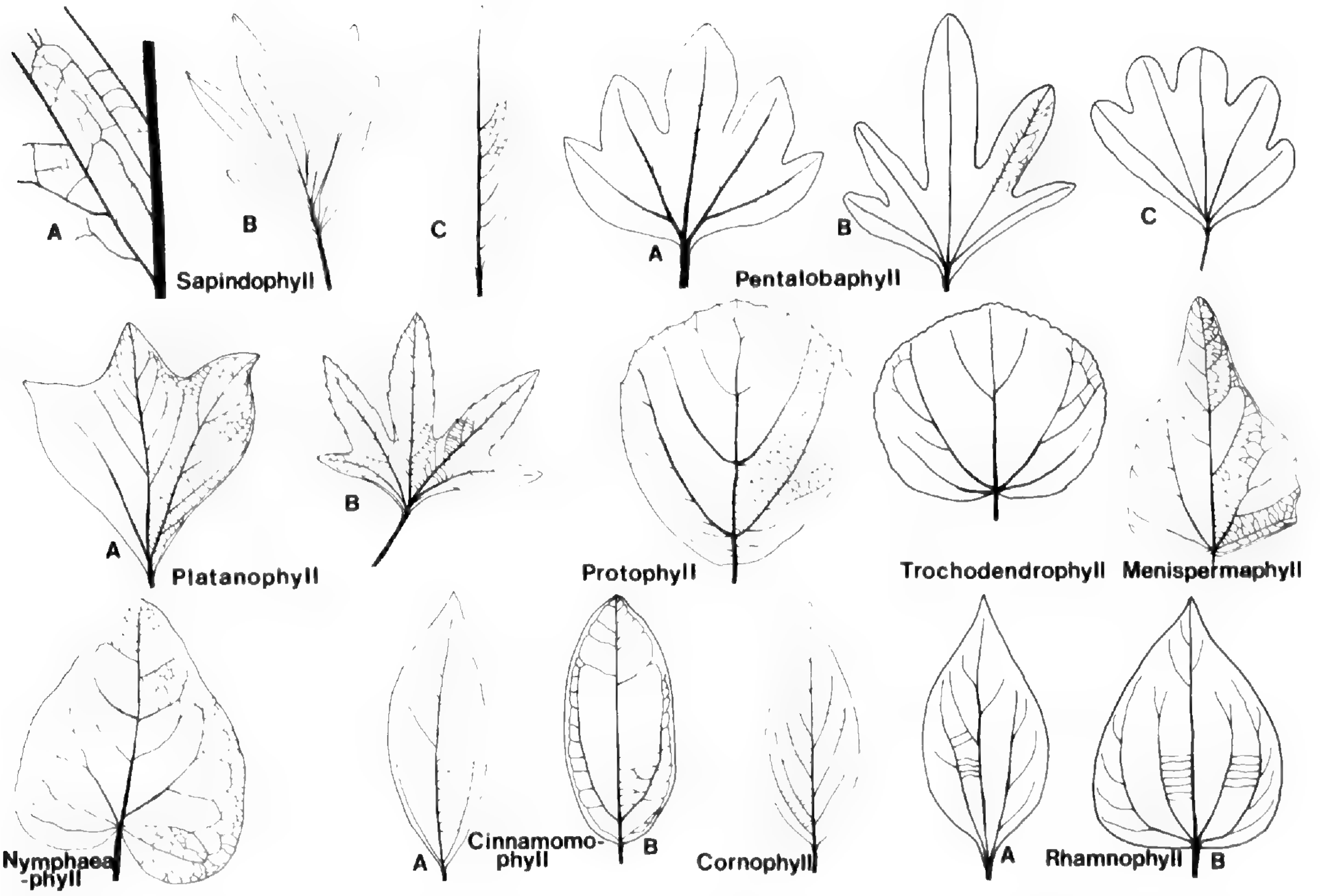

FIGURE 4. Cretaceous dicotyledonous leaf morphotypes. Sources of previously published drawings are indicated. SAPINDOPHYLL:—A. cf. "*Ficus*" *beckwithii* Lesquereux (Crabtree), Dakota Formation, Golden, Colorado (Peabody Museum Paleobotanical Collection no. 5849).—B. *Sapindopsis magnifolia* Fontaine, Patapsco Formation, Virginia (fig. 17 in Doyle & Hickey, 1976).—C. Generalized leaflet. PENTALOBAPHYLL:—A. *Araliaephyllum obtusilobum* Fontaine, Patapsco Formation, Virginia (pl. 164, fig. 3 in Fontaine, 1889).—B. *Araliaephyllum westonii* (Dawson) Bell.—C. *Araliaephyllum rotundata* Dawson. PLATANOPHYLL:—A. *Araliopsoides breviloba* Berry, Raritan Formation, Maryland (pl. 86, fig. 2 in Berry, 1916).—B. "*Aralia*" *saportanea* Lesquereux, Dakota Formation, Kansas (pl. 9, fig. 2 in Lesquereux, 1883). PROTOPHYLL: Generalized leaf. TROCHODENDROPHYLL: Generalized leaf. MENISPERMAPHYLL: *Menispermites obtusilobus* Lesquereux, Dakota Formation, Kansas (pl. 15, fig. 4 in Lesquereux, 1883). NYMPHAEAPHYLL: "*Cocculus*" *haydenianus* Ward, Fort Union Formation, Montana (pl. 59, fig. 2 in Ward, 1885). CINNAMOMOPHYLL:—A. "*Cinnamomum*" *sezannense* Watelet, Dakota Formation, Kansas (pl. 12, figs. 6, 7 in Lesquereux, 1892).—B. Generalized leaf. CORNOPHYLL: "*Cornus*" *forchhammeri* Heer, Raritan Formation, Maryland (pl. 82, fig. 1 in Berry, 1916). RHAMNOPHYLL:—A. "*Cinnamomum*" *intermedium* Newberry (pl. 29, fig. 7 in Hollick, 1906).—B. Generalized leaf.

(Chlonova, 1980). Krassilov's papers propose four intuitively based, latitudinal climatic zones: boreal, temperate, warm-temperate, and subtropical. Relative to these zones, the NRM region is closest to the warm-temperate zone based primarily on the presence in the Albian and Cenomanian of several thermophilous ferns and temperate *Nilssonia*, and in the Campanian by the presence of palms and large-leaved deciduous dicots. A position in the warm-temperate zone is consistent with Campanian floras in Sakhalin, Amur, Altai, western Greenland, and Vancouver Island (Krassilov, 1981). Vakhrameyev (1978) placed the NRM region straddling the boundary between his temperate-warm and subtropical humid zones for the Early Cretaceous. This placement is based on the presence of *Tempskya* and *Cycadeoidea* in Montana and South Dakota. The boundary shifts approximately 100 km to the north in his Late Cretaceous reconstruction, placing it just north of the present 49th parallel (about 55°N paleolatitude). The Late Cretaceous temperate-warm humid zone is based on the occurrence of *Nilssonia* and *Pseudoprotophyllum*, and the subtropical humid zone is based on palms and *Dewalquea*.

Smiley (1967), basing his arguments primarily on North American high-latitude floras, indicated that the climate gradually warmed from the Jurassic into the Albian, after which a general cooling occurred through the Late Cretaceous (at the same time as Alaska was rotating to the south).

Scott & Smiley (1979) reported on the micro- and megafossil flora from the north slope of Alaska. Their treatment indicates that northern floras remain predominantly gymnospermous-pteridophytic until the end of the Late Albian, that they do not exhibit *Classopollis* pollen in any significant quantity (but see Herngreen & Chlonova, 1981), and that they are allied to more southerly Albian floras by abundant spores of Gleicheniaceae and Schizaeaceae. Vakhrameyev (1982) recognized the Early Cretaceous as a time of increasing aridity followed by "humidification and some cooling" by the Albian. Cooling was not extreme, however, as the presence of frost-sensitive ferns throughout the Lower Cretaceous at high latitudes indicates, and did not continue, since palms in the Senonian indicate a generally equable year-round temperature. Krassilov (1973a, 1975, 1981) stated that Late Cretaceous climates in Asia warm into the Campanian and subsequently cool through the end of the Cretaceous.

THE EARLY ANGIOSPERM FLORA

Hickey & Wolfe's (1975) synthesis of the systematic implications of leaf morphology among extant dicots enables paleobotanists to assess the relationship of fossil taxa by extrapolation. Krassilov (1977) and Hickey (1984) used a series of informal descriptive names for early angiosperm leaf fossils that attempt to unify fossil species with similar morphology. Such leaf morphotypes are especially appropriate for Early Cretaceous dicot leaves that have been placed mistakenly in extant genera. Morphotypes are best viewed as serving as a descriptive terminology in lieu of revision.

Most important morphotypes from western North American mid-Cretaceous floras are illustrated in Figure 4 (see also Hickey, 1984). The drawings are based in some cases on individual taxa and in others on an idealized composite of several different taxa (see figure legend). In all cases the drawings represent the general form or range of forms present in the morphotype. Table 1 lists the morphotypes along with the genera that have been used in the past for species belonging to each. Extant genera, such as *Populus,* which has been mistakenly regarded as embracing a large number of disparate fossil taxa, may be listed under more than one morphotype. Extant genera cannot be demonstrated from the mid Cretaceous, with rare exceptions (Doyle, 1969; Walker & Walker, 1984). Extinct genera for which the type species is of Cretaceous age are included under the appropriate morphotype according to the type description. Fossil genera for which the type is younger than Late Cretaceous have not been considered for inclusion, reflecting the intended focus on early angiosperms. Thus, *Laurophyllum* Saporta is named from Tertiary material; hence, I consider it inappropriate as a generic placement for Early Cretaceous angiosperms. Morphotypes, since they are not formal taxonomic classifications, have no types.

I have chosen to discuss the early angiosperm flora of the NRM region using the leaf morphotypes as a descriptive base. For each morphotype I provide a brief description using the leaf architectural terminology of Hickey (1979). In addition, I provide particulars relevant to the distribution in time and space for each morphotype along with observations on relative abundance and diversity. Possible relationships for each morphotype are discussed individually and summarized in Table 1.

The occurrence and distribution of early angiosperms in the NRM region is presented in Table 2, which encompasses the first five million years of angiosperm history in the region. Where possible, species are grouped according to morphotype. All Albian and major floras from the region are included, in addition to several previously unreported collections. Names of taxa appear as originally published except for floras examined by myself, for which I have provided identifications. Ages and locations of floras appear in Figures 1 and 2 and in Appendix I.

Pentalobaphyll (Araliaephyll). Leaves simple, orbicular, 3–5-lobed. Margin entire. Base ± cuneate. Primary venation palinactinodromous, with 3 primary veins diverging from above top of petiole, and 2 subprimary veins branching from lateral primaries just above base. Secondary venation eucamptodromous, rather weakly developed. Tertiary venation reticulate to transverse, AR to AO. Higher order venation and cuticle not observed.

This very distinctive group is first recognized in the region during the Middle Albian. Pentalobaphylls are lobate leaves with five principal veins, the two outermost of which originate as suprabasal branches from the lateral primary veins (Fig. 4). *Araliaephyllum obtusilobum* Fontaine is included in this group on the basis of the

TABLE 1. Botanical affinity and important genera for Cretaceous leaf morphotypes.

Morphotypes	Important genera[1,2]	Botanical affinity
Sapindophyll	*Fontainea* Newberry, *Sapindopsis* Fontaine, "*Andromeda*," "*Diospyros*," "*Ficus*," "*Laurus*," "*Rhus*," "*Salix*," "*Sapindus*," "*Staphylea*"	Rosidae
Pentalobaphyll	*Araliaephyllum* Fontaine, *Sterculites* Dawson, "*Aralia*," "*Hedera*," "*Liquidambar*," "*Sassafras*," "*Sterculia*"	Unknown; possibly Rosidae or Magnoliidae (Laurales)
Platanophyll	"*Araliopsis*," *Araliopsoides* Berry, *Aspidophyllum* Lesquereux, *Platanophyllum* Fontaine, *Pseudoaspidophyllum* Hollick, "*Aralia*," "*Platanus*," "*Sassafras*"	Hamamelididae–Platanales
Protophyll	*Cissites* Debey, *Credneria* Zenker, *Paracredneria* Richter, *Protophyllum* Lesquereux, *Pseudoprotophyllum* Hollick, *Viburnites* Lesquereux, "*Alnus*," "*Betula*," "*Cissus*," "*Parrotia*," "*Platanus*," "*Populus*," "*Tilia*"	Polyphyletic within Hamamelididae—probably Platanales and Hamamelidales
Trochodendrophyll	*Trochodendroides* Berry, "*Cercidiphyllum*," "*Cocculus*," "*Grewia*," "*Paliurus*," "*Populus*," "*Smilax*," "*Zizyphus*"	Trochodendrales and Crecidiphyllales
Menispermaphyll	*Menispermites* Lesquereux, "*Ampelopsis*," "*Cissampelopsis*," "*Cocculus*," "*Hedera*"	Unknown; possibly Ranunculiidae
Nymphaeaphyll	*Castaliites* Hollick, *Hederaephyllum* Fontaine, *Nelumbites* Berry, *Paleonuphar* Hollick, *Populophyllum* Fontaine, *Proteaephyllum* Fontaine, "*Castalia*," "*Hedera*"	Magnoliid–Nymphaeales
Magnoliaephyll	*Liriodendropsis* Newberry, *Liriophyllum* Lesquereux, *Magnoliaephyllum* (Krasser) Seward, "*Bauhinia*," "*Ficus*," "*Laurus*," "*Liriodendron*," "*Magnolia*," "*Persea*," "*Sassafras*"	Polyphyletic; some Magnoliidae, possibly Laurales, Magnoliales.
Cinnamomophyll	*Cinnamomoides* Seward, "*Benzoin*," "*Cinnamomum*," "*Cocculus*," "*Litsea*," "*Oreodaphne*," "*Paliurus*," "*Zizyphus*"	Polyphyletic; some probably Laurales
Cornophyll	*Cornophyllum* Newberry, "*Andromeda*," "*Cornus*," "*Diospyros*," "*Ficus*" "*Rhamnus*"	Polyphyletic; some possibly Rosidae
Rhamnophyll	*Macclintockia* Heer, "*Cinnamomum*," "*Ficus*," "*Paliurus*," "*Piper*," "*Rhamnus*," "*Smilax*," "*Zizyphus*"	Polyphyletic; some possibly palmate Dilleniidae

[1] See text for criteria used for inclusion of genera.
[2] Quotation marks indicate extant genera mistakenly identified in the Cretaceous flora.

characteristic venation, although this and several other species may have three-lobed leaves. Doyle & Hickey (1976) include this species in their Platanoid line, based primarily on the palinactinodromous primary venation. The palmate lobing and palinactinodromous venation of the Pentalobaphylls is here considered to be insufficient evidence to establish relationship with the Platanoid line when viewed along with the balance of leaf-morphological characters. Pentalobaphylls show leaf-morphological characters, including entire margins, eucamptodromous secondary venation, and weak tertiary venation, which serve to distinguish the group from Platanophylls.The tendency towards orthogonal branching of tertiary and quaternary veins so characteristic of Platanophylls is absent in Pentalobaphylls.

Certain palmate leaves from the Albian flora cannot be accommodated under either the Pentalobaphyll or Platanophyll morphotype. These include "*Liquidambar*" *fontanella* Brown, with glandular-toothed margins, and "*Sassafras*" *bradleyi* Brown, which has smooth margins but lacks the suprabasal lateral branches characteristic of Pentalobaphylls.

Fritel (1914) recognized seven species of Pentalobaphylls that were widespread throughout the Laurasian landmass during the Late Albian and Cenomanian. He characterized the group based primarily on the three basal primary veins, the lateral two of which give off prominent lateral veins just above the point of radius, and on the camptodromous secondary venation. However, he included forms exhibiting serrate margins, craspedodromy, and orthogonal reticulate higher order venation such as "*Aralia*" *saportanea* Lesquereux, which I assign to the Platanophylls.

Pentalobaphylls are perhaps the most abundant dicots from Albian floras of the NRM region. Albian Pentalobaphylls from Wyoming (Fig. 5), Montana (Fig. 6), and Alberta (Figs. 7–9) are representative of the group. Fritel (1914) placed the Alberta species *Araliaephyllum westonii* (Dawson) Bell and "*Aralia*" *rotundata* Dawson into synonymy with *Araliaephyllum kowalewskiana* (Saporta & Marion) Fritel from Europe. A more thorough treatment of the group is needed before such conclusions are substantiated. Cuticular detail for the group is unknown with the exception of the Senonian *Araliaephyllum polevoi* (Krystofovich) Krassilov (1973b) from the eastern Soviet Union, for which a similarity to *Sassafras* and *Lindera* is suggested. G. Upchurch (pers. comm.) has suggested a lauralean affinity for leaves of the *A. polevoi* group based on cuticular detail, sinus bracing, mesophyll secretory glands, and possible basilaminar secondary veins. The secondary and tertiary venation (Figs. 4, 8) in this group suggests rosid affinity.

Platanophyll. Leaves simple. Margins entire or serrate, lobed or unlobed. Primary veins usually 3, palinactinodromous with several pectinal secondaries on laterals. Secondary veins straight, forking or exmedially branched, craspedodromous to teeth, brochidodromous if margin entire. Tertiaries and quaternaries forming an orthogonal network. Teeth platanoid, glandular processes often nipple-shaped. Cuticular structure in Upchurch (1984b), Krassilov (1973b), Kvaček (1983), Bůžek et al. (1967), Němejc & Kvaček (1975).

Members of this widespread Laurasian morphotype date from the Middle Albian in North America. The earliest occurrence from the NRM region is "*Platanus*" sp. (Fig. 10) from the upper Middle Albian of Alberta (Bell, 1956). Platanophylls of Middle and Late Albian age occur in several floras from the NRM region (Table 2). A particularly rich assemblage of Platanophylls occurs in the Late Albian Blackleaf Formation in Montana (Figs. 11–14). Several poorly preserved specimens representing the group are reported from the Middle and Upper Albian of Alberta (Bell, 1956). As in the Albian flora of Alaska (Hollick & Martin, 1930) and eastern North America (Doyle & Hickey, 1976), the group is most frequently encountered in coarse fluvial sediments.

Araliopsoides cretacea (Lesquereux) Berry is an early member of this complex and is reported from the Late Albian in the Patapsco Formation in eastern North America (Hickey & Doyle, 1977). *Araliopsoides cretacea* is also reported from the Cenomanian of Texas (Berry, 1922b), Kansas (Lesquereux, 1874), and eastern North America (Berry, 1916; Hickey & Doyle, 1977). In the NRM region *A.* cf. *cretacea* is known from the Late Albian Summit locality in the Blackleaf Formation (Table 2, Fig. 14).

Platanophylls are typically more abundant in higher latitude floras (above approximately paleolatitude 45°N), and the group may appear in the NRM region before eastern North America. Little debate exists over the platanoid affinities of Platanophylls, but the precise timing of the origin of the Recent order and family remains unresolved. Recent *Platanus* is reported as being of Senonian age on the basis of pollen morphology (Pactlova, 1978), with pollen of platanaceous character recorded from the Albian (Pactlova, 1982). Němejc & Kvaček (1975) proposed on the basis of cuticular analysis that Cenomanian *Credneria* spp. (here considered Protophylls) from Bohemia are related to the platanaceous line. Early Platanophylls are related to, and convergent with, other groups of the emerging Hamamelididae, especially the Protophylls.

Fructifications regarded as of platanoid affinity are widespread in the Late Albian and Cenomanian of North America. Notable among these are records of "*Sparganium*" from Washington (Fig. 35) and Wyoming (Fig. 41; Brown, 1933a), and "*Platanus*" from Greenland (Seward & Conway, 1935) and Kansas (Lesquereux, 1892). For further discussion of Cretaceous fructifications of platanoid affinity see Dilcher (1979) and Crane et al. (1986).

Platanophylls are allied to Protophylls on the basis of well-defined, orthogonal-reticulate, tertiary and quaternary venation. Palinactinodromous venation and a greater tendency towards lobation distinguishes the Platanophylls from the Protophylls, which have pinnate organization (Fig. 4). I have chosen to segregate these leaves in the hope that the Cenomanian *Cissites-Betulites-Alnites* complex (Protophylls) might be

TABLE 2. Early angiosperm flora from the northern Rocky Mountain region.[1,2,3]

	Beaver Mines (4)			Lower Gates (6a)	Upper Gates (6b)	Fall River (10)	Pre-Muddy (18)	Boulder Creek (6c)		Pasayten (17)		Kingsvale (14)	Jackass (12)	Mill Creek (16)				Summit (19)	Sun River (20)	Black Eagle (5)	Crowsnest (7)	
	A	B	C					A	B	A	B			A	B	C	D				A	B
Sapindophyll																						
Celastrophyllum acutidens Fontaine											X	X				X	X					
Celastrophyllum sp.																	X					
cf. *Celastrophyllum* sp.																				X		
Daphnophyllum dakotense Lesquereux															X							
Fontainea grandifolia Newberry							X									X	X					X
Fontainea cf. *F. grandifolia* Newberry					X																	
Fontainea sp.																	X					
"*Laurus*" *crassinervis* Dawson														X								
"*Myrica*" *serrata* Penhallow										X												
Proteoides daphnogenoides Heer														X								
"*Quercus*" *flexuosa*? Newberry										X												
"*Salix*" *inaequalix*? Newberry													X				X					
cf. "*Rhus*" *powelliana* Lesquereux							X															
Sapindopsis angusta (Heer) Seward & Conway		X									X	X				X					X	
Sapindopsis cf. *angusta*																						X
Sapindopsis sp. aff. *angusta*			X																			
Sapindopsis belviderensis Berry				X											X	X						
Sapindopsis brevifolia? Fontaine	X																					
Sapindopsis cf. *brevifolia*																						X
Sapindopsis magnifolia Fontaine															X							
Sapindopsis cf. *magnifolia*					X																	X
Sapindopsis sp.			X																			
Sapindopsis sp.						X																
cf. *Sapindopsis* sp.																	X					
cf. *Sapindopsis* sp.																		X				
Pentalobaphyll																						
"*Aralia*" rotundata Dawson														X								
"*Aralia*" westonii Dawson														X								

TABLE 2. Continued.

	Beaver Mines (4)			Lower Gates (6a)	Upper Gates (6b)	Fall River (10)	Pre-Muddy (18)	Boulder Creek (6c)		Pasayten (17)		Kingsvale (14)	Jackass (12)	Mill Creek (16)				Summit (19)	Sun River (20)	Black Eagle (5)	Crowsnest (7)	
	A	B	C					A	B	A	B			A	B	C	D				A	B
Araliaephyllum westonii (Dawson) Bell												X				X	X	X		X		X
Araliaephyllum? sp.				X																		
Araliaephyllum sp.																	X					
"*Liquidambar*" *integrifolium* Lesquereux														X								
"*Sassafras*" *mudgii*? Lesquereux															X							
cf. "*Sterculia*" *mucronata* Lesquereux						X																
"*Sterculia*" *vetustula* Dawson														X								
"*Sterculia*" sp.																						X
Protophyll																						
Alnites insignis? Dawson														X								
Cissites? sp.					X																	
cf. *Cissites* sp.									X													
"*Platanus*" *affinis* Lesquereux														X								
"*Platanus*" *affinis* var. *ampla* Dawson														X								
Populites dawsonii Bell																X	X					X
Populites cf. *dawsonii*					X																	
Populites sp.																	X					
cf. *Protophyllum* sp.																		X				
Platanophyll																						
"*Aralia*" *wellingtoniana* Lesquereux					X																	
cf. "*Aralia*" *wellingtoniana*																		X				
Araliopsoides cf. *cretacea* (Newberry) Berry																		X				
cf. *Aspidophyllum trilobatum* Lesquereux																			X			
Platanophyllum sp.																			X			
Platanophyllum sp.						X																
"*Platanus*" *heeri* Lesquereux														X								
"*Platanus*" sp.									X													
"*Platanus*" sp.											X					X						
"*Platanus*" sp.																	X					X
"*Platanus*" n. sp.																	X					
"*Sassafras*" *cretaceum* Newberry										X												
Trochodendrophyll																						
"*Cercidiphyllum*" sp.									X													

Table 2. Continued.

	Beaver Mines (4)			Lower Gates (6a)	Upper Gates (6b)	Fall River (10)	Pre-Muddy (18)	Boulder Creek (6c)		Pasayten (17)		Kingsvale (14)	Jackass (12)	Mill Creek (16)				Summit (19)	Sun River (20)	Black Eagle (5)	Crowsnest (7)	
	A	B	C					A	B	A	B			A	B	C	D				A	B
Menispermites potomacensis Berry								X				X										
Trochodendroides ("*Cercidiphyllum*") *potomacensis* (Ward) Bell												X				X	X					X
Nymphaeaphyll																						
"*Hedera*" *ovalis*? Lesquereux														X								
Menispermites reniformis Dawson								X	X		X				X	X						
Menispermites sp.																X						
Nelumbites sp.												X										
Nymphaeites sp.																			X			
Magnoliaephyll																						
"*Magnolia*" *alternans* Heer															X							
"*Magnolia*" *magnifica* Dawson														X			X					
Cornophyll																						
"*Ficus*" *fontainii*? Berry								X														
Laurophyllum debile Dawson														X								
Rhamnites sp.													X									
"*Rhamnus*" sp.									X													
Cinnamomophyll																						
"*Cinnamomum*" *canadense* Dawson														X								
Cinnamomoides ovalis (Dawson) Bell												X				X	X				X	X
Cinnamomoides cf. *ovalis* (Dawson) Bell																						X
Cinnamomoides sp.																					X	
Cinnamomoides sp.																						X
Cinnamomoides sp.																			X			
Macclintockia cretacea Heer														X								
"*Paliurus*" *ovalis* Dawson														X	X							
Uncertain																						
Capparites? sp.											X											
Dicotylophyllum sp.																	X					
"*Ficus*" cf. *fontainii*																	X					
"*Ficus*" *ovatifolia* Berry					X										X	X						
cf. "*Ficus*" *ovatifolia* Berry																		X				

TABLE 2. Continued.

	Beaver Mines (4)			Lower Gates (6a)	Upper Gates (6b)	Fall River (10)	Pre-Muddy (18)	Boulder Creek (6c)		Pasayten (17)		Kingsvale (14)	Jackass (12)	Mill Creek (16)				Summit (19)	Sun River (20)	Black Eagle (5)	Crowsnest (7)	
	A	B	C					A	B	A	B			A	B	C	D				A	B
Juglandites cretacea Dawson														X								
"*Magnolia*"? sp.																X						
"*Magnolia*" sp.									X													
"*Magnolia*" sp.																	X					
"*Magnolia*" n. sp.																	X					
"*Magnolia*"? sp.																	X					
Menispermites? sp.																	X					
Myrtophyllum boreale Seward & Conway												X										
"*Populus*" cf. *berggrenii* Heer															X							
"*Populus*" *cyclophylla* Heer										X												
Quercophyllum? sp.																	X					
"*Quercus*" *coriacea* Newberry										X												
"*Salix*"? sp.																	X					
"*Salix*" sp.										X												
"*Sassafras*" *parvifolium* Fontaine					X																	

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[1] Numbers in parentheses refer to geographic and stratigraphic position of floras as indicated in Figures 1 and 2.

[2] All species are included as originally cited in the references given below. I have identified the species from the Summit, Sun River, Black Eagle, Fall River, and Pre-Muddy collections.

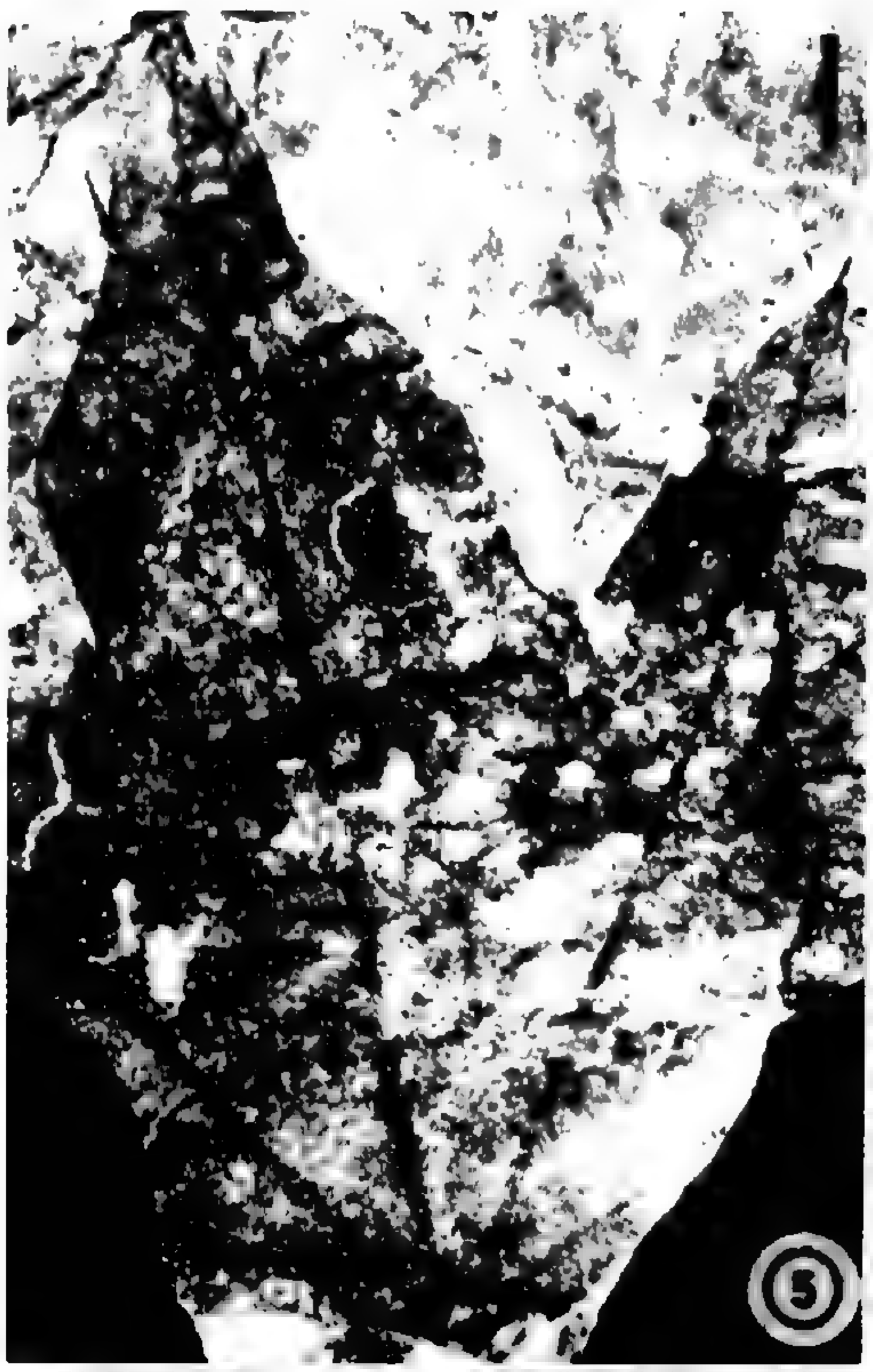
[3] Vertical rows indicate single floristic references as follows: (4)A—Berry, 1929b. (4)B—Bell, 1956. (4)C—Mellon, 1967. (6a)—Stott, 1963. (6b)—Mellon et al., 1963. (6c)A—Bell, 1956. (6c)B—Stott, 1963. (17)A—Penhallow, 1907. (17)B—Bell, 1956. (14)—Bell, 1956. (12)—Bell, 1956. (16)A—Dawson, 1886. (16)B—Berry, 1929c. (16)C—Bell, 1956. (16)D—Mellon, 1967. (7)A—Bell, 1956. (7)B—Mellon, 1967. (10), (18), (19), (20), and (5)—Crabtree, this report. It should be noted that W. A. Bell, in his capacity as paleobotanist with the Geological Survey of Canada, provided the identifications for megafossils reported in Stott (1963), Mellon (1967), and Mellon et al. (1963).

better understood. I suggest that Protophylls are more similar to mainline Hamamelidales on the basis of leaf architecture than are Platanophylls, which are closer to the platanoid line of Hamamelids.

Protophyll. Leaves simple. Margin entire to dentate, occasionally lobed. Venation pinnate, the basal secondaries sometimes strengthened considerably and bearing pectinals. Secondary and higher order venation similar to Platanophylls. Cuticular details in Němejc & Kvaček (1975) and Krassilov (1973b).

Richter (1905) monographed *Credneria* Zenker and *Paracredneria* Richter.

Protophylls can usually be distinguished from Platanophylls by the basically pinnate venation and by the more consistent craspedodromy of the secondary veins (Fig. 4). However, in many cases the two morphotypes intergrade to the extent that recognition is difficult. Protophylls are common in the NRM region but do not exhibit the diversity or dominance found in the coarse facies of the Cenomanian Dakota flora of Nebraska and Kansas (Lesquereux, 1892). Several species from the Albian floras of Alberta are placed in this morphotype (Table 2). Protophylls are present in the Blackleaf flora (Fig. 15). Basal venation in Platanophylls and Protophylls is compared in Figures 16 and 17.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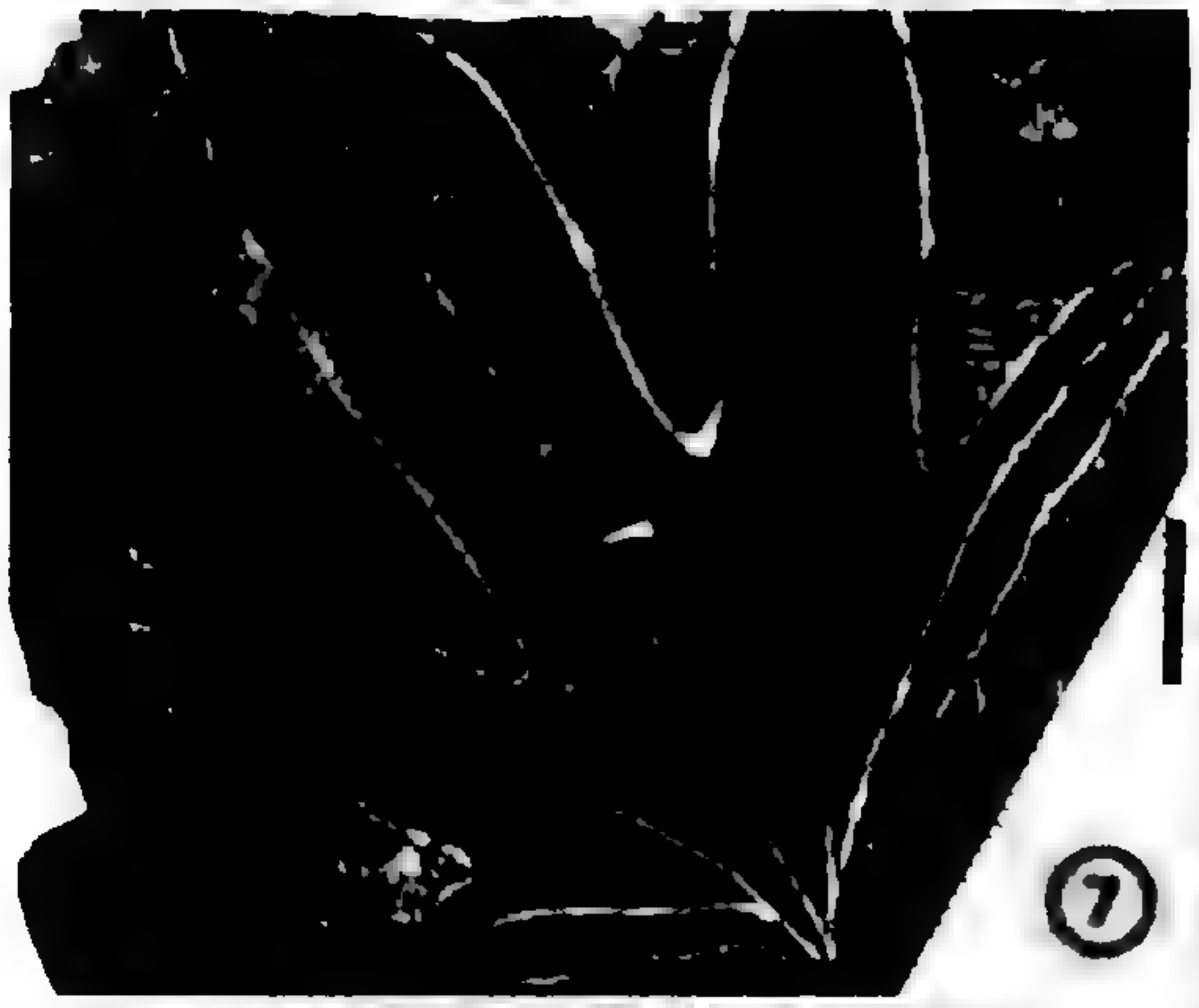
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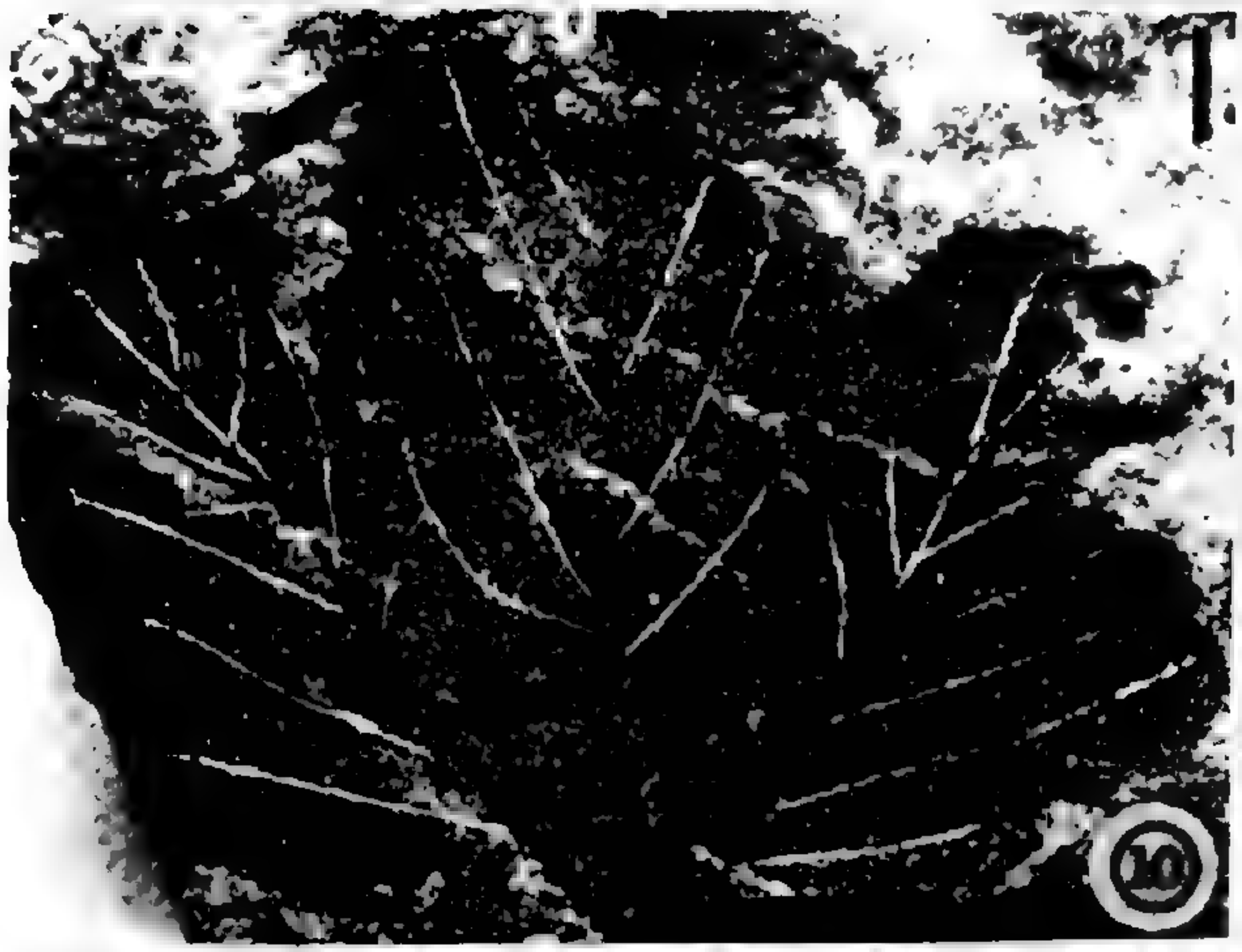
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Sapindophyll. Leaves even to odd pinnatifid or pinnately compound. Leaflets opposite or alternate, sometimes decurrent on rachis. Margins entire to serrate. Teeth apparently cunonioid. Petiole stout. Petiolule stout. Primary vein stout. Secondary veins eucamptodromous or semicraspedodromous, arched-ascending, often numerous, diverging at ± uniform angle of 35–50°. Intersecondary veins typically present. Tertiaries weakly percurrent, transverse, AR but highly variable. Quaternaries irregularly reticulate. Cuticle and tooth morphology in Upchurch (1984b).

This unique Lower and mid-Cretaceous morphotype encompasses fossils with pinnatifid or pinnately compound leaves (Fig. 4). Rachises with attached leaflets have been reported as *Sapindopsis* Fontaine and *Fontainea* Newberry. The widespread Laurasian species "*Andromeda*" *parlatorii* Heer, "*Ficus*" *daphnogenoides* (Heer) Berry, "*F.*" *beckwithii* Lesquereux, "*Sapindus*" *morrisonii* Lesquereux, and "*Rhus*" *powelliana* Lesquereux represent dispersed leaflets of Sapindophylls. Dissected leaves with palmate organization, cf. *Halyserites* Sternberg and *Cussoniophyllum* Velenovsky, are excluded from the Sapindophylls and have not been observed in the NRM region.

Sapindophylls are an important component of many North American Albian and Cenomanian floras (Berry, 1922a, 1922b; Fontaine, 1889; Hickey & Doyle, 1977; Lesquereux, 1874, 1883, 1892; MacNeal, 1958; Upchurch, 1984b). The morphotype is generally considered to be more abundant in floras from regions to the south of the NRM region and is sometimes regarded as representing thermophilous plants. Nonetheless, the morphotype is common in mid-latitude floras from the NRM region and Greenland (Seward & Conway, 1935), and occurs in southern Alaska ("*Ficus*" *daphnogenoides* in Hollick & Martin, 1930) and the north slope (pers. obs.).

This morphotype is represented by several species in the NRM region (Table 2). A probable new species of *Sapindopsis* of Middle Albian age is illustrated from rocks equivalent to the Thermopolis Shale in southwestern Montana (Fig. 18). It appears to be related to the Cenomanian species "*Sapindus*" *morrisonii* and "*Ficus*" *beckwithii.* A Sapindophyll similar to *Sapindopsis variabilis* Fontaine is present in the Blackleaf Formation of Montana (Fig. 19). Sapindophylls are present in the Albian of Alberta (Table 2, Fig. 20), British Columbia (Fig. 27), and Washington (Figs. 28–32). A putative Sapindophyll (cf. *Sapindopsis* sp.) from the Upper Albian of Idaho is tentatively assigned to this morphotype (Figs. 21–23). This species is allied to the morphotype by admedial orientation of the tertiary veins (Fig. 21) and dissected leaves with decurrent leaflets (Figs. 22, 23), but shows the irregular laminar furcations of *Halyserites.*

Sapindophylls may be most closely allied to Recent basal Saxifragales and to other rosid groups such as the Sapindales and Rutales. This relationship is based on the pinnately compound leaves, eucamptodromous venation, admedial orientation of the transverse tertiary veins (Hickey & Doyle, 1977), cunonioid teeth in some species (Upchurch, 1984b), and cuticular features (Upchurch, 1984b). Crane et al. (1986) discussed possible relationships between Sapindophylls and Platanophylls in the context of the Late Albian radiation of dicotyledons that produced tricolpate pollen (viz. Hamamelididae and

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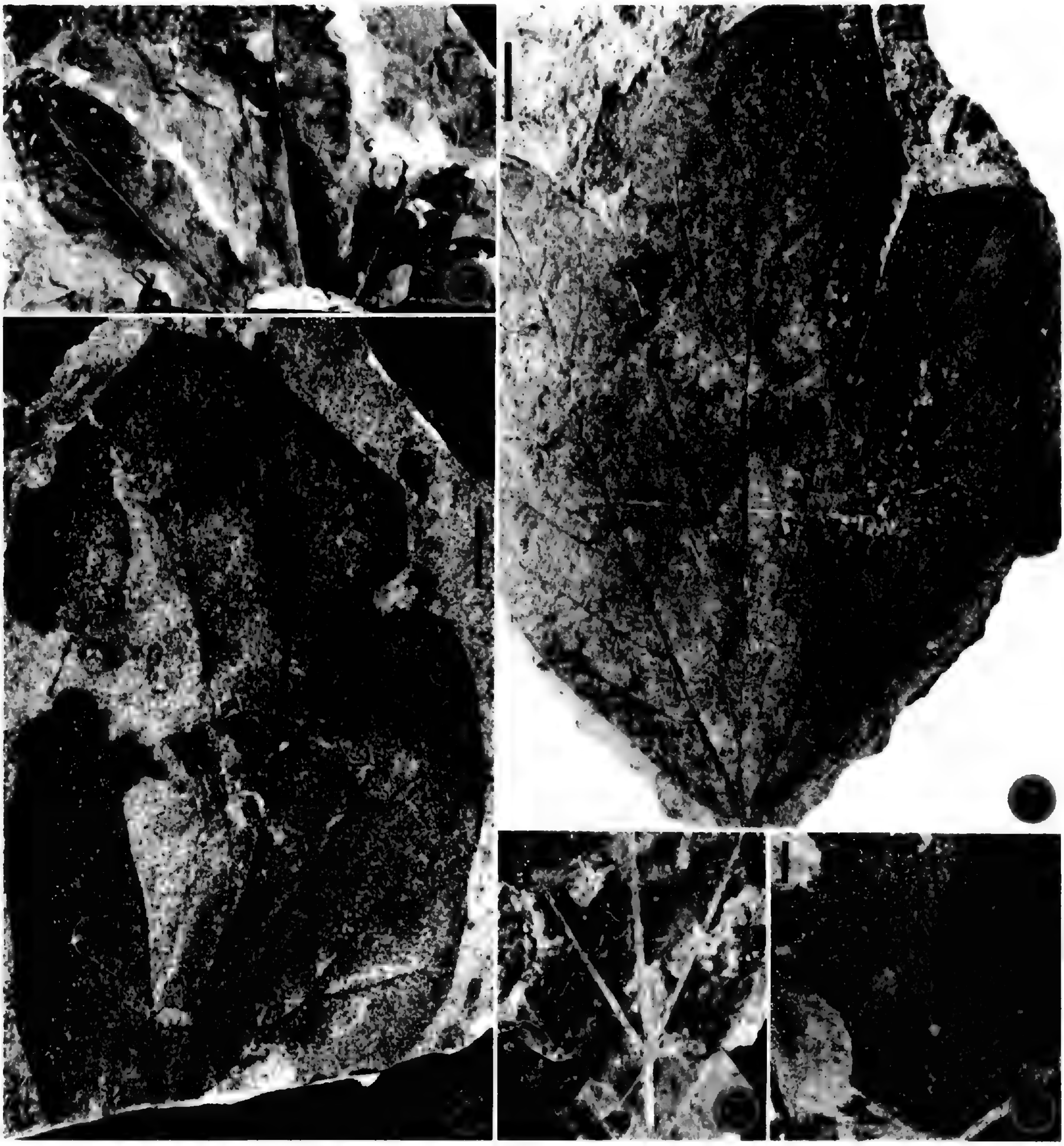
FIGURES 5–58. Representative dicotyledonous leaves from the Albian through middle Campanian of the NRM region. All figures with centimeter scales. Specimens from the U.S. National Museum are provided with USGS field locality numbers, and those from the Geological Survey of Canada are provided with GSC locality numbers. Types and other cataloged specimens are indicated where appropriate, along with U.S. National Museum (USNM) and Geological Survey of Canada (GSC) accession numbers. Names applied to illustrated specimens are as originally published or as identified in paleobotanical collections at the USNM and GSC. I have provided names only for species from the Fall River, Blackleaf, Pre-Muddy, Pasayten, Mowry, Winthrop, and Two Medicine floras.

FIGURES 5–12. Albian age dicotyledonous leaves of the Pentalobaphyll and Platanophyll morphotypes. 5–9. Pentalobaphylls.—5. cf. "*Sterculia*" *mucronata* Lesquereux, Fall River Formation, USGS locality 7404. 6–8. *Araliaephyllum westonii* (Dawson) Bell.—6. Blackleaf Formation, USGS locality 9439. 7, 8. Mill Creek Formation.—7. GSC locality 1815, GSC 5117, holotype.—8. GSC locality 3066, GSC 5874.—9. "*Aralia*" *rotundata* Dawson, Mill Creek Formation, GSC locality 1815, GSC 5116, holotype. 10–12. Platanophylls.—10. "*Platanus*" sp., Mill Creek Formation, GSC locality 1815, GSC 5106.—11. *Platanophyllum* sp., Blackleaf Formation, USGS locality 9437.—12. cf. *Aspidophyllum trilobatum* Lesquereux, Blackleaf Formation, USGS locality 9437.



FIGURES 13–17. Albian age dicotyledonous leaves of the Platanophyll and Protophyll morphotypes. 13, 14. Platanophylls.—13. cf. "*Aralia*" *wellingtoniana* Lesquereux, Blackleaf Formation, USGS locality 5984.—14. *Araliopsoides* cf. *cretacea* (Newberry) Berry, Blackleaf Formation. 15. Protophyll, cf. *Protophyllum* sp., Blackleaf Formation, USGS locality 5986. 16, 17. Comparison of basal venation of Platanophyll and Protophyll.—16. Platanophyll, *Platanophyllum* sp., Blackleaf Formation, USGS locality 5939.—17. Protophyll, *Protophyllum* sp., Blackleaf Formation, USGS locality 5986.

Rosidae). Friis & Skarby (1982) and Basinger & Dilcher (1984) discussed Cretaceous flowers and pollen of early Rosidae.

Sapindophylls are restricted to Albian and Cenomanian floras in the NRM region. I am not familiar with their Late Cretaceous range elsewhere. The rosid affinities of Sapindophylls need to be confirmed by further study, as does the relationship between the group and the putative Upper Cretaceous and Paleocene derivative *Averhoites*.

Trochodendrophyll. Leaves simple, ovate to reniform. Margin crenate. Teeth convex-convex (A–1), chloranthoid. Venation actinodromous. Primary veins usually 3 or 5, sometimes more, arched apically. Secondary venation semicraspedodromous with ± prominent brochidodromous arches present apically. Tertiary and higher order venation not well known, appearing reticulate in some with tendency towards orthogonal branching.

This group is characterized by actinodromous primary venation and crenate margins bearing chloranthoid teeth (Fig. 4). The latter character distinguishes the group from those Menispermaphylls with actinodromous venation. Trochodendrophylls are reported in low frequencies during the Albian, and are represented in the NRM region primarily from Alberta and British Columbia (Table 2). *Trochodendroides* ("*Cercidiphyllum*") *potomacensis* (Ward) Bell conforms most closely to the concept of the morphotype with five primary veins, brochidodromous secondary veins, and crenate margin (Figs. 24, 25).

Trochodendrophylls have been assigned to rather unlikely genera (Table 1). Cuticular studies of *Menispermites potomacensis* Berry from the Lower Cretaceous Potomac Group (Upchurch, 1984b; pers. comm.) indicate that the stomatal structure of this species does not conform to that of extant Cercidiphyllales and Trochodendrales. Probable members of the lineage are reported in high frequencies from Senonian and latest Cretaceous deposits, but these are more advanced in morphology and in some cases can be appropriately assigned to the Recent Trochodendraceae and Cercidiphyllaceae (see Krassilov, 1973b). Trochodendrophylls, along with a series of pinnately veined Lower Cretaceous leaves with chloranthoid teeth and open craspedodromous secondaries (see Upchurch, 1984b; Fig. 36, this report), may represent an ancestral plexus from which Recent Trochodendrales and Cercidiphyllales evolved during the Cretaceous (but see Wolfe, 1973). The Campanian Two Medicine flora (see below) includes four leaf taxa which have chloranthoid teeth, but which exhibit variations of primary and higher order venation that suggest mosaic development of leaf characters in Cercidiphyllales, Trochodendrales, and Chloranthales.

Menispermaphyll. Leaves apparently simple, broadly deltoid and ± trilobed to circular or ovate-elliptic. Base cordate to obtuse. Margins entire or lobate forms occasionally with teeth. Venation acrodromous or actinodromous with 3–9 primary veins. Primary veins craspedodrome or becoming camptodrome just before margin. Secondary veins irregularly spaced, camptodrome in many but craspedodrome to the teeth in nonentire forms. Tertiary veins random-reticulate to transverse. Higher order venation not observed. Cuticle unknown.

This group (Fig. 4) superficially resembles Nymphaeaphylls but is never peltate and never has an expanded, multistranded petiole. Cordate leaves with major veins unbranched to the margin are best placed in Menispermaphylls, whereas such leaves with highly branched primary and secondary veins are more appropriately placed in Nymphaeaphylls. Trochodendrophylls may be distinguished by their crenate margin.

Menispermaphylls are morphologically convergent with extant Menispermaceae (Ranunculiidae). The modern family includes both simple-leaved and ternately compound members. The leaves and leaflets are deltoid to ovate with entire or sparingly toothed margins. Tooth morphology is a modification of the chloranthoid type (Hickey & Wolfe, 1975). Primary venation is actinodromous or acrodromous, and major veins terminate in a fimbrial vein, thus appearing craspedodromous. Many Recent species exhibit a mucronate leaf apex; simple, unbranched trichomes; and well-developed, orthogonal-reticulate, higher order venation.

Menispermaphylls resemble Recent Menispermaceae in shape, margin, and venation. However, before relationship to the family can be established it is necessary to demonstrate the presence in the fossils of such characters as fimbrial veins and simple, unbranched trichomes. Nevertheless, the unusual combination of entire margin and craspedodrome primary veins is an important point of agreement between the fossils and Recent Menispermaceae.

Menispermaphylls show their greatest diversity in the Dakota flora of Kansas and Nebraska (Lesquereux, 1892). However, here, as in the NRM region (Table 2), they are a relatively minor component of the flora. The Campanian Two Medicine flora (see below) includes a species that is entirely consistent with the leaf morphology of extant Menispermaceae.

Magnoliaephyll. Leaves simple, ovate to elliptical. Margin entire or 2- or 3-lobed. Primary venation pinnate in entire forms, with 3 primary veins from base in lobed forms. Secondary venation brochidodromous or festooned brochidodromous. Higher order venation variable.

This morphotype (Table 1) comprises a large number of problematic taxa that form an im-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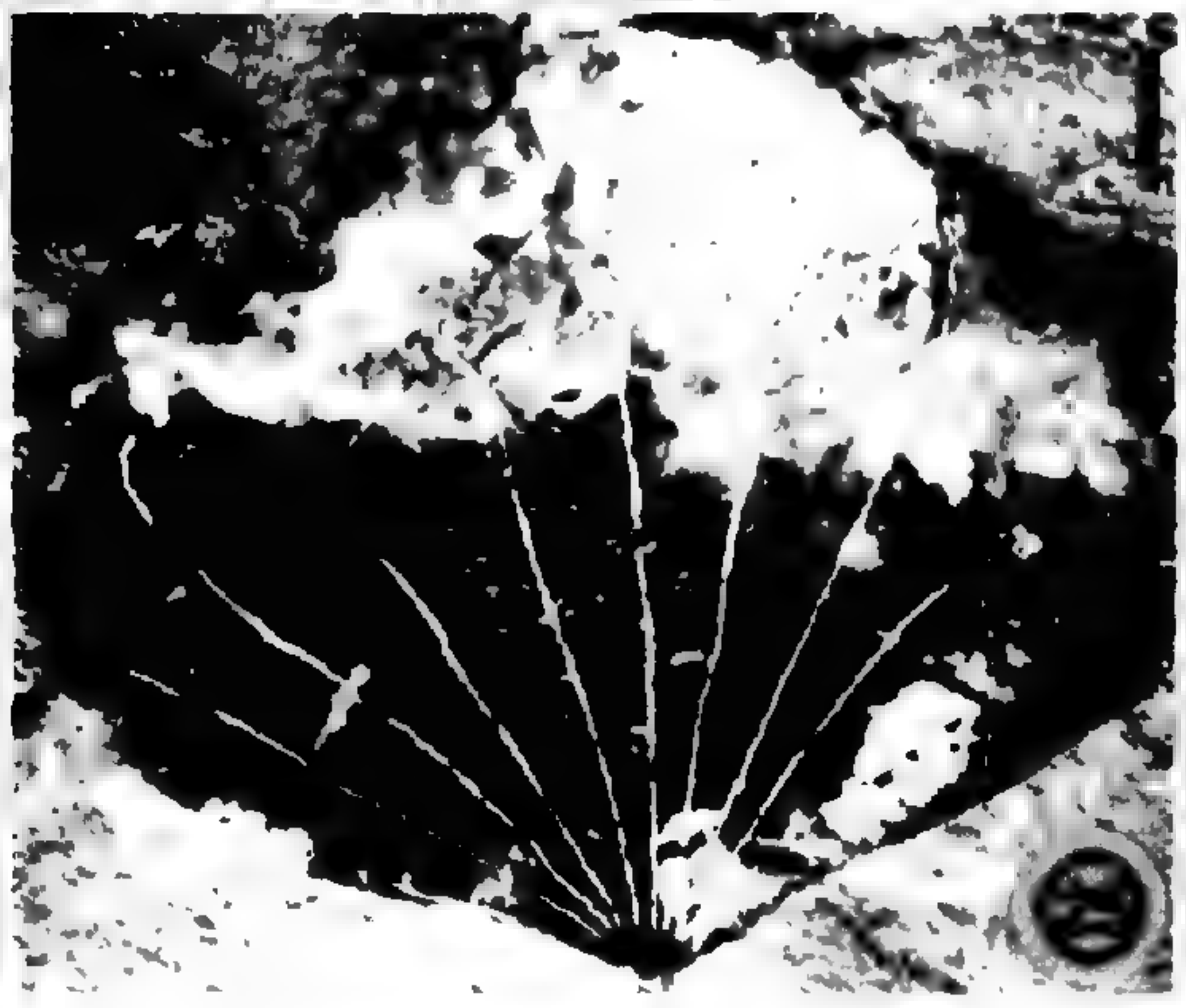
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portant part of all but extreme northern Laurasian floras. The group is erected primarily for convenience due to the enigmatic positions of most of its members. Some Potomac Group Magnoliaephylls for which cuticular evidence is available (Upchurch, 1984a, 1984b) appear to be related to Laurales and Illiciales. "*Magnolia*" *magnifica* Dawson is illustrated as an example of the morphotype (Fig. 26). Early members of the morphotype from the NRM region are listed in Table 2.

Putative magnoliid infructescences are known from the mid Cretaceous of central North America (Dilcher, 1979), Japan (Nishida, 1985), and Greenland (Seward & Conway, 1935). Walker et al. (1983) reported pollen of Winteraceae from the Lower Cretaceous of Israel.

Cinnamomophyll. Leaves simple. Margin entire. Venation pinnate. Prominent suprabasal secondary veins arching apically. Secondary venation brochidodromous. Basilaminar secondary veins sometimes present. Tertiary veins transverse, regular or somewhat irregular in spacing and course. Quaternary veins weak, random-reticulate. Cuticle unknown.

This morphotype (Fig. 4) is widely reported from NRM region floras and is an important component of the angiosperm vegetation during the Albian (Table 2). Although not present in all Cinnamomophylls, basilaminar secondary veins indicate that some may be related to extant Laurales. Cinnamomophylls are most important in floras from middle latitudes in Laurasia where they are consistently represented in the Albian floras.

Nymphaeaphyll. Leaves simple, orbicular to reniform. Margin entire. Petiole often multistranded. Base cordate or peltate. Venation actinodromous or pinnate with strong lateral veins radiating from a congested base. Primary and secondary veins branching ± equally. Marginal venation forming weak brochidodromous arches, craspedodromous in "*Castalia*" and *Castaliites*. Cuticle unknown.

This morphotype converges with Trochodendrophylls, from which it is distinguished by its entire margin, and with Menispermaphylls (see discussion of Menispermaphylls and Fig. 4).

Several species of Nymphaeaphylls exhibit leaf architecture consistent with those of extant Nymphaeales and Nelumbonales. Evidence from cuticles and fruits is needed to confirm the relationship.

Cordate and peltate leaves with actinodromous venation and entire margins are abundant and diverse in the North American mid Cretaceous, but they are not well represented in the NRM flora (Table 2). Nymphaeaphylls may represent an adaptational syndrome for aquatic habitats as suggested by Samylina (1968), Axelrod (1970), and Krassilov (1977). Hughes (1976) suggested that this leaf morphology may represent simply an early "experimental" shape that is not correlated with aquatic habitats.

Rhamnophyll. Leaves simple. Margin entire or crenate-dentate. Base acute to truncate. Venation acrodromous. Primary veins 3–5, arising from within the petiole and arching apically. Secondary venation brochidodromous or semicraspedodromous to teeth, often with several regular and prominent secondary veins originating on outermost primary veins and arching apically along margins. Tertiary veins transverse, regularly spaced and usually numerous. Higher order venation not observed. Cuticle unknown.

Rhamnophylls are rare from floras of Albian age in the NRM region (Table 2). The group occurs with greater frequency in Late Cretaceous floras throughout western North America (Hickey, 1984). Rhamnophylls can be distinguished from Cinnamomophylls (Fig. 4) by the petiolar divergence of the acrodromous primary veins and by the presence of teeth in some. The botanical affinities of the former remain unknown.

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FIGURES 18–26. Albian age dicotyledonous leaves of the Sapindophyll, Trochodendrophyll, and Magnoliaephyll morphotypes. 18–23. Sapindophylls.—18. cf. "*Rhus*" *powelliana* Lesquereux, Pre-Muddy collection.—19. cf. *Sapindopsis* sp., Blackleaf Formation, USGS locality 6007.—20. *Fontainea grandifolia* Newberry, Commotion Formation, GSC locality 3204, hypotype (as labeled in GSC collections), GSC 6639. 21–23. cf. *Sapindopsis* sp., Wayan Formation. 24–25. Trochodendrophylls, *Trochodendroides* ("*Cercidiphyllum*") *potomacensis* (Ward) Bell, Kingsvale Formation.—24. GSC locality 3449, GSC 6654.—25. GSC locality 3125, GSC 5907.—26. Magnoliaephylls, "*Magnolia*" *magnifica* Dawson, GSC locality 290, GSC 5133, holotype.

Cornophyll. Leaves simple. Margin entire. Primary venation pinnate. Secondary venation camptodromous, arching apically. Tertiary veins transverse, regularly spaced, more or less numerous. Higher order venation and cuticle unknown.

Cornophylls occur in limited diversity and abundance in the Albian floras of the region (Table 2). The group assumes a more important position in later Cretaceous floras. The botanical affinity of the group is unknown, but some members appear to exhibit morphological similarities to Rosidae.

Dryophyll. Leaves palmately compound. Leaflets ovate to lanceolate. Margin serrate. Primary venation pinnate. Secondary venation craspedodromous. Higher order venation not observed. Cuticle in Krassilov (1973b) and Němejc & Kvaček (1975).

This group of palmately compound leaves with serrate margins is not present in the early angiosperm floras. They appear first in the uppermost Albian and Cenomanian. Serrate forms with craspedodromous venation and lanceolate leaflets (cf. *Dryophyllum* Debey) can be shown to share morphological similarities with Fagales, although this is a tenuous association for most Cretaceous forms (Wolfe, 1973).

FLORISTIC PROVINCIALITY OF THE NORTHERN ROCKY MOUNTAIN REGION DURING THE ALBIAN

Discussion of floristic provinciality during the Cretaceous ultimately depends on accurate correlation of stage and substage boundaries between the proposed provinces. The Upper–Lower Cretaceous boundary and the position of the Albian substages in the NRM region are placed based on ammonites in the United States (Cobban & Reeside, 1951, 1952a) and on a varied molluscan fauna in Canada (Jeletsky, 1968; Kauffman, 1975). Geologists have generally placed the boundary between the Upper and Lower Cretaceous in the NRM region at the top of the Mowry Shale. This boundary coincides with the uppermost widespread occurrence of *Neogastroplites* (Cobban & Reeside, 1951). It also coincides with the first occurrence of tricolporate pollen in the region (Nichols et al., 1983; Norris et al., 1975). Nonetheless, uncertainty exists over the correlation of the regional boundary to the European standard. The boundary in the western interior is radiometrically dated as 94 Ma (Obradovich & Cobban, 1975; but also see Fouch et al., 1983), whereas in Europe it is dated as 97.5 Ma (Harland et al., 1982).

Brenner (1976) recognized a Northern Laurasian Province and a Southern Laurasian Province based on the palynology of Lower Cretaceous deposits. The northern province is recognized by a coniferous palynoflora less diverse and more heavily bisaccate than the southern province. The NRM region lies on the boundary between provinces. Such provinciality is supported by Srivastava (1981) and by Hickey & Doyle (1977) and rejected by Herngreen & Chlonova (1981). Angiosperm pollen has been used for the recognition of Late Cretaceous provinciality (Srivastava, 1981). The extension of angiosperm palynofloral provinces into the Early Cretaceous seems reasonable in light of the elaboration of the timing of the migration of angiosperms provided by Brenner (1976) and by Hickey & Doyle (1977).

The poleward migration of early angiosperms was first recognized from megafossils (Axelrod, 1959) and subsequently refined through palynological studies (Brenner, 1976; Hickey & Doyle, 1977). Early angiosperms appear to have arisen in northern Gondwana and to have crossed the Tethys into Laurasia in the Late Barremian and Aptian (Hickey & Doyle, 1977). Entry of monosulcate-producing angiosperms into northern latitudes of Laurasia was delayed by several million years. This may be attributed to climatic or other environmental barriers, inadequate dispersal mechanisms, or merely to stalwart pre-existing vegetation. Tricolpate taxa exhibit a far shorter lag period. The first major radiation of the tricolpate group occurs on a worldwide scale during the late Middle Albian (excepting at the very highest latitudes).

Considerations of floral provinciality of early angiosperms must address two common problems with palynological investigations: 1) underspeciation, i.e., approximate equivalency of a palynological species with a natural genus (Muller, 1970; Tschudy & Tschudy, 1986), especially in the Paleozoic and Mesozoic, and 2) spurious conspecificity, i.e., the tendency to assign pollen grains to existing taxa. Both problems obscure provincialism at lower taxonomic levels. Penny (1969) commented on the impoverished appearance of Cenomanian pollen floras relative to leaf floras of that age. A related problem, which is more or less confined to the early angiosperm pollen floras, is the general absence of differentiation of grains with respect to ornamentation, shape, and gross morphology. In addition, Mesozoic palynologists do not normally elaborate species frequency as is common for Holocene workers, a situation that makes it difficult to review existing literature for data which could be used to determine provinciality based on dominance and importance of species. On the other hand, a common problem with megafloral taxonomy has been overspeciation due to failure to recognize physiognomic variation in leaf morphology within natural species. Both megafloral and microfloral treatments are restricted by the taphonomic biases implicit in any depositional environment.

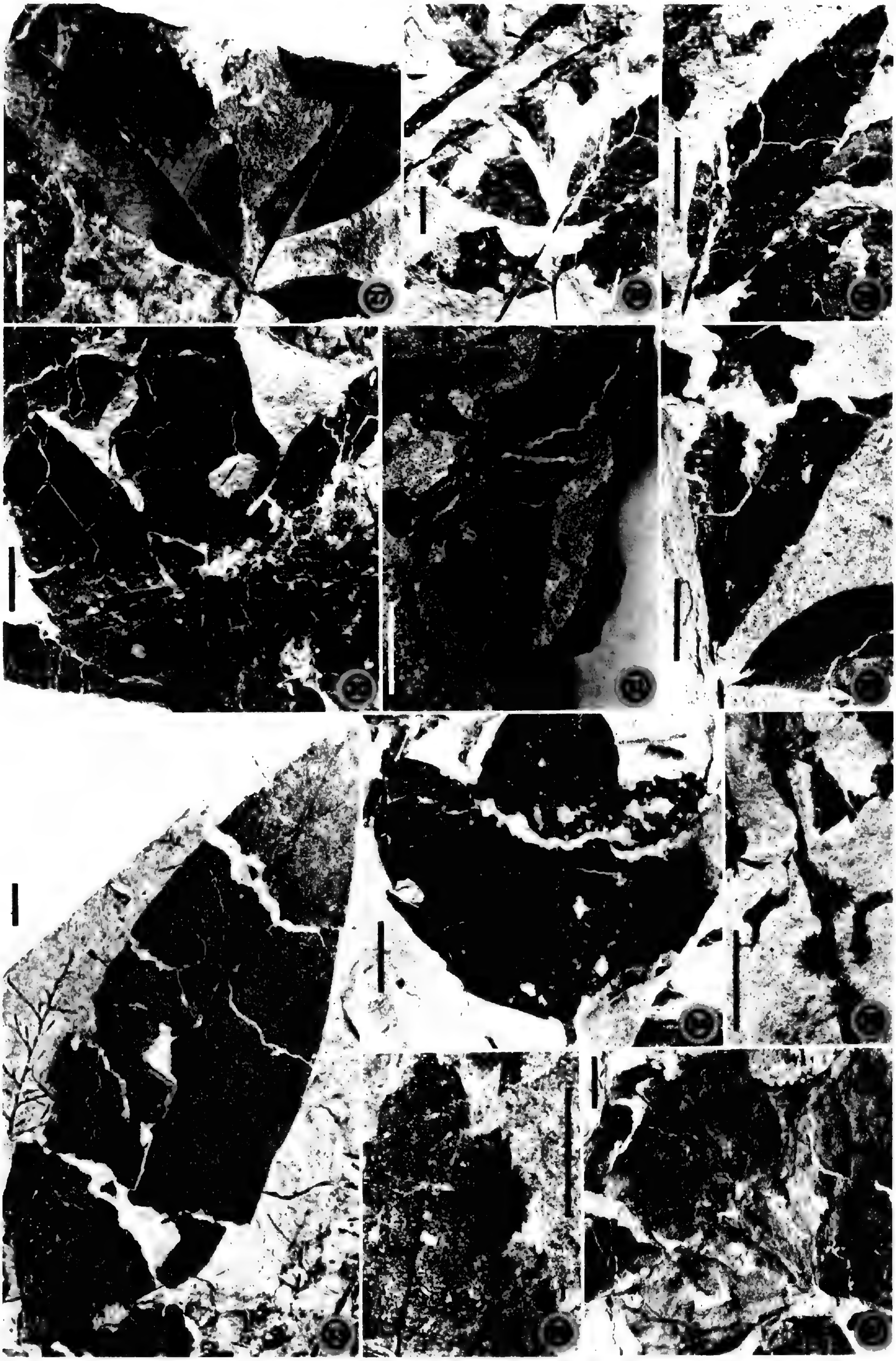
The first angiosperms known from the lower Middle Albian (Potomac subzone IIB) of the NRM region are two grains of *Tricolpites micromunus* (Groot & Penny) Singh from the upper Loon River Formation in northwest Alberta (Singh, 1971) and monosulcate grains from the Cloverly Formation in Wyoming (Davis, 1963). Pollen and megafossils are known throughout the NRM region with certainty from the middle Middle Albian (Bell, 1956; Davis, 1963; Nichols & Jacobson, 1982; Norris, 1967; Singh, 1975; Roberts, 1972). Singh (1971) reported nine species of middle Middle Albian angiosperm pollen from northwest Alberta. By upper Middle Albian (Potomac subzone IIB), angiosperm pollen becomes a persistent element of moderate frequency in the microflora. This upper Middle Albian surge in frequency seems to be common to most of North America other than far northern latitudes.

The first angiosperm megafossil from the region, *Sapindopsis angusta* (Heer) Seward, occurs in the lower Middle Albian (Potomac subzone IIB). Localities in British Columbia of equal age yield *Sapindopsis* and a limited diversity of other dicot leaves (Table 2). The first diverse assemblages of megafossils are of middle Middle and upper Middle Albian age and include Sapindophylls, Pentalobaphylls, Platanophylls, *Cinnamomoides, Trochodendroides,* and *Menispermites* in order of frequency in collections. The components of this megaflora continue into the lower Upper Albian with little apparent change. The early angiosperm flora of the region is distinct from more southerly floras in its high representation of Pentalobaphylls, Cinnamomophylls, and to a lesser degree *Trochodendroides,* and several endemic species are present.

I compared the Lower Cretaceous palynoflora of the Patapsco Formation of Maryland (Brenner, 1963) with that of the Loon River and Peace River formations of northwest Alberta (Singh, 1971) to contrast composition, abundance, and diversity of Middle and Late Albian floras of eastern North America with those of the NRM region. More recent treatments of the Patapsco palynoflora exist (Doyle, 1969; Doyle & Hickey, 1976; Hickey & Doyle, 1977), but Brenner's work remains the standard for taxonomic comparison in the absence of a revision. Brenner apparently was conservative in recognition of taxa, thus it is likely that some of his taxa represent species complexes or genera.

Monosulcates first occur in the latest Barremian or early Aptian in eastern floras, considerably antedating their lower Middle Albian occurrence in the NRM region. Seven of the twelve Patapsco species of angiosperm pollen are tricolpate. The tricolpates appear during the Lower and Middle Albian and continue upsection to the top of the formation (middle Upper Albian) with no addition of new species (Brenner, 1963; but also see Doyle & Hickey, 1976). Of these seven species, *Tricolpites micromunus* occurs in the lower Middle Albian Loon River Formation, and six of the seven tricolpates occur in the middle Middle Albian Harmon Member of the Peace River Formation. Such palynological data indicate close similarity between lower and middle Middle Albian dicots in the eastern and western floras of North America, at least at the generic level.

An endemic flora in the region is indicated by angiosperm pollen recovered from the Peace River Group (Singh, 1971), which was deposited during and after the maximum transgression of the middle Albian seaway. Nineteen species comprise the angiosperm palynoflora in the upper Middle Albian Cadotte Member of the Peace River Formation. Nine of these, including five tricolpates, are reported from the Patapsco, still a high degree of similarity, but strikingly less than that of the earlier flora. Furthermore, five Cadotte taxa have not been reported from Cretaceous palynofloras outside the NRM region. Eastern groups apparently moved north and east into the NRM region during the Middle Albian and persisted in the western flora; however, by the upper Middle Albian, tricolpate and monosulcate taxa indicate endemism in the region. Among the endemics are the monosulcate species *Liliacidites trichotomosulcatus* Singh and the tricolpates *Retitricolpites maximus* Singh, *Tricol-*



pites sagax Norris, *T. parvus* Stanley, and *Fraxinaipollenites venustus* Singh.

The endemic character of the flora appears to result largely from separation of the region from eastern North America by the Skull Creek Seaway for approximately two million years during the upper Middle and lower Upper Albian. Thus, shortly after angiosperms entered the region, they were cut off from their presumed ancestral stock to the south and east in an area some 20° further north and potentially subject to substantially different selective pressures. However, it should be noted that available palynofloras make it difficult to resolve an east-to-west adaptive radiation within groups producing small, reticulate, tricolpate pollen, since the equivalence of named species to biological species is debatable. In contrast to the simple tricolpate pollen, leaf architectures and cuticles of Lower Cretaceous angiosperms provide an expanded suite of characters from which biological species can be circumscribed. A detailed comparison of North American floras of Albian age is beyond the scope of this paper.

WINTHROP FLORA

A large collection of fossil foliage from the type locality of the Late Albian or Early Cenomanian (Barksdale, 1975) Winthrop Formation in central Washington (Figs. 1, 2) appears to be the latest occurring "archaic" flora in the region. The flora contains abundant Sapindophylls and Pentalobaphylls that are closely related to but not conspecific with those of earlier Albian floras from the NRM region.

Several small collections of plant fossils from the Winthrop have appeared as floral lists in geological papers (see Barksdale, 1975). Apparently the collections were sent to the U.S. National Museum and examined by F. Knowlton and R. Brown. Reevaluation of these collections in 1986 by S. Wing and J. Wolfe (pers. comm.) indicated a Paleocene age for the flora, and hence their origin in the Winthrop Formation must be questioned. The present report includes only those specimens collected from the type locality (Appendix I) by R. Rau, J. Robison, and myself.

The Winthrop flora is a moderately diverse assemblage consisting of about 20 species of ferns, conifers, dicotyledons, and *Sagenopteris* (Caytoniales). Dicotyledonous species include *Sapindopsis* sp. (Figs. 28–32), *Magnoliaephyllum* sp. (Fig. 33), *Araliaephyllum* sp. (Fig. 34), *Araliaephyllum westonii*, "*Sparganium*" sp. (Fig. 35), an unidentified dicot with craspedodromous secondary venation and chloranthoid teeth (Fig. 36), *Nelumbites* sp. (Fig. 37), "*Ficus*" *ovalifolia*, *Menispermites* sp., *Eucalyptophyllum* sp., and several poorly preserved species.

UPPERMOST ALBIAN, CENOMANIAN, AND TURONIAN FLORAS

Three well-developed floras, the Aspen, Frontier, and Dunvegan (Table 3), provide much of the megafossil evidence for the angiosperm flora of the NRM region during the uppermost Albian and Cenomanian (Fig. 2). The Dunvegan flora is near the northern limit of the region; the Aspen and Frontier are at the southern limit (Fig. 1). Collections from the Albino Member of the Mowry Formation and the Wayan Formation (Figs. 1, 2) provide a few additional species.

The Albian angiosperm flora of the region shows an underlying unity due to the occurrence in most assemblages of Sapindophylls, Pentalobaphylls, Platanophylls, Protophylls, and Cinnamomophylls, which give the flora an "archaic" appearance when contrasted to the flora of the post-Albian. The post-Albian flora shows the development of north–south provinciality in the region. However, because of the small number of floras known from this period (Fig. 2), and the restricted volcaniclastic facies of the Aspen and Frontier floras, such provinciality is at this time somewhat conjectural. Moreover, because the early angiosperm flora is known primarily from deposits in the northern half of the region, there is uncertainty over how widespread and uniform the early flora was.

The development of intraregional provincial-

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FIGURES 27–37. Dicotyledonous leaves from the Pasayten and Winthrop formations. 27. Pasayten Formation, *Sapindopsis* sp. 28–37. Winthrop Formation. 28–32. *Sapindopsis* sp.—28. Upper part of compound leaf.—29. Enlarged leaflet of specimen in Figure 28.—30. Upper part of compound leaf.—31. Base of leaf.—32. Base of joined upper three leaflets.—33. *Magnoliaephyllum* sp.—34. *Araliaephyllum* sp.—35. "*Sparganium*" sp.—36. Unidentified leaf with craspedodrome secondaries and chloranthoid teeth.—37. *Nelumbites* sp.

TABLE 3. Angiosperm flora from the uppermost Albian, Cenomanian and Turonian of the northern Rocky Mountain region.[1,2,3]

	Aspen (2)	Lower Frontier (11a)	Dunvegan (8)		Upper Frontier (11b)
			A	B	
Sapindophyll					
"*Andromeda*"? *spatula* Bell				X	
"*Ficus*" *daphnogenoides* (Heer) Berry				X	
"*Myrica*" *nervosa* Knowlton		X			
Sapindopsis schultzii Brown	X				
Rosidlike Leaves					
"*Diospyros*" *nitida* Dawson			X		
"*Hymenaea*" *fayettensis* Berry				X	
"*Laurus*" *aspensis* Brown	X				
Phyllites dentata Knowlton		X			
"*Prunus*" *aspensis* Brown	X				
"*Salix*" *cumberlandensis* Knowlton		X			
"*Staphylea*"? *fremontii* Knowlton	X	X			
Platanophyll					
Ampelophyllites attenuatus (Lesquereux) Knowlton				X	
"*Aralia*" cf. *parvidens* Hollick				X	
"*Aralia*" *veatchii* Knowlton		X			
Aspidophyllum dentatum? Lesquereux				X	
"*Hedera*" cf. *cretacea* Lesquereux				X	
"*Platanus*" *latiloba* Newberry				X	
Pseudoaspidophyllum latifolium Hollick				X	
"*Quercus*" *stantonii* Knowlton		X			
"*Sparganium*" *aspensis* Brown	X				
Protophyll					
Credneria macrophylla Heer				X	
Credneria truncatodenticulata Bell				X	
"*Platanus*" *affinis* Lesquereux				X	
"*Platanus*" *williamsii* Bell				X	
Populites cyclophylla Dawson			X		
Protophyllum boreale Dawson			X		
Protophyllum leconteanum? Dawson			X		
Protophyllum multinerve? Lesquereux				X	
Protophyllum rugosum Lesquereux			X		
Pseudoprotophyllum boreale (Dawson) Hollick				X	
Pentalobaphyll					
Araliaephyllum rotundiloba (Newberry) Fritel				X	
Araliaephyllum groenlandica? Heer				X	
"*Sterculia*" *towneri* (Lesquereux) Berry					X
Dryophyll					
Dewalquea pulchella Knowlton		X			
Dryandroides lanceolata Knowlton	X	X			
Dryophyllum gracile Debey				X	
Dryophyllum lanceolatum (Knowlton) Berry	X				X
Trochodendrophyll					
Castaliites cf. *cordatus* Hollick (in part)				X	
Trochodendroides ("*Cercidiphyllum*") *potomacensis* (Ward) Berry				X	

TABLE 3. Continued.

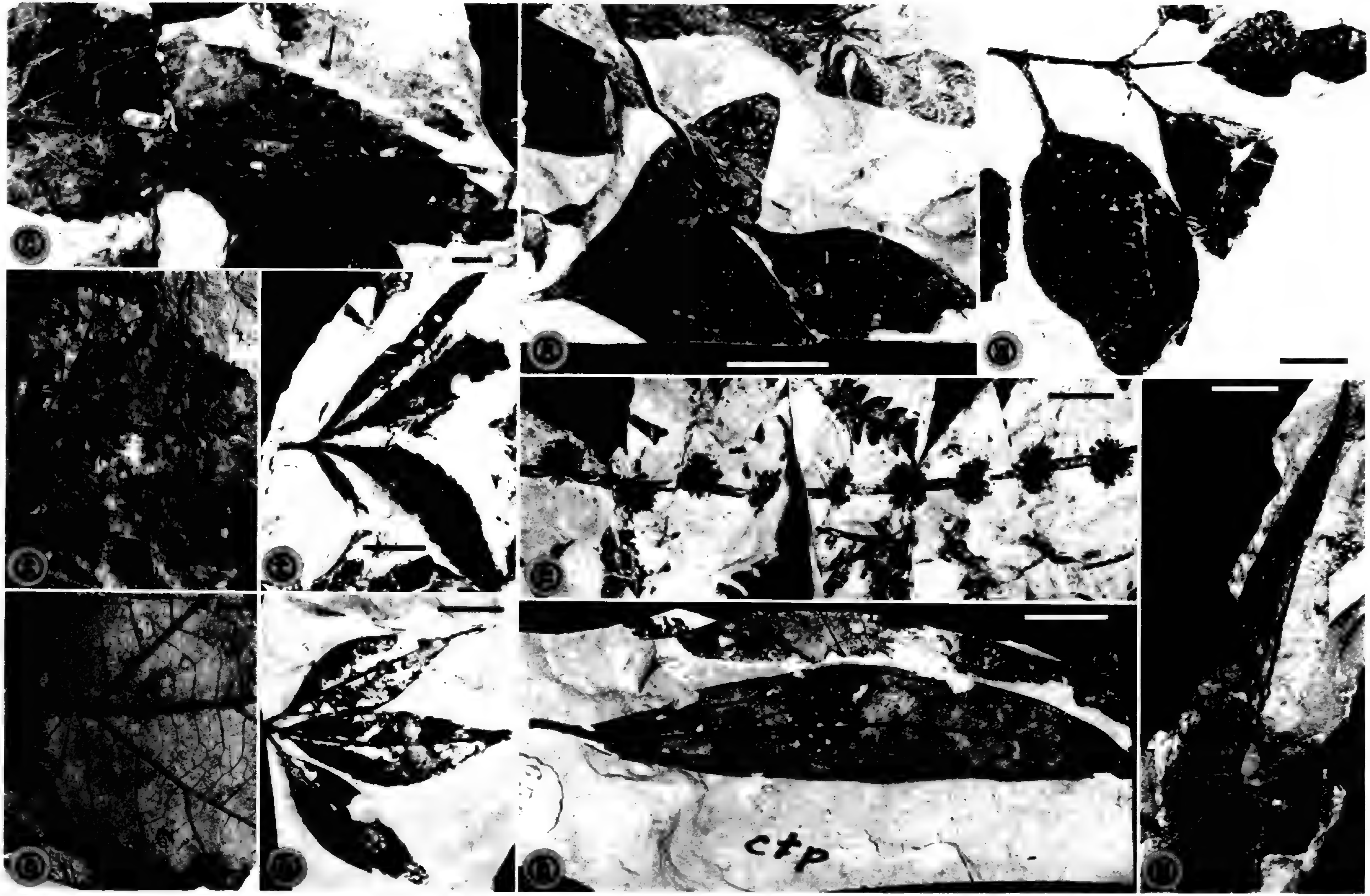
	Aspen (2)	Lower Frontier (11a)	Dunvegan (8)		Upper Frontier (11b)
			A	B	
Cinnamomophyll					
"*Cinnamomum*" *heeri* Lesquereux				X	
"*Cinnamomum*" *hesperium* Knowlton		X			
"*Cinnamomum*" sp.		X			
Phyllites sp.		X			
Nymphaeaphyll					
Castaliites cf. *cordatus* (in part)				X	
Menispermites reniformis Dawson			X	X	
"*Nelumbo*" *weymouthii* Brown	X				
Nymphaeites exemplaris Hollick				X	
Paleonuphar nordenskioldii (Heer) Bell				X	
Magnoliaephyll					
"*Ficus*" *maxima* Dawson			X		
"*Liriodendron*" *giganteum* Lesquereux				X	
"*Magnolia*" *boulayana* Lesquereux				X	
"*Magnolia*" *hollickii* Berry				X	
"*Magnolia*" *lacoeana* Lesquereux				X	
"*Magnolia*" *magnifica* Dawson			X	X	
"*Magnolia*" cf. *rotundifolia* Newberry				X	
"*Magnolia*" *tenuifolia* Dawson			X		
"*Sassafras*" *bradleyi* Brown	X				
Cornophyll					
"*Diospyros*" *lesquereuxii* Knowlton & Cockerell				X	
"*Ficus*" *fremontii* Knowlton		X			X
Laurophyllum debile Dawson			X		
"*Magnolia*" *rhamnoides* Bell				X	
Monocots					
Sabalites sp.					X
Uncertain					
"*Bauhinia*"? *cretacea*? Newberry				X	
"*Dalbergia*" *hyperborea* Heer				X	
Dicotylophyllum sp. A. Bell				X	
"*Fagus*" *protonucifera* Dawson			X		
"*Ficus*" *glascoeana* Lesquereux				X	
"*Ficus*" *inaequalis* Lesquereux					X
"*Ficus*"? sp.				X	
"*Ficus*" sp.		X			X
Laurophyllum flexuosum (Newberry) Bell				X	
Leguminosites spatulatus Bell				X	

[1] Numbers in parentheses refer to geographic and stratigraphic position of floras as indicated in Figures 1 and 2.

[2] All species are included as originally cited in the references given below.

[3] Vertical rows indicate single floristic references as follows: (2)—Brown, 1933a. (11a)—Knowlton, 1917. (8)A—Dawson, 1883. (8)B—Bell, 1963. (11b)—Berry, 1929d.

ity in the uppermost Albian and Cenomanian is correlated with the ebb of the Albian epeiric seaway. As previously discussed, the seaway may have influenced the development of endemism in the flora by restricting movement of eastern species into the region during much of the Upper Albian. As the seaway withdrew towards the north at the end of the Albian, immigration from east-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ern and southern regions may have altered the floristics of the southern part of the NRM region. Although this scenario is hypothetical, the uppermost Albian and Cenomanian floras of Wyoming contain *Dewalquea,* a genus characteristic of floras to the south and east of the region.

A large collection of fossil leaves from the Wayan Formation in southeast Idaho (Figs. 1, 2) is dominated by pteridophytes (Crabtree, 1983) that are undescribed but appear to be similar to those from the Frontier Formation in southwest Wyoming (Knowlton, 1917). The Wayan contains a single angiosperm, cf. *Sapindopsis* sp. (Figs. 21–23), which appears to be a new species. Andrews (1948) and Andrews & Kern (1947) described a large collection of pteridophytic petrifactions (*Tempskya*) from the Wayan (Appendix I).

Another undescribed megaflora is known from several localities in the Albino Member of the Mowry Formation in southern Montana (Figs. 1, 2, Appendix I). An extensive fern community is preserved in the deltaic deposits of the Albino (Vuke, 1982; Crabtree, 1983). Dicot leaf mats have been excavated at one locality in the Albino (Appendix I). Unfortunately, work on these fossils is incomplete and the floristics of this site remain poorly known. Figure 38 shows a specimen from the Albino that appears to be a pinnately compound leaf, possibly of rosid affinity, but the venation is too poorly preserved to confirm such a determination.

The uppermost Albian Aspen flora (Brown, 1933a, 1933b) from southwest Wyoming (Figs. 1, 2, Table 3) comprises nine species of angiosperms. No species from the Aspen are known from the older floras of the region, although some are recorded from the nearby and slightly younger Frontier Formation (Table 3). Notable in the flora is "*Liquidambar*" *fontanella* Brown (Fig. 39), which possesses glandular teeth similar to those of Recent *Liquidambar* and *Altingia.* "*Sassafras*" *bradleyi* Brown (Fig. 40) is preserved in a semicoalified state, which makes higher order venation difficult to distinguish. This species shows smooth-margined, palinactinodromous leaves with three lobes such as in extant Lauraceae and certain palmate Dilleniid families. "*Sparganium*" *aspensis* Brown (Fig. 41) is believed to be a Hamamelid fructification. Such fossils are most commonly attributed to Platanoids; however, associated leaves of this form are not present in the Aspen. It is possible that the fructification was produced by *Liquidambar fontanella.* An advanced Sapindophyll, *Sapindopsis schultzii* Brown, is present in the Aspen, as well as several other species of putative rosid affinity (Table 3).

The Cenomanian flora from the Frontier Formation of southwest Wyoming (Hall, 1845; Knowlton, 1917; Andrews & Pearsall, 1941) is a mixed pteridophyte–angiosperm assemblage preserved in volcanic sediments similar to those which yield the Aspen and Albino floras. The flora is from the lowermost part of the Frontier Formation and is referred to as the Lower Frontier flora in Figures 1 and 2 and in Table 3.

"*Cinnamomum*" *hesperium* Knowlton (Fig. 42) is very similar to Cinnamomophylls from the Middle and Late Albian, and as such is the only archaic element in this flora. Platanophylls are represented by "*Aralia*" *veatchii* Knowlton (Fig. 43), which is advanced over earlier members of the morphotype by its deeply divided lamina. *Dewalquea pulchella* Knowlton (Fig. 44) is a toothed, palmately compound leaf of uncertain affinity. The entire-margined, palmately compound leaf of "*Staphylea*"? *fremontii* Knowlton (Fig. 45), which also occurs in the Aspen flora (Table 3), shows well-developed, eucamptodromous secondary venation such as characterized many Rosidae. Palmately compound leaves are restricted to extant Ranunculiidae, Rosidae, and palmate Dilleniidae. Species with and without entire margins can be found in each of these groups. More detailed analysis of the venation and tooth morphology of the palmately compound leaves from the mid Creta-

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FIGURES 38–47. Dicotyledonous leaves from the Mowry, Aspen, Frontier, and Dunvegan formations. 38. Pinnately compound leaf, Mowry Formation. 39–41. Aspen Formation, USGS locality 8169.—39. "*Liquidambar*" *fontanella* Brown, USNM 39146, holotype.—40. "*Sassafras*" *bradleyi* Brown, USNM 39144, holotype.—41. "*Sparganium*" *aspensis* Brown, USNM 39140A, holotype. 42–47. Frontier Formation.—42. "*Cinnamomum*" *hesperium* Knowlton, USGS locality 6527, USNM 35260, holotype. 43–45. USGS locality 5049.—43. "*Aralia*" *veatchii* Knowlton, portion of palmately divided leaf, USNM 35258, holotype.—44. *Dewalquea pulchella* Knowlton, USNM 35255, holotype.—45. "*Staphylea*"? *fremontii* Knowlton, USNM 35230, holotype. 46, 47. Dunvegan Formation.—46. *Pseudoaspidophyllum latifolia* Hollick, GSC locality 4197.—47. *Protophyllum boreale* Dawson, GSC locality 4205, GSC 5398, holotype.

ceous of the region (*Dewalquea pulchella*, "*Diospyros*" *nitida* Dawson = "*Hymenaea*" *fayettensis* Berry, *Dryophyllum gracile* Debey, *D. lanceolatum* (Knowlton) Berry, and "*Staphylea*"? *fremontii*) is necessary before further conclusions are possible.

Far to the north of the floras just mentioned, the Dunvegan flora (Figs. 1, 2; Dawson, 1883; Bell, 1963, 1965) was recovered from coarse fluvial deposits in marked contrast to the volcaniclastic southern deposits. The Dunvegan flora, unlike the more southerly floras, contains several leaf genera that indicate considerable affinity with early angiosperm floras (*Araliaephyllum, Trochodendroides*, and "*Cinnamomum*"), as well as new forms. Platanophylls (Fig. 46) and Protophylls (Fig. 47) are numerically dominant in the Dunvegan assemblage. Entire-margined, palmately compound leaves and Dryophylls relate this flora to the Frontier and Aspen floras. The Dunvegan flora contains a suite of large, entire-margined leaves of the Magnoliaephyll morphotype (Table 3).

The Turonian flora (Berry, 1929d) from the upper part of the Frontier Formation (Table 3, Appendix I) comprises cycadophytes, taxodiaceous conifers, Cornophylls, Pentalobaphylls, and fragments of the laminae of a putative palm to which Berry (1929d) applied the name *Sabalites*, although the specimens lack evidence of costapalmate morphology. In addition, several rosidlike leaves are reported from the upper Frontier (Table 3).

SANTONIAN FLORAS

The lower Santonian Badheart flora from northeast British Columbia is notable for an abundance of Trochodendrophylls (*Trochodendroides arctica* (Heer) Berry and "*Zizyphus*" *mcgregorii* (Bell)). These occur in association with the common Upper Cretaceous araucarian conifer *Geinitzia formosa* Heer (Bell, 1963).

LOWER CAMPANIAN FLORAS

The floristic record from this time rivals that for the Albian. Near equivalent floras are known from the Milk River, Eagle, and Two Medicine formations in Alberta and Montana (Figs. 1, 2). Floristics of the individual floras vary within a context of dominant Hamamelididae. Also important are Cornophylls and Rhamnophylls. Some collections contain an abundance of araucarian, taxodiaceous, and cupressaceous foliage. The small-leaved aquatic dicot *Quereuxia* (cf. "*Trapa*"? *microphylla* Lesquereux) is found in the Two Medicine. The earliest pinnate palm from the region is present in the Two Medicine.

The woody dicotyledonous flora (Bell, 1963, 1965) of the Milk River Formation in southern Alberta (Figs. 1, 2) is preserved in coarse fluvial sandstones and associated sediments. Unusual is the complete absence of Platanophylls from the flora. Other than Trochodendrophylls, there is an overall dearth of Hamamelidids. Trochodendrophylls (*Trochodendroides arctica* and *T. dorfii* Bell), Cornophylls ("*Magnolia*"? *coalvillensis* Knowlton and *Celastrinites* sp.), and Rhamnophylls ("*Ficus*" *trinervis* Knowlton) are the most abundant dicotyledonous leaf fossils.

The Eagle Formation extends through most of central Montana and northern Wyoming. A number of fossil localities are known, and some collecting has been done (see Appendix I), but our knowledge of the Eagle flora is based at present on the work of Knowlton (1900) in central Montana, and Bell (1963) in northcentral Montana. I was not able to locate the original collections for either of these treatments (see Appendix I), so my discussion is based on the published accounts.

Bell (1963) recognized five dicotyledons from the Eagle. The composition of the flora is very similar to that of the Milk River with *Trochodendroides dorfii*, Cornophylls, and Rhamnophylls. In addition, the flora contains a magnoliid-grade leaf "*Ficus*" *missouriensis* Knowlton, which was first described from the Eagle in central Montana (Knowlton, 1900).

Knowlton (1900) described a small, poorly preserved collection from the banks of the Missouri River (Appendix I). The flora contains a Platanophyll ("*Platanus*"? *wardii* Knowlton), which seems to be reliable to the family level. A Rhamnophyll ("*Ficus*" *trinervis*) and a rosid leaf ("*Juglans*" *missouriensis* Knowlton) are present. The latter may be sapindalean or juglandalean, based on the semicraspedodromous secondary veins that terminate near the sinuses of the teeth, margins with rosid teeth and rosidlike sinus bracing, and percurrent, transverse tertiary venation. "*Liriodendron*" *alatum* Newberry, a large leaf of probable magnolialean affinity, was also reported by Knowlton (1900). Knowlton's specimen shows little more than secondary venation, and identity with the type from the Amboy Clays (Newberry, 1895) must be considered tentative.

A more extensive, well-preserved assemblage from the lower Campanian Two Medicine Formation in northern Montana (Figs. 1, 2) is currently under investigation as part of my doctoral program. The flora consists of about 30 species of angiosperms, two conifers, and six ferns, and was recovered in Oilfield Coulee (Appendix I) from a single fluvial system extending in outcrop for two kilometers. It records the vegetation along a coastal plain river.

Pinnate palm fronds (Fig. 37) dominate the channel margin facies throughout the outcrop. The fronds are up to two meters long and are incompletely divided into induplicate segments. The fossil palm could be assigned to the form genus *Phoenicites* (sensu Read & Hickey, 1972) were it not for the absence of spines at the base of the frond. Occasional interbedded paludal facies contain "*Trapa*" (*Quereuxia*). Taxodiaceous and cupressaceous conifers are found in the basal lag deposits of paludal facies. *Nymphaeites* sp. foliage occurs in restricted parts of the outcrop.

Levee and other near-channel facies contain a diverse dicotyledonous flora that is dominated by leaves of Hamamelididae. Nonhamamelidid dicot leaves typically comprise about 10% of the megafossils. Dicot 43 (Fig. 49) is characterized by coriaceous texture, entire margins, and weakly percurrent tertiary venation irregularly spaced, eucamptodromous secondary veins that originate almost perpendicular to the midvein and turn upward rather abruptly near the margin. The leaf morphology indicates closest relationship to extant Rutales but should be considered tentative since Rutales have pinnately compound leaves, a feature not demonstrated for Dicot 43. A putative dilleniid (Dicot 1, Fig. 50) shows theoid teeth and closely spaced, thin, transverse-percurrent, tertiary venation. Several other minor components of the Oilfield Coulee flora have affinities to Dilleniidae on the basis of tooth morphology. Two species (Dicots 57 and 19, unfigured) of entire-margined, imperfectly actinodromous leaves with thin, percurrent, tertiary veins arranged in concentric series relative to the base of the leaf indicate palmate dilleniids.

A complex of four species (three of which are illustrated in Figs. 51–53) are related by their chloranthoid teeth and form an important and pervasive element at Oilfield Coulee. Dicot 11 (Fig. 51) is pinnately veined with secondary veins clustered at the base; these are weakly craspedodromous, and the tertiaries are thin and transverse-percurrent. The leaf shows closest affinity with Trochodendrales but cannot be accommodated in either of the extant genera *Trochodendron* or *Tetracentron*. Another leaf in this complex (Dicot 12, not figured) more closely resembles extant *Trochodendron*, especially in details of tertiary and quaternary venation. Dicot 53 (Fig. 52) is a small, broadly elliptic leaf with pinnate venation and with secondary veins clustered at the base. Dicot 53 shares with extant *Cercidiphyllum* such features as shape, orientation and behavior of tertiary and higher order venation, and chloranthoid teeth with a tripod-like arrangement of accessory veins. *Cercidiphyllum* differs from the fossil in its well-developed actinodromous venation and greater tendency for tertiary veins to bifurcate. Dicot 53 is sufficiently like extant *Cercidiphyllum* that it can be placed into Cercidiphyllales. Dicot 50 (Fig. 53) has pinnate venation, craspedodromous secondary veins with the basal pair strengthened, and acute chloranthoid teeth. Tooth morphology most closely approaches extant Atherospermataceae; however, the craspedodromous secondaries and strong basal secondary veins of Dicot 50 make it a problematic species intermediate in morphology between Laurales/Chloranthales and Trochodendrales.

Dicot 25 (Fig. 54) has a morphology close to some extant Hamamelidaceae, notably Recent *Fortunearia*. The fossil has strong craspedodromous secondary veins that end in scalloped teeth with spinose tips; the tertiary and quaternary venation is strong and branched orthogonally. Dicot 25 is the most abundant and widespread of the Two Medicine dicot taxa and probably represented a deciduous plant with large, chartaceous leaves. Another hamamelid (Dicot 36, not figured) shows leaf morphological features convergent with extant *Hamamelis* and *Fothergilla*. Second in overall abundance at Oilfield Coulee are two species of Platanaceae (Figs. 56, 57). Both are large, rhombic leaves with palinactinodromous venation, pectinal veins, nipple-shaped teeth, and orthogonal tertiary and quaternary venation.

Much of the diverse Oilfield Coulee flora cannot be treated fully here. One leaf species (Dicot 17, not figured) is entirely consistent with the leaf morphology of extant Menispermaceae. Several taxa of magnoliid-grade leaf morphology are present (e.g., Fig. 55).

Other poorly known collections from the Two Medicine exist (Appendix I). Because the Two Medicine Formation extends upsection to the top of the Campanian, and I have not revisited


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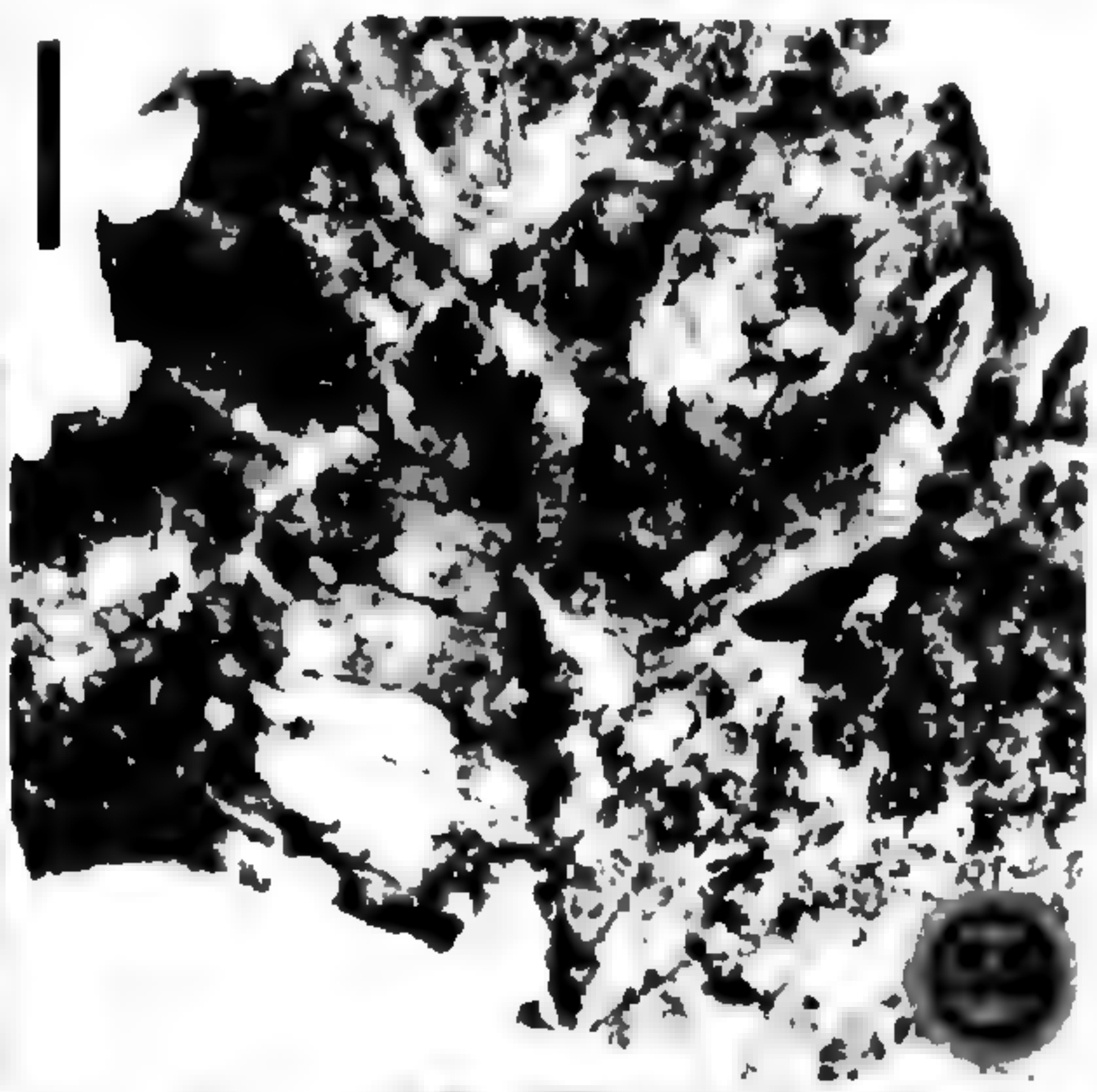
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the collecting localities, it is difficult to assess the age of these collections. One specimen is illustrated (Fig. 47) from these localities. The leaf fits the Cinnamomophyll morphotype and may represent Laurales based on the presence of basilaminar secondary veins, basal secondaries at a lower angle than superadjacent secondaries, admedial orientation of tertiary venation, subparallel and irregularly branched quaternary venation, and possible mesophyll secretory bodies.

MIDDLE CAMPANIAN FLORAS

Floras are known from the Judith River Formation in central Montana (Knowlton, 1905) and the Oldman Formation in southern Alberta (Penhallow, 1908; Bell, 1963, 1965). The two floras were recovered from fluvial sandstones and exhibit a similar composition. Simple leaves with serrate margins and pinnate, craspedodromous venation allied to Hamamelidaceae predominate. There is some evidence for the presence of Trochodendrophylls (Hickey, 1984). Diverse Platanophylls, including "*Platanus*" *affinis* Lesquereux, are found in the Oldman flora. "*Artocarpus*" sp. (Bell, 1965) from the Oldman is a pinnately compound leaf, the leaflets of which are pinnately veined with eucamptodromous secondary veins and many intersecondaries. This morphology relates it to rosid groups, including Sapindales, Rutales, and Rosales. Dawson (1886, 1887) described plants from the Belly River series, which is equivalent to the Judith River–Oldman floras. His species appear unusually advanced for the Campanian, an attribute Knowlton (1900) ascribed to stratigraphic mixing of the collections. Ramanujan (1972) reported on permineralized coniferous woods of Taxodiaceae and Podocarpaceae from the Oldman Formation.

Several other lower and middle Campanian floras exist from the NRM region. They are the Allison flora from southwest Alberta (Berry, 1929d), the Maudlow flora (Skip & McGrew, 1977), and the Livingston flora (Knowlton, 1893) from southcentral Montana, the Adaville flora from southwest Wyoming (Dorf, 1955), and the Point of Rocks flora from southcentral Wyoming (Brown, 1956; Dorf, 1955; Knowlton, 1900; Lesquereux, 1878; Newberry, 1898; Ward, 1885, 1887).

SUMMARY

During an approximate three million year period of the Middle and Late Albian, angiosperms displaced gymnosperms as the dominant lowland vegetation of the NRM region. This occurred shortly after the entry of angiosperms into the region. Upland vegetation retained a predominantly gymnospermous composition. Pteridophytes remained important through this period, although composition changed. Ginkgophytes, Cycadophytes, and Pteridosperms decreased dramatically.

Although the arrival of angiosperms can be seen as the essential agent of change, several environmental factors correlate with the floristic changes in the Albian. The Cretaceous epeiric seaway expanded across the mid-continent for the first time during the Albian. Climatic seasonality may have increased due to increased orogenic activity in the Cordillera and increased temperatures.

Early angiosperms with low rank leaves such as *Rogersia* and *Ficophyllum* are not recognized in the NRM region. The Middle Albian flora is closely allied to time equivalent floras at lower latitudes in North America. The similarity is most pronounced at the level of genus, although a few species appear to have ranged across North America during this time. As in the Potomac flora, Sapindophylls and Platanophylls form a conspicuous element. Other groups, such as the Cinnamomophylls and Pentalobaphylls, appear to have achieved prominence earlier in the NRM region than elsewhere in North America and impart a uniqueness to the regional flora.

Leaf morphologies indicate that early mem-

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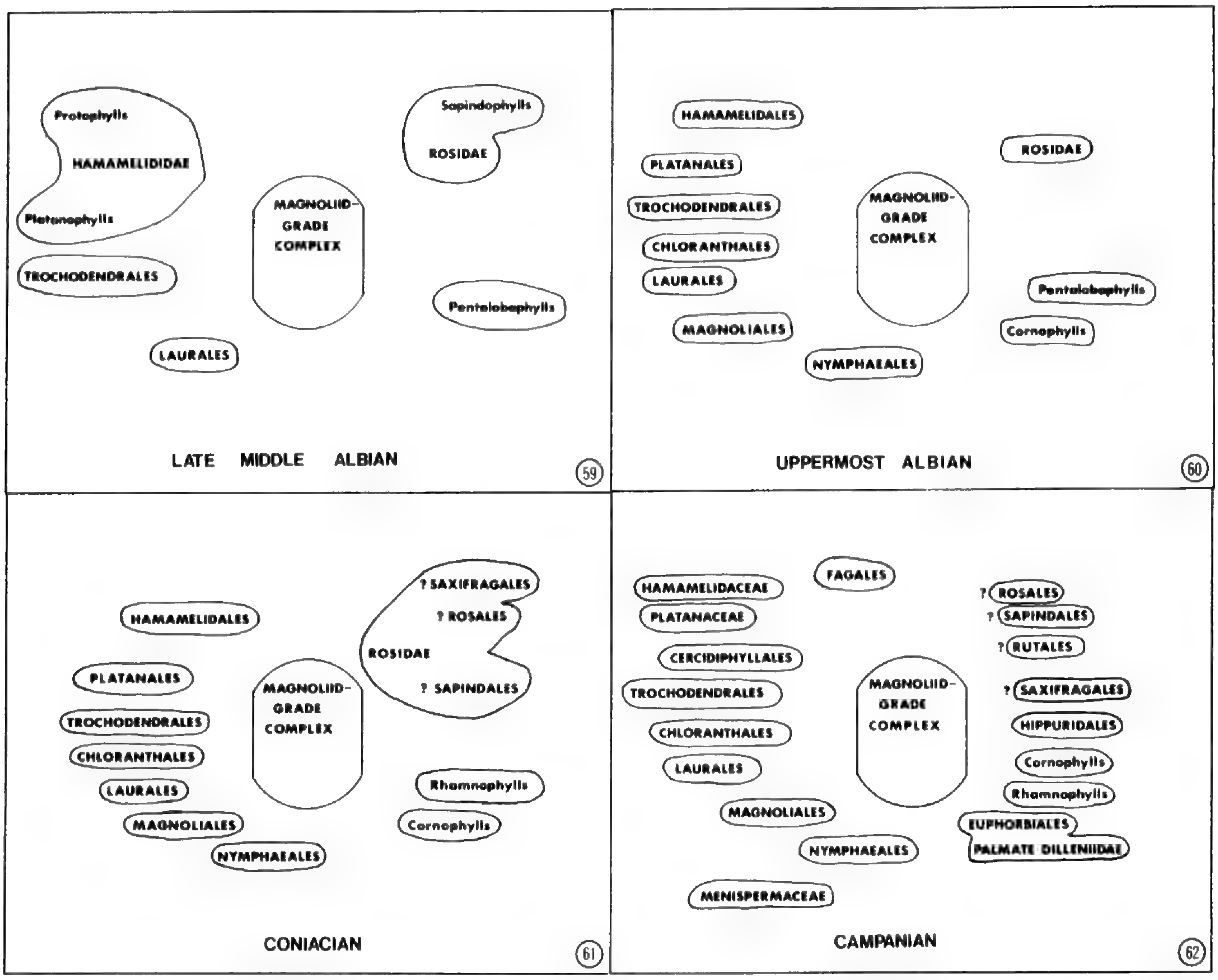
FIGURES 48–58. Angiosperm megafossils from the Two Medicine Formation. Specimen numbers correspond to the research collection housed at the Department of Botany, University of Montana. 48–57. "Oilfield Coulee" locality.—48. Pinnate palm, 23A/M1/003.—49. Rutales?, Dicot 43, 56A/43/001.—50. Dilleniidae, Dicot 1, 40A/01/001.—51. Trochodendrales, Dicot 11, 50A/11/001.—52. Cercidiphyllales, Dicot 53, 57A/53/001.—53. Indeterminate leaf with craspedodrome secondaries, strong basal secondary veins, and chloranthoid teeth, Dicot 50, 55A/50/001.—54. Hamamelidaceae, Dicot 25, S174A/25/010.—55. Magnoliid-grade leaf of uncertain affinity, Dicot 27, 39B/27/002. 56, 57. Platanaceae.—56. Dicot 32, HPC/32/022.—57. Dicot 6, 24A/06/021.—58. Laurales, USGS locality 6015.



FIGURES 59–62. Changing diversity and floristic affinity of the pre-Maastrichtian dicotyledonous flora of the northern Rocky Mountain region. Occurrences of taxa are based on interpretation of leaf morphology except in the following cases: Chloranthales (*Clavatipollenites*), Hippuridales (*Retitricolpites microreticulatus* Brenner), Fagales (*Tricolporopollenites* sp.), and Euphorbiales (*Erdtmanipollis*). Muller (1981) accepted these occurrences as indicative of the presence of the taxa (see also Norris et al., 1975; Rouse et al., 1971).

bers of several Recent higher taxonomic categories of angiosperms existed in the Albian flora (Figs. 59, 60). Sapindophylls appear to be allied to primitive Rosidae. Hamamelididae is well represented by Platanophylls, Protophylls, and Trochodendrophylls. Magnoliidae allied to Laurales, Magnoliales, Chloranthales, and Nymphaeales are probable. Monocotyledons are not apparent in the megaflora of the NRM region until the Late Cretaceous.

The early angiosperm flora includes several prominent groups with no clear relationship to Recent taxa (Table 1). Pentalobaphylls exhibit some affinity with Rosidae and Magnoliidae. The morphotypes Cinnamomophyll, Rhamnophyll, Cornophyll, and Magnoliaephyll are informal categories based on leaf morphology. The names do not imply relationship to any modern group, merely convergence in leaf morphology with modern forms. Much of the diversity of early dicotyledons is manifest in these morphotypes. New higher level taxa will probably be necessary to allow for their adequate classification.

Cenomanian floras in the region retain some older elements (Platanophylls, Protophylls, Cinnamomophylls, and Trochodendrophylls are worthy of mention), but on the whole are more modern in aspect, contain higher rank leaves, and are more diverse than Albian floras. Latest Albian and Cenomanian floras from lower latitudes within the region contain Dryophylls and *Dewalquea*.

Post-Cenomanian floras continue to diversify, attaining levels of advancement consistent with several modern orders and families (Figs. 61, 62). Hamamelididae (Platanaceae, Trochodendrales, Hamamelidaceae, Cercidiphyllales, and Fagales), palmate Dilleniidae, and Rosidae are a persistent part of the flora. Magnoliidae (Laurales, Chloranthales, Nymphaeales, and Magnoliales) appear as members of individual floras. Ranunculiidae (Menispermaceae) is recognized from the lower Campanian in Montana. Pinnate palms date from the Lower Campanian. The group is historically associated with stream margin environments.

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APPENDIX I

LOCALITY INFORMATION, CHRONOSTRATIGRAPHIC REFERENCES, AND LOCATIONS OF COLLECTIONS FOR NORTHERN ROCKY MOUNTAIN REGION FLORAS

Megafossil collections referred to in this report are listed below in alphabetical order. Numbers in parentheses following name of collection correspond to those used in Figures 2 and 3 and in Tables 2 and 3. Chronostratigraphic references are placed in parentheses immediately following the age. Specific locality information is provided only for collections that have not been published or have been published but with locality information absent or sketchy. All others are referenced to the publications that provide locality specifications. Institutions where collections are housed are indicated.

ALBINO (1). Upper Upper Albian (Roberts, 1972). I made a small collection from leaf mats in the Albino Member of the Mowry Formation along Beaver Creek, Gallatin County, Montana. This locality is in pink and white volcaniclastic siltstones of the Albino Member of the Mowry Formation in the NW ¼, SW ¼, sec. 18, T. 7 S, R. 4 E. Collections are housed at the Department of Botany, University of Montana. An extensive fern flora is also known from the Albino Member (Crabtree, 1983).

ASPEN (2). Upper Upper Albian (Cobban & Reeside, 1952a; Nichols & Jacobson, 1982). This collection is from the predominantly marine Aspen Formation at USGS locality 8168 located in the NW ¼, sec. 6, T. 24 N, R. 115 W northwest of Kemmerer, Lincoln County, Wyoming. The formation is 1,000 feet thick here, and the plants occur 125 feet from the top (Brown, 1933a). Collections are housed at the U.S. National Museum.

BADHEART (3). Lower Santonian (Stott, 1961, 1963; Bell, 1963). Collections are from the Badheart Formation in the vicinity of Belcourt Ridge, eastcentral British Columbia. Collections are housed at the Geological Survey of Canada.

BEAVER MINES (4). Lower Middle Albian (Bell, 1956; Mellon, 1967; Mellon & Wall, 1963; Stott, 1968; Singh, 1971). Collections are from the Beaver Mines Formation in the vicinity of Crowsnest Pass, southwest Alberta. Collections are housed at the Geological Survey of Canada.

BLACKLEAF (5, 19, 20). Lower Upper Albian (Cannon, 1966; Rice & Cobban, 1977). Collections come from several USGS localities in the Vaughn Member of the Blackleaf Formation in northwestern Montana. Collections are described under three headings which correspond to geographic locations:

Black Eagle (5). The single locality is in the NW ¼, SE ¼, NE ¼, sec. 13, T. 21 N, R. 3 E about 5 km north of Great Falls, Cascade County, Montana. Collections are housed at the Department of Botany, University of Montana.

Summit (19). Collecting localities are scattered for about 10 km along the east side of Marias Pass along the Burlington Northern Railroad, USGS field localities 5984, 5985, 5986, 6007, and 9439 in Glacier County, Montana. A separate area exists on the west side of the pass in the S ½, sec. 1, T. 29 N, R. 14 W Flathead County, Montana. Collections are housed at the U.S. National Museum with the exception of a small collection from ½ mile west of Marias Pass, which is at the Department of Botany, University of Montana.

Sun River (20). USGS locality 9437 from the SW ¼, SE ¼, NE ¼, sec. 36, T. 22 N, R. 13 W on the north side of the Sun River, Teton County, Montana. Collections are housed at the U.S. National Museum.

COMMOTION (6a, 6b, 6c). Collections are from three members of the Commotion Formation and are housed at the Redpath Museum and the Geological Survey of Canada. Each member is treated separately below.

Lower Gates (6a). Lower Middle Albian (Bell, 1956; Mellon et al., 1963; Stott, 1960, 1968; Singh, 1971). Collections are from the lower Gates Member in the vicinity of Pine River, northeast British Columbia.

Upper Gates (6b). Middle Middle Albian (Bell, 1956; Mellon et al., 1963; Stott, 1960, 1968; Singh, 1971). Collections are from the upper part of the Gates Member along Belcourt Ridge, eastcentral British Columbia.

Boulder Creek (6c). Middle Middle Albian (Bell, 1956; Stott, 1968; Singh, 1971). Collections are from the Boulder Creek Member in the vicinity of Pine River, northeast British Columbia.

CROWSNEST (7). Lower Upper Albian (Bell, 1956; Mellon & Wall, 1963; Mellon, 1967). Collections are from the Mill Creek Formation in the vicinity of Crowsnest Pass, and along the eastern side of the Front Range in southwest Alberta. Collections are housed at the Geological Survey of Canada.

DUNVEGAN (8). Cenomanian (Bell, 1963; Stott, 1960, 1968). Collections are from the Dunvegan Formation in the vicinity of Pine, Smokey and Peace rivers, northwest Alberta and northeast British Columbia and are housed at the Redpath Museum and the Geological Survey of Canada.

EAGLE (9). Lower Campanian (Cobban & Reeside, 1952a; Russell, 1970). The Eagle flora reported by Knowlton (1900) was collected by Lester Ward in 1883. Knowlton's description of the location is vague: "the south side of the Missouri River near Bear Creek." Knowlton's specimens, several of them types, are missing from the U.S. National Museum.

I attempted to relocate Ward's site and found a small assemblage from along the Missouri River below Rattlesnake Coulee about 12 km south of Coal Banks, Chouteau County, Montana, in section 24, T. 26 N, R. 12 E. This collection is at the Department of Botany, University of Montana.

Bell (1963) reported a flora from Buckley and Red Coulees, Toole County, Montana, in the vicinity of the International Boundary south of the town of Milk River, Alberta (see Evans, 1930). I was unable to locate this collection at the Geological Survey of Canada.

In recent years, collecting has been carried out at USGS locality 7633 from the Eagle Formation by L. J. Hickey in Elk Basin, Park County, Wyoming, in the SE ¼, NE ¼, NW ¼, NW ¼, sec. 21, T. 58 N, R. 99 W. His collections are housed at the U.S. National Museum.

FALL RIVER (10). Upper Albian (Crabtree, pers. obs.). While at the U.S. National Museum I examined several specimens from USGS locality 7312 in the general collection. The ledger of field collection sites indicates that these plants were found in the Fall River Sandstone near Pine Creek, Wyoming. This is probably the Pine Creek mentioned by Ward (1899). As best I can judge from Ward's descriptions, the fossils are from R. 62 W, T. 55 N in Crook County, Wyoming, from a level 60 feet below the Dakota contact. This locality could be as old as Middle Albian.

FRONTIER (11a, 11b). Two main stratigraphic levels in the Frontier Formation have yielded plant megafossils. These are treated separately below.

Lower Frontier (11a). Lower Cenomanian (Cobban & Reeside, 1952b; Nichols & Jacobson, 1982). Many collections were made from the lower Frontier Formation as the result of geological fieldwork. Hall (1845) reported on the earliest collections from the Frontier made by the Charles Fremont Expedition. This site was apparently along Little Muddy Creek, Lincoln County, Wyoming, in the S ½, sec. 29, T. 19 N, R. 116 W. U.S. Geological Survey collections from this area and the adjacent sec. 6, T. 18 N, R. 116 W include USGS field localities 8676, 3671, 5048, and 5049. Knowlton (1917) reported on collections primarily from locality 5049. Subsequent collections from this and nearby localities were reported by Andrews & Pearsall (1941). All of these localities are from the same stratigraphic level about 1,200 feet below the Oyster Ridge Sandstone and are considered to be of lower Cenomanian age. Hall's original collection no longer exists. Knowlton's published collections are housed at the U.S. National Museum. Andrews's collection, primarily ferns, is at the Department of Biological Sciences, University of Connecticut. Unstudied collections are at the U.S. National Museum.

Upper Frontier (11b). Turonian (Nichols & Jacobson, 1982). Collections from the Frontier near Lander, Wyoming (Berry, 1929d) are from well above the Oyster Ridge Sandstone. These collections are housed at the U.S. National Museum.

JACKASS MOUNTAIN (12). Middle Middle Albian (Bell, 1956). Collections are from localities in the Jackass Mountain Formation in southcentral British Columbia and are housed at the Geological Survey of Canada.

JUDITH RIVER-OLDMAN (13). Middle Campanian (Cobban & Reeside, 1952a; Russell, 1970). The collections from the Judith River Formation described by Knowlton (1905) were collected at USGS locality 3272 along Willow Creek about 1.4 km east of old Fort Maginnis, Musselshell County, Montana. I can find no locality information for the Oldman Formation in southern Alberta, but see Ramanujan (1972) and Bell

(1965). Judith River collections are housed at the U.S. National Museum.

KINGSVALE (14). Middle Middle Albian (Bell, 1956). From localities in the Kingsvale Formation in southcentral British Columbia. Collections are housed at the Geological Survey of Canada.

MILK RIVER (15). Lower Campanian (Bell, 1963; Russell, 1970). Localities are in the Milk River Formation along Milk River, south Alberta (Bell, 1963). Collections are housed at the Geological Survey of Canada.

MILL CREEK (16). Lower Upper Albian (Mellon & Wall, 1963; Mellon, 1967). Collections are from the Mill Creek Formation near Crowsnest Pass and north along the foothills in southeast Alberta. They are housed at the Geological Survey of Canada.

PASAYTEN (17). Middle Upper Albian (Barksdale, 1975; Bell, 1956). From the Pasayten Formation in southcentral British Columbia. Collections are housed at the Geological Survey of Canada. The specimen in Figure 27 is at the Department of Botany, University of Montana.

PRE-MUDDY (18). Middle Middle Albian (Roberts, 1972). S. Vuke made this collection from beds below the Muddy Sandstone along Buck Creek, Gallatin County, Montana, in T. 8 S, R. 3 E. It is housed at the Department of Botany, University of Montana.

TWO MEDICINE (21). Lower Campanian (Russell, 1970; Lorenz, 1981). Collections are from the lower part of the Two Medicine Formation in "Oilfield Coulee" about 20 m above the contact with the Virgelle Sandstone in the SW ¼, sec. 18, T. 32 N, R. 5 W about 6 km south of Cut Bank, Glacier County, Montana. These are housed at the Department of Botany, University of Montana. Unstudied collections from USGS localities 6009, 6010, 6011, 6013, 6015, 6129, 6388, 6390, 8574, and 9449 in Glacier County, Montana, are housed at the U.S. National Museum.

WAYAN (22). Upper Upper Albian or Lower Cenomanian (Cobban & Reeside, 1952a; Moritz, 1953). During the course of many years, an amateur collector named Thomas Henry made a very large collection of *Tempskya* and other fossils from the Wayan Formation in the vicinity of Wayan, Caribou County, Idaho. The exact locality (-ies) is not known, but appears to have been in sec. 24, T. 5 S, R. 43 E and secs. 19 and 20, T. 5 S, R. 44 E. I could not relocate the sites during my own visits to the area in 1983. Most of the Wayan material is housed at the Department of Geology, Idaho State University. The specimens figured in this report (Figs. 21–23) are housed in the Department of Botany, University of Montana.

WINTHROP (23). Upper Albian or Cenomanian (Barksdale, 1975; R. Rau, pers. comm.). Collections housed at the U.S. National Museum and reputed to be from the Winthrop Formation are probably Paleocene in age (J. Wolfe, pers. comm.). Material in this report was collected by myself, R. Rau, and J. Robison from the type locality of the Winthrop Formation near the Boesel Ranch along the Methow River road in the NW ¼, NE ¼, SE ¼, sec. 14, T. 35 N, R. 20 E, Okanogan County, Washington. This collection is housed at the Department of Botany, University of Montana.

EOCENE AND OLIGOCENE FLORAS AND VEGETATION OF THE ROCKY MOUNTAINS[1]

SCOTT L. WING[2]

ABSTRACT

The Eocene and Oligocene epochs were times of major evolutionary, biogeographic, and vegetational changes in terrestrial plants. From a floristic perspective three major trends characterize this period in the Rocky Mountain region: 1) development of more distinct phytogeographic provinces from a relatively homogeneous Paleocene holarctic flora, 2) the early diversification in Eocene upland areas of presently important temperate families, and 3) the first appearances of many extant angiosperm genera and disappearance of many typically Cretaceous and Paleocene forms. From a vegetational perspective there are two strong trends. Initially there was an early Eocene spread of broad-leaved, evergreen forest to high northern latitudes (60°N), possibly the greatest geographic coverage such vegetation ever achieved. This was followed by the subsequent fragmentation of these forests to produce more open vegetation of lower stature in many areas. These floristic and vegetational trends were of great consequence for angiosperm evolution and biogeography. They were also significant in creating the ecological milieu for the evolution of early and mid Tertiary animals.

The Paleogene rocks and fossils of the Rocky Mountains and adjacent areas provide an exceptional window on the flora and vegetation of the time and place. Eocene and Oligocene rocks cover some 40% of the surface of the state of Wyoming (106,000 km^2), and their total outcrop area in the Rocky Mountain region is in the range of 300,000^2 km (Fig. 1). Over much of this vast outcrop, weathering has exposed the strata, making them available for paleontological and geological study. Eocene–Oligocene deposits from a variety of fluvial, lacustrine, and volcanically influenced settings have produced tens of thousands of fossils collected at hundreds of localities. These Paleogene sequences have the potential to yield one of the most complete and geographically extensive records of evolutionary and ecological change in a terrestrial biota. A century or more of paleontological and geological research has only begun to explore this potential, in part because of the vast area and great thickness of the sedimentary sequences.

This paper is intended to serve three goals. First, to set out the basic data on the location, stratigraphic positions, and relative ages of the fossil floras. Second, to summarize published work on Eocene and Oligocene flora and vegetation of the region and discuss previous hypotheses in light of current data. Third, to suggest new directions for future research aimed at a regional understanding of Paleogene floras that takes full advantage of the potential of such a widespread and prolific fossil record.

GEOLOGIC SETTING

The Rocky Mountain region is geologically diverse, and its Cenozoic history has been reviewed in a number of recent volumes (e.g., Robinson, 1972; Curtis, 1975; Flores & Kaplan, 1985). Eocene and Oligocene plant fossils are best known from the large intermontane basin fill deposits of the eastern Rocky Mountain area and from the primarily volcanic deposits of western Montana, northwestern Wyoming, Idaho, Oregon, and Washington. The separate depositional histories of these two areas are important for interpreting historical change in their floras.

The intermontane basins of the eastern Rocky Mountain area (Fig. 1) began to develop in the Late Cretaceous as parts of a relatively continuous Rocky Mountain foreland region that intermittently was covered by a mid-continent seaway. Uplift of local, initially east–west trending, mountain ranges during the latest Cretaceous–Paleocene began to divide the foreland basin into structurally, topographically, and sedimentologically discrete units. Consequently, each of the present intermontane basins has a separate Cenozoic history, yet some general trends have affected most or all of the basins.

Fluvial to paludal environments were preva-

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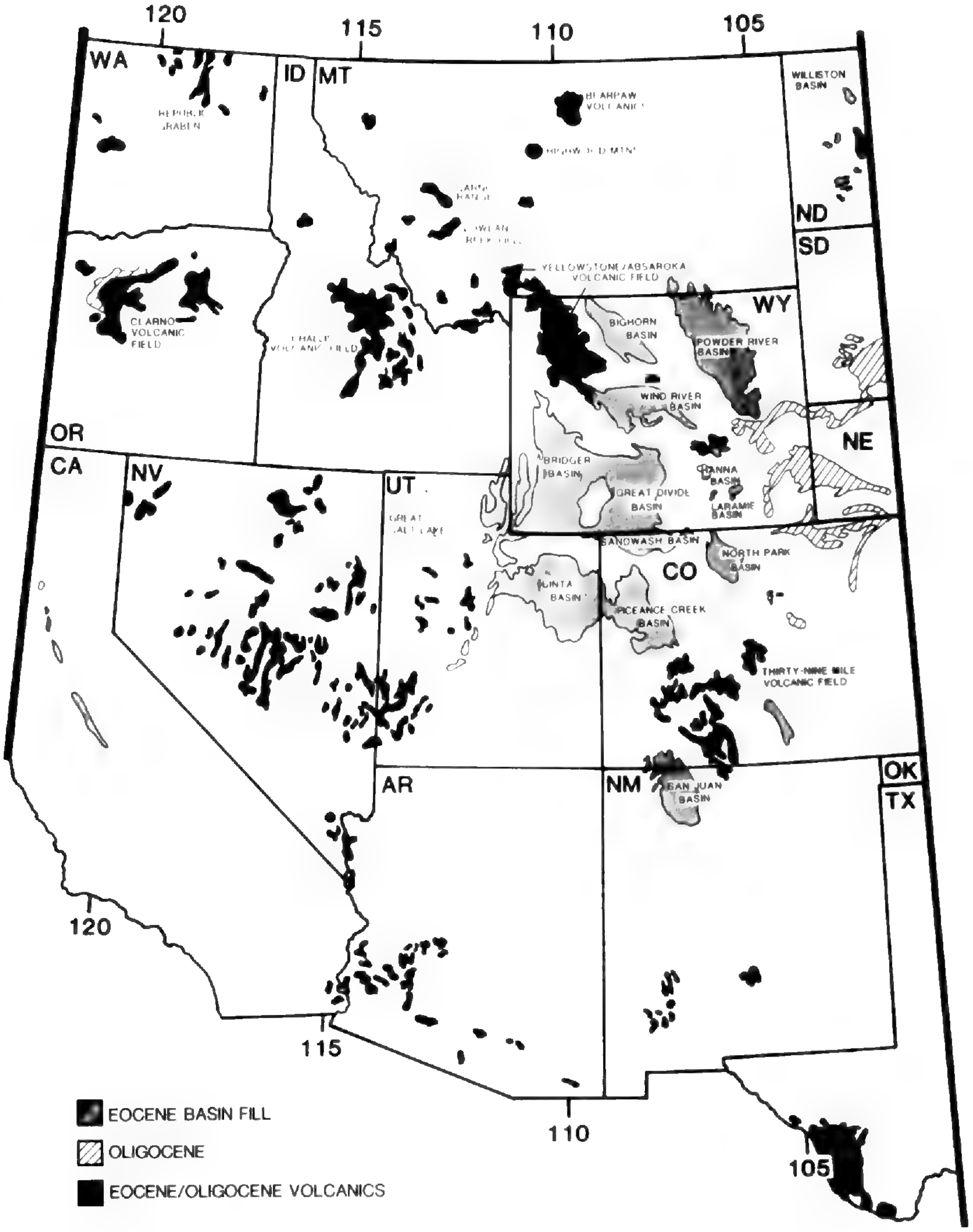

FIGURE 1. Outcrop area of Eocene and Oligocene rocks in the greater Rocky Mountain area.

lent throughout most of the area in the Paleocene and were environments of deposition for coals in the Powder River, Bighorn, Green River, and other basins. Fresh or brackish water lakes formed in the Uinta, Wind River, and Bighorn basins during the latter half of the Paleocene (Johnson, 1985; Keefer, 1965; Yuretich et al., 1984). Beginning in the Clarkforkian[3] and continuing into the Wasatchian, paludal deposition of organic-rich sediment waned in most of the basins, and alluvial floodplain sediments began to be modified by oxidizing pedogenic processes (Bown, 1979; Bown & Kraus, 1981). The onset of this kind of pedogenic modification was probably controlled by a combination of local tectonic and physiographic factors, as well as by regional climatic change (Wing & Bown, 1985).

In the later Wasatchian and Bridgerian, large lakes again developed in many of the basins (Bighorn, Green River, Uinta–Piceance). In at least some cases this appears to reflect hydraulic closure of the basin rather than climatic change (Johnson, 1985), and the lakes of the Green River and Uinta–Piceance Basins are known to have been saline during much of their later histories.

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[3] Through much of this paper, North American provincial land mammal ages (NALMA) will be used in favor of standard epochal subdivisions because NALMA are known to be relatively synchronous throughout western North America (Flynn et al., 1984) and because it is easier to correlate floras with nearby mammalian sites than with the type age/stages of Europe. Correlation of NALMA with epochal boundaries and time are given in Figure 2.

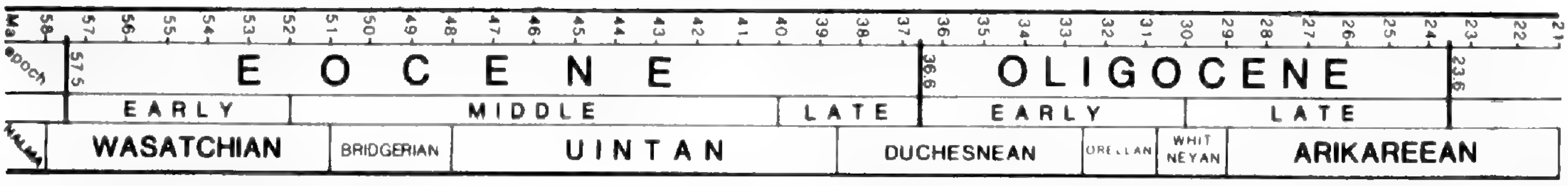

FIGURE 2. Correspondence of North American Land Mammal Ages (NALMA) with epochal and stage boundaries (after Berggren et al., 1985).

Much of the sediment filling these middle Eocene lakes and forming coeval fluvial deposits was derived from newly active volcanic fields in western Wyoming and Idaho.

During the later Bridgerian and Uintan most of the intermontane basins began to fill with sediment, and during the Duschesnean and Chadronian these sediments began to lap outward onto the tops of the bordering ranges. During the Oligocene, volcanically derived sediment continued accumulating at relatively slower rates in the eastern Rocky Mountains and Great Plains. Oligocene formations over much of the northern Rocky Mountains and Great Plains are typically thin, widespread units that were probably deposited on a surface of low relief.

The history of the volcanic centers in the western part of the northern Rocky Mountains is largely independent of that of the intermontane basin region. Volcanic activity was sporadic in southwestern Montana (the Elkhorn volcanic field) beginning in the latest Cretaceous and throughout the Paleocene (Roberts, 1972). However, the greatest pulse of volcanic activity began in the late Wasatchian to Bridgerian and continued through to the end of the Eocene.

From about 53 to 38 Ma there was volcanism across much of western Montana (Bearpaw, Garnet Range, Lowland Creek, Gallatin, and Beaverhead Canyon fields), northwestern Wyoming (Yellowstone–Absaroka Field), and Idaho (Challis Field), and in the Clarno area of Oregon, the Republic graben of northern Washington, and southern British Columbia (Chadwick, 1985). Although the intrusive and sedimentary rocks associated with these volcanic areas presently cover on the order of 10^5 km, it is likely that most of their original extent has been removed by erosion. Armstrong (1974) suggested that the Challis volcanic field once covered much of Idaho.

The extent and thickness of these broadly coeval volcanic deposits in the northern Rocky Mountain area indicate the region may have been a rugged, but more or less connected, volcanic highland during much of the Eocene (Axelrod, 1968; Fritz & Harrison, 1985). The prevalence of volcanic conglomerates and mudflows, and analogy with present day volcanic terrains, suggest strong topographic relief, which Fritz & Harrison (1985) estimated at 1,000–2,500 m difference between adjacent valleys and peaks.

Following the end of the Eocene, heavy volcanic activity shifted southward to southern Colorado, New Mexico, Arizona, and west Texas, and extensional tectonics began to affect the northern Rocky Mountains (Chadwick, 1985). A number of small, fault-bounded basins developed in western Montana during the Late Eocene and Oligocene. These basins filled with primarily fluvial and lacustrine deposits that were derived from both local sources and volcanics as far away as the Cascade Range of Oregon (Fields et al., 1985).

The geological events summarized above are highly relevant to the floristic and vegetational history of western North America. The development of a volcanic highland region in the northern Rocky Mountain region during the Eocene had several major effects on plant life, including: 1) dividing lowland areas that formerly had been continuous from the West Coast to the eastern Rocky Mountain region, 2) reducing the flow of Pacific-influenced air into the interior of North America, and 3) changing soil and groundwater conditions by the influx of airborne volcanic ash. Prior to and during the onset of these effects the low-lying area in the eastern Rocky Mountains was itself broken into a series of topographically isolated and somewhat climatically different basins. Thus the overall effect of geological events during the Eocene and Oligocene was fragmentation of a relatively homogeneous landscape along both north–south and east–west axes.

DISTRIBUTION OF FOSSIL FLORAS

No single source provides a comprehensive list of Tertiary plant localities in western North America. The list of localities given here (Appendix I) represents an attempt to bring together the bulk of Eocene and Oligocene localities of the greater Rocky Mountain region. I estimate that this list is 60–80% complete.

The locality information was derived from a number of published and unpublished sources. Previous works listing a significant number of localities include those by Axelrod (1966a, 1966b, 1968), Axelrod & Raven (1985), Brown (1937), Hickey (1977), Leopold & MacGinitie (1972), MacGinitie (1941, 1953, 1969, 1974), and Wolfe (1981, 1985). Unpublished locality information was derived from collections at the U.S. National Museum of Natural History (including those of the USNM, the U.S. Geological Survey, and some formerly belonging to Princeton University), and from collections at the Museum of Paleontology (University of California, Berkeley) and the Yale Peabody Museum.

Not all of the 240 "localities" compiled here are strictly equivalent. Some floras commonly considered as units actually consist of the summed floral lists of a number of separate quarry sites (e.g., the Ruby paper shale flora of Becker, 1961, was collected at 15 quarries), whereas others were derived from a single excavation (e.g., Copper Basin flora of Axelrod, 1966a). Most of the listed localities are individual quarry sites, but for some floras listed in the literature it was not possible to determine how many sites contributed to the flora.

Criteria used in correlating and determining the ages of floral localities included mammalian biostratigraphy, lithostratigraphic equivalence, magnetic polarity stratigraphy, and radiometric dates. In order to avoid circularity, floras were *not* correlated on the basis of their taxonomic composition or physiognomic characteristics. The Tertiary time scale used here is that of Berggren et al. (1985). Chronological boundaries for North American Land Mammal Ages are from West et al. (in press), and Prothero (1985a, 1985b). There is controversy over the precise age of the Eocene/Oligocene boundary. The date used here (36.6 Ma) is the most recent opinion, but many authors (e.g., Wolfe, this volume) use a date of about 34 Ma. Radiometric dates from older publications have been corrected for new constants using the tables published by Dalrymple (1979).

Fossil floras of Eocene and Oligocene age have a highly uneven geographic and stratigraphic distribution. Stratigraphically, the Wasatchian and Bridgerian are by far the best-represented time intervals, with the number of floras diminishing sharply through the Uintan and Duschesnean, and into the Oligocene (Fig. 3). Geographically, the northern Rocky Mountain region is far better sampled than the southern region (Fig. 4). These inequities in distribution result from at least four factors. 1) Bias of the author: my work has centered on the lower Eocene of Wyoming, so I am particularly aware of these localities. 2) Wasatchian, Bridgerian, and early Uintan sections are thicker and more widely exposed than later Eocene and Oligocene rocks. 3) Later Eocene and Oligocene rocks are generally less fossiliferous than early Eocene rocks, probably reflecting less favorable conditions for plant preservation associated with a drying climate in the Western Interior. 4) Collecting has been more intense in some areas than in others.

In addition to the uneven distribution of floras in space and time, there are also changes through time in environments of deposition. Nearly all Wasatchian plant assemblages were recovered from rocks deposited in fluvial or fluvial/paludal settings. Although some Bridgerian and later floras are from fluvial deposits, the best known (e.g., Green River, Florissant) are from lacustrine sediments. Floral samples drawn from fluvial environments represent the flora differently than do those from lacustrine environments.

Fluvial assemblages, particularly those deposited on low-energy flood basins, are largely derived from local vegetation (Scheihing & Pfefferkorn, 1984; Spicer & Greer, 1986; Burnham, in press). This results in considerable spatial heterogeneity in the fossil assemblage that probably reflects original variation in the local vegetation (Hickey, 1980; Wing, 1980, 1984).

By contrast, lakes receive input from surrounding lakeshore vegetation and from inflowing rivers (Spicer, 1981). These different elements may be mixed to various degrees and scattered across the lake bottom. Although lacustrine assemblages are overwhelmingly dominated by plant parts derived from nearby vegetation (Drake & Burrows, 1980; Spicer & Wolfe, 1987), they tend not to preserve in situ variation in vegetation. They may, however, preserve more of the species that were present in the regional flora. As a result of being derived from a larger source area and of predepositional transport and mixing, lacustrine assemblages are probably more diverse than fluvial assemblages, and specimens are more evenly distributed among the taxa present.

As a consequence of the inequities in distribution of fossil floras and nonequivalence in their

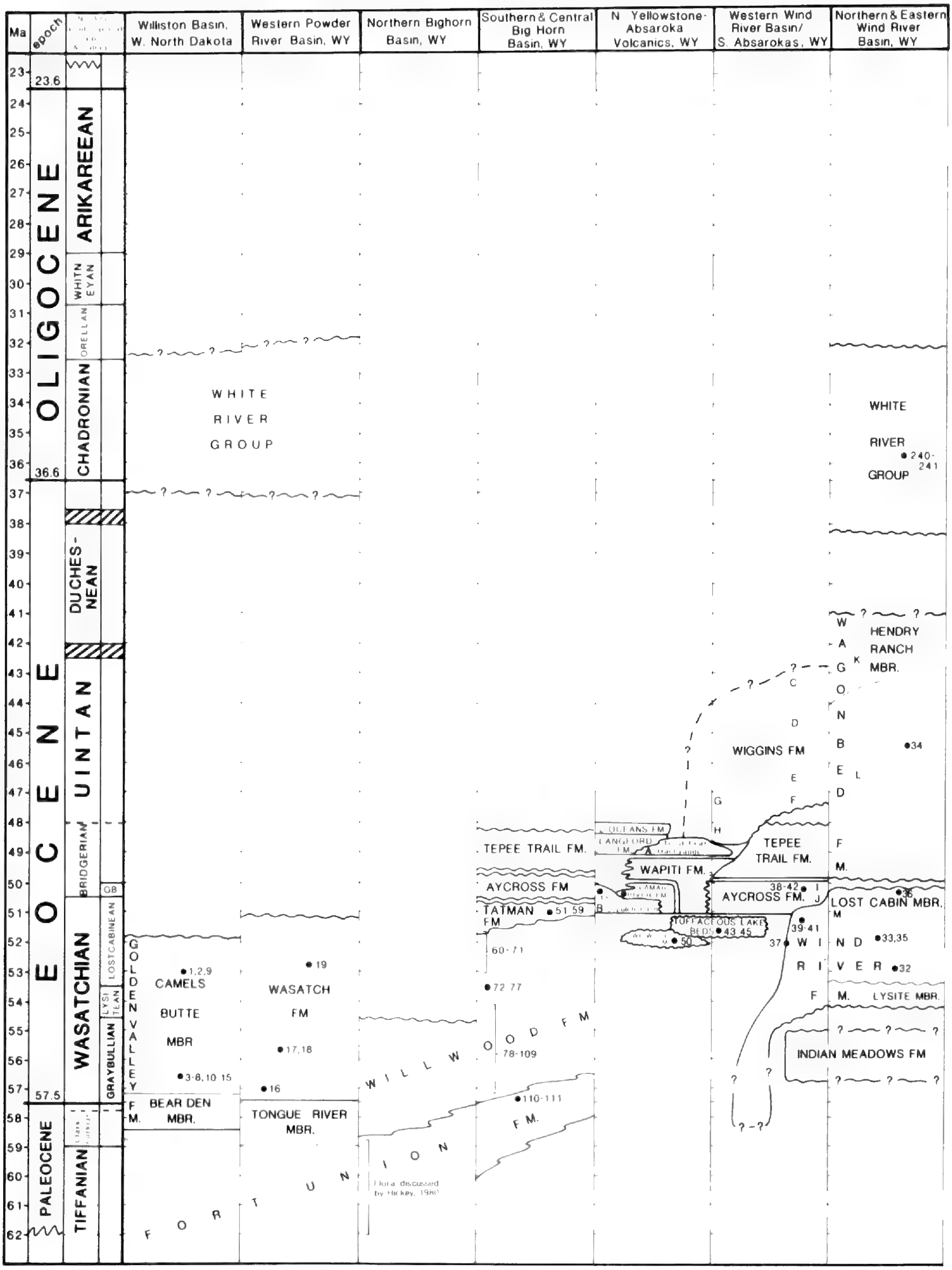

FIGURE 3. Correlation chart of Eocene and Oligocene floras from the Rocky Mountains and surrounding areas. Numbers indicate floras listed in Appendix I; letters (A–FF) indicate radiometric dates listed in Table 1.

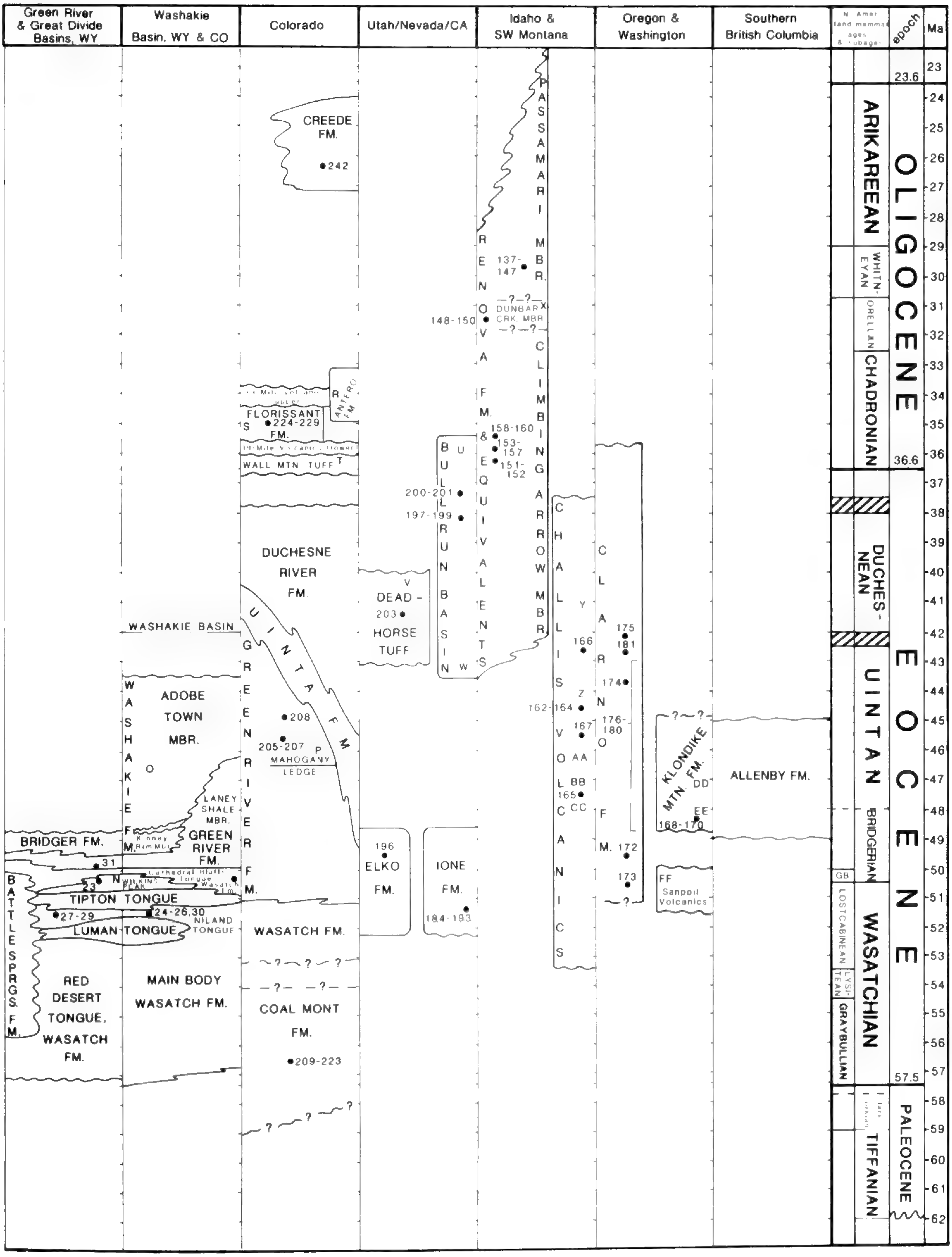

FIGURE 3. Continued.

TABLE 1. Radiometric dates of Tertiary floras in Figure 3.

Age		Stratigraphic Unit	Publication
A,	49.2 ± 0.7	Trout Peak Trachyandesite	Smedes & Prostka, 1972
B,	50.5 ± 1.55	Sepulcher Formation	Smedes & Prostka, 1972
C,	43.1	Wiggins Formation	Bown, 1982
D,	44.6	Wiggins Formation	Bown, 1982
E,	46.7	Wiggins Formation	Bown, 1982
F,	47.1	Wiggins Formation	Bown, 1982
G,	47.9 ± 0.5	Wiggins Formation	Bown, 1982
H,	48.5	Wiggins Formation	Bown, 1982
I,	50.4	Aycross Formation	MacGinitie, 1974
J,	50.6	Aycross Formation	MacGinitie, 1974
K,	42.3 ± 1.4	Henry Ranch Member, Wagon Bed Formation	Black, 1969
L,	46.2	Wagon Bed Formation, near Badwater, Wyoming	Evernden et al., 1964
M,	50.5	Halfway Draw Tuff, Wind River Formation	Evernden et al., 1964
N,	50.2	Little Mountain Tuff, Wilkins Peak Member, Green River Formation	Mauger, 1977
O,	46.7 ± 0.9	Washakie Formation, Bed 664 of Roehler	Mauger, 1977
P,	46.2	several hundred feet above Mahogany Ledge, Parachute Creek Member, Green River Formation	MacGinitie, 1974
Q,	26.5	Creede Formation	Axelrod, 1987
R,	34	Antero Formation	Epis & Chapin, 1975
S,	35	Florissant Formation	Epis & Chapin, 1975
T,	36–37	Wall Mountain Tuff	Epis & Chapin, 1975
U,	36	"Chicken Creek Formation," 5 feet above highest floral locality	Axelrod, 1966b
V,	41 ± 1	Deadhorse Tuff	Axelrod, 1966b
W,	43	"Frost Creek Formation," 1,500 feet below lowest floral locality	Axelrod, 1966b
X,	31.1	Williams Creek basalt	Fields et al., 1985
Y,	41.1 ± 1.6	Salmon area tuffs	Fritz & Harrison, 1985
Z,	44.2 ± 1.7	Salmon area tuffs	Fritz & Harrison, 1985
AA,	46.3 ± 1.0	rhyolite below "Dewey Beds"	Fritz & Harrison, 1985
BB,	47.2 ± 1.8	basalt above Germer Tuffaceous member	Edelman, 1975
CC,	48.0 ± 1.0	Latite-andesite Member, Challis Volcanics	Edelman, 1975
DD,	47.0 ± 1.8	Klondike Mountain Formation	Wolfe & Wehr, 1987
EE,	48.2 ± 1.6	Klondike Mountain Formation	Wolfe & Wehr, 1987
FF,	50–51	Sanpoil Volcanics	Wolfe & Wehr, 1987

depositional environments, there are obvious difficulties in interpreting patterns of vegetational and floristic change through time. In spite of these difficulties, a number of durable generalizations have emerged concerning the early Tertiary development of the Rocky Mountain flora.

FLORISTIC AND VEGETATIONAL HISTORY

Three major floristic trends are indicated by Eocene–Oligocene fossil assemblages from the Rocky Mountain area: the modernization of the angiosperm flora at the generic level, the breakup of the Paleocene North American province into distinct phytogeographic subregions, and the major diversification of many present-day microthermal lineages (e.g., Rosaceae, Betulaceae, Aceraceae). There were also three major vegetational periods during the Eocene and Oligocene. During the Wasatchian and Bridgerian there appears to have been a major poleward expansion of subtropical and paratropical forest types in response to global climatic warming (Wolfe, 1985). Perhaps beginning as early as the Clarkforkian in some areas, and of increasing importance during Bridgerian and later time, there is evidence that these forests were replaced in some parts of the region by more open subtropical vegetation of lower stature, probably as a result of local or regional orographic drying (e.g., MacGinitie, 1969). Finally, during the latest

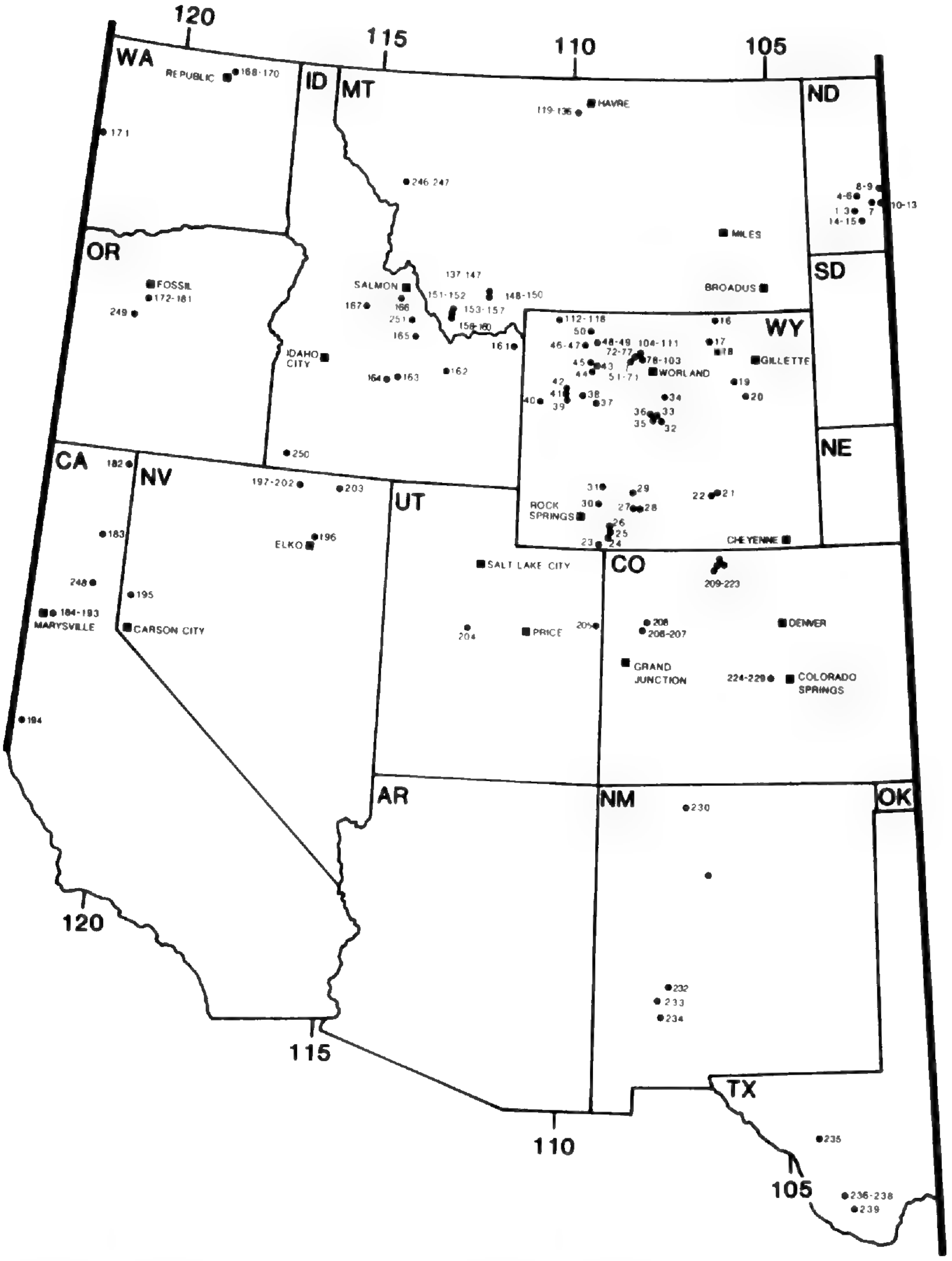

FIGURE 4. Map position of Eocene and Oligocene floras mentioned in the text and in Figure 3. Numbers refer to floras listed in Appendix I.

Eocene and Oligocene, vegetation of the Rocky Mountain region became dominated by a mixture of conifers and broad-leaved deciduous forms.

MODERNIZATION

Paleobotanical systematics of the last century and early in this century was based largely on superficial characteristics of leaves. This led to exaggerated estimates of the similiarities between extinct and modern floras. More recent systematic work has focused on detailed comparisons of leaf venation (e.g., Hickey, 1977) and on greater use of multiple organs (e.g., Manchester, 1986). One result of such work has been the realization that many Paleocene angiosperms represent extinct genera or intermediates between several related living genera.

In contrast, many, if not most, angiosperm remains younger than Late Eocene can be assigned to extant genera with little ambiguity, although sectional or other subgeneric-level affinities may be unclear (see Manchester & Crane, 1983 and Wolfe & Tanai, 1987 for well-documented exceptions). The temporal pattern of appearance of extant genera has not been quantified, nor has it been determined the extent to which this modernization reflects evolution within lineages as opposed to extinction of archaic lines and replacement by modern ones. Although this generic modernization of angiosperms is a striking systematic pattern, little has been said about its biological significance. Modernization at the generic level may reflect a true radiation of angiosperms, perhaps in response to changing climatic and topographic conditions in western North America, or it may be an artifact of our retrospective view. That is, the appearance of many modern genera in the Eocene occurred because angiosperms in a number of independent lineages accumulated enough recognizable generic characters to be pigeonholed easily in present-day categories. This question could be resolved by measuring and comparing rates of morphological change during the Paleocene and Eocene.

PROVINCIALITY

The Eocene divergence of Rocky Mountain and West Coast floras and its relationship to East Asian–North American disjunct distributions in a number of living plant groups is probably the most discussed aspect of the Tertiary paleobotanical record in western North America (e.g., MacGinitie, 1941; Leopold & MacGinitie, 1972; Wolfe, 1972; Hickey, 1977). Consequently, I will summarize the pattern only briefly.

Paleocene floras from across northern North America and to some extent of Europe and Siberia are relatively homogeneous (Wolfe, 1966). Leaf assemblages typically are of low diversity and dominated by a group of taxa including *Ginkgo, Metasequoia, Glyptostrobus, Macginitiea* ("*Platanus*") *nobilis,* "*Carya*" *antiquorum,* "*Ampelopsis*" *acerifolia,* and members of the *Cercidiphyllum* complex, among others. Such floras have been reported from Alaska (Wolfe, 1972), many areas of the northern conterminous U.S. (Brown, 1962), the Canadian high Arctic (Hickey et al., 1983), and Greenland (Koch, 1963).

Because some of these Holarctic Paleocene taxa (e.g., *Metasequoia, Cercidiphyllum*) are now East Asian endemics, Paleocene floras sometimes have been described as having "East Asian" affinities (although they are only East Asian in a modern context). During the Eocene many of these Paleocene ("East Asian") forms were eliminated from floras in the eastern Rocky Mountains, presumably as a result of their inability to withstand seasonal dryness (Leopold & MacGinitie, 1972). In contrast, some of the same lineages survived into the Neogene along the West Coast and in the northern intermountain region of North America. At the same time that the "East Asian" forms were being eliminated in the eastern Rocky Mountains, some of the new genera appearing there were "Central American"; that is, their closest living relatives are in the seasonally dry subtropics of Mexico and Central America (MacGinitie, 1969; Leopold & MacGinitie, 1972). This general pattern has been confirmed by additional work in the intermontane basins of the eastern Rocky Mountains, but three modifications should be noted.

Paleocene megafloral samples may be more uniform than actual Paleocene floras because the fossil assemblages have been collected from a limited and similar array of paleoenvironments that tend to have low floral diversity. This would accentuate the impression that a homogeneous floral province was being broken up in the Eocene.

The regional extinction of taxa with East Asian affinities and the appearance of taxa with Central American affinities began in the Clarkforkian and was well under way in some areas by the mid Wasatchian, considerably earlier than was recognized by Leopold & MacGinitie (1972), who lacked floras from the Paleocene–Eocene transition period. Clarkforkian taxa with closest living relatives in Central America include *Chaetoptelea microphylla, Woodwardia gravida,* and species of *Populus* sect. *Abaso.* By late Graybullian or Lysitean time, some taxa with closest living relatives in East Asia, such as *Metasequoia* and some members of the *Cercidiphyllum* complex, were already regionally extinct in basinal floras of the eastern Rocky Mountains.

The shift from East Asian to Central American affinities in the flora of the eastern Rocky Mountains was not a uniform process, and some significant taxa do not follow the pattern. For instance, the genus *Platycarya,* now confined to East Asia, did not appear in western North America until the early Wasatchian and achieved maximum abundance throughout the region in the latest Wasatchian and early Bridgerian before going regionally extinct (Leopold & MacGinitie, 1972; Wing & Hickey, 1984). This pattern also appears to hold true for several undescribed species in the Icacinaceae, Flacourtiaceae, and Menispermaceae. *Ailanthus,* also now endemic to East Asia, appeared in North America during the early to mid Eocene (Chalk Bluffs flora, Green River flora, Rate Homestead flora, MacGinitie, 1941, 1969), and was abundant in Oligocene floras from southwestern Montana (Becker, 1961,

1969) before going regionally extinct in the later Tertiary.

Floristic segregation of northern and southern areas was probably occurring at the same time as the better-documented and better-discussed east–west divergence (Axelrod & Raven, 1985). Unfortunately, few Wasatchian–Bridgerian floras have been reported from the southern Rocky Mountains (Fig. 4). One small Lysitean flora from the San Juan Basin (Tidwell et al., 1981) shows that two taxa common in the Gardnerbuttean and Bridgerian of Wyoming ("*Sapindus*" *dentonii* and *Eugenia americana*) appeared two to three million years earlier in New Mexico. This suggests the possibility that some taxa were migrating northward during the climatic warming of the early Eocene. A similar geographic pattern has been observed in some mammalian species (Beard, pers. comm., 1986).

DIVERSIFICATION OF MICROTHERMAL LINEAGES

The Wasatchian and Bridgerian floras from the eastern Rocky Mountain region are a mixture of taxa now associated with temperate and subtropical to paratropical climates. For instance, mesothermal to microthermal groups like the Betulaceae (*Alnus, Paleocarpinus*), Cercidiphyllaceae, and Hamamelidaceae (Hamamelidoideae) are frequently associated with members of megathermal groups such as the Icacinaceae (*Paleophytocrene*), Lauraceae (*Phoebe*), Palmae, and Cyatheaceae (*Cnemidaria*). In most of these floras the microthermal elements are not diverse, although they may be important in terms of abundance (Wolfe, 1972, 1977).

In contrast, floras of similar or somewhat younger age from the volcanic areas farther west may be strongly dominated in both abundance and diversity by microthermal taxa. This has been attributed to the relatively high paleoelevation of these floras (Axelrod, 1966b, 1968; Wolfe & Wehr, 1987). Currently the best known of these floras is from Republic, Washington (Fig. 4; Wolfe & Wehr, 1987, and unpubl.). The vegetation at Republic is inferred to have been a Mixed Coniferous forest, but the diversity of microthermal angiosperm groups is striking: Hamamelidoideae, 4 species; Fagaceae, 4 species; Betulaceae, 5 species; Rosaceae, 19 species; Aceraceae, 7 species (Wolfe & Wehr, 1987; pers. comm., 1987). Although the Copper Basin flora of northern Nevada (Axelrod, 1966a) is younger and less diverse, it shows a similar domination by microthermal taxa. *Alnus* is represented by 2 species, one of which accounts for 85% of the specimens, and there are 3 species of *Mahonia*, 6 of Rosaceae, 3 of *Acer*, and 3 of Ericaceae.

Although upland floras of Paleocene or greater age are not known, it seems possible that the first major diversification of many present-day microthermal lineages took place during the Eocene in upland areas like the volcanic highland of the northwestern United States (Wolfe, 1986, this volume). Some of these groups were represented by relatively generalized species in later Paleocene or early Eocene lowland floras. Thus the adjustment of basically megathermal or mesothermal lines to cooler climates initially may have taken place along altitudinal gradients (Wolfe, pers. comm., 1986). Following mid-Tertiary climatic cooling, these upland lineages spread and diversified over much of the Northern Hemisphere, whereas their megathermal or mesothermal sister taxa now have relictual southerly distributions.

One particularly good example of this pattern is seen in the genus *Populus*. Species of the primitive section *Abaso* are common in Clarkforkian, Wasatchian, and Bridgerian floras over much of North America (Eckenwalder, 1977; Wing, 1981), usually in lowland settings, although *Populus adamantea* does occur in probable Oligocene upland floras described by Becker (1960, 1972, 1973). The extant species of this section, *P. mexicana*, is distributed only in limited parts of northeastern and northwestern Mexico. The earliest record of the more advanced sections that account for most of the present-day diversity and distribution of the genus is in the late Eocene Bull Run flora (Axelrod, 1966a). A number of species belonging to the more advanced sections are common in later Tertiary floras, but there is no known fossil record of sect. *Abaso* poplars following the early Oligocene.

PATTERNS OF VEGETATIONAL CHANGE

The general pattern of vegetational change during the Eocene and Oligocene in western North America has been outlined in a number of publications (e.g., Axelrod, 1958, 1968; Axelrod & Raven, 1985; MacGinitie, 1941, 1969; Wolfe, 1971, 1975, 1985). Despite considerable disagreement on details, there is overall agreement about the large-scale trends. Broad-leaved evergreen forests were dominant over most of the area during most of the Eocene, with two main exceptions. Some areas in the eastern Rocky Mountains may have been dry enough to create more open, partially deciduous vegetation. Volcanic activity in the western Rockies during the late Wasatchian, Bridgerian, and Uintan generated uplands where conifers and broad-leaved deciduous taxa became important components of the vegetation. Climatic cooling and drying during the late Eocene and Oligocene brought about increasing dominance of mixed coniferous and broad-leaved deciduous forest.

Late Paleocene vegetation in most areas of western North America was broad-leaved evergreen forest with an admixture of deciduous elements (e.g., Golden Valley flora of Hickey, 1977). During the latest Paleocene and early Eocene (Wasatchian) world climates were warming (Savin, 1977; Wolfe, 1971, 1978; Wolfe & Poore, 1982), possibly as a result of elevated levels of atmospheric CO_2 and associated effects on circulation patterns (Owen & Rea, 1985; Rea et al., 1985). At this time evergreen broad-leaved taxa increased in importance within local floras.

Floras from the Willwood Formation of northwestern Wyoming span most of the Wasatchian and show an upward increase in the number of entire-margined (41% to 52%) and thick-textured leaves, although there are also changes in sedimentary environment that may be causally related to this shift (Wing, 1981). Using data on living vegetation presented by Wolfe (1979), these leaf-margin percentages correspond with Microphyllous or Notophyllous Broad-leaved Evergreen Forest. Wolfe (1985) interpreted slightly older (Clarkforkian) floras from the adjacent Powder River Basin as representing Paratropical Rainforest, suggesting that an overrepresentation of streamside taxa in Bighorn Basin floras from the Fort Union and Willwood formations, or a relatively higher elevation, has given them a "cooler" aspect. I think it more likely that the less entire-margined, presumably more deciduous, floras of the Bighorn Basin were under the influence of a seasonally dry climate as early as the middle Clarkforkian. This is also suggested by the development of oxidized soil horizons in floodplain sediments of this age in the Bighorn Basin (Gingerich et al., 1980). A resolution of this apparent conflict would involve detailed comparison of depositional settings of the floras or independent evidence for paleoelevation. Regardless of these somewhat different interpretations of vegetation in northern Wyoming, it is apparent that some form of broad-leaved evergreen forest extended as far north as 65° during the Wasatchian (Wolfe, 1985).

A great many Lostcabinian-aged (late Wasatchian) fossil localities are known from all over the state of Wyoming and from the Golden Valley Formation of western North Dakota (e.g., numbers 1, 2, 9, 19, 27–30, 32–33, 50–71; Fig. 3, Appendix I). These floras are mostly uniform in composition and dominated by one of two species of *Platycarya,* with important subdominants being *Alnus,* "*Dombeya*" *novi-mundi,* "*Dalbergia,*" *Zingiberopsis isonervosa,* and species of Icacinaceae, Lauraceae, Magnoliales, and Palmae. Common pteridophytes are *Cnemidaria magna, Lygodium kaulfussii, Thelypteris weedii, T. iddingsii,* and a large-statured species of *Equisetum.* The similarity in these floras may in part reflect similar environments of deposition occurring in a number of intermontane basins at approximately the same time. Given, however, that some range of depositional environments is spanned by these floras, it is likely that the successional vegetation most likely to be preserved in fluvial sediments was truly similar over this large region. This in turn implies the existence of few sharp climatic differences across the area, which is in distinct contrast with the early Bridgerian floras discussed in the next section.

Vegetation during early Bridgerian time (about 50 Ma). Although the latest Wasatchian and Bridgerian were the times of maximum poleward extent of broad-leaved evergreen forests, vegetation of the Rocky Mountain region began to differentiate more strongly during this time interval. This differentiation is illustrated by comparing four floras: the Little Mountain flora from the upper Wilkins Peak Member of the Green River Formation in southern Wyoming (23 in Figs. 3 & 4, Appendix I), the Boysen flora from the upper part of the Wind River Formation in the northcentral Wind River Basin (36), the Kisinger Lakes-Tipperary flora from the Aycross Formation in the western Wind River Basin (38, 42), and the flora of the lower Sepulcher and Lamar River formations in Yellowstone National Park in northwestern Wyoming (112–118). All four of these floras are approximately 50–51 Ma and correlate with Gardnerbuttean (early Bridgerian) mammalian faunas.

Based on floristic affinities, foliar physiognomy, and sedimentological data, MacGinitie (1969) inferred that the Little Mountain flora was derived from open woodland vegetation. (MacGinitie used the term "savanna woodland," although he pointed out this might misleadingly imply that grasses played an important role in the vegetation.) More recently, Wolfe (1985) stated that leaf size in the Green River floras is too large for scrub or savanna vegetation and is more consistent with semideciduous subtropical to paratropical forest. The 22 species of dicotyledonous leaves from the Little Mountain flora are generally small and thick textured, and a number of the species belong to families or genera typical of seasonally dry subtropical vegetation (e.g., *Alchornea, Cardiospermum, Populus* sect. *Abaso,* and a number of microphyllous Leguminosae; MacGinitie, 1969: 67–68). Recent sedimentological work on the Wilkins Peak Member suggests that deposition took place in and around the margins of a playa lake that lay in an orographic desert basin (Smoot, 1983). The upper part of the Wilkins Peak Member apparently represents the maximum transgression of the lake and hence the wettest period during the deposition of this part of the Green River Formation (Smoot, 1983).

The Boysen flora is largely undescribed, although it was referred to in a treatment of the Green River flora (MacGinitie, 1969). This flora occurs in fluvially deposited, irregularly fissile, tuffaceous mudstones at the southern edge of the Owl Creek Mountains. The assemblage has approximately 15 species and is heavily dominated by palm leaves, *Lygodium kaulfussii,* and an entire-margined dicot leaf resembling *Sapindus* spp. Other common elements include "*Populus*" *wyomingiana, Canavalia diuturna,* cf. *Typha, Zingiberopsis isonervosa,* and *Musophyllum complicatum.* The importance of palms, herbaceous monocots, and vines suggests low-stature, perhaps relatively open, floodplain vegetation. Somewhat similar vegetation may have been responsible for forming the Lostcabinian-aged Vermillion Creek coal in southern Wyoming (Nichols, in press).

The Kissinger Lakes-Tipperary flora consists of 5 ferns, 1 horsetail, 2 conifers (*Glyptostrobus* and *Chamaecyparis*), and 44 angiosperms (MacGinitie, 1974). Of the 36 well-defined dicotyledonous leaf types, 55% have nonentire margins, and judging by their closest living relatives, some 60% were deciduous. A number of the genera in the fossil assemblage are presently restricted to subtropical or tropical climates (e.g., *Acrostichum, Apeiba, Canavalia, Dendropanax, Thelypteris*). Based on foliar physiognomy and the distribution of living relatives, MacGinitie (1974) inferred that the Kisinger Lakes flora was derived from a subtropical to tropical, semideciduous forest resembling those native to the southwest coast of Mexico at elevations of about 1,000 m. These inferences are consistent with the diverse palynoflora, which in most samples is dominated by angiosperms and ferns (Leopold, 1974).

The fossil floras of Yellowstone National Park were first described by Knowlton (1899) and have not been subjected to a general revision since. Therefore, most of the published identifications are probably incorrect. Furthermore, much of the megafossil material comes from sites that are imprecisely located and of unknown stratigraphic relationship. It may be that significant temporal change within the "Yellowstone flora" has remained undetected as a result. In spite of these problems, most of the Yellowstone assemblages were derived from vegetation that was quite different from the kind inferred for the assemblages discussed above.

Four genera of conifers are known from megafossil remains (*Sequoia, Glyptostrobus, Pinus,* and ?*Podocarpus*), and the first three are abundant at many localities (Dorf, 1960; Aguirre, 1977). As might be expected, the importance of conifers is even more strongly indicated by the palynoflora, where they are diverse (12 genera) and consistently make up about half of the flora (Fisk, 1976). Ferns are also highly diverse and abundant at many localities in the Sepulcher Formation. Fisk (1976) reported 28 species of pteridophyte spores from the Yellowstone Park palynoflora, and there are 10–15 named species from the macroflora. The local abundance of ferns at some localities (particularly *Thelypteris weedii* and *Allantoidiopsis erosa*) may be related to the frequency of disturbance by volcanic events. A similar dominance of ferns in the colonizing vegetation has been noted following eruption and deposition in the vicinity of El Chichón volcano in Mexico (Spicer et al., 1985).

The foliar physiognomy of the Yellowstone National Park floras has not been studied in detail, but dicot leaves in the collections at the U.S. National Museum of Natural History are mostly in the notophyll and mesophyll size categories. Drip tips are present on a few taxa, and roughly half of the species have entire-margined leaves. Although the percentage of entire-margined species is similar at Yellowstone (approximately

50%) and Kisinger Lakes (54%), leaf size in the Kisinger Lakes flora is generally in the microphyll to notophyll range (Wing, unpubl. data; Wolfe, pers. comm., 1987). These physiognomic aspects of the Yellowstone assemblages, in addition to the importance of conifers, suggest that the vegetation grew under a somewhat cooler and perhaps less seasonally dry climate. The forest from which the Yellowstone flora was derived appears to have been a variety of broad-leaved evergreen forest that included a substantial element of conifers in some local environments.

The question of taphonomic mixing of floral assemblages is ever present but has been a particular focus of debate with regard to fossil floras from Yellowstone National Park (Fisk, 1976; Fritz & Fisk, 1978; Fritz, 1980a, 1980b, 1981a, 1981b; Retallack, 1981; Yuretich, 1984; Karowe & Jefferson, 1987). The mixture of "tropical" and "temperate" elements (e.g., *Thuja* and presumed evergreen members of the Lauraceae) in the Yellowstone floras has been attributed to transport of plant remains derived from vegetation growing at a range of elevations (Fisk, 1976; Fritz, 1980a, 1986), and the upright stumps and autochthonous "fossil forests" described by Knowlton (1899) and Dorf (1964) have been explained in part as the consequence of transport by mudflows associated with volcanic activity (Coffin, 1976; Fritz, 1980a, 1980b, 1986; Fritz & Harrison, 1985).

Observations of present-day volcanic systems have shown that high-energy mudflows can transport upright stumps from higher to lower elevations, and that stumps weighted by soil trapped in their roots may float upright for a time in lacustrine situations (Fritz, 1980a, 1980b, 1986; Coffin, 1983). Furthermore, sedimentological and stratigraphic studies of the Sepulcher and Lamar River formations and other Eocene volcanic units have highlighted the importance of high-energy deposits that are presumably indicators of steep paleotopography (Fritz, 1980c; Fritz & Harrison, 1985). In spite of these important observations, several lines of evidence suggest that the Yellowstone megafossil assemblages are not highly allochthonous.

First, although many fossil trees in the Specimen Ridge section may be prone rather than upright, this is not always the case. The presence of paleosols around some of the upright stumps is evidence that these were fossilized in place rather than transported upright to the site of burial and preservation (Retallack, 1981). Yuretich (1984) and Karowe & Jefferson (1987) have presented petrographic and sedimentological evidence that the upright stumps are generally in situ. 1) Tree stumps are rooted in fine-grained sediments, not in conglomerates. 2) Some conglomerates have structures showing that they flowed around trunks in place. 3) Upper parts of inclined axes are abraded, but parts contained in finer-grained rock are not. 4) Petrographic sections of sediment containing fossil tree roots show no signs of extensive current bedding but do show indications of pedogenesis. Many of the leaf compression assemblages, which also show mixed "temperate" and "tropical" forms, are derived from fine-grained fluvial sediments and thus are unlikely to be highly transported (Wing, unpubl. data). Some fine- to medium-grained, airfall tuffs have the potential to entomb plant assemblages that quite accurately reflect local vegetation (Burnham & Spicer, 1986).

Second, the presence in the same sedimentary units of trees showing distinct seasonal growth with trees lacking distinct growth rings (Wheeler et al., 1977, 1978) has been cited as evidence that plants that grew under more than one climatic regime are present (Fritz & Fisk, 1978). This interpretation is not justified. Tree species have varying genetic capacities for seasonal growth, and individual trees are variably influenced by microclimatic and edaphic factors. The result is that different trees in the same region may show different patterns of growth (e.g., Tomlinson & Craighead, 1972). Fossil log assemblages containing specimens with both seasonal and aseasonal growth have been observed in sedimentary environments that could not have produced long-distance transport (Bown et al., 1982).

Third, most of the extreme examples of dissonance in the climatic tolerances of elements in the flora are generated by comparing the palynoflora with the megaflora. Pollen of *Abies* and *Larix* were less than 1% of the assemblages in which they occurred, which in turn were only a few of the 20 samples taken by Fisk (1976). Obviously, these could be highly allochthonous pollen grains derived from vegetation growing at higher elevations than the site of deposition. *Picea* occurred as 1–3 grains in 12 of the 20 samples, and reached 2%–6% of the flora in three samples (Fisk, 1976). Cross & Taggart (1982) have noted that abundance of *Picea* pollen is generally in rough proportion to its importance in the source vegetation, implying that spruce could have been a minor part of local vegetation, probably at higher elevations in the watershed containing the site of deposition.

Fourth, almost all early Eocene floras from western North America contain some taxa that presently have mutually exclusive climatic requirements (MacGinitie, 1969, 1974; Wolfe, 1980). In many floras the depositional setting argues strongly against explaining the presence of these dissonant elements by transport. For instance, backswamp compression fossil assemblages from the Willwood Formation, perhaps one million years older than the Yellowstone flora, have abundant palms, *Cnemidaria* (cyatheaceous tree fern), and *Alnus* (Wing, 1981). The Willwood Formation is a mostly fine-grained, basin-fill formation deposited by low-energy streams (Bown, 1979); low paleotopography is further indicated by thin, laterally extensive sheet sands (Kraus, 1980) and paleosol horizons that are traceable over many kilometers (Bown & Kraus, 1981). Many of the collecting sites for the Willwood flora were near the center of the basin, at least 100 km from the uplifted basin margins. The assemblages were derived from fine-grained mudstones (Wing, 1984), and similar assemblages are characteristic of this lithology over a large part of Wyoming (Wing, unpubl. data). Given this depositional environment, the potential for long-distance transport of leaves is miniscule, and the assemblages must be autochthonous or transported only a short distance. Therefore there has been change through time in the climatic requirements of the taxa involved and/or early Tertiary climates permitted the coexistence of genera that at present have largely nonoverlapping ranges.

In conclusion, recent stratigraphic and sedimentological studies of volcanic strata in Yellowstone National Park and other Paleogene volcanic sequences have demonstrated the importance of high-energy mudflow deposition and have made it clear that such deposits are characterized by a high degree of lateral variability. However, these studies have failed to demonstrate that the majority of the megafossil assemblages from such deposits are allochthonous. Currently, prevailing evidence suggests that plant megafossils, especially compression assemblages of leaves, generally accumulated from local sources during quiet periods between violent, localized, mudflow deposition.

Although the Republic flora (168–170; Figs. 3, 4) is approximately 2 Ma younger than the four floras discussed above, it is similar to the Yellowstone flora in having abundant conifers in both the megaflora and palynoflora. Wolfe & Wehr (1987) argued that the Republic paleovegetation was a mixed coniferous forest dominated by conifers because: 1) *Chamaecyparis* and *Pinus* are abundant at the Graphite Creek locality, 2) bisaccate pollen dominates the palynoflora, and 3) conifers are quite diverse (including *Thuja, Abies, Picea, Tsuga,* and *Pseudolarix* in the megaflora). Deciduous angiosperms are the most abundant and diverse group at the other two localities, but broad-leaved evergreens are present, including *Phoebe, Photinia, Ternstroemites* spp., and a new extinct genus. Based on the physiognomy of the assemblage, Wolfe & Wehr (1987) inferred a mean annual temperature of 12–13°C and a mean annual range of temperature of 5–6°C. By comparing these temperature estimates with those inferred for approximately coeval floras from the Puget Group, Wolfe & Wehr (1987) estimated the paleoelevation of the Republic flora as 725–910 m. The greater importance of conifers and deciduous broad-leaved plants at Republic than in the Yellowstone flora probably does not reflect a higher paleoelevation if estimates for the two areas are even approximately correct. Therefore, the compositional and physiognomic differences between the two floras probably result from differing taphonomic processes, climatic cooling during Bridgerian time, or both.

Vegetation during the Chadronian (38–33 Ma). Comparison of the approximately contemporaneous Little Mountain, Boysen, Kisinger Lakes, and Yellowstone floras illustrates the kinds of vegetational and floristic differences that existed over one part of the northern Rockies at about 50 Ma. The regional importance of coniferous and broad-leaved deciduous elements seems to have increased during the later Eocene and Oligocene, with dominantly coniferous forests probably becoming established at higher elevations. However, later Eocene and Oligocene floras provide less evidence of the kinds of vegetational boundaries implied by the contrasts between the four floras discussed above. This may reflect in part a less adequate sample of coeval floras.

One time interval in the remainder of the Eocene and Oligocene contains enough fossil floras to permit an attempt at analyzing vegetational variability in the Rocky Mountain region.

Ten floras in Appendix I are from rocks of probable Chadronian age: Missoula, from westcentral Montana (245–246; Jennings, 1920); Christensen Ranch, Horse Prairie, and Medicine Lodge from southwestern Montana (151–152, 153–157, 159–160; the Beaverhead Basins floras of Becker, 1969); uppermost Bull Run from northeastern Nevada (202; Axelrod, 1966a, 1966b); Florissant from central Colorado (224–229; MacGinitie, 1953); Red Rock Ranch, Hermosa, and Hillsboro from the Rio Grande Rift of New Mexico (232, 233, 234; Axelrod & Bailey, 1976; Meyer, 1986); and a small flora from the White River Group in the Flagstaff Rim area of central Wyoming (240).

The Missoula flora was derived from a sequence of coal and lacustrine ash beds that Jennings (1920) believed were correlative with the lower part of the White River Formation in South Dakota. The flora has not been studied since 1920, and many of Jennings's identifications are questionable. However the flora appears to be dominated by *Metasequoia, Sequoia,* and one or more species of Betulaceae. *Equisetum, ?Thuites, ?Populus* sect. *Abaso, Acer,* and *?Cercidiphyllum* are also present. It is difficult to reach any conclusion about vegetation based on such a small assemblage of relatively ubiquitous taxa.

Becker (1969) considered the Beaverhead Basins floras to be of latest Oligocene to Miocene age, but this was based on the thickness of the local stratigraphic sequence and on floral correlation; the latter was in turn based on an incomplete understanding of the taxa involved. More recent geological and paleontological work suggests that the sections are thinner than originally thought, and that the "Medicine Lodge Beds," from which the floras were collected, may correlate with sediments producing Chadronian vertebrates (Fields et al., 1985). All three of the Beaverhead Basins floras represent mixed coniferous and deciduous broad-leaved forest, which Becker (1969) felt reflected a subhumid climate. The subhumid elements include such taxa as *Mahonia, Juniperus,* and various nanophyllous Leguminosae. Common broad-leaved deciduous taxa are *Fagopsis longifolia, Cercidiphyllum, Populus, Sassafras,* and various Betulaceae and Ulmoideae. Upsection changes in floral composition are relatively modest, although the upper two floras have 14 (Medicine Lodge) and 16 (Horse Prairie) species of conifers to the 10 species found in the lowest flora. There is a pronounced physiognomic change between the Christensen Ranch flora and the upper two in that the percentage of species with entire-margined leaves increases from 18% to 34% and 37%. The significance of this shift is cast into some doubt by concomitant changes in depositional environment and floral diversity, and by the lower reliability of leaf margin data from coniferous vegetation (Wolfe, 1979), but taken at face value the increase in percentage of species with entire-margined leaves would indicate an increase in mean annual temperature from 7° to 12°C.

Axelrod (1966a, 1966b) stated that the upper Bull Run floras represented montane forest almost totally dominated by conifers, including *Abies, Picea, Pinus, Pseudotsuga, Tsuga, Chamaecyparis,* and *Thuja.* The angiosperm components are small-leaved and, with the exception of *Mahonia,* deciduous genera such as *Alnus, Betula, Ribes,* and *Zelkova.* This low diversity, strongly conifer-dominated assemblage contrasts markedly with the Beaverhead Basins floras, and although the upper Bull Run floras may be slightly older than those of the Beaverhead Basins (the highest locality is five feet below a tuff dated at 36 Ma; Axelrod, 1966a; Table 1), it seems probable that a difference in paleoelevation is also involved.

The small flora from the Chadronian of the Flagstaff Rim area was collected from clastic dike fillings that also preserve vertebrate skeletons (Emry, pers. comm., 1986). This peculiar mode of deposition makes comparisons between this flora and others questionable, but the low diversity (about six forms) and the small leaf size (microphylls or nanophylls) probably indicate relatively dry conditions. The identifiable taxa are *Mahonia, ?Ribes,* ?Ulmaceae, Leguminosae, and an undetermined conifer. This small flora may represent interfluve vegetation better than typical collections obtained from rocks deposited in paludal or lacustrine settings.

The Florissant flora is the most diverse from the Oligocene of the Rocky Mountain area. Based on a combination of floristic and physiognomic criteria, MacGinitie (1953) inferred that the Florissant fossil assemblage represented two main types of vegetation: a mesic, broad-leaved deciduous forest along streams and lakeshores and a drier scrub forest and grass vegetation on slopes and interfluve areas. The ten most common species in the flora comprise 60% of the specimens collected: *Fagopsis longifolia, Zelkova drymeja, Chamaecyparis, Typha, Populus crassa, Rhus stellariaefolia, Sequoia affinis, Cercocarpus* *myricaefolius, Staphylea acuminata,* and *Athyana haydenii.* The broad-leaved evergreen component of the Florissant is not dominant, but the diversity and abundance of conifers is much less than in either the Beaverhead Basins or the upper Bull Run floras.

Chadronian floras from New Mexico (Axelrod & Bailey, 1976; Meyer, 1986) appear to represent two different types of vegetation. The Red Rock Ranch flora is numerically dominated by specimens of *Pinus* subsection *Balfourianae* and contains species of *Picea, Abies, Zelkova,* and possibly *Salix* and *Rosa* (Meyer, 1986). Based on a list by Farkas (1969), Axelrod & Bailey (1976) reported several additional taxa including *Fagopsis, Halesia, Mahonia, Rhus,* and *Sapindus,* but, with the exception of *Mahonia,* these were not confirmed by Meyer (1986). Although the Red Rock Ranch flora is small, on the basis of relatively high conifer diversity and abundance and low broad-leaf diversity, Meyer (1986) concluded that it most likely represents a mixed coniferous forest. This flora was correlated with Florissant (35 Ma) by Axelrod & Bailey (1976), but the more recent and direct radiometric date obtained by Meyer (1986) indicates the flora is no younger than 36.7 ± 1.1 Ma, or about 2 Ma older than Florissant.

The Hermosa and Hillsboro floras are derived from sediments associated with the infilling of the moat of the Emory caldera, and both were dated at about 32 Ma by Axelrod & Bailey (1976). New radiometric dates reported by Meyer (1986) indicate the Hillsboro flora is probably 28.1–30.6 Ma (Whitneyan or early Arikareean) and that the Hermosa flora is about 33.6 ± 1.0 Ma (Chadronian). The floras are similar in composition, with an overwhelming dominance of specimens of *Pinus* subsection *Balfourianae,* along with a few small leaves of *Mahonia,* and possibly *Picea* and *Crataegus.* These floristic and physiognomic attributes indicate a taiga-type forest growing under a cold temperate climate (Meyer, 1986). Axelrod & Bailey (1976) argued that the difference between the Red Rock Ranch and Hermosa/Hillsboro floras was a response to higher paleoelevation of the latter floras; however, Meyer (1986) pointed out that these floras may bracket the major decrease in mean annual temperature and increase in mean annual range of temperature that occurred at about 33 Ma (Wolfe & Hopkins, 1967; Wolfe, 1986).

The pattern of geographic variation in Chadronian vegetation is less obvious than that of the earliest Bridgerian, and this can be attributed to several causes. First, the Chadronian floras are less tightly correlated and probably occurred over a longer interval of time, perhaps 5 Ma. Second, several of the floras are of low diversity or are not completely described, with the result that they are poorer samples of regional vegetation. Third, there may be a greater altitudinal range represented by the floras. Fourth, the youngest floras in the set (Hermosa/Hillsboro) may lie on the opposite side of a major temperature decrease from the other floras. In spite of these problems, the three floras of presumed intermediate elevation (Beaverhead Basins, Florissant, Red Rock Ranch) seem to have broadly similar compositions and to represent mixed coniferous and broad-leaved deciduous forest growing under a seasonally dry climate. The higher diversity of conifers and mesic taxa in the Montana floras may indicate higher rainfall and/or lower rates of evapotranspiration in the northern part of the Rocky Mountains. The subhumid aspect of all of these floras when compared with those of similar age from the Pacific Northwest demonstrates the continuation of the pattern of regional climatic variation that began during the early Eocene/latest Paleocene.

The mid Tertiary climatic deterioration. Much of the evidence for the major decrease in mean annual temperature and increase in mean annual range of temperature that occurred at approximately 33 Ma is derived from lowland floras from the Pacific Coast of North America (Wolfe & Hopkins, 1967; Wolfe, 1971, 1986). Is there unambiguous evidence of this major climatological change in floras from the Rocky Mountain region? Presently this does not seem to be the case. Using the dates and correlations presented in Figure 3, there are six floras that closely follow after the 34 Ma date: Mormon Creek, Metzel Ranch, York Ranch, Ruby paper shales, Hermosa, and possibly Hillsboro. The dating of the Montana floras has been uncertain since their initial descriptions (Becker, 1960, 1961, 1972, 1973), and opinions on the age of the Mormon Creek flora have embraced some 20 Ma. Recent geological and mammalian biostratigraphic correlations suggest the Mormon Creek, Metzel Ranch, and York Ranch floras are of Orellan age (32.2–30.8 Ma) and that the Ruby paper shale flora is Whitneyan (30.8–29.2 Ma). These floras were judged by Becker (1960, 1961, 1972, 1973) to represent mixed coniferous and broad-leaved deciduous forest and shrubland growing under temperate to dry-temperate climates. Although the Ruby paper shale flora is inferred to have been somewhat dryer than the other three, they all bear substantial resemblance to one another and to the older (Chadronian) Beaverhead Basins floras. As noted above, the New Mexican floras are derived from a setting of some paleotopographic and structural complexity, so that it is difficult to separate potential effects of elevation and regional climatic change.

Thus the only floras of suitable age do not provide good evidence of a major temperature decrease at 33 Ma. This absence of evidence may result from the confounding effects of changing elevations and dryer climates in the Rocky Mountains, or it may simply be a problem of insufficient data and poor stratigraphic control.

PRESENT METHODS AND FUTURE STUDY

Perhaps the most useful result of summarizing current knowledge and opinions in a field of study is that this activity reveals gaps in the data base and reveals possible directions for future research. At present, research in Tertiary paleobotany follows two main themes: the systematic/evolutionary approach is concerned primarily with describing new fossil forms and understanding their implications for the evolutionary history of lineages and relationships among living groups of plants; the paleoecological/environmental approach focuses largely on understanding habits of extinct species, structure of extinct vegetation, and patterns of ancient climates. Historically these approaches often were combined in the treatment of a single fossil flora. More recently, as standards have become higher and techniques more sophisticated in both approaches, workers have specialized on one or the other. This probably reflects a more general separation of ecology from systematics, but the disjunction in viewpoints should not be accepted as inevitable or desirable. Ecological and systematic approaches must be combined in order to reach a full understanding of evolution, because ecological data provide the context for understanding the genealogical changes that are inferred from systematic studies. Furthermore, in paleobotany both approaches are united at a practical level by the study of the same sites and specimens.

FIELD DATA

As noted in the section on the data base for Eocene and Oligocene floras, the stratigraphic and geographic distribution of sites is very uneven. The total number of sites from which collections have been made is also small, considering the commonness of plant fossils and the large outcrop area. The meagerness of the data set results from there being few paleobotanists, from a tendency for the same sites to be collected repeatedly, and from relatively small efforts toward finding new sites. The largest "holes" in the record would be filled by: 1) more late Eocene and Oligocene floras from the eastern Rocky Mountain area; 2) more Paleogene floras from the southern Rocky Mountains; and 3) more fluvially deposited late Eocene or Oligocene assemblages (or conversely, more Paleocene and early Eocene lacustrine assemblages).

Field data that would enhance reports of fossil plants include: number of quarry sites collected; size of quarry; precise locality information; stratigraphic unit; detailed lithological description; abundance of fossils and relative abundance of species; and, where available, biostratigraphic correlation, radiometric age, and paleomagnetic correlation. If such data were available, even as preliminary approximations, the published record of Tertiary fossils would be more useful for interpreting paleovegetation, paleoclimate, and possible associations of dispersed organs.

SYSTEMATICS

During the last 15 to 20 years several new methods have brought increased resolution and rigor to systematic studies of Tertiary angiosperms. Comparative studies of the leaf architecture of living dicotyledons have created a much firmer basis for interpreting the systematic affinities of fossil leaves (Hickey & Wolfe, 1975). The range of characters being studied has increased greatly, and important systematic data are now being gained from fossil cuticle (e.g., Upchurch, 1984a, 1984b; Jones, 1986), structure and ultrastructure of fossil pollen (e.g., Crepet et al., 1980), and from more detailed analyses of fossil flowers (e.g., Crepet & Daghlian, 1981, 1983). At the same time, more studies have come to base their systematic conclusions on multiple fossil organs belonging to the same species (e.g., Manchester & Crane, 1983; Wing & Hickey, 1984; Manchester, 1986). Finally, in many areas of paleobotany, refinements in methods of systematic analysis have resulted in sharper definition of characters and character states and have made the reasoning behind systematic decisions more explicit (e.g., Stein et al., 1984).

Although major advances have been made in methodology, the vast majority of fossil angiosperms from western North America are as yet very poorly understood. For most times and places the floras either have not been described or the only descriptions are those of late-19th century workers whose goals were more biostratigraphic than systematic. New methods will have to be applied repeatedly before the botanical relationships of any significant number of Tertiary fossils will be understood.

Methodology has remained underdeveloped in the quantification of variability. Comparative leaf architecture was an important advance in analyzing higher-level systematic affinities but has been much less useful at the level of species. With few exceptions (e.g., Dolph, 1975; Burnham, 1986a, 1986b; Wing & Eckenwalder, 1987), paleobotanists have been little concerned with quantifying the variability of their taxa. Yet individuating taxa in a paleobotanical sample is the initial step in subsequent systematic, biostratigraphic, and paleoecological syntheses. Detection and quantification of low-level morphological variability is also a key to uncovering patterns of temporal change in closely spaced stratigraphic samples.

PALEOECOLOGY

Traditional paleoecological interpretation of fossil angiosperm floras has been based on floristic analogy and on leaf physiognomic analysis. The floristic method assumes that the ecological/climatic requirements of the fossil taxa were similar to those of their closest living relatives. This kind of direct analogy suffers from several defects (see Wolfe, 1979). First, it assumes that the botanical relationships of the fossils have been determined correctly. Second, it assumes that little evolutionary change has occurred in the climatic or ecological preferences of the lineages under study. Justification for both of these assumptions diminishes as one considers older floras, because evolution is more likely to have occurred in the intervening time, making it more difficult to determine close living relatives of older fossil plants. A third problem with floristic inference is that it implies that the present-day distribution of a taxon accurately reflects even its present climatic tolerances. Given the rapid climatic fluctuations typical of the last two million years, it may be that the current distributions of many taxa are strongly influenced by migration rate, plant competitors, or other nonclimatic factors (Davis, 1976).

The second commonly used method of paleovegetational/paleoclimatic inference is analysis of leaf physiognomy. Physiognomic analysis primarily relies on a relationship observed in living floras; the percent of species in a local flora that have entire-margined leaves rises with the mean annual temperature of the site (Bailey & Sinnott, 1915, 1916). Thus tropical floras have nearly 100% species with entire leaves, whereas temperate floras are dominated by species with toothed or lobed leaves. This relationship has been worked out with some precision based on the humid floras of East Asia (Wolfe, 1979). Studies based on smaller regions have been used to question the resolution of leaf-margin inferences (Dolph, 1976, 1978a, 1978b, 1979; Dolph & Dilcher, 1979), but the basic pattern of climate change as inferred from Tertiary floras agrees with data from a variety of other sources (e.g., Savin, 1977; Wolfe & Poore, 1982; Hutchison, 1982; Owen & Rea, 1985; Rea et al., 1985). Physiognomic analysis also considers the average size of leaves in a fossil assemblage, their apparent thickness, cuticle thickness, pubescence, the number of leaf types with drip tips, and the number of species that are probable lianes (those with cordate-based leaves). Generally these attributes increase with increasing tropicality of vegetation.

Although physiognomic analysis offers significant improvement on the floristic method, it has defects. In addition to their correlation with mean annual temperature, physiognomic characteristics of leaves are also correlated with water availability, intensity and angle of incident radiation, and a variety of other factors. Consequently, changes in the leaf physiognomy of fossil assemblages cannot always be read unambiguously as changes in mean annual temperature. An increase in climatically or edaphically induced water stress could produce vegetation with small, thick, entire-margined leaves and few lianes. Greater representation of canopy species in a fossil flora would produce an assemblage with smaller leaves (Roth & Dilcher, 1978). This is because canopy leaves tend to be smaller than interior leaves in order to radiate heat more efficiently and maintain an optimal photosynthetic rate. Perhaps the most serious factor biasing leaf physiognomic analysis of fossil assemblages is the probable overrepresentation of early successional and streamside plants, which grow close to sites of deposition in fluvial and volcanic settings (MacGinitie, 1969). Successional and riparian vegetation in most climatic zones is dominated by species with lobed, toothed, or compound leaves, probably because these species hold individual leaves for only a short time, and these leaf shapes provide a large photosynthetic surface at a small cost of support tissue (Givnish, 1978). Thus a change in the frequency with which fossil vegetation was disturbed might produce a change in leaf physiognomy that might be interpreted as a change in mean annual temperature.

In spite of their defects, both the floristic and leaf physiognomic methods produce inferences about paleovegetation that are generally consistent with paleoclimatic reconstructions based on other, independent data sets. Furthermore, they generally agree with one another (e.g., MacGinitie, 1974; Hickey, 1977). The problem with these methods is not that they produce grossly incorrect interpretations of past vegetational structure, but rather that the inferences lack detail, frustrating the most interesting comparisons that might be made between extinct and living forests.

For instance, because of strong seasonality of light and a low angle of incident radiation, it is likely that the structure of high latitude, broadleaved, evergreen forests in the early Tertiary was significantly different from that of living broadleaved evergreen forests, even though the two types of vegetation are similar in leaf physiognomy and floristic composition. This hypothesis can only be examined by finding more ways to compare fossil and living vegetation. These new methods of comparison will probably require collecting data on the distribution of fossils in the sediment. These distributional data (e.g., alpha and beta diversity, relative abundance, spatial heterogeneity) may reflect actual synecological characteristics of the vegetation that produced a fossil assemblage; the difficulty in interpretation arises from the probability that taphonomic processes have also influenced the distribution of fossils. In spite of recent work on the taphonomy of fossil plants (Spicer, 1981; Scheihing & Pfefferkorn, 1984; Spicer & Greer, 1986; Ferguson, 1985; Gastaldo, 1986; Burnham & Spicer, 1986; Spicer & Wolfe, 1987), there are as yet no general recommendations for how leaf assemblages can be sampled to reflect best given characteristics of the former vegetation. This kind of work will have to be done in order to make the best use of the paleoecological information preserved in fossil plant assemblages.

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APPENDIX I

Name, source, North American land mammal age, and stratigraphic position of localities in Figures 3 and 4. Abbreviations for North American Land Mammal Ages (NALMA):

GB = Graybullian
LY = Lysitean
LC = Lostcabinian
WA = Wasatchian
GA = Gardnerbuttean
BR = Bridgerian
UI = Uintan
DU = Duschesnean
CH = Chadronian
OR = Orellan
WH = Whitneyan
AR = Arikareean

Number	Locality	Source	NALMA	Stratigraphic Unit
1	USNM 14048	Hickey, 1977	LC	upper Camels Butte Member, Golden Valley Fm.
2	USNM 14141	Hickey, 1977	LC	upper Camels Butte Member, Golden Valley Fm.
3	USNM 14117	Hickey, 1977	GB	lower Camels Butte Member, Golden Valley Fm.
4	USNM 14094	Hickey, 1977	GB	lower Camels Butte Member, Golden Valley Fm.
5	USNM 14092	Hickey, 1977	GB	lower Camels Butte Member, Golden Valley Fm.
6	USNM 14089	Hickey, 1977	GB	lower Camels Butte Member, Golden Valley Fm.
7	USNM 14088	Hickey, 1977	GB	lower Camels Butte Member, Golden Valley Fm.
8	USNM 14054	Hickey, 1977	GB	lower Camels Butte Member, Golden Valley Fm.
9	USNM 14099	Hickey, 1977	LC	upper Camels Butte Member, Golden Valley Fm.
10	USNM 14066	Hickey, 1977	GB	lower Camels Butte Member, Golden Valley Fm.
11	USNM 14052	Hickey, 1977	GB	lower Camels Butte Member, Golden Valley Fm.
12	USNM 14053	Hickey, 1977	GB	lower Camels Butte Member, Golden Valley Fm.
13	USNM 14056	Hickey, 1977	GB	lower Camels Butte Member, Golden Valley Fm.
14	USNM 14068	Hickey, 1977	GB	lower Camels Butte Member, Golden Valley Fm.
15	USNM 14025	Hickey, 1977	GB	lower Camels Butte Member, Golden Valley Fm.
16	USGS 8892	unpublished	WA	Wasatch Fm., above Roland Coal
17	USGS 8891	unpublished	WA	Wasatch Fm.
18	USGS 8890	unpublished	WA	Wasatch Fm.
19	USGS 9394	unpublished	LC	upper Wasatch Fm. on Pumpkin Buttes
20	USGS 9483	unpublished	WA	?
21	USGS 6985	unpublished	?WA	Hanna Fm.?
22	USGS 6978	unpublished	?WA	Hanna Fm.?
23	Little Mountain; PA116	MacGinitie, 1969	GA/BR	upper Wilkins Peak Mbr., Green River Fm.
24	USGS 8588	unpublished	?LC	Wasatch Fm.
25	USGS 5263	unpublished	?LC	Wasatch Fm.
26	USGS 5255	unpublished	?LC	Wasatch Fm.
27	USGS 9495	unpublished	?LC	Niland Tongue, Wasatch Fm.
28	USGS 9179	unpublished	?LC	Niland Tongue, Wasatch Fm.
29	USGS 9397	unpublished	LC	Niland Tongue, Wasatch Fm.
30	USGS 4811	unpublished	?LC	Niland Tongue, Wasatch Fm.
31	Eden Valley	Kruse, 1954; MacGinitie, 1969	BR	base of Laney Mbr., Green River Fm.
32	USGS 9051; Schoening	MacGinitie, 1974	LC	lower Lost Cabin Mbr., Wind River Fm.
33	USGS 9537	unpublished	LC	Lost Cabin Mbr., Wind River Fm.
34	USGS 9040; Rate Homestead	MacGinitie, 1969	UI	Wagonbed Fm.

APPENDIX I. Continued.

Number	Locality	Source	NALMA	Stratigraphic Unit
35	USGS 8784	unpublished	LC	Lost Cabin Mbr., Wind River Fm.
36	USGS 9052; Boysen Locality; PA-111	MacGinitie, 1974	GA	upper Lost Cabin Mbr., Wind River Fm.
37	USGS 8770; Crowheart Locality	unpublished	?LC	upper Wind River Fm.
38	Tipperary; USGS 8785	MacGinitie, 1974	BR	Aycross Fm.
39	Coyote Creek	MacGinitie, 1974	?BR	Aycross Fm.
40	Rhodes Ranch	MacGinitie, 1974	?BR	Aycross Fm.
41	Wind River flora; USGS 8912; PA-104	Leopold & MacGinitie, 1972	LC	lower Aycross Fm.
42	Kisinger Lakes	MacGinitie, 1974	BR	Aycross Fm.
43	USGS 9519; Princeton "Willwood"	unpublished	LC/GA	tuffaceous lake beds above Willwood Fm. (Bown, 1982)
44	USGS 10022; Princeton "Willwood"	unpublished	LC/GA	tuffaceous lake beds above Willwood Fm. (Bown, 1982)
45	USGS 8496; Princeton "Willwood"	unpublished	LC/GA	tuffaceous lake beds above Willwood Fm. (Bown, 1982)
46	USGS 8586	unpublished	?BR	Aycross Fm.
47	USGS 8909	unpublished	?BR	Aycross Fm.
48	USGS 6389	unpublished	?	?
49	USGS 6177	unpublished	?	?
50	USGS 8894; Jim Creek	unpublished	LC	uppermost Willwood Fm.
51	T2; USNM 37687	Wing, 1981	LC	lower Tatman Fm.
52	TAT79; USNM 37686	Wing, 1981	LC	lower Tatman Fm.
53	BCT4; USNM 37685	Wing, 1981	LC	lower Tatman Fm.
54	BCT3; USNM 37684	Wing, 1981	LC	lower Tatman Fm.
55	BCT2; USNM 37683	Wing, 1981	LC	lower Tatman Fm.
56	BCT; USNM 37682	Wing, 1981	LC	lower Tatman Fm.
57	WhBgL; USNM 37681	Wing, 1981	LC	lower Tatman Fm.
58	WhBg; USNM 37680	Wing, 1981	LC	lower Tatman Fm.
59	B; USNM 37679	Wing, 1981	LC	lower Tatman Fm.
60	MQ; USNM 37678	Wing, 1981	LC	upper Willwood Fm.
61	AL; USNM 37677	Wing, 1981	LC	upper Willwood Fm.
62	Brosh; USNM 37676	Wing, 1981	LC	upper Willwood Fm.
63	T; USNM 37675	Wing, 1981	LC	upper Willwood Fm.
64	Fl; USNM 37674	Wing, 1981	LC	upper Willwood Fm.
65	TL; USNM 37673	Wing, 1981	LC	upper Willwood Fm.
66	CQ; USNM 37672	Wing, 1981	LC	upper Willwood Fm.
67	15M; USNM 37671	Wing, 1981	LC	upper Willwood Fm.
68	15ME; USNM 37670	Wing, 1981	LC	upper Willwood Fm.
69	SL; USNM 37669	Wing, 1981	LC	upper Willwood Fm.
70	M; USNM 37668	Wing, 1981	LC	upper Willwood Fm.
71	A; USNM 37667	Wing, 1981	LC	upper Willwood Fm.
72	MBR; USNM 37666	Wing, 1981	LY	middle Willwood Fm.
73	Pn; USNM 37560	Wing, 1981	LY	middle Willwood Fm.
74	125; USNM 37664	Wing, 1981	LY	middle Willwood Fm.

Appendix I. Continued.

Number	Locality	Source	NALMA	Stratigraphic Unit
75	67; USNM 37663	Wing, 1981	LY	middle Willwood Fm.
76	320; USNM 37662	Wing, 1981	LY	middle Willwood Fm.
77	H; USNM 37661	Wing, 1981	GB	middle Willwood Fm.
78	281-3; USNM 37660	Wing, 1981	GB	middle Willwood Fm.
79	281-2; USNM 37659	Wing, 1981	GB	middle Willwood Fm.
80	281; USNM 37657	Wing, 1981	GB	middle Willwood Fm.
81	DCF; USNM 37656	Wing, 1981	GB	middle Willwood Fm.
82	DC1; USNM 37655	Wing, 1981	GB	middle Willwood Fm.
83	LB; USNM 37654	Wing, 1981	GB	middle Willwood Fm.
84	RR5; USNM 37653	Wing, 1981	GB	lower Willwood Fm.
85	98; USNM 37652	Wing, 1981	GB	lower Willwood Fm.
86	RR1; USNM 37626	Wing, 1981	GB	lower Willwood Fm.
87	WCS8-2; USNM 37651	Wing, 1981	GB	lower Willwood Fm.
88	WCS8-1; USNM 37650	Wing, 1981	GB	lower Willwood Fm.
89	RC; USNM 37649	Wing, 1981	GB	lower Willwood Fm.
90	HsII; USNM 37648	Wing, 1981	GB	lower Willwood Fm.
91	Hs; USNM 37563	Wing, 1981	GB	lower Willwood Fm.
92	UU; USNM 37646	Wing, 1981	GB	lower Willwood Fm.
93	BRII; USNM 37645	Wing, 1981	GB	lower Willwood Fm.
94	BR1.5; USNM 37644	Wing, 1981	GB	lower Willwood Fm.
95	BR; USNM 37643	Wing, 1981	GB	lower Willwood Fm.
96	Bs; USNM 37642	Wing, 1981	GB	lower Willwood Fm.
97	CnII; USNM 37641	Wing, 1981	GB	lower Willwood Fm.
98	CnI; USNM 37640	Wing, 1981	GB	lower Willwood Fm.
99	P; USNM 37639	Wing, 1981	GB	lower Willwood Fm.
100	S; USNM 37638	Wing, 1981	GB	lower Willwood Fm.
101	WCS6; USNM 37637	Wing, 1981	GB	lower Willwood Fm.
102	GER; USNM 37591	Wing, 1981	GB	lower Willwood Fm.
103	RR4; USNM 37635	Wing, 1981	GB	lower Willwood Fm.
104	USGS 6177	Wing, 1981	GB	lower Willwood Fm.
105	LHE; USNM 37633	Wing, 1981	GB	lower Willwood Fm.
106	VS1; USNM 37584	Wing, 1981	GB	lower Willwood Fm.
107	RR2; USNM 37631	Wing, 1981	GB	lower Willwood Fm.
108	LW; USNM 37630	Wing, 1981	GB	lower Willwood Fm.
109	LR1; USNM 37629	Wing, 1981	GB	lower Willwood Fm.
110	HFU; USNM 37628	Wing, 1981	GB	upper Fort Union Fm.
111	FUCS1; USNM 37627	Wing, 1981	GB	upper Fort Union Fm.
112	Yellowstone flora (Princeton)	Dorf, unpubl.	WA/BR	Lamar River Fm. on Specimen Ridge
113	Yellowstone flora (Princeton)	Dorf, unpubl.	WA/BR	Sepulcher Fm. on Yellowstone River
114	Yellowstone flora (Princeton)	Dorf, unpubl.	WA/BR	Sepulcher Fm. on Crescent Hill

Appendix I. Continued.

Number	Locality	Source	NALMA	Stratigraphic Unit
115	Yellowstone flora (Princeton)	Dorf, unpubl.	WA/BR	Sepulcher Fm. near Elk Creek
116	Yellowstone flora (Princeton)	Dorf, unpubl.	WA/BR	Sepulcher Fm. on N. bank of Lamar River
117	Yellowstone flora (Princeton)	Dorf, unpubl.	WA/BR	Sepulcher Fm. opposite mouth Hellroaring Crk.
118	Yellowstone flora (Princeton)	Dorf, unpubl.	WA/BR	Sepulcher Fm., east side, Yellowstone river
119	Bearpaw Mtns.; USGS 8902	Brown & Pecora, 1949	BR	unnamed volcanics overlying Wasatch equivalent
120	Bearpaw Mtns.; USGS 9959	Brown & Pecora, 1949	BR	unnamed volcanics overlying Wasatch equivalent
121	Bearpaw Mtns.; USGS 9186	Brown & Pecora, 1949	BR	unnamed volcanics overlying Wasatch equivalent
122	Bearpaw Mtns.; USGS 9957	Brown & Pecora, 1949	BR	unnamed volcanics overlying Wasatch equivalent
123	Bearpaw Mtns.; USGS 9355	Brown & Pecora, 1949	BR	unnamed volcanics overlying Wasatch equivalent
124	Bearpaw Mtns.; USGS 9222	Brown & Pecora, 1949	BR	unnamed volcanics overlying Wasatch equivalent
125	Bearpaw Mtns.; USGS 9354	Brown & Pecora, 1949	BR	unnamed volcanics overlying Wasatch equivalent
126	Bearpaw Mtns.; USGS 9958	Brown & Pecora, 1949	BR	unnamed volcanics overlying Wasatch equivalent
127	Bearpaw Mtns.; USGS 9960	Brown & Pecora, 1949	BR	unnamed volcanics overlying Wasatch equivalent
128	Bearpaw Mtns.; USGS 9187	Brown & Pecora, 1949	BR	unnamed volcanics overlying Wasatch equivalent
129	Bearpaw Mtns.; USGS 9218	Brown & Pecora, 1949	BR	unnamed volcanics overlying Wasatch equivalent
130	Bearpaw Mtns.; USGS 9956	Brown & Pecora, 1949	BR	unnamed volcanics overlying Wasatch equivalent
131	Bearpaw Mtns.; USGS 9124	Brown & Pecora, 1949	BR	unnamed volcanics overlying Wasatch equivalent
132	Bearpaw Mtns.; USGS 9216	Brown & Pecora, 1949	BR	unnamed volcanics overlying Wasatch equivalent
133	Bearpaw Mtns.; USGS 9146	Brown & Pecora, 1949	BR	unnamed volcanics overlying Wasatch equivalent
134	Bearpaw Mtns.; USGS 9137	Brown & Pecora, 1949	BR	unnamed volcanics overlying Wasatch equivalent
135	Bearpaw Mtns.; USGS 9133	Brown & Pecora, 1949	BR	unnamed volcanics overlying Wastach equivalent
136	Bearpaw Mtns.; USGS 9290	Brown & Pecora, 1949	BR	unnamed volcanics overlying Wasatch equivalent
137	Upper Ruby River 1 (blocky shale)	Becker, 1961	WH	Passamari Mbr., Renova Fm.
138	Upper Ruby River 2 (paper shale)	Becker, 1961	WH	Passamari Mbr., Renova Fm.
139	Upper Ruby River 3 (paper shale)	Becker, 1961	WH	Passamari Mbr., Renova Fm.
140	Upper Ruby River 4 (paper shale)	Becker, 1961	WH	Passamari Mbr., Renova Fm.
141	Upper Ruby River 5 (paper shale)	Becker, 1961	WH	Passamari Mbr., Renova Fm.
142	Upper Ruby River 6 (paper shale)	Becker, 1961	WH	Passamari Mbr., Renova Fm.
143	Upper Ruby River 7 (paper shale)	Becker, 1961	WH	Passamari Mbr., Renova Fm.
144	Upper Ruby River 8 (paper shale)	Becker, 1961	WH	Passamari Mbr., Renova Fm.
145	Upper Ruby River 9 (paper shale)	Becker, 1961	WH	Passamari Mbr., Renova Fm.
146	Upper Ruby River 10 (paper shale)	Becker, 1961	WH	Passamari Mbr., Renova Fm.
147	Upper Ruby River 11 (paper shale)	Becker, 1961	WH	Passamari Mbr., Renova Fm.
148	Mormon Creek	Becker, 1960	OR	Dunbar Crk. Mbr., Renova Fm.
149	Metzel Ranch	Becker, 1972	OR	Dunbar Crk. Mbr., Renova Fm.
150	York Ranch	Becker, 1973	OR	Dunbar Crk. Mbr., Renova Fm.
151	Christensen Ranch (lower)	Becker, 1969	CH?	"Medicine Lodge Beds" (Fields et al., 1985)
152	Christensen Ranch (upper)	Becker, 1969	CH?	"Medicine Lodge Beds" (Fields et al., 1985)
153	Horse Prairie	Becker, 1969	CH?	"Medicine Lodge Beds" (Fields et al., 1985)

APPENDIX I. Continued.

Number	Locality	Source	NALMA	Stratigraphic Unit
154	Horse Prairie	Becker, 1969	CH?	"Medicine Lodge Beds" (Fields et al., 1985)
155	Horse Prairie	Becker, 1969	CH?	"Medicine Lodge Beds" (Fields et al., 1985)
156	Horse Prairie	Becker, 1969	CH?	"Medicine Lodge Beds" (Fields et al., 1985)
157	Horse Prairie	Becker, 1969	CH?	"Medicine Lodge Beds" (Fields et al., 1985)
158	Medicine Lodge	Becker, 1969	CH?	"Medicine Lodge Beds" (Fields et al., 1985)
159	Medicine Lodge	Becker, 1969	CH?	"Medicine Lodge Beds" (Fields et al., 1985)
160	Medicine Lodge	Becker, 1969	CH?	"Medicine Lodge Beds" (Fields et al., 1985)
161	Targhee Flora	Axelrod, 1968	?	?
162	Coal Creek, Idaho	Axelrod, 1968	UI	Challis Volcanics
163	Democrat Creek	Axelrod, 1968	UI	Challis Volcanics
164	Bullion Gulch	Axelrod, 1968	UI	Challis Volcanics
165	Germer Basin	Edelman, 1975	UI	Germer Tuffaceous Mbr., Challis Volcanics
166	Salmon flora	Brown, 1937; Axelrod, 1968	UI/DU	Germer Tuffaceous Mbr., Challis Volcanics
167	Thunder Mountain	Axelrod, 1966b, 1968	UI	"Dewey Beds," Challis Volcanics
168	Republic flora, main locality	Wolfe & Wehr, 1987	UI	Klondike Mtn. Fm.
169	Republic flora, Resner Canyon	Wolfe & Wehr, 1987	UI	Klondike Mtn. Fm.
170	Republic flora, Graphite Creek	Wolfe & Wehr, 1987	UI	Klondike Mtn. Fm.
171	Roslyn	Wolfe, 1968; Axelrod, 1968	?	?
172	Clarno Nut Beds; OMSI-225	Scott, 1954; Bones, 1979	BR	Clarno Fm.
173	W. Branch Creek; USGS 8637; OMSI-230	Manchester, 1986	WA-BR	Clarno Fm.
174	Hancock Canyon mudflow; OMSI-49	Manchester, 1986	BR-DU	Clarno Fm.
175	Hancock Tree Canyon; OMSI-69	Manchester, 1986	UI-DU	Clarno Fm.
176	Gosner Road; OMSI-238	Manchester, 1986	BR-UI	Clarno Fm.
177	Indian Rocks; OMSI-239	Manchester, 1986	BR-UI	Clarno Fm.
178	W. Branch Crk. lacustrine; OMSI-226	Manchester, 1986	BR-UI	Clarno Fm.
179	W. Branch Crk. shale; OMSI-228	Manchester, 1986	BR-UI	Clarno Fm.
180	Alex Canyon lacustrine; OMSI-229	Manchester, 1986	BR-UI	Clarno Fm.
181	Dry Hollow mudflow tuff; OMSI-253	Manchester, 1986	UI-DU	Clarno Fm.
182	Lower Cedarville flora	Axelrod, 1966a	DU	lower Cedarville Fm.
183	Susanville flora	Wolfe, pers. comm.		
184	Iowa & Independence Hill; loc. 42	MacGinitie, 1941	WA	Ione Fm.
185	Chalk Bluffs; P3318	MacGinitie, 1941	WA	Ione Fm.
186	Chalk Bluffs; P3324	MacGinitie, 1941	WA	Ione Fm.
187	Chalk Bluffs; P3325	MacGinitie, 1941	WA	Ione Fm.
188	Chalk Bluffs; P3345	MacGinitie, 1941	WA	Ione Fm.
189	Buckeye Flat; loc. 104	MacGinitie, 1941	WA	Ione Fm.
190	Buckeye Flat; P3370	MacGinitie, 1941	WA	Ione Fm.
191	Quaker Flat; P3346	MacGinitie, 1941	WA	Ione Fm.
192	Sailor Flat; P3347	MacGinitie, 1941	WA	Ione Fm.
193	Cherokee Mine; loc. 206	MacGinitie, 1941	WA	Ione Fm.

APPENDIX I. Continued.

Number	Locality	Source	NALMA	Stratigraphic Unit
194	Corral Hollow	Axelrod, 1968		
195	Coal Creek, Nevada	Axelrod, 1968		
196	Coal Mine Canyon palynoflora	Axelrod, 1966a, 1968	WA/GA	Elko Fm.
197	Bull Run flora (lower; Mori Road)	Axelrod, 1966a, 1968	DU	"Mori Rd. Fm."
198	Bull Run flora (lower; Summit)	Axelrod, 1966a, 1968	DU/CH	"I L Fm."
199	Bull Run flora (lower)	Axelrod, 1966a, 1968	DU/CH	"I L Fm."
200	Bull Run flora (upper)	Axelrod, 1966a, 1968	DU/CH	"Chicken Creek Fm."
201	Bull Run flora (upper)	Axelrod, 1966a, 1968	DU/CH	"Chicken Creek Fm."
202	Bull Run flora (upper)	Axelrod, 1966a, 1968	CH	"Chicken Creek Fm."
203	Copper Basin flora	Axelrod, 1966a, 1968	DU	Deadhorse Tuff
204	Sage Creek	Axelrod, 1968		
205	Rainbow, Utah; PA-107	MacGinitie, 1969	UI	upper Parachute Creek Mbr., Green River Fm.
206	Wardell Ranch; PA-106	MacGinitie, 1969	UI	upper Parachute Creek Mbr., Green River Fm.
207	West of Wardell Ranch; PA-321	MacGinitie, 1969	UI	upper Parachute Creek Mbr., Green River Fm.
208	Stewart Gulch; PA-326	MacGinitie, 1969	UI	430 feet above Mahogany Ledge, Green River Fm.
209	North Park; USGS 5987	unpublished	WA	Coalmont Fm.
210	North Park; USGS 6102	unpublished	WA	Coalmont Fm.
211	North Park; USGS 6437	unpublished	WA	Coalmont Fm.
212	North Park; USGS 5994	unpublished	WA	Coalmont Fm.
213	North Park; USGS 6110	unpublished	WA	Coalmont Fm.
214	North Park; USGS 6105	unpublished	WA	Coalmont Fm.
215	North Park; USGS 6103	unpublished	WA	Coalmont Fm.
216	North Park; USGS 5991	unpublished	WA	Coalmont Fm.
217	North Park; USGS 6107	unpublished	WA	Coalmont Fm.
218	North Park; USGS 6000	unpublished	WA	Coalmont Fm.
219	North Park; USGS 6111	unpublished	WA	Coalmont Fm.
220	North Park; USGS 6005	unpublished	WA	Coalmont Fm.
221	North Park; USGS 5997	unpublished	WA	Coalmont Fm.
222	North Park; USGS 6440	unpublished	WA	Coalmont Fm.
223	North Park; USGS 9446	unpublished	WA	Coalmont Fm.
224	Florissant; Denver Museum locality	MacGinitie, 1953	CH	Florissant Fm.
225	Florissant; P3731	MacGinitie, 1953	CH	Florissant Fm.
226	Florissant; P3732	MacGinitie, 1953	CH	Florissant Fm.
227	Florissant; P3733	MacGinitie, 1953	CH	Florissant Fm.
228	Florissant; Princeton locality	MacGinitie, 1953	CH	Florissant Fm.
229	Florissant; Scudder's locality	MacGinitie, 1953	CH	Florissant Fm.
230	unnamed	Tidwell et al., 1981	LY	Rosarita Mbr., San Jose Fm.
231	Galisteo palynoflora	Leopold & MacGinitie, 1972	UI	Galisteo Fm.
232	Red Rock Ranch	Meyer, 1986	CH	Red Rock Ranch Fm.
233	Hermosa	Meyer, 1986	CH	Mimbres Peak Fm.?
234	Hillsboro	Meyer, 1986	WH/AR	sediments overlying Emory caldera lake beds

APPENDIX I. Continued.

Number	Locality	Source	NALMA	Stratigraphic Unit
235	Barilla	Berry, 1919	DU?	Huelster Fm.
236	unnamed	Wilson, pers. comm.		
237	unnamed	Wilson, pers. comm.		
238	unnamed	Wilson, pers. comm.		
239	unnamed	Wilson, pers. comm.		
240	unnamed	Emry, pers. comm.	CH	White River Fm., below ash D
241	Poison Springs palynoflora	Leopold & MacGinitie, 1972	CH	White River Fm.
242	Creede, 5-Mile Bridge; 571A, B, C	Axelrod, 1987	AR	Creede Fm.
243	Creede, Birdsey Gulch; 574A, B, C	Axelrod, 1987	AR	Creede Fm.
244	Creede, Dry Gulch; 572A, B, C, D	Axelrod, 1987	AR	Creede Fm.
245	Creede, Wason Cliffs; 573A, B, C, D	Axelrod, 1987	AR	Creede Fm.
246	Missoula (loc. 165)	Jennings, 1920	CH	Renova Fm.?
247	Missoula (loc. 196)	Jennings, 1920	CH	Renova Fm.?
248	LaPorte			
249	Bridge Creek			
250	Alvord Creek			
251	Cow Creek			

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AN OVERVIEW OF THE ORIGINS OF THE MODERN VEGETATION AND FLORA OF THE NORTHERN ROCKY MOUNTAINS[1]

JACK A. WOLFE[2]

ABSTRACT

The present flora of the northern Rocky Mountains has diverse origins. The Late Cretaceous mesothermal to megathermal evergreen vegetation of this region had few taxa, even at the familial level, that live in the northern Rocky Mountains today. The terminal Cretaceous event resulted in broad-leaved deciduous taxa occupying mesothermal climate in the northern Rocky Mountain region, where they underwent major diversification. The early Eocene thermal maximum severely restricted the areas of microthermal climate and created a climatic/geographic bottleneck for microthermal lineages. By the early middle Eocene, volcanic uplands that supported microthermal coniferous forests of Pinaceae and Cupressaceae had developed in parts of the northern Rocky Mountain region. These Eocene coniferous forests contained a diverse broad-leaved subsidiary element, most of which represented adaptive radiations of mesothermal clades into newly created microthermal climate. During the later Eocene, microthermal vegetation was progressively enriched by internal diversification and by adaptation of mesothermal groups to microthermal climate; extinction also was a major factor in the changing composition of the microthermal flora. The Eocene volcanic uplands of western North America played a major role in the diversification of arcto-tertiary clades; dispersals between western North America and Eurasia of members of these clades was readily accomplished during the later Eocene by way of Beringia. Some of the Eocene microthermal lineages survive relatively unchanged in the northern Rocky Mountains today, and other extant lineages, although ultimately derived from taxa in the Eocene uplands, represent morphological types that originated and diverged in Eurasia, arriving in North America by migration. Oligocene and Neogene floras are largely unknown in the northern Rocky Mountains, although the Columbia Plateaus to the west contain many assemblages of these ages. These assemblages represent microthermal broad-leaved deciduous or coniferous forests, and most constituent taxa represent lineages that were derived from Eocene upland vegetation following the terminal Eocene temperature deterioration. With the presence of many extant northern Rocky Mountain lineages, the Columbia Plateaus assemblages provide evidence that the northern Rocky Mountain region was probably occupied primarily by coniferous forest during the Oligocene and most of the Neogene. During the mid-Miocene thermal maximum, numerous microthermal lineages were exchanged between western North America and Eurasia. Other extant northern Rocky Mountain lineages are known during the Miocene only in areas such as Alaska and probably represent migrants into the northern Rocky Mountains during the late Neogene. The present flora of the northern Rocky Mountains therefore clearly represents a complex overlay of numerous historical biogeographic patterns.

The modern vegetation of the northern Rocky Mountain region is primarily steppe at low altitudes and coniferous forest at higher altitudes (Habeck, 1987). Temperatures are entirely microthermal.[3] The lower and drier part of the coniferous forest belongs to the *Pinus ponderosa* zone, whereas most of the mesic coniferous forest at higher altitudes belongs to the *Abies grandis* zone (Franklin & Dyrness, 1969). The vegetational/climatic types that have occupied the northern Rocky Mountain region are documented by successive microfossil and megafossil plant assemblages. In some instances, lack of assemblages that represent particular intervals makes it necessary to infer climate and vegetation from the fossil record of adjacent regions. This report addresses vegetational (physiognomic) types that have occupied the northern Rocky Mountain region in the past and the history of the lineages that comprise the modern flora. Throughout, the focus is primarily on the woody flora.

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[3] Microthermal = mean annual temperature <13°C, mesothermal = mean annual temperature 13–20°C, megathermal = mean annual temperature >20°C.

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The extant woody flora is composed of 10 genera and 19 species of conifers and 30 genera and 80 species of woody dicotyledons. The dominant conifers are *Abies grandis, Larix occidentalis,* and other members of Pinaceae, as well as a few members of the Cupressaceae. The dicotyledons are primarily adjuncts in coniferous forest or form streamside communities. Conspicuous dicotyledonous families, as elsewhere in Northern Hemisphere vegetation, include Betulaceae, Ericaceae, Salicaceae, Rosaceae, and Caprifoliaceae, with a few Aceraceae.

The origins of the flora of a region such as the northern Rocky Mountains are, of course, highly complex. Each component species, genus, and family has a unique history, although some histories may approximate others in space and time. Indeed, the search for patterns to which numerous histories approximately conform is a primary concern of historical plant geography. Such patterns might be indicative of similar responses to specific historical factors, particularly responses to environmental changes, including various parameters of climate and topographic changes resulting from orogenic factors. However, because two taxa are now in association or have similar present distributions does not imply similar histories.

The classical methodology for determining the histories of biogeographic patterns involves reconstruction of phylogenies from phenetic similarities of extant and fossil taxa, observing distribution patterns of extant taxa, and determining the patterns of distribution of fossils in time and space. The relative completeness of the fossil record is the major problem in using it in biogeographic analyses. The problem is underscored in the present case by the almost total absence of Oligocene and Neogene assemblages of plant megafossils in the northern Rocky Mountains. Although some palynomorph assemblages fill this gap, the typical taxonomic resolution of palynological morphology is typically at a generic or higher level (Muller, 1970) and is of limited assistance in determining histories of lineages on the scale desirable in biogeographic analyses. Further, the upland Eocene megafossil assemblages from the northern Rocky Mountain region have been actively collected and studied for only the last two decades. These assemblages are critical because they contain the records of diversification of many microthermal groups (see below), and additional collecting and study are needed. In contrast, the Oligocene and Neogene plant-megafossil assemblages from adjoining regions such as the Columbia Plateaus and from possible source areas such as Beringia are well known. Estimates based on the geographic and climatic distribution of fossil and extant taxa indicate that, at least in the Beringian Neogene, the lineages represented in the fossil record are thought to be more than 95% complete for woody plants.

Inferences also can be made regarding histories of lineages if a cladistic analysis of a group is combined with detailed knowledge of history of the physical environment. This approach, termed "vicariance biogeography" (e.g., Platnick & Nelson, 1978) has considerable merit for groups that have poor or no fossil records. However, it rests on major assumptions and requirements:

(1) Cladistic analyses inherently rest on the assumption of parsimony in evolution of characters.
(2) Cladistic analyses must be based on valid determination of polarities of character states.
(3) History of the physical environments in all areas must be known in detail.
(4) The final biogeographic analysis also rests on the assumption of parsimony in dispersals.

In most recent applications, vicariance biogeographers have either ignored the fossil record or, at best, have incorporated fossil taxa in cladistic analyses without reference to stratigraphy, although Grande (1985) emphasized the significance of the age relations of fossil taxa, which provide additional geographic data on distributions. Another major tendency has been to consider the history of the physical environment solely in terms of plate tectonics, thus ignoring particularly climatic changes. Because climates of a given area generally determine vegetational types and, in turn, vegetation organizes the environment into a variety of microenvironments (Upchurch & Wolfe, 1987) that determine whether a particular organism can live in a given area, the history of vegetation assumes paramount importance for interpreting the biogeographic histories of land organisms.

The fossil record can be of major significance in any analysis in vicariance biogeography, as Grande (1985) emphasized. However, partly because Grande was examining the fossil record from the standpoint of icthyology, some contributions of paleontology to vicariance biogeography were not stressed or were overlooked:

(1) The stratigraphic sequence of grades, if cautiously interpreted, can determine polarity states (Hennig, 1966).
(2) The fossil record can supply evidence of environments in particular areas at particular times.
(3) The fossil record can supply evidence of the existence of dispersal barriers and routes other than those related to plate tectonics.
(4) The fossil record can supply minimal times of divergences in a cladogram, and these times can then be placed in the framework of the then-existing environments to determine probabilities of dipersals of the resulting, diverging lineages.
(5) The fossil record can independently test the assumptions of parsimony in both evolution and dispersal.

Unfortunately, almost no cladistic analyses of groups of concern in the northern Rocky Mountains have been carried out. However, the results of a cladistic analysis of *Acer* (Wolfe & Tanai, 1987) when compared with the known fossil record of *Acer* (especially in North America) indicate:

(1) The known relative times of appearances of sections of *Acer* generally correspond to those predicted from the cladogram; those few that do not correspond probably resulted from the absence of collections from the appropriate environment or areas.
(2) Phylogeny reconstructed on a phenetic paleobotanical basis compares well with phylogeny reconstructed on a cladistic basis.
(3) Dispersals have not been as parsimonious as would be predicted from vicariance biogeography.
(4) The present distributions of species and sections of *Acer* are complex and have resulted from a variety of environmental, particularly climatic, factors.

As more cladistic analyses of extant groups are completed, they will provide a framework for evaluating phenetic paleobotanical phylogenies, but cladistic analyses, because of biogeographic "noise," can provide only highly generalized concepts of histories of biogeographic patterns, some of which are much more complex than indicated by cladistics alone and some of which are invalid (Wolfe, 1981b). In essence, cladistic analyses test phenetic phylogenies based on the fossil record, whereas the fossil record tests models developed from vicariance biogeography.

The divergence that apparently exists between "vicariance" and "dispersalist" schools of biogeography has resulted from psychological and sociological factors. Each school typically has rejected the totality of the other's methods and results. Both have inherent problems that can be resolved by reference to the other's methods and/or by using the other's conclusions. Indeed, Grande's (1985) discussion of vicariance biogeography basically incorporates some dispersalist concepts and uses some dispersalist data that support his conclusions; he argued for systematic/biogeographic analyses on successive time planes to attempt to filter out biogeographic "noise" introduced by subsequent dispersal events. The approach used in the present report similarly will involve both cladistic and dispersalist concepts and data.

CRETACEOUS

The northern Rocky Mountain region was occupied by a mesothermal, broad-leaved evergreen forest during the Late Cretaceous (Dorf, 1942). Some conifers (e.g., Araucariaceae, evergreen Taxodiaceae) probably were emergents in this vegetation (Wolfe & Upchurch, 1987b), and broad-leaved deciduous plants were restricted largely to successional or disturbed vegetation, especially along streams. General absence of drip-tips and a somewhat small leaf size indicate slightly subhumid conditions (Wolfe & Upchurch, 1986, 1987a). Analyses of woods from the North American mesothermal region suggest little seasonality of either temperature or precipitation (Wolfe & Upchurch, 1987b). Presence of extensive marine rocks of Late Cretaceous age throughout much of the Western Interior indicates generally low altitudes.

Miller (1987) emphasized the great floristic disparity between known Early Cretaceous floras, including those of the northern Rocky Mountain region, and the modern flora of this region. Even with the rise to dominance of the angiosperms in the early Late Cretaceous, the flora has an archaic aspect, dominated by generalized members of Hamamelididae and Rosidae (Crabtree, 1987). Whether any of these ultimately gave rise to taxa that now occur in the northern Rocky Mountains cannot now be determined. By the later part of the Late Cretaceous, some families that today have microthermal members become recognizable. Aceraceae, for example, occur in the latest Cretaceous of central Alberta, represented by an extinct genus interpreted as a sister group to *Acer* (Wolfe & Tanai, 1987). Even at high paleolatitudes, the flora was composed largely of trochodendroids, hamamelidaleans, and deciduous Taxodiaceae (Spicer et al., 1987); this high-latitude flora has some floristic similarities to that of the early Tertiary of the northern Rocky Mountains but no similarity to the extant flora of this region.

PALEOCENE

In areas such as eastern Montana, the Cretaceous–Tertiary boundary is marked by a presumed fallout layer that has anomalously high amounts of iridium and shocked minerals (Bohor et al., 1984); these are considered to be evidence of an impact by an extraterrestrial body (Alvarez et al., 1984). This event at the end of the Cretaceous had a profound effect on the flora and vegetation of the northern Rocky Mountain region (Wolfe & Upchurch, 1986). At least 50–60% of the latest Cretaceous lineages became extinct (Hickey, 1981). Most extinctions were in the previously dominant broad-leaved evergreen element; in addition, araucarians and many other evergreen conifers became extinct in this region. Immediately above the presumed fallout horizon, palynofloras contain almost exclusively fern spores (Hotton, 1984; Tschudy & Tschudy, 1986). Within a few centimeters above this horizon, angiosperm pollen occurs with the fern spores; the associated leaf flora contains both fern pinnae and a compound-leaved rosid, which is thin-leaved and probably deciduous. About 10 meters higher in the section, the leaf assemblage of about 15 species consists almost entirely of deciduous angiosperms (trochodendroids, hamamelidaleans, Tiliaceae) and deciduous conifers (Taxodiaceae).

The eastern Montana sequence immediately above the Cretaceous–Tertiary boundary resembles normal secondary succession following a volcanic eruption (Richards, 1952); in mesothermal, broad-leaved evergreen regions, deciduous plants are typically dominant in secondary successions (Wang, 1961). However, in the northern Rocky Mountain region, broad-leaved deciduous plants dominated north of the Colorado–Wyoming border (Brown, 1962), and the broad-leaved evergreen element did not return to dominance until almost the end of the Paleocene, about 10 Ma following the Cretaceous. Hickey (1981, 1984) attributed the deciduousness of this Paleocene vegetation to an overall decline in temperature that persisted through most of the Paleocene. The occurrence of large (and presumably ectothermic) reptiles (crocodilians, champsosaurs, large turtles) with this deciduous vegetation, however, indicates the probable absence of low winter temperatures that would select for deciduousness. That is, the faunal data indicate strongly that the deciduousness of the vegetation is anomalous; just as significantly, megathermal, broad-leaved evergreen vegetation persisted in the early Paleocene at about the Colorado–Wyoming border.

Wolfe & Upchurch (1986) suggested instead that the terminal Cretaceous event resulted in a brief low-temperature excursion that devastated the vegetation of both mesothermal and megathermal regions of North America. Some megathermal, broad-leaved evergreen lineages survived (perhaps in refugia; Tschudy et al., 1984), and megathermal vegetation continued to be dominantly evergreen. The megathermal vegetation underwent physiognomic change and gradually increasing diversity during the Paleocene, a phenomenon mimicking short-term secondary succession and termed "quasisuccession" by Wolfe & Upchurch (1986, 1987a). However, almost none of the mesothermal, broad-leaved evergreen lineages survived, and replenishment of them would have had to occur by adaptation of some megathermal lineages to mesothermal climate on an evolutionary (not successional) time scale.

The anomalously deciduous character of Paleocene mesothermal vegetation throughout North America (and in Eurasia) gave deciduous angiosperms a unique opportunity. These deciduous lineages were derived primarily from elements that were uncommon in Late Cretaceous mesothermal evergreen vegetation and/or dominant in Late Cretaceous, high-latitude deciduous vegetation (Wolfe & Upchurch, 1986). In mesothermal regions, dominantly deciduous taxa (e.g., Hamamelidaceae, Fagaceae, Betulaceae, Ulmoideae, Juglandaceae) diversified during the Paleocene (e.g., Nichols & Ott, 1978; Manchester, 1987). By the end of the Paleocene, the Northern Hemisphere had a considerable diversity of broad-leaved deciduous plants, and many families of woody angiosperms that now occur in the Rocky Mountain region were extant.

A major increase in precipitation occurred at the Cretaceous–Tertiary boundary. In the northern Rocky Mountain region this is evidenced by a substantial increase in leaf size and by the initiation of wide-scale peat deposition that typically marks the early Paleocene in this region (Wolfe & Upchurch, 1986). Not only would increased precipitation result in an increase in biomass, but water tables also would be raised and more swamps developed.

Pre-Eocene microthermal vegetation contrasts markedly with Eocene and later microthermal vegetation in floristic composition. Pre-Eocene microthermal vegetation was restricted to high latitudes and, probably due to low winter light levels, was almost entirely deciduous (Wolfe, 1985; Spicer & Parrish, 1986). The flora primarily comprised deciduous Taxodiaceae, deciduous Pinaceae (*Pseudolarix*), and deciduous dicotyledons, the great majority of which represents a few clades of trochodendraleans, platanoids, and other hamamelidaleans (Spicer et al., 1987; Wolfe, 1987). Although these clades later contributed some lineages first to the mesothermal deciduous vegetation of the Paleocene and then to the Eocene upland microthermal vegetation, they comprise a small fraction of the Eocene and later microthermal flora. The microthermal vegetation and flora of the Late Cretaceous and the Paleocene have few similiarities to Eocene and later vegetation and flora.

EOCENE

A warming initiated during the latest Paleocene culminated in the early Eocene thermal maximum (Savin, 1977; Wolfe & Poore, 1982; Wolfe, 1985). Vegetation in areas such as northwestern Wyoming was dominantly broad-leaved evergreen and represented warm mesothermal temperatures (Wing, 1981, 1987). At somewhat lower altitudes (and particularly in the lowland Pacific Northwest), vegetation represented megathermal rain forests (Wolfe, 1978, 1985). That the eastern part of the Rocky Mountain region was still generally of low altitudes is indicated by the persistence of large lakes from the early into late Eocene in areas such as southwestern Wyoming and adjacent Utah. The early Eocene vegetation indicates abundant precipitation, but later Eocene vegetation indicates increased seasonality of precipitation and development of subhumid, seasonal climate (MacGinitie, 1969; Leopold & MacGinitie, 1972).

The warm mesothermal to megathermal vegetation of the early and middle Eocene has few floristic similarities to the extant flora of the northern Rocky Mountains. A few extant northern Rocky Mountain genera (e.g., *Alnus, Populus,* and *Acer*) are present in this vegetation, but the species represented are not closely related to extant species in this region.

Extensive vulcanism and associated tectonism resulted in a major upland region that extended from northern Nevada and central Idaho north into British Columbia during the middle Eocene (Axelrod, 1966a, 1966b); this upland may have actually been a series of upland volcanic centers. Known upland assemblages of early middle Eocene age (Fig. 1) occur from northeastern Washington (Republic and associated floras) northward into central British Columbia (Princeton, Chu Chua Creek, and coeval floras). Extensive vulcanism of early Eocene age became less intense during the early middle Eocene, and tectonism resulted in a series of grabens, in which the plant-bearing lacustrine sediments were deposited (Pearson & Obradovich, 1977). Altitude of the Republic basin of deposition is estimated to have been about 900 m (Wolfe & Wehr, 1987).

Later in the middle Eocene and in the early part of the late Eocene, major volcanic centers occurred in central Idaho (Challis Volcanics), central Oregon (Clarno Formation), and northeastern Nevada (rocks containing the Copper Basin and Bull Run floras of Axelrod, 1966b). Most Clarno assemblages represent only low altitudes, but a newly collected assemblage (Sheep Rock Creek) from the Crooked River Basin is probably microthermal and indicates the presence of higher altitudes. By the late Eocene, tectonism in the central Idaho region resulted in the formation of grabens and associated lakes on the post-Challis surface; these lake beds contain floras such as the Salmon. A similar depositional regime occurred in southwestern Montana (the numerous floras described by Becker); to the north in western Montana are plant-bearing lacustrine beds that have been collected recently by C. N. Miller and associates.

The development of this upland region, concomitant with a general decline of temperature following the early Eocene thermal maximum, resulted in the presence of microthermal climates. Early middle Eocene microthermal vegetation, such as that at Republic (Wolfe & Wehr, 1987), represents the oldest known coniferous forest dominated by Pinaceae (*Abies, Picea, Pinus, Pseudolarix,* and *Tsuga*) and Cupressaceae (*Chamaecyparis* and *Thuja*). These genera were of low diversity in the early middle Eocene, but had increased in diversity by the end of the

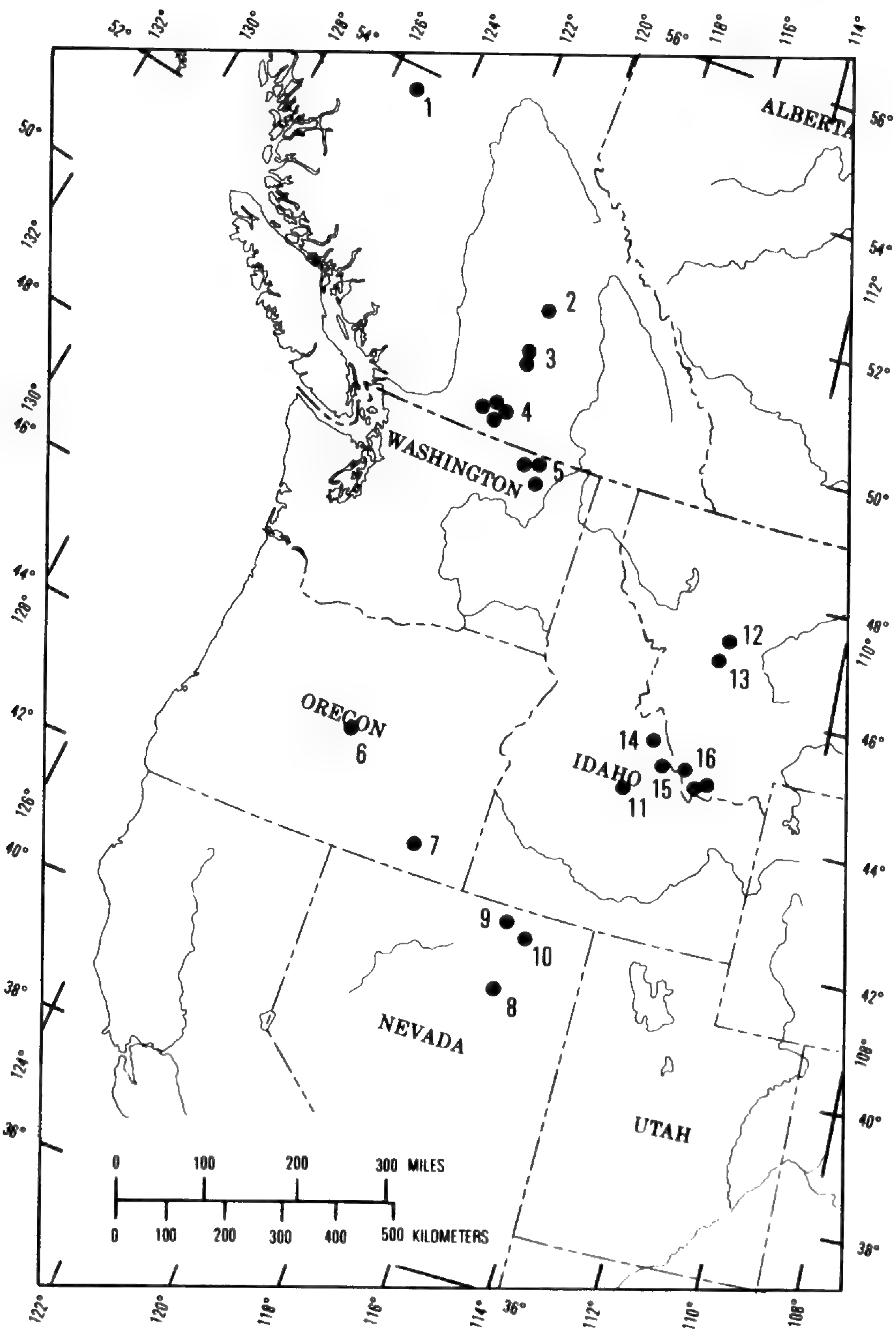

FIGURE 1. Map showing location of Eocene microthermal plant assemblages in western conterminous United States and adjacent Canada. For each assemblage or group of assemblages, either published references or repositories of largely unpublished assemblages are cited. These repositories are: GSC (Geological Survey of Canada); OMSI (Oregon Museum of Science and Industry); TMP (Tyrrell Museum of Paleontology); UAPC (University of Alberta Paleobotany Collections); UBC (University of British Columbia); UCMP (University of California Museum of Paleontology); UMPC (University of Montana Paleobotany Collections); USGS (U.S. Geological Survey); UWBM (University of Washington Burke Museum). Early middle Eocene: 1. Smithers (UWBM); 2. Chu Chua Creek (Berry, 1926); 3. Kamloops assemblages (TMP); 4. Princeton assemblages (GSC, UAPC, UWBM); 5. Republic assemblages (Wolfe & Wehr, 1987; UWBM). Late middle to early late Eocene: 6. Sheep Rock Creek (OMSI); 7. Alvord Creek (Axelrod, 1944b); 8. Elko assemblages (UCMP, USGS); 9. Bull Run assemblages (UCMP); 10. Copper Basin (Axelrod, 1966a); 11. Thunder Mountain (Brown, 1937). Latest Eocene: 12. Beaver Creek (UMPC); 13. Drummond (Pearson, 1972); 14. Salmon (Brown, 1937; USGS); 15. Cow Creek (USGS); 16. Beaverhead, Metzel Ranch, Mormon Creek, Ruby, and York Ranch (Becker, 1960, 1961, 1969, 1972, 1973).

Eocene. As discussed later, major diversification also occurred in numerous woody dicotyledonous families. This probably resulted from (1) the areal restriction of microthermal climate during the early Eocene and (2) the opportunistic expansion of mesothermal lineages into newly created microthermal climate in the uplands.

Areas of microthermal climate were probably highly restricted during the early Eocene thermal maximum. Indeed, I know of no latest Paleocene or early Eocene Northern Hemisphere plant assemblage that represents microthermal vegetation; possibly only on mountains in polar latitudes could such vegetation have been present (Wolfe, 1985, fig. 5). Because of the absence or extreme restriction of microthermal climates during the early Eocene, probably few pre-Eocene microthermal taxa were able to survive this climatic-geographic bottleneck, leaving the newly expanding microthermal regions available for opportunistic mesothermal lineages. Further, topographic and edaphic diversity, juxtaposition of many microclimates, and relative isolation of one volcanic center from another would all lead to rapid diversification of lineages in the uplands. Geographic proximity to lowland mesothermal vegetation would allow a continuing supply of new clades.

Probable instability of community composition during the middle Eocene is indicated by two lines of evidence. First, from one approximately coeval depositional site to another, species composition varies markedly; almost all the localities are in lacustrine shales and presumably represent similar ecologic settings. Spatial heterogeneity more resembled that of mesothermal or even megathermal vegetation than that of microthermal vegetation. Second, floristic comparisons of early middle Eocene lacustrine assemblages with late middle to early late Eocene assemblages indicate large changes in composition, some related to evolution of lineages within microthermal vegetation and some related to additions from mesothermal vegetation, as well as to extinction.

Numerous mesothermal (or mesothermal/megathermal) evergreen dicotyledonous clades had adapted to the microthermal climate by the early middle Eocene, although these typically are rare elements. Such taxa include *Talauma* (Magnoliaceae), *Phoebe* (Lauraceae), *Gordonia* (Theaceae), *Barghoornia* (Burseraceae), *Paullinia, Serjania,* and *Allophylus* (Sapindaceae), *Paleophytocrene* (Icacinaceae), and *Schoepfia* (Olacaceae). None of these genera are known to have survived into microthermal vegetation of the late Eocene and they can best be considered as unsuccessful experiments, although other evergreen dicotyledons successfully adapted to the microthermal climate during the Eocene. The presence of evergreen dicotyledons in microthermal coniferous forests during the Eocene is consistent with the low (ca. 5°C) mean annual range of temperature inferred for coeval lowland assemblages (Wolfe, 1978). Modern microthermal coniferous vegetation of low-latitude, upland areas (e.g., Taiwan, Himalayas) also has many taxa of evergreen dicotyledons.

Also included in the upland early middle Eocene vegetation are numerous extant genera of trees and shrubs that contributed to broad-leaved deciduous and coniferous forests of the Neogene and Holocene, although not present in the northern Rocky Mountain region today. Included are: *Sassafras, Cercidiphyllum, Corylopsis, Comptonia, Castanea, Fagus, Tilia, Ulmus, Itea, Photinia, Decodon, Rhus,* and *Aesculus.*

Overall, diversity among woody angiosperms appears to have been higher in the initial phase (early middle Eocene) of development of the microthermal coniferous forests than later in the Eocene. At least 95 genera and 140 species of woody angiosperms are known in the Republic and Princeton floras, which are still not thoroughly collected. In contrast, about 70 genera and 110 species of woody angiosperms are known in the extensively collected and described latest Eocene coniferous forests from western Montana (Becker, 1960, 1961, 1969, 1972, 1973). This general decrease is particularly notable in presumed large trees, which were perhaps gradually replaced by newly evolved species of conifers.

Very few of the extant northern Rocky Mountain lineages are recognizable by the early middle Eocene. The oldest known *Betula* clearly allied to the *B. papyrifera–B. occidentalis* complex occurs at Republic, as does an *Acer* allied to *A. negundo.* However, the *Acer,* although possibly ancestral to *A. negundo,* is assignable to an extinct section (Wolfe & Tanai, 1987). Many other extant native microthermal genera were also participants in this early middle Eocene vegetation (e.g., *Alnus, Corylus, Ribes, Rubus, Spiraea, Crataegus, Prunus,* and *Cornus*), but the species cannot be placed directly in the ancestry of extant northern Rocky Mountain lineages.

The early middle Eocene microthermal flora of western North America had numerous archaic elements in terms of Neogene or Holocene microthermal vegetation. Other than the unsuccessful thermophilic experiments previously listed, the vegetation had extinct genera of Trochodendraceae, Cercidiphyllaceae, Hamamelidaceae, Platanaceae, Fagaceae, Betulaceae, Rosaceae, and other families; about 40% of the genera are totally extinct (Wolfe & Wehr, 1987, unpubl. data).

By the late middle to late Eocene, upland microthermal vegetation had been floristically altered as the result of:

(1) Extinction, e.g., the unsuccessful thermophilic experiments.
(2) Gradual evolution in phylads, e.g., in a phylad ultimately leading to *Chamaebatiaria* (Rosaceae), the early middle and late Eocene members represent distinct genera.
(3) Major diversification of early middle Eocene microthermal clades, e.g., whereas early middle Eocene *Acer* comprised 10 species and 3 extinct sections, late middle to late Eocene *Acer* comprised 35 species and 17 sections, 14 of which are extant (including the first members of sects. *Negundo* and *Macrophylla*).
(4) Adaptation of members of previously mesothermal clades to microthermal climates, e.g., invasion of newly evolved species of *Quercus*, *Mahonia*, Salicaceae, and Leguminosae.

Rosaceae and Aceraceae underwent major diversification in Eocene upland microthermal vegetation. Both are today primarily bee-pollinated; entomophily would have been advantageous to small trees and shrubs in densely stocked coniferous forests. Diaspores of Rosaceae are typically biotically dispersed, as are those from some extant acers. Anemophily and abiotic dispersal, in contrast, probably characterized woody angiosperms that are abundantly represented in the fossil assemblages and that were presumably of fluviatile habitats: trochodendroids, hamamelidaleans, *Fagopsis*, most Betulaceae, *Comptonia*, and Ulmoideae. However, the fluviatile habitat and concomitant anemophily/abiotic dispersal syndrome did not lead to more than species-level diversification in most of these groups.

The great majority of extant genera of woody microthermal angiosperms had evolved by the end of the Eocene, yet diversification in some genera and perhaps families had yet to occur:

(1) In *Salix*, all known Eocene species are referable to subg. *Salix*.
(2) Ericaceae were of low generic and specific diversity in the Eocene; thus far only *Rhododendron* (subg. *Rhododendron*) has been found in the upland Eocene vegetation, although several small Eocene leaves that lack diagnostic characters have been referred to *Vaccinium*.
(3) Only a few scattered Eocene palynological records of Caprifoliaceae s. str. are known, e.g., *Diervilla* in the latest Eocene of Alaska (E. B. Leopold, written comm., 1970). A few nondiagnostic, microphyllous leaves have been referred to *Symphoricarpos*.

OLIGOCENE AND NEOGENE

Wide-scale deposition of lacustrine sediments apparently ended in the northern Rocky Mountains by the end of the Eocene (ca. 33 Ma)[4]. This termination presumably resulted from considerable uplift, leading to downcutting and erosion. At approximately the same time, a worldwide major climatic deterioration occurred (Wolfe, 1978), resulting in development of microthermal, broad-leaved, deciduous forest at low altitudes of middle latitudes and broad-leaved deciduous and coniferous forests at high latitudes (Wolfe, 1985). This deterioration involved a decline in mean annual temperature and a major increase in mean annual range of temperature (Wolfe, 1978).

Megafloras of Oligocene and Neogene age are not known from the northern Rocky Mountains. Wing (1987) and Leopold & Denton (1987) have therefore largely concentrated on well-known assemblages from the adjacent Columbia Plateaus (Fig. 2). From the Oligocene into the middle Miocene (ca. 13–14 Ma), the Columbia Plateaus were occupied largely by Mixed Mesophytic forest; during the middle Miocene, this forest was replaced by Mixed Coniferous forest (Wolfe, 1981a).

That Miocene basalts of the Columbia River Group generally lap onto highlands to the east and north indicates that certainly the region of the northern Rocky Mountains was higher than

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[4] Many workers place the Eocene–Oligocene boundary at about 37 Ma and would include the latest Eocene floras discussed above in the early Oligocene. Whichever placement is valid does not affect relative or actual ages of the floras or paleoclimatic changes.

the Columbia Plateaus. Based on the temperature relations of extant vegetational types (Wolfe, 1979), I infer that during the Oligocene through middle Miocene, the northern Rocky Mountains had a lower altitudinal belt of Mixed Northern Hardwood forest (Fig. 3) and an upper belt of High Montane Mixed Coniferous forest (the vegetational type that generally occupies mesic sites within the present northern Rocky Mountains).

The terminal Eocene temperature deterioration resulted both in numerous microthermal lineages migrating downslope from Eocene uplands into Oligocene lowlands and in extinction of many microthermal lineages. For example, the relationships of most Bridge Creek (early Oligocene) taxa are with Eocene upland taxa (MacGinitie, 1953) and not with Eocene high-latitude taxa. Among the Oligocene taxa that illustrate this relationship are: *Cercidiphyllum crenatum, Castanea orientalis, Fagus pacifica, Quercus clarnensis, Alnus "carpinoides," Betula* aff. *papyrifera, "Carpinus grandis," Mahonia simplex, Plafkeria* sp., "*Ulmus*" *brownelli, Amelanchier* sp., *Crataegus newberryi, Acer* (*Negundo*) sp., *A.* (*Macrophylla*) *osmonti, A.* (*Lithocarpa*) sp., *Bohlenia* sp. (an extinct sapindaceous genus that = *Dipteronia* auct.), and "*Holmskioldia*" *speirii.* Some lowland Oligocene taxa were probably derived from mesothermal to megathermal taxa of the Eocene lowlands: *Liquidambar, Platanus, Engelhardtia,* and *Paleophytocrene.* Although such taxa are few, both *Liquidambar* and *Platanus* were vegetationally important during the Neogene. None of the Bridge Creek lineages appear to be derived from a northern source.

Although the Oligocene data base is not as complete as desired, many Eocene microthermal lineages are unknown in the Oligocene. Taxa that apparently became extinct at the end of the Eocene include *Fagopsis,* some genera of Rosaceae, and the sister genus of *Acer* ("*Acer*" *arcticum* group). Some Eocene microthermal lineages that participated in Oligocene vegetation of the Columbia Plateaus did not survive into the Miocene (e.g., "*Zelkova,*" *Plafkeria, Bohlenia,* "*Holmskioldia*"). Clearly, extinction continued to play a significant role.

The Oligocene vegetation in high-latitude regions such as Alaska was of low diversity (Wolfe, 1972, 1985) and provided a limited reservoir for mid-latitude lineages. Only near the end of the Oligocene did taxonomic diversity increase in high-latitude regions, largely from migration from lower latitudes and some diversification of immigrant clades; the influence at mid latitudes of the high-latitude flora was generally not felt until the middle and late Miocene.

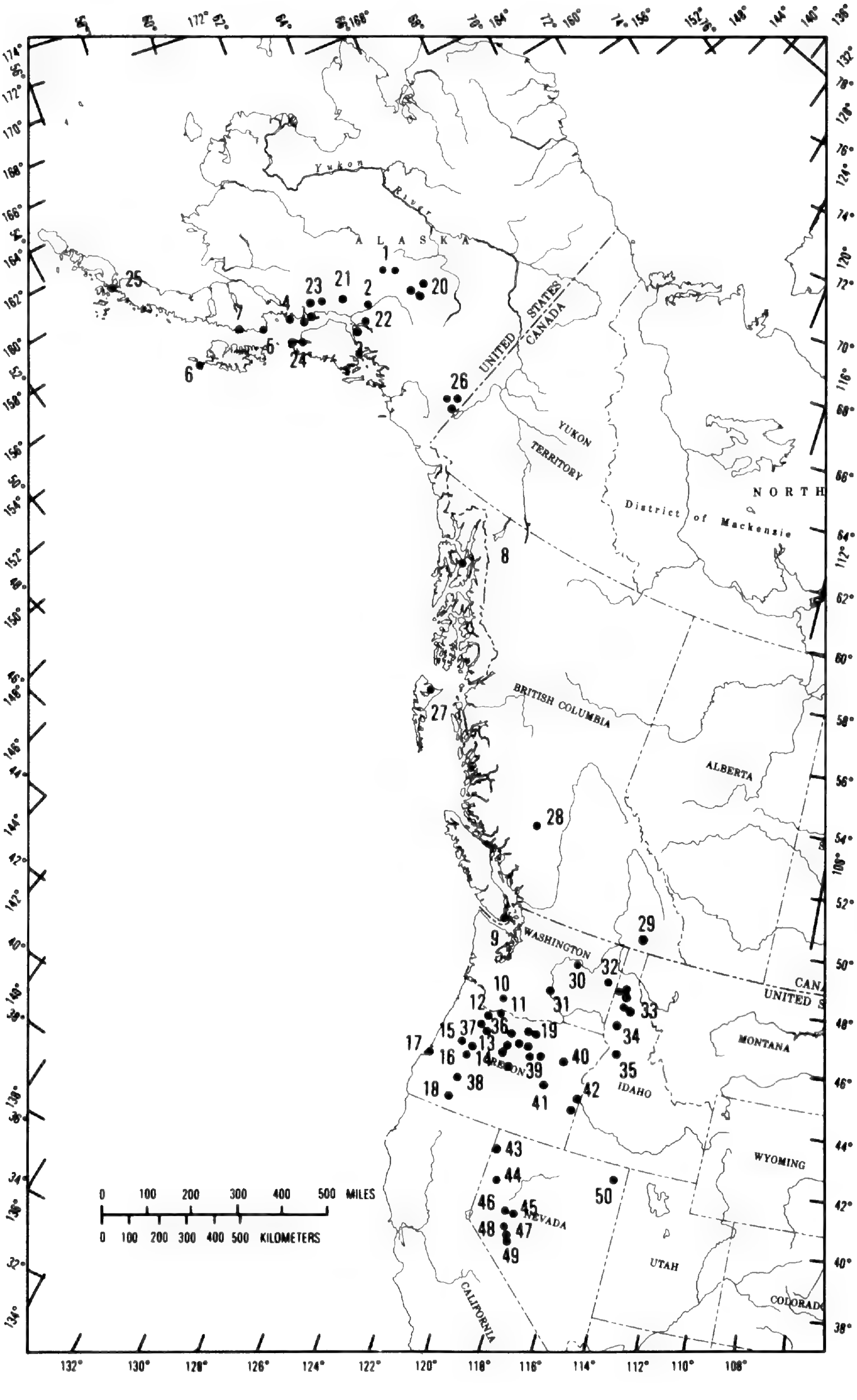
By the early to middle Miocene, the flora of the Columbia Plateaus had increased in diversity relative to the Oligocene. This diversity increase resulted from three major factors (Wolfe, 1972, 1977):

(1) Adaptation of mesothermal lineages to microthermal climates (e.g., *Magnolia,* some Lauraceae, and *Exbucklandia*).
(2) Diversification of Oligocene microthermal clades (e.g., *Fagus, Alnus, Ulmus, Carya,* and *Acer*).
(3) Northward migration of Asian mid-latitude lineages into Beringia and subsequent southward migration onto the Columbia Plateaus (e.g., four lineages of *Acer* belonging to sections *Macrantha, Platanoidea,* and *Parviflora*).

Maximal diversity on the Columbia Plateaus and adjacent areas was reached during the middle Miocene (ca. 13–16 Ma).

Notable are the few species shared between middle Miocene floras on the Columbia Plateaus and the Kilgore flora of Nebraska (MacGinitie, 1962). Even a putative shared species (*Acer* "*heterodentatum,*" in sect. *Negundo*) is represented in either region by distinct subspecies. Further, most Columbia Plateaus species have only a distant relationship to extant species of eastern North America. Divergences between most western and eastern American lineages had probably occurred during, or at the end of, the Eocene, which led to a distinctive western American element (Wolfe & Tanai, 1980: 16–18). By the Miocene (if not the Oligocene), the Rocky Mountain region must have formed an effective climatic barrier to migrations of most warm microthermal plants (Leopold & Denton, 1987).

An exception is series *Saccharodendron* of *Acer,* which was apparently able to disperse from eastern into western North America. Members of this series appear suddenly at middle latitudes of western North America during the early Miocene and have no Beringian record. Cladistic relationships and the fossil record both suggest dispersal across the North Atlantic during the Miocene (Wolfe, 1981b; Wolfe & Tanai, 1987), and the two lineages of series *Saccharodendron* present in the western American Neogene are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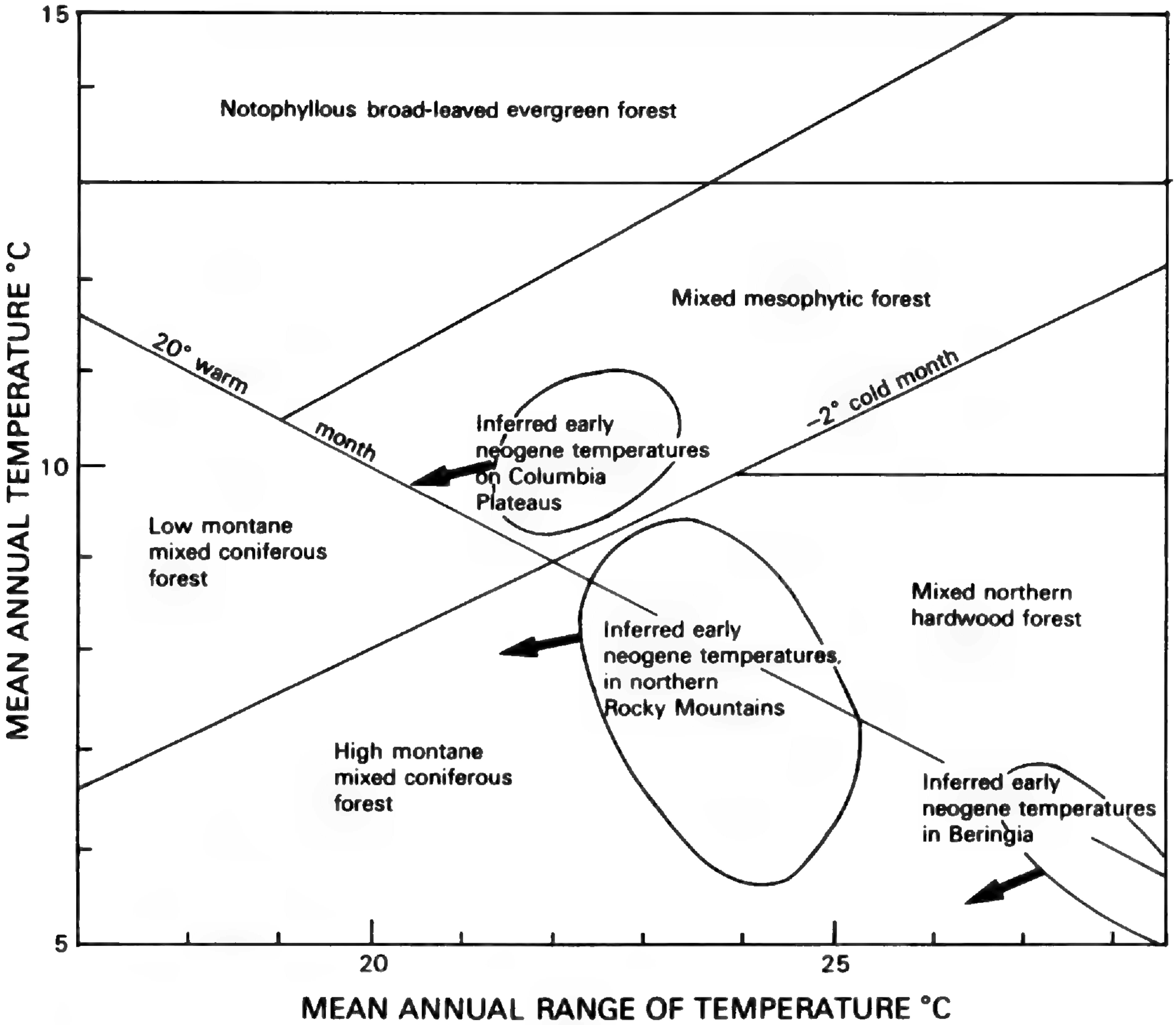

FIGURE 3. Nomogram showing inferred temperatures for the northern Rocky Mountains during the early Neogene. Classification and temperature relations of forests adapted from Wolfe (1979). Inferred temperatures for Columbia Plateaus and Beringian assemblages adapted from Wolfe & Tanai (1980) and Wolfe (1981a). Arrows indicate direction of Neogene temperature trends.

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FIGURE 2. Map showing location of some Oligocene and early Neogene (>13 Ma) plant assemblages in western North America. For each assemblage or group of assemblages, either published references or repositories of largely unpublished assemblages are cited; see Figure 1 for explanation of repositories. Oligocene: 1. Cheeneetnuk River assemblages (USGS); 2. Colorado Creek (USGS); 3. Eagle River (Wolfe et al., 1966); 4. Harriet Point, Harriet Creek, and Redoubt Point (USGS); 5. Douglas Mountain (USGS); 6. Sitkinak Island (USGS); 7. Kukak Bay assemblages (Knowlton, 1904; USGS); 8. Kootznahoo assemblages (Wolfe in Lathram et al., 1965); 9. Sooke (LaMotte, 1935; GSC); 10. Gumboot Mountain (UCMP); 11. Cascade Locks (USGS); 12. Sandstone Creek (USGS); 13. Cascadia (UCMP); 14. Lyons (Meyer, 1973); 15. Willamette (UCMP); 16. Rujada (Lakhanpal, 1958); 17. Yaquina (McClammer, 1978); 18. Shale City (USGS); 19. Bridge Creek assemblages (Chaney, 1927; OMSI, UCMP USGS). Early Neogene: 20. Nenana coal field assemblages (Wahrhaftig et al., 1969); 21. Lower Cache Creek (Wolfe et al., 1966); 22. Houston (Wolfe et al., 1966); 23. Capps Glacier (Wolfe, 1966; USGS); 24. Seldovia Point assemblages (Wolfe & Tanai, 1980); 25. Coal Bay (USGS); 26. Frederika (Wolfe, 1972; USGS); 27. Skonun (UBC); 28. Hanceville (GSC); 29. St. Eugene (Hollick, 1927); 30. Grand Coullee (Berry, 1931); 31. Vantage (UCMP); 32. Latah assemblages (Knowlton, 1926; Berry, 1929; Brown, 1937); 33. Clarkia (Smiley et al., 1975); 34. Orofino Creek (Brown, 1940); 35. Whitebird (Berry, 1934); 36. Eagle Creek assemblages (Chaney, 1920); 37. Collawash and Fish Creek (USGS); 38. Little Butte Creek (USGS); 39. Mascall assemblages (Chaney & Axelrod, 1959); 40. Baker (USGS); 41. Skull Spring (USGS); 42. Succor Creek assemblages (Graham, 1964, in part; cf. Fields, 1983); 43. '49 Camp (LaMotte, 1936); 44. Rabbit Hole (USGS); 45. Eastgate (Axelrod, 1985); 46. Middlegate (Axelrod, 1985); 47. Goldyke (UCMP); 48. Fingerrock (Wolfe, 1964); 49. San Antonio (UCMP); 50. Thurston Ranch (UCMP).

inferred to have crossed the Rocky Mountains; consistent with such crossings are the present distributions of the related *A. brachypterum* and the descendant *A. grandidentatum,* both of which live in the Rocky Mountains today. Thus some probably very limited floristic interchange between eastern and western North America occurred during the Neogene.

In the absence of actual assemblages, the flora of the northern Rocky Mountain region during the post-Eocene can be inferred only from assemblages outside the region. Except for floras to the west and southwest on the Columbia Plateaus, however, floras from adjacent regions are few. To the north in central British Columbia, the probable early Miocene assemblage from near Hanceville on the Chilcotin River appears to represent a High Montane Mixed Coniferous forest. In southern Colorado, the late Oligocene Creede assemblage represents subalpine coniferous vegetation. In Nebraska, the middle Miocene Kilgore assemblages largely represent a mesothermal gallery forest (MacGinitie, 1962).

Taxa that occurred both in Mixed Northern Hardwood forest of Alaska and in Mixed Mesophytic forest of the Columbia Plateaus represent taxa that (1) could exist under temperatures inferred for the northern Rocky Mountain region and (2) are known to have occurred adjacent to the northern Rocky Mountains. Such taxa thus can be reasonably inferred to have been in the northern Rocky Mountain region. Included in this category are lineages that are extant in the northern Rocky Mountains: *Alnus* aff. *incana, A.* aff. *viridis, Betula* aff. *papyrifera, Populus* aff. *trichocarpa, Salix* aff. *lasiandra, Prunus* aff. *virginiana, Acer* aff. *negundo,* and *A.* aff. *macrophyllum.* Also included are species of now extinct lineages: *Nordenskioldia* ("*Cocculus*" *auriculata*), *Cercidiphyllum alaskanum, Liquidambar pachyphylla, Alnus fairii, A. healeyensis, Ostrya oregoniana, Populus kenaiana, Ulmus knowltonii, U. speciosa, U. owyheensis, Zelkova brownii, Carya bendirei, Pterocarya nigella, Acer scottiae, A. septilobatum, A. tigilense,* and *Nyssa knowltonii.* Both lists contain primarily arcto-tertiary genera, genera that are now disjunct between eastern Asia and eastern North America or genera that are now characteristic of forests of north temperate regions (Engler, 1879). These genera (and many subgeneric groups), however, were represented in the Eocene upland microthermal vegetation; their inferred presence in the northern Rocky Mountain region is not necessarily the result of southward migration from high latitudes.

Composition of the northern Rocky Mountain coniferous element during the Oligocene and Miocene must also be inferred. In the middle Miocene of Nevada, the conifers are primarily those that now inhabit Low Montane Mixed Coniferous forest (e.g., *Abies* aff. *concolor, Picea* aff. *breweriana, Pinus* aff. *monticola, P.* aff. *ponderosa, Tsuga* aff. *heterophylla,* and *Chamaecyparis* aff. *nootkatensis*). Most of these conifers were also dominants of the Columbia Plateaus vegetation between 10 and 13 Ma (Fig. 4). In at least one instance, the fossil species is a sister species to the lineage that gave rise to the extant species (Edwards, 1983), suggesting that the fossil may have been adapted to a different environment than the extant species.

In the Beringian Neogene, most coniferous lineages were distinct from mid-latitude lineages. The *Abies* belong to a group of which the extant *A. sibirica* and *A. grandis* are members. *Larix* was a diverse and major element in the Beringian Neogene; no valid *Larix* is known during the Miocene at middle latitudes of western North America (H. E. Schorn, pers. comm., 1984). The Beringian *Picea* either are related to extant Asian species or represent the *P. glauca* group (including an extinct, large-coned species that survived into the Wisconsin glacial of southeastern North America according to Critchfield, 1984). Thus, the conifers (*Abies grandis, Larix,* and *Picea glauca*) that are now the most distinctive element of the northern Rocky Mountain region relative to other regions of the western United States appear to be derived from a high-latitude source.

Precisely when the Beringian coniferous element arrived in the northern Rocky Mountains is unknown. I suggest, however, that the arrival was probably post-Miocene. Coniferous lineages allied to taxa that are now restricted to Low Montane Mixed Coniferous forest occupied the Columbia Plateaus and Nevada during the Neogene and presumably represent ecotypes distinct from extant relatives (Wolfe, 1964); such extinct ecotypes also may have occupied the northern Rocky Mountains during the Neogene. During the late Neogene, many of these northern Rocky Mountain conifers possibly became extinct as the Beringian lineages migrated south. Perhaps significant is that the first record of the coastal ecotype of *Abies grandis* at middle latitudes is in the Pliocene–Pleistocene Sonoma assemblage of California (Axelrod, 1944a).

Various dicotyledons also may have penetrated southward from high latitudes during the Neogene. All North American (including Beringian) Eocene *Salix* represent subg. *Salix.* In Beringia, subg. *Vetrix* appears in the late Oligocene, approximately coincidental with the first appearance of other taxa of Asian affinities; members of sect. *Glauceae* appear in Beringia by the early Miocene. Sect. *Retusae* of subg. *Chamaetia* appear by the end of the Miocene. Skvortsov (1968) suggested that subg. *Vetrix* and subg. *Chamaetia* were of Asian origin, based on the present distribution of species that have inferred primitive morphologies. Although Asian fossil data are lacking, certainly the Beringian data are consistent with Skvortsov's interpretations. During the Neogene, various members of subg. *Vetrix* and sect. *Glauceae* underwent diversification at high latitudes. A few lineages penetrated southward in North America by the late early Miocene and middle Miocene, but most lineages of subg. *Vetrix* and subg. *Chamaetia* now extant at middle latitudes of western North America are probably late Neogene immigrants.

Representatives of Caprifoliaceae such as *Diervilla, Lonicera,* and *Symphoricarpos* were also significant and diverse elements in the Beringian Miocene, as were Ericaceae such as *Rhododendron* (subg. *Anthodendron = Azalea*) and *Vaccinium.* These are generally absent in Neogene floras at middle latitudes, although *Symphoricarpos* is known in the late middle Miocene of Nevada (Axelrod, 1956) and the late Miocene of Idaho (Chaney & Axelrod, 1959). Presumably most Caprifoliaceae and Ericaceae also represent late Neogene immigrants into the northern Rocky Mountain region.

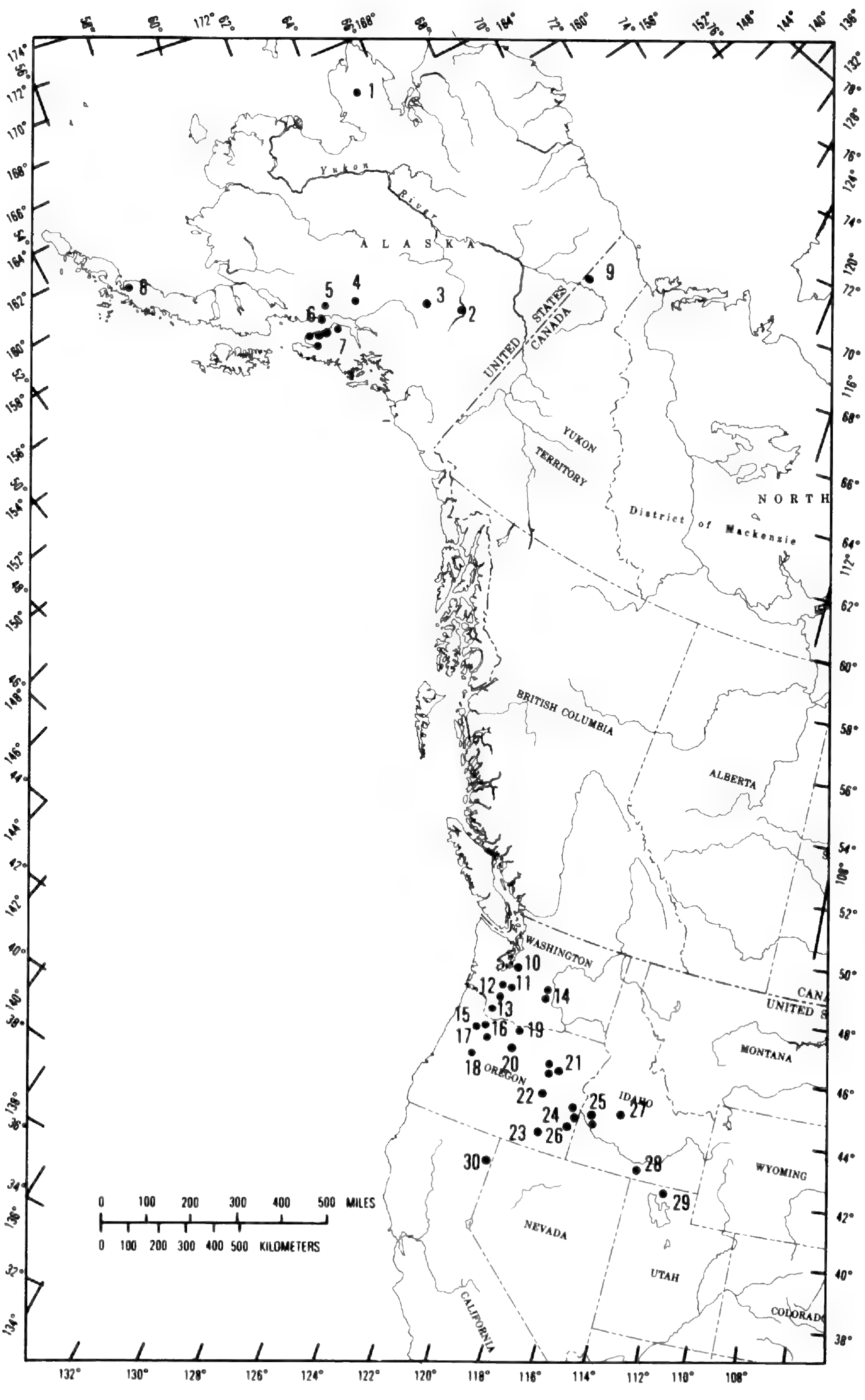
Some extant northern Rocky Mountain Rosaceae (e.g., *Amelanchier*) appear to be derived from lineages that have lived in or near the northern Rocky Mountain region since the Eocene. Other Rosaceae, however, probably belong to the late Neogene Beringian element. Although *Rubus* was represented in the Eocene upland microthermal vegetation, the extant *R. idaeus* has a probable ancestor in the Beringian Miocene. Similarly, *Prunus* subg. *Padus* has a continuous record in western North America during the Eocene and later, but subg. *Prunophora* first appears in western North America in Beringia during the Miocene, and the extant Pacific Northwest *Prunus subcordata* appears to represent a late Neogene immigrant from Beringia.

A pattern somewhat similar to that of *Prunus* is indicated for *Alnus.* Members of subg. *Alnus* were present in the northern Rocky Mountain region as early as late Paleocene, and all the upland Eocene *Alnus* represent this subgenus. The mid-latitude members of the subgenus differentiated by the Oligocene into a lineage leading to the extant *A. oregona,* and the lineage is clearly recognizable in the early Miocene of Oregon. High-latitude members of the subgenus are recognizable as belonging to the *A. crispa* lineage by the Oligocene, and this lineage had penetrated into middle latitudes by the middle Miocene. Members of subg. *Alnobetula* are high-latitude in distribution through the Miocene, and the entry of the extant *A. viridis* into middle latitudes probably occurred during the late Neogene.

Discussion

The terminal Cretaceous event selected for deciduousness and created a mesothermal region in the Northern Hemisphere almost devoid of broad-leaved evergreens, allowing by default occupation of this region by many deciduous groups. These groups then underwent major generic-level diversification. The elimination (or nearly so) of microthermal climates by the early Eocene thermal maximum and the following creation of microthermal, mid-latitude uplands of the later Eocene provided the opportunity for adaptive radiation of these deciduous mesothermal clades into the new microthermal environments and the opportunity for continuing diversification. Fundamentally, microthermal ecosystems became extinct during the early Eocene thermal maximum and arose again *de novo* following the thermal maximum. The continuing and major alterations in floristic composition during the Eocene, the apparent high degree of community instability during at least the early middle Eocene, and the rapid diversification of groups such as Rosaceae and Aceraceae during the Eocene can be viewed as symptomatic of the evolution of this new ecosystem. Insofar as known, the western North American volcanic uplands made up the only major, mid-latitude upland region in the Northern Hemisphere during the Eocene. These volcanic uplands thus occupy a central place in the diversification of many (if not most) microthermal clades of arcto-tertiary type.

Primarily during the middle and late Eocene, many microthermal, arcto-tertiary lineages were able to disperse readily from North America into Eurasia as adjuncts of a continuous expanse of coniferous forests (Wolfe, 1985, fig. 10). Partic-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Yukon River
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District of Mackenzie
NORTH
BRITISH COLUMBIA
ALBERTA
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MONTANA
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NEVADA
UTAH
CALIFORNIA
COLORADO
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ularly with the general cooling that characterized the later Eocene (Savin, 1977), microthermal climates were found at increasingly lower latitudes and produced a greater area available for occupation by microthermal vegetation. As migrating lineages elaborated over this area, diversification would continue and some new divergences that occurred in other regions would probably, in turn, migrate into North America. Thus, even in the Eocene, complexities were probably introduced into historical patterns of a given lineage.

Histories of the component lineages now in the flora of the northern Rocky Mountains are varied.

(1) Some lineages can be traced back, more or less continuously, into microthermal vegetation of the Eocene uplands (e.g., *Betula papyrifera* complex).
(2) Some lineages have generic representation in this upland vegetation, but divergences that led to the extant species probably occurred in the Oligocene or Neogene at middle latitudes (e.g., *Alnus oregona*) and some at high latitudes (e.g., *A. viridis*).
(3) Some lineages represented in the Eocene uplands probably dispersed into Asia, underwent major divergences into new subgenera, returned to Beringia by the Neogene, underwent species-level diversification, and entered the northern Rocky Mountain region in the late Neogene (e.g., species of *Salix* subg. *Vetrix*).
(4) Some lineages represented in the Eocene uplands dispersed into Eurasia, underwent diversification at the sectional level and returned to North America via long-distance dispersal from Europe (e.g., *Acer* series *Saccharodendron*).
(5) Some lineages have long Beringian histories and entered the northern Rocky Mountain region during the late Neogene (e.g., *Lonicera*).
(6) Another major pattern must be inferred for many alpine tundra plants; Arctic tundra is not recognizable until about the Pliocene–Pleistocene boundary (Wolfe, 1985), and elements shared between Arctic tundra and alpine tundra of the northern Rocky Mountain region may have entered the northern Rocky Mountains during the Quaternary.
(7) Another pattern must be inferred for plants of subhumid to xeric, southern affinities (Barnosky, 1984; Leopold & Denton, 1987); some of these belong to families that did not originate until about 25 Ma (Muller, 1981). The Neogene spread of Compositae was rapid, probably in relation to the high degree of dispersibility of their diaspores; however, the spread appears to be associated also with the development of dry climates.
(8) Pollen indicates that *Sarcobatus* (Chenopodiaceae) was a member of mesic coniferous forest during the later Miocene in areas such as southern Idaho (Wolfe, 1969); adaptation of *Sarcobatus* to xeric climate may be a late Neogene phenomenon.

No single pattern explains the origin of the majority of the modern flora of the northern Rocky Mountain region or even the majority of the flora of a given vegetational type or zone in the region. Certainly late Neogene cooling (probably along with orogenic movements) created climates in the northern Rocky Mountains favorable to Beringian taxa, but these are intermixed with taxa whose ancestry goes back to the Eocene in the northern Rocky Mountains. Further, Be-

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FIGURE 4. Map showing location of some late Neogene (<13 Ma) plant assemblages in western North America. For each assemblage or group of assemblages, either published references or repositories of largely unpublished assemblages are cited; see Figure 1 for explanation of repositories. 1. Hoogendoorn (Hopkins et al., 1971); 2. McCallum Creek (USGS); 3. Grubstake (Wahrhaftig et al., 1969); 4. Upper Cache Creek (Wolfe et al., 1966); 5. Chuitna River (Wolfe, 1966); 6. Tyonek (Wolfe et al., 1966); 7. Assemblages of type and referred sections of Homerian and Clamgulchian Stages (Wolfe et al., 1966; Wolfe, 1966); 8. Herendeen Bay (USGS); 9. Porcupine River (UAPC); 10. Hammer Bluff (USGS); 11. Mashel assemblages (USGS); 12. Wilkes assemblages (USGS); 13. Woodland (UWBM); 14. Ellensburg assemblages (Smiley, 1963); 15. Troutdale (Chaney, 1944b); 16. Faraday (USGS); 17. Weyerhauser and Molalla (UCMP, USGS); 18. Hidden Lake (USGS); 19. The Dalles (Chaney, 1944a); 20. Deschutes (Chaney, 1938); 21. Austin, Tipton and Vinegar Creek (Chaney, 1959; Chaney & Axelrod, 1959); 22. Stinking Water (Chaney & Axelrod, 1959); 23. Trout Creek (MacGinitie, 1933; Graham, 1964); 24. Succor Creek assemblages (Graham, 1964, in part; cf. Fields, 1983); 25. Hog Creek (Dorf, 1936); 26. Payette assemblages (UCMP; cf. Fields, 1983); 27. Thorn Creek (Smith, 1941); 28. Trapper Creek (Axelrod, 1964); 29. Cache Valley (Brown, 1949); 30. Pit River (LaMotte, 1936).

ringian taxa entered at different times during the Neogene and even Quaternary.

Despite considerable resemblance at the generic level to the modern flora of the northern Rocky Mountains, the microthermal upland vegetation of the Eocene had many genera that are now extinct and many genera that are now exotic to the region. Microthermal vegetation of western North America experienced major floristic alteration during the Eocene and later in response to various extrinsic climatic factors and intrinsic biotic factors such as competition.

The primary floristic result of the terminal Eocene temperature deterioration for microthermal vegetation was the elimination of many dicotyledonous genera, particularly those containing evergreens. Many deciduous dicotyledons, however, also suffered extinction. For example, numerous lineages in *Acer* became extinct, including all North American members of sections *Acer, Platanoidea, Campestria,* and *Macrantha* (all of which survived in Eurasia). Patterns of survival among deciduous taxa differed markedly between Eurasia and North America, probably due to intrinsic factors.

The relatively depauperate flora of the early Oligocene offered opportunities for radiation and diversification, with a general increase in diversity and blurring of the regional Oligocene generic and subgeneric endemism, especially between western North America and eastern Asia; for example, both *Platanoidea* and *Macrantha* reappeared in western North America during the Neogene. Migrations across Beringia were enhanced by the mid-Miocene warm interval, when broad-leaved deciduous forests were probably continuous from the Pacific Northwest across Beringia and into middle latitudes of eastern Asia (Wolfe, 1985, fig. 11).

Cooling at about 13 Ma (late middle Miocene), concomitant with a general Neogene decline in summer temperatures and decline in mean annual ranges of temperature (Wolfe, 1981a), eliminated many broad-leaved taxa of trees and shrubs from the Columbia Plateaus, Beringia, and presumably the northern Rocky Mountains. Coniferous forests probably occupied a continuous belt from the Columbia Plateaus and the northern Rocky Mountains north into Beringia. Mixed Northern Hardwood forest would have been totally eliminated from western North America. Climates in the northern Rocky Mountain region during the Neogene may have initially exhibited the trend toward lower mean annual ranges of temperature. However, by the late Miocene, increase in altitudes of mountains along the Pacific Coast would have countered this trend, allowing incursions of Arctic air masses; these masses are inferred to have influenced eastern North America after 13 Ma (Wolfe, 1985).

During the Neogene a summer-dry precipitation regime gradually encroached from the south (Wolfe, 1978), and during the late Miocene (ca. 5–11 Ma) increase in altitude of the Cascade Range created a significant rain shadow east of the range (Chaney, 1944c; Smiley, 1963). At lower altitudes on the Columbia Plateaus, forests were replaced by steppe vegetation during the late Miocene (Leopold & Denton, 1987; Wolfe, 1985). An analogous replacement was occurring in the northern Rocky Mountain region (Barnosky, 1984).

Considering the complexities of climatic changes and the complexities of orogenic activity in the northern Rocky Mountain and nearby regions, determination of historical biogeographic patterns, without recourse to the fossil record of extant lineages and analyses of successive fossil biotas, can be highly problematic. As Grande (1985) emphasized, vicariance methodology as typically applied is incapable of dealing with such complexities; several patterns can be overprinted on one another in such a region. Numerous patterns have been detected in the modern flora of the northern Rocky Mountains by recourse to the fossil record, and different species within the same genus can represent different patterns. Lineages, some closely related, can be subjected to the same extrinsic environmental factors and can respond in different ways, a fact that further increases the general complexity of the biogeographic tapestry in a region such as the northern Rocky Mountains.

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PRESENT-DAY VEGETATION IN THE NORTHERN ROCKY MOUNTAINS[1]

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ABSTRACT

The present-day northern Rocky Mountain vegetation is the product of a long history of geologic and climatic events that have interacted with the species populations composing the regional flora. General concepts relating to the organization, classification, and dynamic nature of vegetation are reviewed. Distributional and structural features of the vegetation cover between the Colorado Rockies and the Southern Canadian Rockies are discussed. Alpine, upper timberline, subalpine, montane, lower timberline, and grassland/steppe zones are treated. Climatic, physiographic, edaphic, and geologic factors operate interactively as complex local and regional gradients in patterning Rocky Mountain vegetation. It is likely that members of the modern Rocky Mountain flora are not in equilibrium with present-day environments but are shifting and adjusting to geographic dislocations associated with post-Pleistocene climatic alterations. Fire suppression, agriculture, domestic grazing, construction activities, timber harvesting, strip mining, species introductions, and air, soil, and water quality are having major impacts on Rocky Mountain vegetation. Present plant communities feature altered structures and compositions that may represent new ecosystem equilibria which could be irreversible under present-day climates.

Vegetation ecology encompasses the description and interpretation of distribution patterns exhibited by plants and plant communities occupying a given geographical area (Miles, 1979; McIntosh, 1985; Walter, 1985). The objective of this symposium is centered on an interpretation of the evolutionary development of the Northern Rocky Mountain (NRM) flora and vegetation, including the earliest origins and ages evidenced. This effort closely complements the reviews of the origins of the cordilleran flora (Great Basin and southern Rocky Mountains) provided by Reveal's (1979) and Axelrod & Raven's (1985) biogeographic treatments of the western intermountain region, and Peet's (1988) detailed analysis of structure, distribution, and production of forests from throughout the Rocky Mountains. My description of NRM vegetation serves to orient readers to other symposium contributions that consider the roles of past events in shaping this region's flora and vegetation.

THE NATURE OF VEGETATION

Literature on vegetation science reminds us of the dynamic nature of floras and plant communities (Knapp, 1974; Mueller-Dombois & Ellensberg, 1974; Miles, 1979; Chabot & Mooney, 1985; McIntosh, 1985). Many botanists engaged in the study of floras and plant communities agree that vegetation units associated with any landscape arise over time as chance combinations or assemblages of plant populations, with each species following more or less independent or individualistic ecological responses and migrational pathways, as Gleason (1926) hypothesized. Such ideas have been substantiated by Whittaker (1953), Curtis (1959), McIntosh (1985), and others over the past half century.

In his recent remarks addressing vegetation history in the northern Great Basin and Pacific Northwest, Mehringer (1985: 168) stated, "Plants responded as vagaries of climate, dispersal potential, competition, selection, soils, topography, volcanic eruptions, fire, man and chance dictated. A hazy outline of these responses has been traced through pictures painted with pollen extracted from yesterday's mud. Sketchy as the images may be, they prove the dynamic nature of this area's vegetation."

Floristic changes over time, whether gradual or abrupt, underlie the dynamic nature of the NRM vegetation. Post-Pleistocene pollen sequences in this region reveal "unquestionable fluctuations in vegetation wrought by short, sharp climatic episodes, by fire and by volcanic eruptions" (Mehringer, 1985: 185). Wells (1983), analyzing wood rat middens throughout western

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North America, provided descriptions and historical documentations of the paleobiogeographic shifts of western vegetation zones.

Davis (1976, 1981) and Webb (1981), in their analyses of forest vegetation stability during the Quaternary, also addressed postglacial vegetation dynamics and suggested that eastern North American plant populations are displaying differential rates of range reoccupancy following the Wisconsin glacial phase. Both Davis and Webb urged us not to assume that an equilibrium exists between modern plant distributions and the present climate. The NRM assuredly experienced its own Pleistocene stresses and phytogeographic rearrangements, and it is likely that the modern flora and vegetation in this area are not in equilibrium with modern climate.

Numerous environmental variables have influenced the NRM flora and vegetation over time. Lassoie et al. (1985), Smith (1985), and Peet (1988) provided summary interpretations of the ecophysiology of Pacific Northwest and Rocky Mountain conifer forests. Factors such as mountain building, differences in soil chemistry and physical structure, precipitation and temperature gradients, seasonal surpluses and water deficits, evaporation potentials, and wildfire, all interacting with each other and locally conditioned by physiographic factors, create a multitude of specific habitats for plant occupancy. Over time, plant populations sort themselves out differentially among available habitats. The spatial or geographic pattern (local and regional range limits) of each species is at least partially based on adaptive features. The physiological studies cited above emphasize how well the Rocky Mountain conifer species are adapted and adjusted to their environment.

Within the context of her eastern North American studies, Davis (1981) supported the view that species with long histories of co-occurrences in similar plant communities or habitats have co-evolved adaptive adjustments to reduce interspecific competition. Davis warned, however, that it is important for ecologists to individually assess as to whether sufficient time has elapsed for coevolution to have happened among closely associated plant species. Often these sorts of assessments represent research that must still be undertaken on our western vegetation types.

Each plant population is unique in its degree of adaptive expression or amplitude of tolerance. This uniqueness, founded in the genetic constitution of a species, is reflected in its rates of range extension or retreat, its present ecologic range limits, and its specific habitat. Differential rates of migration will affect vegetation distribution patterns, as well as the presence or absence of a species in a given vegetation association. The dynamic nature of plant populations and plant communities requires that ecologists recognize that they are dealing with a vegetational phenomenon that exhibits short-term stability but lacks long-term permanency.

Rocky Mountain Vegetation Studies

The earliest efforts to provide descriptive summaries of Rocky Mountain vegetation date back to the turn of the century. C. Hart Merriam (1889), a prominent figure in the history of North American vegetation ecology, developed a system of life zones that stressed the importance of temperature in explaining vegetation patterns. He popularized such life zone terms as Boreal, Transitional, Canadian, and Hudsonian. Little of Merriam's scheme is used today. P. A. Rydberg, an early botanist associated with the New York Botanical Garden, made major contributions to our understanding of the phytogeography of the Rocky Mountains (Rydberg, 1916, and numerous "phytogeographical notes" published in the Bulletin of the Torrey Botanical Club between 1913 and 1917). Rydberg's typical reporting format involved listing the flora of each mountain zone with its geographic origin and limits.

J. E. Kirkwood, pioneer botanist at the University of Montana, published (1918, 1922) some of the first in-depth ecological interpretations of northern Rocky Mountain forest compositions and distributions, applying to this region much of the basic ecological insight promulgated by Schimper (1903). Kirkwood provided a detailed literature review of NRM vegetation studies available at that time. He clearly emphasized that vegetation distribution patterns would be interpreted best when the "individualities" of the "constituent species" were understood, an idea that Gleason (1926) also advocated. Kirkwood stated that "the complex interaction of climatic, edaphic, biotic and other influences that guide and control the distribution of species is of keen interest to the student of phytogeography, and no treatment of the subject is fair that does not seek to give full weight to the many factors involved and especially to the nature and requirements of the individual species" (1922: 15). He also pointed out that Merriam's life zones often

FIGURE 1. Kuchler's (K) potential natural vegetation types (1964), with dominant species listed.—A. K-11 = western ponderosa pine forest (*Pinus ponderosa* var. *ponderosa*; K-16 = eastern ponderosa pine forest (*P. ponderosa* var. *scopulorum*).—B. K-12 = Douglas-fir forest (*Pseudotsuga menziesii* var. *glauca*).—C. K-13 = cedar-hemlock-pine forest (*Thuja plicata, Tsuga heterophylla* and *Pinus monticola*).—D. K-14 = grand fir & Douglas-fir (*Abies grandis* and *Pseudotsuga menziesii*).

lacked spatial distinction (discontinuity) because of elevational intermingling of the conifer dominants in the northern Rockies.

The many contributions made by R. F. Daubenmire to our knowledge of northern Rocky Mountain vegetation must also be recognized. In a career spanning nearly a half century, Daubenmire provided historical interpretations of the origins of the Rocky Mountain flora, studied the ecophysiological features of NRM plants, and was instrumental in developing the habitat type classification system widely employed in the Rockies (1943, 1966, 1968, 1969, 1970, 1975, 1978, 1980, 1981). Daubenmire's classic review paper, "Vegetation Zonation in the Rocky Mountains" (1943), summarized 175 ecological studies that bear on the extant vegetation of the Rocky Mountains. He reviewed floristic origins and provided interpretations of relationships between vegetation zonation and mountain climates.

Following these pioneers, many recent efforts

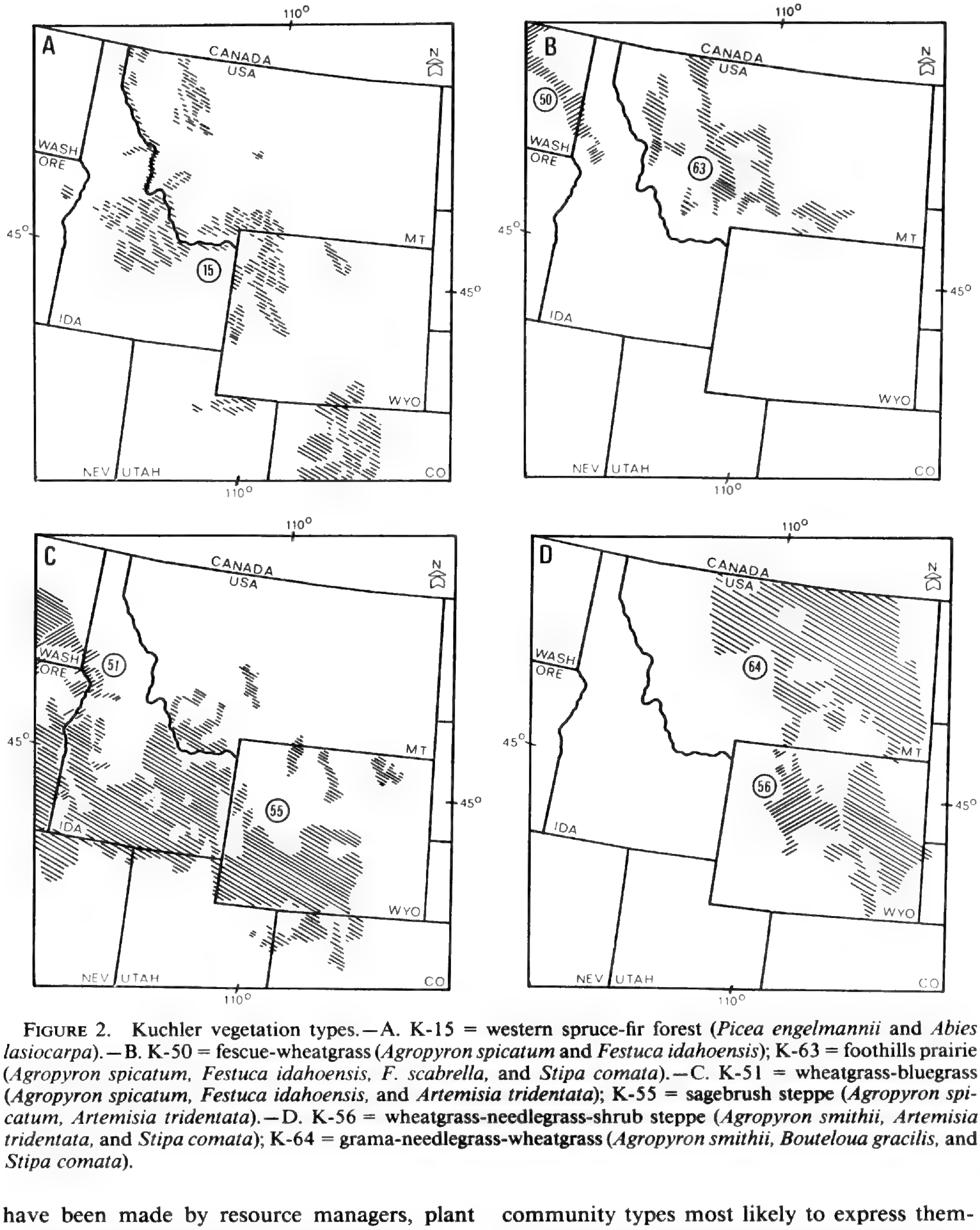

FIGURE 2. Kuchler vegetation types.—A. K-15 = western spruce-fir forest (*Picea engelmannii* and *Abies lasiocarpa*).—B. K-50 = fescue-wheatgrass (*Agropyron spicatum* and *Festuca idahoensis*); K-63 = foothills prairie (*Agropyron spicatum, Festuca idahoensis, F. scabrella,* and *Stipa comata*).—C. K-51 = wheatgrass-bluegrass (*Agropyron spicatum, Festuca idahoensis,* and *Artemisia tridentata*); K-55 = sagebrush steppe (*Agropyron spicatum, Artemisia tridentata*).—D. K-56 = wheatgrass-needlegrass-shrub steppe (*Agropyron smithii, Artemisia tridentata,* and *Stipa comata*); K-64 = grama-needlegrass-wheatgrass (*Agropyron smithii, Bouteloua gracilis,* and *Stipa comata*).

have been made by resource managers, plant ecologists, and geographers to describe, interpret, map, and classify parts or all of the Rocky Mountain vegetation (Kuchler, 1964; Daubenmire & Daubenmire, 1968; Pfister et al., 1977; Peet, 1981, 1988; Arno & Hammerly, 1984; Smith, 1985). Kuchler (1964) published a map of what he termed the "potential natural vegetation" of the coterminous United States. His map portrayed the present-day vegetation in terms of those community types most likely to express themselves in the absence of human influence. Kuchler realized that the presence or absence of wildfire and/or grazing alters the specific nature of vegetation cover; this complicated his mapping efforts. Figures 1, 2, and 3 show the general distributions of Kuchler's northern Rocky Mountain vegetation types.

Pfister et al. (1977) and Pfister (1984) provided detailed literature reviews of the vegetation clas-

FIGURE 3. Kuchler vegetation types.—A. K-40 = saltbush-greasewood (*Atriplex confertifolia* and *Sarcobatus vermiculatus*).—B. K-18 = ponderosa pine–Douglas-fir (*Pinus ponderosa* and *Pseudotsuga menziesii*); K-38 = Greatbasin sagebrush (*Artemisia tridentata*).—C. K-23 = juniper–pinyon woodland (*Juniperus monosperma, J. osteosperma, Pinus edulis* (east), *P. monophylla* (west), and *Quercus* spp.).—D. K-37 = mountain mahogany–oak scrub (*Cercocarpus ledifolius, Quercus gambelii,* and *Acer grandidentatum*).

sification efforts in the Rocky Mountains. Classifications are often individualized by each author's philosophy and objectives, and the absence of universally accepted concepts and principles hampers wide acceptance of any one classification approach. Many Rocky Mountain vegetation classifications have been developed for resource management, mapping, information storage, and vegetation preservation. These approaches often assume the existence of repeating combinations or assemblages of plant populations, in association with more or less specific site qualities.

Pfister (1984) supplied a recent concise summary of the history and current progress of forest and grassland classification efforts in the NRM. These have often involved delineation of site categories called "habitat types": physical settings definable in terms of the potential climax vegetation they are capable of supporting (Daubenmire, 1966). Habitat type classifications cover large parts of the Rocky Mountains. However, these classification efforts have elicited some critical commentary from other ecologists who have studied in the same regions (Antos & Habeck, 1981; McCune & Antos, 1981; Baker, 1984; Cloonan & Habeck, 1985; Crawford & Johnson, 1985; McCune & Allen, 1985a, 1985b).

Baker (1984), working with the Colorado Natural Heritage Inventory, maintained that vegetation classification in the Rocky Mountains is handicapped by the absence of a standardized nomenclature. He suggested, however, that no unique classification may be possible because of the vegetational variability, as noted above. Baker provided his own classification of Colorado's natural vegetation, a hierarchical listing of plant community types. Peet (1981) successfully employed gradient analysis and ordination techniques to the Colorado Front Range vegetation and derived a workable classification of forests in that area. An outline of Peet's results will be presented later.

My literature evaluation revealed that regional climatic patterns, physiographic provinces, elevation zonations, soil features, topographic-moisture gradients, habitat types (potential climax), seasonal moisture regimes, drought stress categories, plant life forms, community life forms, ecological interactions between dominants, as well as human intuition, have all been used to design classifications of Rocky Mountain vegetation. Furthermore, since the natural ecologic role of wildfire in the Rockies has become better understood (Habeck & Mutch, 1973; Arno, 1980; McCune, 1983; Habeck, 1985), some recent vegetation classifications have also encompassed fire-disturbed plant community types (Arno et al., 1985), as well as the multiplicity of seral vegetation types created by human activities. Successful fire suppression during a century of grazing and crop production has significantly altered the natural plant cover in the NRM. Fire-dependent vegetation types in the Rockies, especially, have changed drastically in the past century (Gruell, 1983).

Weaver & Dale (1974), Pfister et al. (1977), Arno (1979), Weaver (1979, 1980), Johnson & Pfister (1981, 1982), Peet (1981, 1988), Steele et al. (1981, 1983), and Arno & Hammerly (1984) contributed recent summaries of the climatic and physiographic features of the Rocky Mountains and detailed descriptive interpretations of the existing vegetation covering this region. These publications serve as my primary references; they are based on extensive field studies and in-depth literature reviews covering eastern Washington and northern Idaho, northeastern Oregon, western and central Montana, central and eastern Idaho, Wyoming, the Yellowstone Park area, and parts of Utah and Colorado.

Arno & Hammerly (1984) described and interpreted the lower (warm) timberline and upper (cold) timberline vegetation zones throughout the mountainous regions of western North America, with supplementary comments on vegetation types adjacent to or between timberlines. Johnson & Pfister's studies (1981, 1982) centered on identification and description of naturally occurring geologic and ecologic units in the middle and northern Rocky Mountains.

Smith (1985) made an effort to provide an ecophysiological explanation for the distribution patterns within western montane forests. Various factors—including moisture, solar radiation, and temperature—exhibiting seasonal variations within the western mountain complex and interactive with soil structure and nutrient content, form the environmental complex that defines plant community distributions and successional patterns. Smith emphasized the importance of "biophysical coupling" of site factors, fire, and various disturbances in dictating successional pathways. Additional ecophysiological data are needed before more complete explanations of vegetation patterns can be made (Peet, 1988). Future studies should also emphasize the long-term importance of human disturbances.

THE ROCKY MOUNTAIN SETTING: PHYTOGEOGRAPHIC SUBREGIONS

The region typically designated as the northern Rocky Mountains extends from the Snake River Plain in southern Idaho to the international border, joining with the southern Canadian Rockies in British Columbia and Alberta. This region averages 500 km in width, extending from near Yellowstone Park (northwestern Wyoming) westward to Hell's Canyon on the Idaho–Oregon state lines. Northward, the principal region extends from central Montana westward to northeastern Washington.

Peet's (1988) description and interpretation of the forest vegetation of the entire Rocky Mountain system recognized the existence of four floristic regions: far-northern, northern, southern, and madrean. My review encompasses all of the northern and part of the southern regions. The latter closely coincides with Daubenmire's (1943)

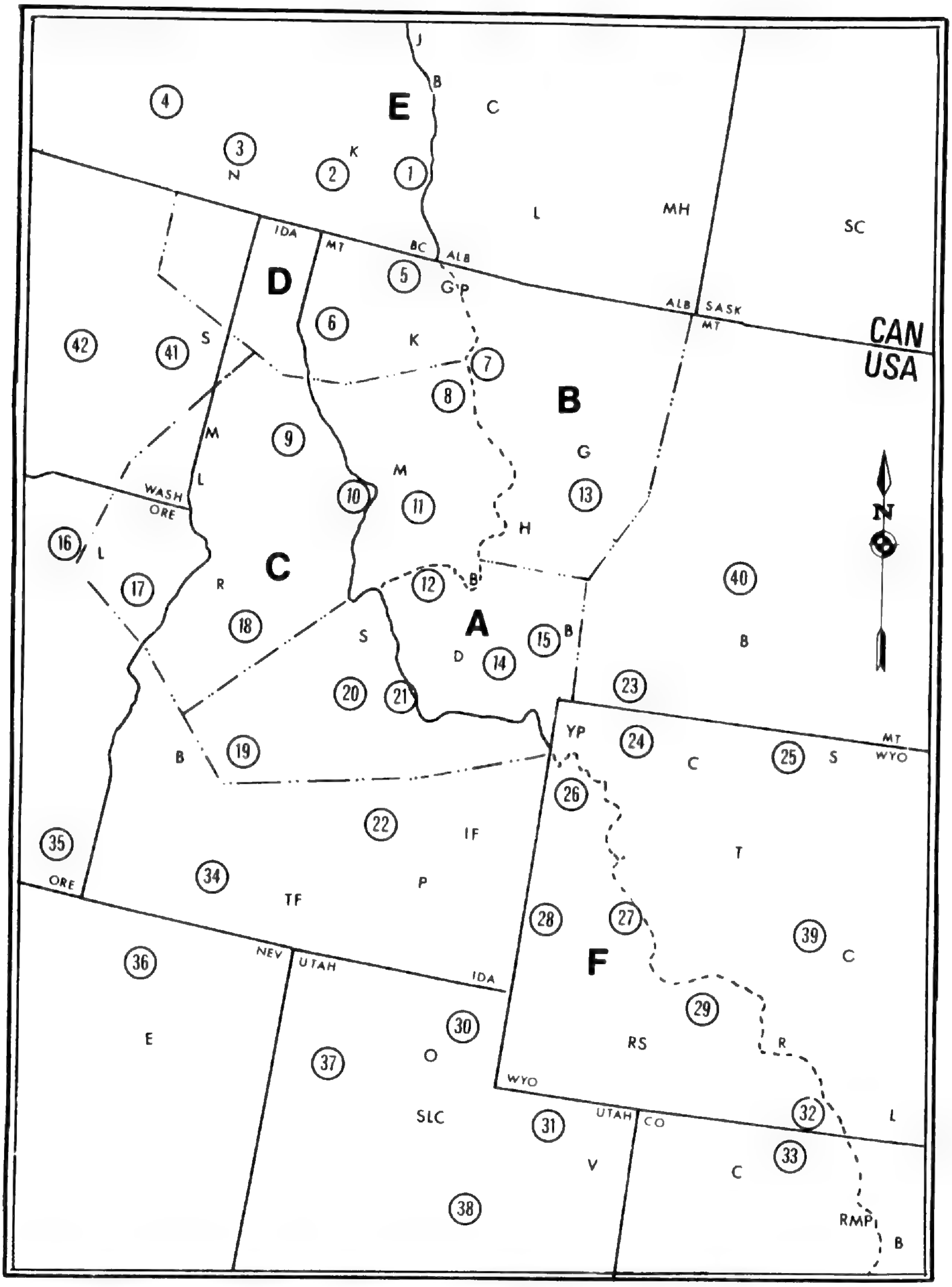

FIGURE 4. Northern Rocky Mountains with designated geographic regions (after Arno & Hammerly, 1984; see text): **A**—Southern Continental Ranges; **B**—Northern Continental Ranges; **C**—Intermountain Ranges; **D**—Inland Maritime Ranges; **E**—Southern Canadian Rocky Mountains; **F**—Middle Rocky Mountains. The Continental Divide is shown as a dashed line. States, provinces, cities, national parks, mountain ranges, and other features are shown by number and letter symbols keyed as follows: 1—Canadian "Great Divide" (BC, ALB); 2—Purcell Mountains (BC, MT); 3—Selkirk Mountains (BC, IDA); 4—Monashee Mountains (BC); 5—Whitefish Range (MT, BC); 6—Cabinet Range (MT); 7—USA Continental Divide (MT, IDA, WYO, CO); 8—Swan Range (MT); 9—Clearwater Mountains (IDA); 10—Bitterroot Mountains (MT, IDA); 11—Sapphire Mountains (MT); 12—Anaconda-Pintler Range (MT); 13—Little Belt and Big Belt Mountains (MT); 14—Gravely Range (MT); 15—Madison Range (MT); 16—Blue Mountains (ORE); 17—Wallowa Mountains (ORE); 18—Idaho Batholith & Salmon River Mountains (IDA); 19—Sawtooth Mountains (IDA); 20—Lost River Range (IDA); 21—Lemhi Range (IDA); 22—Craters of the Moon National Monument (IDA); 23—Beartooth Plateau (MT, WYO); 24—Absaroka Range & Yellowstone Park (WYO); 25—Big Horn Mountains (WYO); 26—Teton Range & Grand Teton Park (WYO); 27—Wind River Range (WYO); 28—Salt River & Wyoming Ranges (WYO); 29—Wyoming Basin & Great Divide Basin (WYO); 30—Wasatch Mountains (UTAH); 31—Uinta Mountains (UTAH); 32—

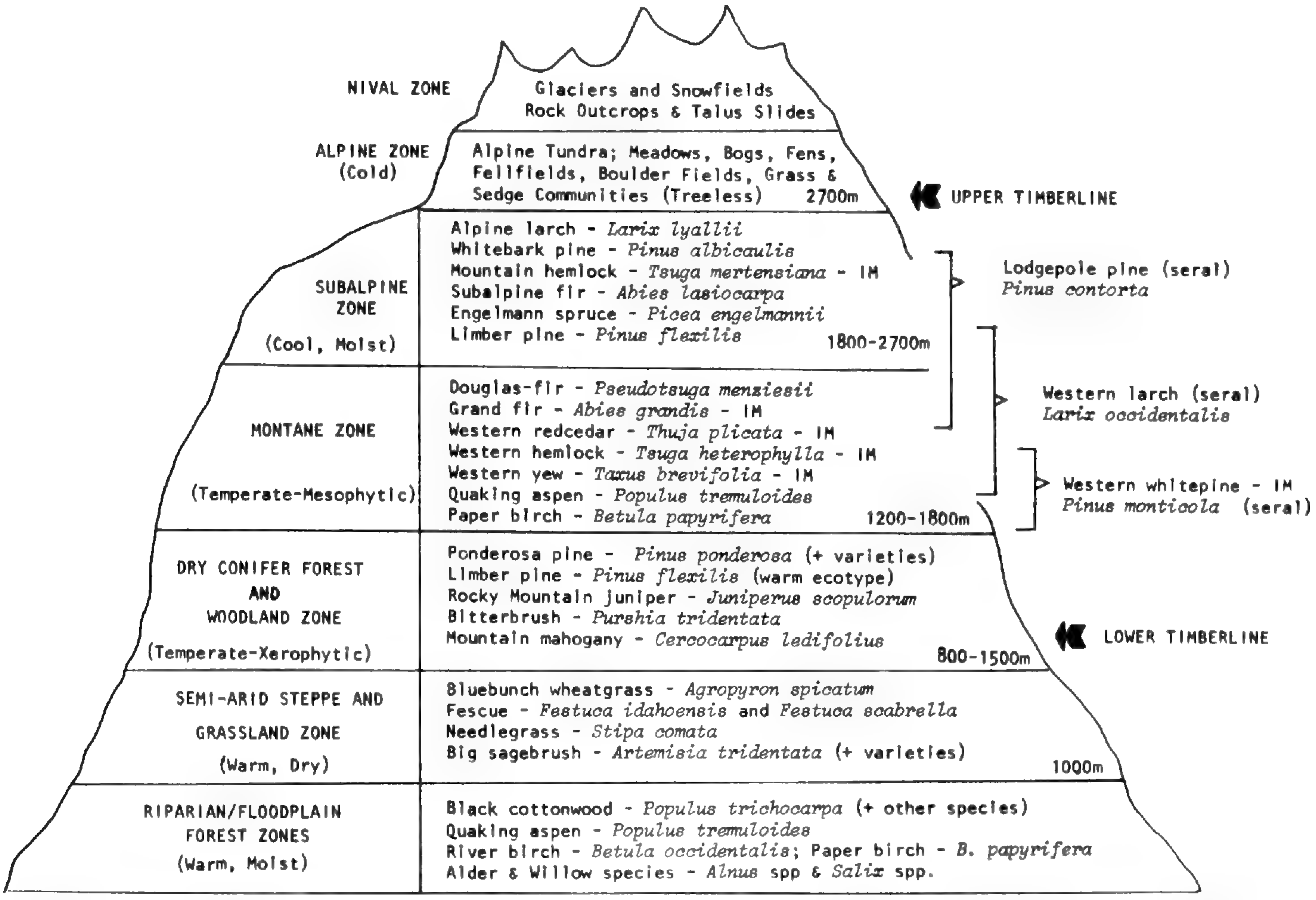

FIGURE 5. Vegetation zones in the northern Rocky Mountains, typical of Montana, northern Idaho, and adjacent parts of British Columbia and Alberta. Approximate elevational limits of these zones are given, as are average positions of the lower and upper timberlines. IM = restricted to Inland Maritime region.

"central Rockies," and in my review will be referred to as the "middle Rockies," after Arno & Hammerly (1984). Figure 4 shows the geographic units employed in this review.

The Southern Canadian Rocky Mountains (SCRM), which extend from the international boundary northward, are closely related physiographically and floristically to the NRM in the United States, as defined above (Rowe, 1959; Arno & Hammerly, 1984). The region designated as the Middle Rocky Mountains (MRM) is located south of the Yellowstone River in Montana and extends southward through Wyoming to parts of Utah and Colorado; it includes the Uinta and Wasatch mountains, Medicine Bow Mountains, and the Colorado Front Range (Fig. 4). Both the SCRM and MRM will be discussed, but emphasis will be placed on the traditional NRM province.

The importance of elevation and topographic-

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Medicine Bow Range (WYO, CO); 33—Park Range (CO); 34—Snake River Plain (IDA); 35—Steens Mountains (ORE); 36—Northeastern Great Basin (NEV); 37—Great Basin (UTAH); 38—Juniper–Pinyon Woodland (UTAH); 39—Wyoming Basin Sagebrush-Steppe (WYO); 40—Plains Grasslands (MT); 41—Palouse Prairie (WASH, IDA); 42—Sagebrush Steppe (WASH). N-BC—Nelson, British Columbia; K-BC—Kimberley, British Columbia; J-ALB—Jasper National Park, Alberta; B-ALB—Banff National Park, Alberta; C-ALB—Calgary, Alberta; L-ALB—Lethbridge, Alberta; MH-ALB—Medicine Hat, Alberta; SC-SASK—Swift Current, Saskatchewan; S-WASH—Spokane, Washington; L-ORE—LaGrande, Oregon; M-IDA—Moscow, Idaho; L-IDA—Lewiston, Idaho; R-IDA—Riggins, Idaho; S-IDA—Salmon, Idaho; B-IDA—Boise, Idaho; IF-IDA—Idaho Falls, Idaho; P-IDA—Pocatello, Idaho; TF-IDA—Twin Falls, Idaho; GP-MT—Glacier National Park, Montana; K-MT—Kalispell, Montana; M-MT—Missoula, Montana; G-MT—Great Falls, Montana; H-MT—Helena, Montana; B-MT—(west)—Butte, Montana; B-MT (east)—Billings, Montana; D-MT—Dillon, Montana; YP-WYO—Yellowstone National Park, Wyoming; C-WYO (north)—Cody, Wyoming; C-WYO (south)—Casper, Wyoming; T-WYO—Thermopolis, Wvoming; RS-WYO—Rock Springs, Wyoming; R-WYO—Rawlins, Wyoming; L-WYO—Laramie, Wyoming; E-NEV—Elko, Nevada; O-UTAH—Ogden, Utah; SLC-UTAH—Salt Lake City, Utah; V-UTAH—Vernal, Utah; C-CO—Craig, Colorado; RMP-CO—Rocky Mountain National Park, Colorado; B-CO—Boulder, Colorado.

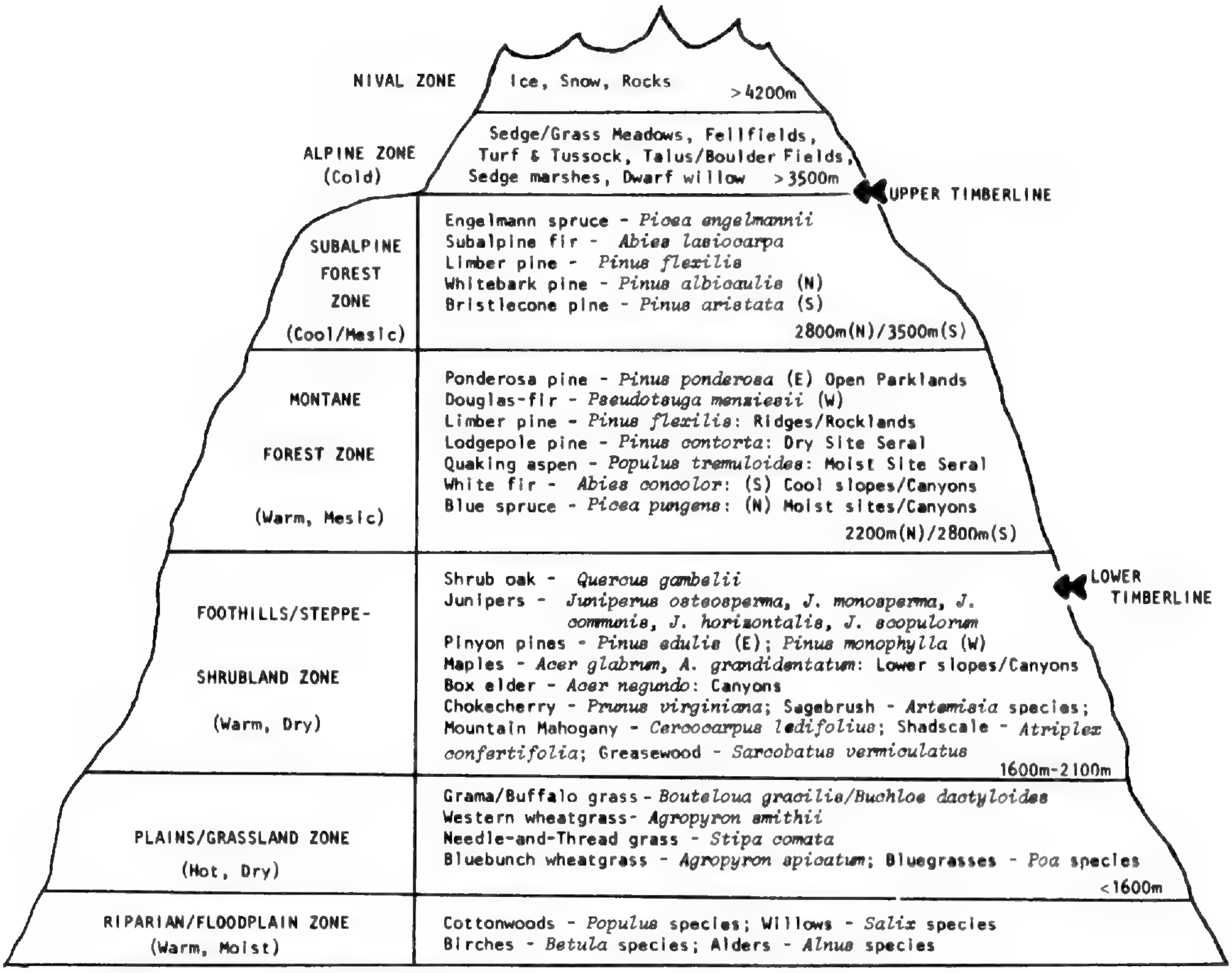

FIGURE 6. Vegetation zones typical of the middle Rocky Mountains. Major dominants in each life zone are listed.

moisture gradients in determining Rocky Mountain forest distribution patterns was emphasized by Peet (1988). He provided a series of "gradient mosaic diagrams" which portray the latitudinal shifts in forest composition along the entire length of the Rocky Mountains. Soil constitutes a third environmental variable important in interpreting Rocky Mountain vegetation patterns (Weaver, 1978; Peet, 1988).

Figures 5 and 6 show generalized vegetation zonations in the northern and middle Rockies. Daubenmire (1980) also documented that NRM vegetation closely follows environmental gradients from warm-and-dry to cold-and-wet, regardless of altitude. He stated that elevation above sea level is of reduced significance in the NRM because of the interdigitation of vegetation types within the mountain topography.

Within the NRM, there are significant climatic gradients which play major roles in modern vegetation distribution patterns. In the northwestern sector of this region (which includes northeastern Washington, northern Idaho, and northwestern Montana to the west slope of the Continental Divide in Glacier Park), there exists a moist inland-maritime zone that features a well-developed oceanic influence (Kirkwood, 1922; Larsen, 1930; Daubenmire, 1943; McMinn, 1952; Weaver, 1979, 1980; Lassoie et al., 1985; Peet, 1988). Here the NRM exhibits nearly continuous forest cover composed of several conifers with Pacific coastal affinities. These include *Thuja plicata, Tsuga heterophylla, T. mertensiana. Taxus brevifolia, Abies grandis,* and *Pinus monticola,* as well as coastal shrubs, herbs, and nonvascular plants (McCune, 1984). The lower slopes and valleys are also heavily forested, without a well-defined lower timberline.

As the maritime influence diminishes, much of the remaining NRM region experiences a significantly colder and drier continental climate. The mountain peaks of this region are also much higher than those of the inland maritime region, and coastal tree species are absent. Well-developed, high-elevation, cold timberline/alpine zones occur, and lower timberlines composed of savanna, grassland, and shrubland vegetation types are caused by the much warmer and drier continental conditions. Here *Pseudotsuga menziesii* var. *glauca, Pinus ponderosa* var. *ponder-*

osa, P. ponderosa var. *scopulorum, Picea engelmannii* (and hybrids between *P. engelmannii* and *P. glauca*), *Abies lasiocarpa, Pinus contorta* var. *latifolia, P. flexilis,* and *P. albicaulis* are the characteristic tree species.

Arno & Hammerly (1984) established several NRM subregions based on geographic and bioclimatic criteria. Each of these includes several mountain ranges (Fig. 4): A. Southern Continental ranges, B. Northern Continental ranges, C. Intermountain ranges, and D. Inland Maritime ranges. The SCRM and MRM ranges were discussed separately. In their reviews, Johnson & Pfister (1981, 1982) made use of "physiographic provinces," as well as forest "climax series" similar to those used in the habitat type classifications cited above.

A very comprehensive biophysical land classification for the southern Canadian Rockies, including an in-depth treatment of the vegetation, is provided by Corns & Achuff (1982). Their study focused on Banff and Jasper National Parks but has general usefulness for the SCRM. They established a series of physiognomic classes: A. Closed Forest, B. Open Forest, C. Shrub, D. Low Shrub-Herb, and E. Herb Dwarf-Shrub. Corns & Achuff used these vegetation types, combined with climatic and soil factors, to define "ecoregions" in Banff and Jasper National Parks.

VEGETATION OF THE NORTHERN ROCKY MOUNTAINS

The following description of the present-day NRM vegetation will make use of the geographic-biophysical subregions established by Arno & Hammerly (1984). The information will emphasize the forested zones as depicted in Figure 5, with supplementary material on associated nonforest types.

SOUTHERN CONTINENTAL MOUNTAINS

The southern continental mountains include those found in eastcentral Idaho and southwestern Montana (Fig. 4, Region A). The Sawtooth Mountains, Lost River Range, Lemhi Range, Beaverhead Range, Anaconda-Pintler Range, Gravelly Range, and Madison Range are included. This region is dry and cool; the low moisture (20–40 cm annually) is due to a rainshadow effect caused by Oregon's Blue and Wallowa mountains and other Idaho ranges. Steppe and grassland types are present on lower slopes and valleys, dominated by several species of *Artemisia* and bunchgrasses (mostly *Agropyron spicatum* and *Festuca idahoensis*). The forest cover is confined to a relatively narrow zone between the lower timberline at 2,000 m and the upper timberline at about 2,700 m.

Pinus ponderosa is not well represented in the lowest forested zones of this part of the NRM because of the cold climate and short growing season at lower timberline (Arno & Hammerly, 1984). Instead, *Pseudotsuga menziesii* is the more common dominant tree adjacent to the steppe zone, sometimes mixing with *Pinus flexilis* at or near the lower timberline (1,800–2,300 m). In dry mountain ranges (Lost River Range), krummholz forms of *Pinus flexilis* and *Picea engelmannii* define the upper tree line at 2,875 m, while on more mesic upper timberline sites (Sawtooth Range, Beaverhead Range, and Madison Range) *Abies lasiocarpa* and *Pinus albicaulis* join *Picea* (Arno & Hammerly, 1984). Some southern continental mountain ranges have such severe moisture shortages that sagebrush-grassland vegetation extends up to and through the subalpine zone.

Forest understories in the southern continental region are low in species richness. Semiarid steppe and grasslands dominated by *Festuca idahoensis, Agropyron spicatum, Stipa comata,* and *Artemisia tridentata* form a mosaic among the *Pseudotsuga menziesii* forests. At higher elevations, *Symphoricarpos albus, S. oreophilus, Carex geyeri, Mahonia repens, Calamagrostis rubescens, Vaccinium globulare, Arnica cordifolia, Spiraea betulifolia,* and *Acer glabrum* are common understory associates. Some of these shrubs and herbs extend into the subalpine zone where they are joined by *Vaccinium scoparium, Linnaea borealis, Smilacina stellata,* and *Arnica latifolia.*

According to Dunwiddie (1977), Young & Evans (1981), Arno & Gruell (1983), Arno & Hammerly (1984), and Butler (1986), fire suppression since 1900, climatic changes, and livestock grazing have contributed to conifer invasions into the steppe-grassland zones at lower and middle elevations throughout the Rocky Mountains. Before 1900, fires swept through these mountain ranges at intervals of 20–30 years, killing many young conifers that were establishing themselves in grasslands and shrublands. Intensive and extensive grazing removes or reduces competing grasses, further facilitating spatial shifts in the forest-grassland boundaries.

The southern continental region also supports woodlands composed mostly of *Juniperus scopulorum.* This vegetation type is found on dry, rocky sites, including outcroppings, generally below the limits of *Pseudotsuga menziesii.* A common associate of juniper is *Cercocarpus ledifolius.* Present but much less common is *Juniperus osteosperma,* which occupies very severe sites and may be found mixed with *Pinus flexilis.* Sagebrush-steppe, dominated by *Agropyron spicatum, Artemisia tridentata, Festuca idahoensis,* and *Purshia tridentata,* occurs throughout Region A in Idaho and Montana (Kuchler, 1964).

NORTHERN CONTINENTAL MOUNTAINS

The northern continental mountains consist of the central Montana mountain ranges east of the Continental Divide (including the Lewis Range and "Rocky Mountain Front"), from the vicinity of Helena and Harlowton (Big Belt Mountains, Crazy Mountains, and Little Belt Mountains) northward to the southern Canadian Rockies in Alberta (Fig. 4, Region B). The isolated Bear Paw Mountains and Sweetgrass Hills in northcentral Montana and the Cypress Hills in southern Alberta can be included in this geographic subunit, although they are located 150 km or more east of the cordilleran Rocky Mountains.

The valley elevations here are lower than in the southern continental mountains but the northern continental ranges experience somewhat less moisture stress (Arno & Hammerly, 1984). This subregion receives 25–30 cm of precipitation annually, causing the lower timberline zone to be expressed at 1,200–1,500 m; continuous forest cover occupies a broader elevational zone. *Pinus ponderosa* forms the lower timberline in parts of central Montana ranges (Arno, 1979) but plays a lesser role north of 47°. Pacific coastal understory species (see Inland Maritime Region) are uncommon in central Montana forests but Great Plains species are present, including *Bouteloua gracilis, B. curtipendula, Andropogon* spp., *Opuntia fragilis,* and *Yucca glauca.*

Pinus ponderosa is replaced by combinations of *Populus tremuloides, Pseudotsuga menziesii, Pinus flexilis,* and *Pinus contorta* north of Great Falls, Montana. Cold winter climates with fluctuating temperatures and 115 kph winds seem to exceed the tolerance of *Pinus ponderosa. Populus tremuloides* and associated conifers that occupy this area are often deformed and/or stunted by the cold winter winds. Good examples of these effects can be seen on the east side of Glacier National Park. With the reduction of fire, *Pinus flexilis* woodlands have extended into the prairie communities in this same region.

The montane zone, occupying the middle elevations of these central Montana mountains (1,500–1,800 m), is dominated by *Pseudotsuga menziesii* and *Pinus contorta* in varying amounts. *Picea engelmannii* is a dominant in areas transitional to the subalpine zone, where it is codominant with *Abies lasiocarpa* and *Pinus albicaulis.* The upper timberline (tree limit) occurs between 2,300–2,600 m, with some terrain above 2,400 m supporting alpine tundra.

Associated undergrowth species near the lower timberline in the northern continental mountains include *Agropyron spicatum, Festuca idahoensis, F. scabrella, Bouteloua gracilis,* and *Stipa richardsonii. Symphoricarpos albus, Spiraea betulifolia, Smilacina stellata, Linnaea borealis, Galium triflorum, Menziesia ferruginea, Vaccinium globulare,* and *V. scoparium* dominate the understories of higher forest zones.

The disjunct Sweetgrass Hills (2,100 m) in northcentral Montana, although completely surrounded by semiarid Great Plains grasslands and foothills prairie, support forests composed of many of the montane and subalpine conifer species listed above, as well as the hybrid spruce *Picea glauca* × *P. engelmannii* (Habeck & Weaver, 1969). According to Thompson & Kuijt (1976), the Sweetgrass Hills were surrounded but not covered by the Laurentide glaciers; the hilltop nunataks may have supported tundra vegetation. Later, the Hills were part of a more continuously forested region in early post-Wisconsin, but climatic changes isolated the forests from the Rockies. The post-Hypsithermal shift towards increased warmth and dryness appears to disfavor maintenance of the present-day subalpine understory species in the Sweetgrass Hills.

INTERMOUNTAIN RANGES

The Intermountain Ranges are found in northeastern Oregon, central Idaho, and westcentral Montana (Fig. 4, Region C). The Blue and Wallowa mountains are in Oregon; the Clearwater Mountains, Salmon River Mountains, and the western edge of the Bitterroot Mountains are in Idaho; the Sapphire Range, Anaconda-Pintler Range (border between Regions A and C), Flint Creek Range, and the southern parts of the Mission and Swan ranges are located in westcentral Montana. The climate is partially influenced by moist maritime air masses that pass nearby, but this region receives less total moisture than does

FIGURE 7. *Pinus ponderosa* forest in Intermountain region, western Montana. Located near Darby, Montana, at 1,050 m within the *Pseudotsuga menziesii* zone. This forest type historically was maintained as open savannas by ground fires. USDA Forest Service.

the more western Inland Maritime region. On the other hand, the more severe continental climate that features temperature extremes, cold dry winter, and stressful chinook winds is not as common in this region (Arno & Hammerly, 1984).

The Intermountain Ranges have well-defined lower and upper timberlines, and the valley bottoms (900–1,050 m) and southern aspects support bunchgrass prairies (*Agropyron* and *Festuca* mixtures) and shrubland communities dominated by *Artemisia tridentata,* its subspecies, and/or *Purshia tridentata. Pinus flexilis* is generally absent from this part of the northern Rockies (a few exist in the easternmost part). The grassland-shrub types were originally interfacing or interspersed with *Pinus ponderosa,* forming the lowest forest zone. In presettlement times, the exact position of the lower timberline was partially conditioned by wildfires caused by lightning and aboriginal man (Gruell, 1983).

Frequent low intensity ground fires perpetuated open *Pinus ponderosa* savannas (Fig. 7), even on mesic sites where *Pseudotsuga menziesii* and *Abies grandis* are now invading (Habeck & Mutch, 1973; Habeck, 1976, 1985; Barrett & Arno, 1982; Freedman & Habeck, 1984). My own analysis of fire scars on 300- to 350-year-old *Pinus ponderosa* specimens occupying a drainage near Missoula indicates that fires occurred at about ten-year intervals before the mid 1700s, but from 1750 to 1870 the fire frequency doubled! That is, intervals between fires were reduced to an average of five years. Indians practiced routine burning throughout the Rocky Mountains before their encounter with Euroamerican influences (Barrett & Arno, 1982; Gruell, 1985; Arno, 1985; Lewis, 1985) but may have started more fires following introduction of horses into western Montana in the 1730s. Such frequent burning maintained even moist *Pseudotsuga* forest sites as grassland savannas. Remnants of the savanna bunchgrass, *Festuca scabrella,* still exist beneath the Douglas-fir forest canopies that have developed without fire since 1900.

Above the *Pinus ponderosa* zone lies the *Pseu-*

FIGURE 8. Old-growth *Larix occidentalis*-dominated forest in Inland Maritime region in Flathead National Forest, Montana (1,100 m). Established following a wildfire, the *Larix* is being replaced by the climax species, *Pseudotsuga menziesii*. USDA Forest Service.

FIGURE 9. Subalpine zone exhibiting unevenly-distributed *Abies lasiocarpa. Pinus albicaulis* and *P. contorta* near Wahoo Pass (2,000 m) in Selway-Bitterroot Wilderness, Montana/Idaho state line. USDA Forest Service.

dotsuga menziesii forest zone, extending from 1,200 to 1,800 m. Within this zone, *Larix occidentalis* prevails as a major pioneer species (Fig. 8). This disturbance-dependent species may achieve diameters of 1–1.5 m (thick basal bark layers that provide fire protection contribute to large girths) and heights over 40 m. Another common but short-lived associate in the upper part of the *Pseudotsuga menziesii* zone is *Pinus contorta*; it is also dependent in the NRM on periodic fires or other site disturbances (Lotan & Perry, 1983; Muir & Lotan, 1985).

Common understory species in the Douglas-fir/western larch forests include *Physocarpus malvaceus, Acer glabrum, Vaccinium globulare, V. caespitosum, Calamagrostis rubescens, Carex geyeri, Spiraea betulifolia, Arctostaphylos uva-ursi, Mahonia repens, Linnaea borealis,* and *Symphoricarpos albus.*

Abies lasiocarpa dominates the zone from 1,800 m to treeline near 2,700 m (Fig. 9). *Pinus contorta* extends into this zone and mixes with *Pinus albicaulis* and *Picea engelmannii.* Again, fire historically occurred in these higher forest zones (Fig. 10) but at long intervals, usually more than 100 years and sometimes at 200- to 300-year intervals (Habeck, 1985).

Dominant understory species associated with Intermountain subalpine forests include *Menziesia ferruginea, Vaccinium globulare, V. scoparium, Xerophyllum tenax, Carex geyeri, Arnica cordifolia, A. latifolia, Calamagrostis rubescens, C. canadensis, Luzula hitchcockii, Clintonia uniflora, Tiarella trifoliata, Anemone piperi,* and *Linnaea borealis.*

Insects and other pathogens are known to have caused periodic ecosystem disruptions in the Intermountain forests. McCune (1983), however, has suggested that man's reduction of wildfires in western Montana has predisposed the forests to greater insect infestations by altering stand structure and composition. Ecological studies employing dendrochronologic analyses of tree growth patterns have been undertaken to investigate these concerns (Carlson & McCaughey, 1982; Anderson, 1985). Their data suggest that

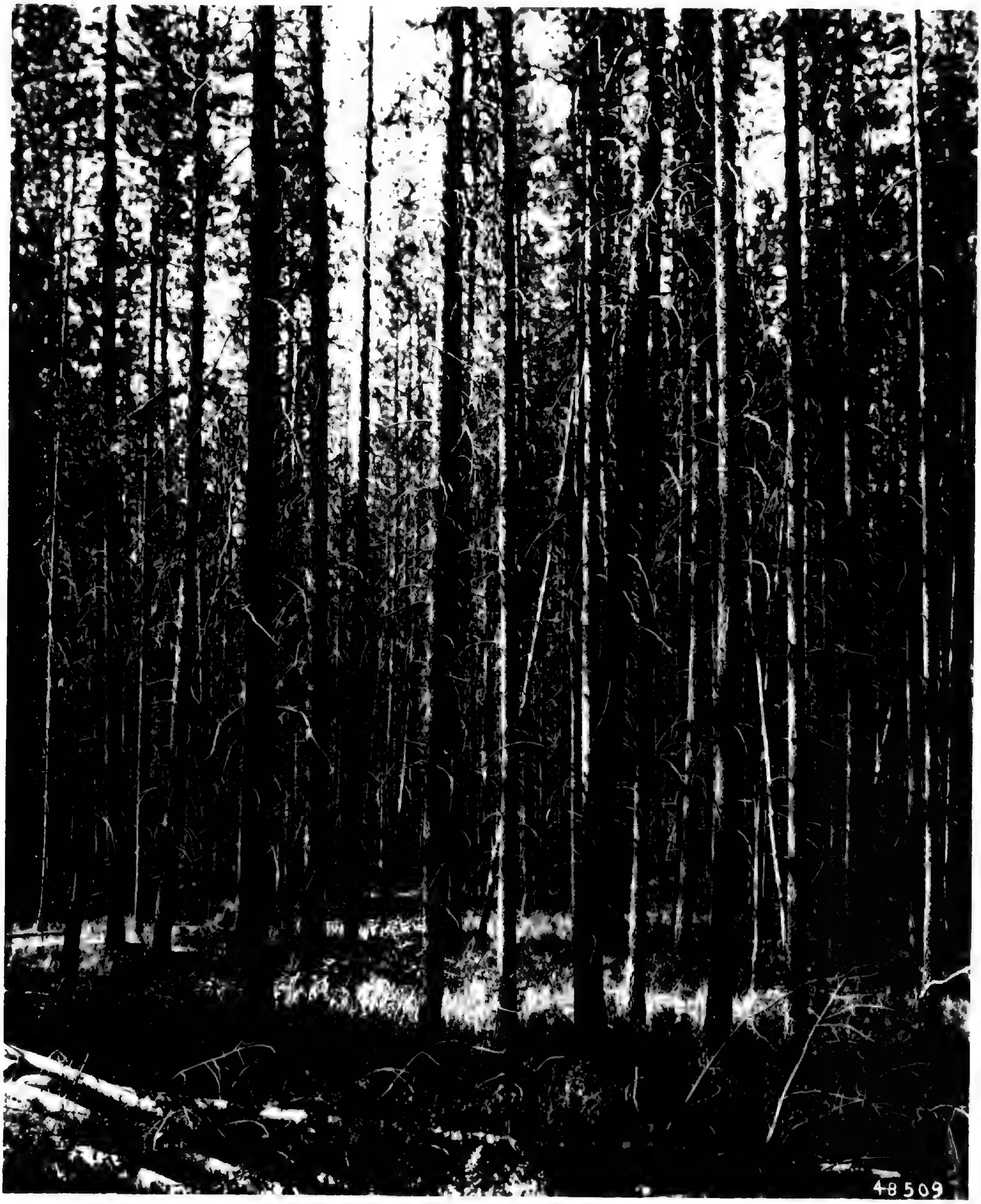

FIGURE 10. Fire-generated, even-aged *Pinus contorta* in the subalpine zone (2,500 m) in northern Rocky Mountains region. USDA Forest Service.

fire suppression and logging practices in the *Pseudotsuga menziesii* forests in western Montana create conditions that encourage outbreaks of western spruce budworm (*Choristoneura occidentalis*) of greater severity and longevity than those experienced prior to fire control. Without fire, forest cover has become more structurally uniform, which facilitates insect spread over large areas.

The upper timberline in the Intermountain Ranges forms at about 2,700 m and is dominated by *Pinus albicaulis*, *Abies lasiocarpa*, *Picea engelmannii* and, not infrequently, *Larix lyallii*. Each of these exhibits a wind timber develop-

FIGURE 11. Wind-shaped *Pinus albicaulis* within upper timberline zone (2,500 m) in southcentral Montana. USDA Forest Service.

ment (dwarfed in size and shape) as each reaches its individual upper limit of growth. *Larix lyallii* is confined to relatively harsh north slopes over 2,100 m and frequently occupies talus slides and boulder fields. Only occasionally does *Larix lyallii* grow on level sites with developed soil (Arno & Habeck, 1972).

Near timberline, *Pinus albicaulis, Picea engelmannii,* and *Larix lyallii* form open-grown, parklike stands. Topography, wind, and snow deposition paths cause a variety of interesting spatial arrangements in the timberline zone, such as "ribbon-forests" and krummholz mats (Billings, 1969; Fig. 11). Some individual timberline specimens of *Pinus albicaulis, Larix lyallii,* and *Picea engelmannii* are relatively large (1.0–1.5 m in diameter) and old (300 to 500 years). *Phyllodoce empetriformis, P. glanduliflora, Cassiope mertensiana, Vaccinium scoparium, Xerophyllum tenax,* and various sedges (*Carex* spp.) and rushes (*Luzula* spp.) are the understory dominants in these timberline forests.

Some bunchgrass communities (*Agropyron spicatum, Festuca scabrella,* and *F. idahoensis*), compositionally similar to lower timberline grasslands, exist islandlike within the Intermountain subalpine forest zone well above 1,800 m. They are believed to be the results of hypsithermal displacements (Daubenmire, 1968, 1975, 1981; Root & Habeck, 1972) and are presently maintained by localized xeric conditions induced by slope, aspect, shallow soils, or unweathered parent rock substrates. Although subject to burning, there is no evidence that fire is required to perpetuate them. Other grasslands, or "grass balds," featuring *Festuca viridula* communities may dominate the subalpine zone in central Idaho and northeastern Oregon, extending to over 2,400 m.

Detailed descriptions and classifications of the lower zone Intermountain grasslands (Fig. 12) have been presented by Mueggler & Stewart (1980). Some of their 30 grassland and shrubland habitat types are similar to those documented by Daubenmire (1970) but others are distinctive for the east front of the Montana Rockies. Major

FIGURE 12. Bunchgrass prairie community on the Deerlodge National Forest (1,750 m), Montana, Intermountain region. *Pseudotsuga menziesii* with groves of *Populus tremuloides* occupying lower elevations. USDA Forest Service.

Intermountain grassland dominants include *Stipa comata, Agropyron spicatum, Festuca idahoensis, F. scabrella, Deschampsia caespitosum, Artemisia tridentata, A. arbuscula, Potentilla fruticosa, Purshia tridentata, Cercocarpus ledifolius, Rhus trilobata,* and *Sarcobatus vermiculatus.*

Other NRM grassland studies have focused on local expressions of prairies on sites surrounded by continuous forests. In many instances, disjunct grasslands are the result of local mountain rainshadows, but soil texture (e.g., coarse glacial till) and past fires have also favored grassland development (Blinn & Habeck, 1967; Koterba & Habeck, 1971; Root & Habeck, 1972). Wright & Wright (1948) have described the grasslands in southcentral Montana; their five types are listed by community dominants (from most mesophytic to more xerophytic): a) *Festuca idahoensis,* b) *Agropyron spicatum,* c) *Agropyron spicatum/Carex filifolia/Bouteloua gracilis,* d) *Bouteloua gracilis/Stipa comata/Koeleria cristata,* and e) *Bouteloua gracilis/Stipa comata.*

Representative shrubland types in the Intermountain region (Fig. 13) were described by Mueggler & Stewart (1980) and by Kuchler (1964). *Cercocarpus ledifolius, Purshia tridentata, Symphoricarpos oreophilus,* and *Artemisia tridentata* all form shrub-bunchgrass communities below lower timberline, occupying dry rocky sites or river floodplains, although these shrubland communities may also be found interspersed within the timbered zones. The grasses are the same as those that form the prairie vegetation types in the valleys and lower slopes, that is, *Agropyron spicatum, Festuca idahoensis, Stipa comata,* and *Poa sandbergii.*

INLAND MARITIME REGION

The Inland Maritime region spans northeastern Washington, northern Idaho, and northwestern Montana (Fig. 4, Region D). The Selkirk Mountains of northern Idaho and adjacent parts of Washington and British Columbia, the north-

FIGURE 13. Sagebrush shrubland and rangeland vegetation types in upper Big Hole drainage (2,000 m), in southern continental ranges, Beaverhead National Forest, Montana. *Pseudotsuga menziesii* forest in distance. USDA Forest Service.

ern Bitterroot Range, the Cabinet Mountains, the Whitefish Range, the northern Swan Range, and the west slope of the Continental Divide (in Glacier Park) collectively comprise this region.

As its name suggests, this region is relatively moist. Coastal moisture follows well-defined storm tracks, which bring an abundance of moisture to all elevations. Most of the lowest valleys receive well over 50 cm annually, although some stations in localized rainshadows may record 40 cm or less. Warm, dry weather usually prevails during July and August. Grassland and *Pinus ponderosa* communities, which exhibit drought tolerance (Minore, 1979; Lassoie et al., 1985), occur locally in some of the driest rainshadow areas. The reduced summer moisture sets the stage for wildfires. Historic fires are believed to have perpetuated xeric vegetation types in climatically moist parts of this geographic subunit (Habeck & Mutch, 1973).

Typically, the forest zones in the Inland Maritime region contain combinations of the following dominants, ranked from highest to lowest in drought resistance (Minore, 1979): *Pinus ponderosa, P. contorta, Pseudotsuga menziesii, Picea engelmannii, Abies grandis, Larix occidentalis, Abies lasiocarpa, Thuja plicata, Taxus brevifolia, Pinus monticola, Tsuga heterophylla,* and *Tsuga mertensiana* (Figs. 14, 15).

Physiological adaptive features of these coastal conifers were reviewed in detail by Lassoie et al. (1985). The mesophytic forests dominated by *Thuja* and *Tsuga* resemble in many ways the forests found on the western slopes of the Coastal and Cascade mountain ranges in Washington and British Columbia (Daubenmire & Daubenmire, 1968; Habeck, 1978; Williams & Lillybridge, 1983; Cooper et al., 1988).

With increased elevation, even greater amounts of precipitation occur, often reaching and exceeding 200 cm annually. A large portion (75–85%) of this precipitation falls as snow between September and March. *Pseudotsuga menziesii, Abies lasiocarpa,* and *Picea engelmannii* occur

FIGURE 14. Mature forest in the Inland Maritime region; Deception Creek, Coeur d'Alene National Forest, Idaho (1,000 m). *Tsuga heterophylla, Abies grandis,* and *Pinus monticola* dominate. Note fire-scarred snag on left. USDA Forest Service.

in abundance on the higher inland Maritime mountain slopes. *Pinus albicaulis* is locally abundant on warm aspects that may experience some July–August moisture shortages.

Between 1,500 and 1,800 m, near the Idaho–Montana state line, *Tsuga mertensiana* joins *Abies lasiocarpa* in forming the highest closed-canopy forest type (Habeck, 1967). *Tsuga mertensiana* is very intolerant of summer drought and heat (Minore, 1979) and severe continental winters, but survives very well in parts of the Inland Maritime Region where suitably mild conditions prevail. *Tsuga mertensiana* is an abundant timberline species in the Coastal and Cascade mountains of western Oregon, western Washington, British Columbia, and southeastern Alaska (Arno & Hammerly, 1984). The Inland Maritime region's timberline, formed at 2,000–2,300 m (Fig. 16), features krummholz of *Abies lasiocarpa* and *Pinus albicaulis*; erect or partly wind-shaped *Larix lyallii* is also present at times (Habeck, 1969; Arno & Habeck, 1972). On glacially scoured parts of the Selkirk Mountains in northern Idaho, *Tsuga mertensiana* and *Larix lyallii* are rare or absent.

Each of the Inland Maritime trees has an individualistic distribution. They can be ordered from most restricted to most widely distributed within this region: *Alnus rubra, Tsuga mertensiana, T. heterophylla, Pinus monticola, Thuja plicata, Taxus brevifolia,* and *Abies grandis.* It has been noted that the individuals or populations occurring at the range limits of these maritime trees, such as *Thuja plicata* near Missoula, Montana, are confined to isolated higher (1,400 m) ravine sites (Habeck, 1978; McCune & Allen, 1985b). Summer moisture deficiencies encountered in westcentral Montana may be counterbalanced by the cooler temperatures in these middle elevation ravine sites.

The undergrowth in the mesic and wet-mesic Inland Maritime region forests is floristically

FIGURE 15. Mature *Thuja plicata* forest on the Thompson River (750 m), Lolo National Forest, western Montana. USDA Forest Service.

FIGURE 16. "Snow ghost" forest in the subalpine zone of northern Idaho's Bald Mountain (2,300 m). Snow-caked trees are *Abies lasiocarpa.* USDA Forest Service.

richer than in any of the other subunits. It includes *Clintonia uniflora, Adenocaulon bicolor, Disporum hookeri, Tiarella trifoliata, Cornus canadensis, Aralia nudicaulis, Rubus parviflorus, Athyrium filix-femina, Gymnocarpium dryopteris, Menziesia ferruginea, Taxus brevifolia, Oplopanax horridum, Pachistima myrsinites,* and many other species.

A limited amount of the arid *Pinus ponderosa/ Festuca idahoensis/Agropyron spicatum* habitat type also occurs within intermontane valleys running through the Inland Maritime region. For example, a steep precipitation-vegetation gradient exists, west to east, between Spokane, Washington (38 cm/yr., pine-grassland savanna) and nearby (40 km east) Coeur d'Alene, Idaho (75 cm/yr., cedar–hemlock–western white pine forests).

Fires occur at lower frequencies (100-year intervals or longer) in this geographic region (Habeck, 1985). When wildfires do occur, however, they are often of much higher intensity ("stand replacement" fires), due to the greater organic matter ("fuel") accumulations in these moist forests. When the right combination of midsummer "fire weather" occurs—characterized by high temperatures, gusty afternoon winds, dry ground fuels, low humidity, and lightning—the Inland Maritime forests may have wildfires capable of removing all aboveground plant cover (Habeck & Mutch, 1973). *Larix occidentalis, Pinus contorta,* and/or *Pinus monticola* are important postfire species, but it is not uncommon for the potential climax species to make an initial entry at the same time. Examples of short interval (less than 10 years) "double" and "triple" burns exist, and forest recovery on such sites may be retarded for many decades.

Deep snow accumulations in the Inland Maritime mountains (Fig. 17) cause frequent avalanches. In minutes, tons of flowing snow and fierce winds may smash and mangle the vegetation in the snow track. Snow slide chutes are often dominated by such woody angiosperms as

FIGURE 17. Snow cornice above *Picea engelmannii* and *Abies lasiocarpa* forest at 2,100 m in Panhandle National Forest, northern Idaho. USDA Forest Service.

Alnus sinuata, Amelanchier alnifolia, Sorbus spp., *Acer glabrum, Populus trichocarpa, P. tremuloides, Salix* spp., and a rich assortment of perennial herbs that seem well adapted to frequent avalanches.

VEGETATION OF THE SOUTHERN CANADIAN ROCKIES

The southern Canadian Rockies are composed of high, rugged terrain with a long history of glaciation. The mountain ranges often reach or exceed 2,400 m, with peaks over 3,000 m. The southern Canadian Rockies embrace several major mountain ranges near the United States/Canada border, including the Selkirk, Purcell, and Monashee mountains, the Continental Divide itself ("The Great Divide") separating Alberta from British Columbia, and several front ranges east of the Great Divide (Fig. 4, Region E).

Frigid polar air masses characterize the continental climate east of the Great Divide in Alberta. The dessicating winter winds are similar to those described for the east front of the Montana Rockies; these winds are responsible for "red belt" mortality among the conifer communities located here. Just west of the Great Divide, the climate is more like that of the Inland Maritime region in northern Idaho and northwestern Montana; mild and wet weather prevails as Pacific coastal storm tracks penetrate eastward (Arno & Hammerly, 1984).

Southeastern British Columbia, parts of which lie in the Cascade Mountains rainshadow, has a warm and dry lower timberline in valley bottoms where only 25–40 cm of precipitation occurs annually. Open *Pinus ponderosa* woodlands, bunchgrass prairies (*Agropyron spicatum* and *Festuca idahoensis*), and sagebrush steppe (*Artemisia tridentata*) form the major plant communities in the semiarid valleys (Tisdale & McLean, 1957; McLean, 1970; Tisdale, 1974). Some of the upper slopes of nearby mountains also have low annual precipitation, and at mid-elevation slopes a forest zone dominated by *Pseudotsuga menziesii* occurs. Above this is the subalpine zone dominated by *Abies lasiocarpa, Picea engelmannii,* and *Pinus albicaulis,* which ultimately form a krummholz on upper slopes above 2,100 m. Past fires in southeastern British Columbia perpetuated extensive stands of *Pinus contorta* at middle and upper elevations (LaRoi & Hnatiuk, 1980; Arno & Hammerly, 1984).

Those parts of southeastern British Columbia that receive greater coastal moisture display forest vegetation similar to that of the Inland Maritime region in the United States. Warm, dry, lower timberlines occur only rarely in this part of the Canadian Rockies, where dominants include *Thuja plicata, Tsuga heterophylla, Abies grandis, Pseudotsuga menziesii, Picea engelmannii,* and *P. engelmannii* × *P. glauca* hybrids. *Pinus contorta, Abies lasiocarpa, Tsuga mertensiana, Pinus albicaulis,* and *Larix lyallii* are the major timberline dominants in the Selkirk and Purcell mountains. Timberline in these ranges typically occurs at elevations below 2,100 m; however, it may occur below 1,500 m in areas of deep snow accumulations. The highest mountain peaks (over 3,000 m) support permanent snowfields and glaciers (Shaw, 1916).

The Alberta Rockies consist of the mountains forming the Great Divide. From Waterton Park northward to Banff and Jasper National Parks, the Divide peaks reach from 2,800 m to nearly 3,650 m in height. The continental climate in Alberta disfavors the occurrence of tree species adapted to milder maritime conditions. Annual precipitation is near 150 cm at the higher elevations but less than 50 cm on the east front at Calgary. The subalpine and montane forest zones are dominated by the same species listed above for British Columbia, except that maritime trees like *Thuja* and *Tsuga* are missing. At timberline, *Abies lasiocarpa, Picea engelmannii, Larix lyallii,* and *Pinus albicaulis* form the upper treeline communities, including the krummholz zone (Moss, 1955; Ogilvie, 1963, 1976; Day, 1972; Corns & Achuff, 1982).

The lower forest zones adjoining the grasslands are mixtures of *Pseudotsuga menziesii, Picea glauca* (and hybrids *P. glauca* × *P. engelmannii*), and *Populus tremuloides.* Local moisture-stressed sites support *Pinus flexilis* (Moss, 1944; Rowe, 1959; Stringer & LaRoi, 1970). *Pinus ponderosa* is absent, according to Arno & Hammerly (1984), seemingly unable to tolerate winter desiccation and rapid temperature changes. As was described for other areas of the NRM, frequent high intensity wildfires helped develop and perpetuate extensive stands of *Pinus contorta* throughout much of the Alberta Rockies, from the lower to the upper timberline (Tande, 1979).

The natural grasslands in southern Alberta east of the Great Divide occur where precipitation becomes lower, temperatures are warmer, Chinook winds prevail, and evaporation rates are high (Moss, 1944; Moss & Campbell, 1947). Moss (1944) described three prairie community types: *Bouteloua gracilis/Stipa comata, Agropyron/Stipa/Carex,* and *Festuca scabrella/F. idahoensis/Danthonia intermedia/D. parryi.* Much of the native prairie no longer exists because of modern levels of grazing and mowing.

VEGETATION OF THE MIDDLE ROCKY MOUNTAINS

The last part of the Rocky Mountains to be treated here lies north of Provo and Salt Lake City, Utah, in the vicinity of 40°N, and includes the adjacent parts of northwestern Colorado, the Medicine Bow Mountains in southeastern Wyoming, the remainder of Wyoming west and north of the Wyoming Basin desert, north to south-central Montana (Beartooth Plateau), and west to the Snake River Plain in southern Idaho (Fig. 4, Region F). This region coincides with the "Middle Rockies" as discussed by Oosting & Reed (1952), Johnson & Pfister (1982), Arno & Hammerly (1984), and Mutel & Emerick (1984), and includes the northeastern part of the Rockies that Reveal (1979) designated "the Intermountain Region." Figure 6 shows the typical vegetation zones in this part of the Rocky Mountains.

The Utah portions of the middle Rocky Mountains support a flora that contains many elements that are geographically centered further to the south and southwest, characteristic of the pinyon-juniper, chaparral, and Great Basin desert vegetation types. In contrast, western Wyoming ranges are without these floristic inclusions and display more elements common to the East Front of the Rockies in central Montana (Arno & Hammerly, 1984). The forest vegetation of this region is usually dependent on melting of deep winter snow packs (from Pacific storms) to supply needed summer moisture. The inland continental climate lacks a maritime component of the sort described earlier (Baker, 1944).

Arno & Hammerly (1984) described the middle Rockies as an area of well-separated ranges diverse in geologic structure and rock types. Johnson & Pfister (1982) provided detailed interpretive summaries of the geology of this region. Three geologic mountain types exist (see Fig. 4 for locations): 1) anticlinal mountains (Beartooth Plateau, Big Horn–Pryor Mountains, Uinta Mountains, and Wind River Range); 2) mountains of the overthrust belt (Tetons, Wyoming, and Wasatch ranges); and 3) volcanic mountains (Yellowstone Plateau and Absaroka Range). The highest points in the middle Rocky Mountains reach up to approximately 4,200 m (Gannett Peak and Grand Teton), although more typical heights range between 3,000 and 3,600 m.

The Wasatch and Uinta ranges have broken patches and stringers of timber on their upper mountain slopes, a result of frequent avalanches clearing wide tracks through the timber. Several tree species achieve dominance here, including *Pseudotsuga menziesii, Pinus flexilis, Picea pungens, Abies concolor,* and *Populus tremuloides. Pinus contorta* is present in the northern part of the Wasatch Range but *Pinus ponderosa* is scarce. The lower Wasatch slopes are covered with *Quercus gambelii, Cercocarpus ledifolius,* and *Acer grandidentatum.* This mountain shrub or chaparral type replaces the pinyon-juniper vegetation zone found further westward in Nevada (Hayward, 1945, 1948; Arno & Hammerly, 1984).

The Uinta Mountains, which have an east–west orientation, are capped with an extensive alpine zone above 3,300 m (Hayward, 1952). Below this and forming the krummholz and upper subalpine zones are stands of *Picea engelmannii, Abies lasiocarpa,* and *Pinus flexilis*; this region is beyond the distribution of *Pinus albicaulis.* Extending down to 2,700 m below these zones are *Pinus contorta* forests. A wide band of *Populus tremuloides,* serving as a major seral species in the middle Rockies, occurs below the *Pinus contorta* zone. *Pinus ponderosa* is scattered on south slopes and found more extensively on north ones at the lower Uinta timberline down to 2,100 m. Mid elevations support extensive stands of *Pseudotsuga menziesii*; moist drainages (riparian sites) contain *Picea pungens* communities.

Arno & Hammerly (1984) and Ellison (1954) provided additional descriptions of the contrasting climatic and vegetational features between the Wasatch and nearby Uinta ranges. In contrast to the Wasatch Range, the Uintas lack the oak-maple chaparral but support a pinyon-juniper type. In both areas, the lowest and driest shrub zones are dominated by a dozen different species and varieties of sagebrush (*Artemisia* spp.) and *Atriplex canescens, A. confertifolia,* and *Cercocarpus ledifolius.* Variations in summer rainfall, geologic and topographic features, and contracting patterns of past plant migrations have all contributed to these differences.

The modern forest vegetation occurring in Colorado's Front Range (Fig. 4, vicinity of Rocky Mountain National Park) has been the subject of many studies dating back 80 or more years. The most recent and comprehensive among these is the detailed treatment provided by Peet (1981), who reviewed much of the previous vegetation literature for this part of the middle Rocky Mountains. Employing modified gradient analysis techniques, he derived a classification of the Front Range vegetation that accommodated both developmental (successional) and mature (late seral/climax) community types, relating them to a moisture-elevational complex. Peet classified the Front Range vegetation (1981, his fig. 5) into community series as follows: A. *Pinus ponderosa* woodland series; B. *Pinus ponderosa/Pseudotsuga menziesii* forest series; C. Mesic montane forest series (a heterogeneous group that includes *Picea, Abies, Pseudotsuga, Populus, Betula,* and *alnus*); D. *Pinus contorta* forest series; E. *Picea/Abies* forest series; F. *Pinus flexilis* forest series; G. Alpine transition (krummholz) series. His classification also delimits community type subunits within these series. Subsequently, Greenland et al. (1985) described a methodology for defining bioclimatic zones in the Colorado Front Range utilizing a one-dimensional version of Peet's vegetation ordination model.

The importance of 19th century anthropogenic disturbances within the montane forests of the Front Range have been investigated by Veblen & Lorenz (1986). Patterns of forest recovery following severe logging and burning disturbances inflicted during the Colorado mining booms were studied. Their findings clarify the successional pathways that forest recovery has followed during the last century in this part of the Rocky Mountains.

The upper-elevation forests in a representative watershed within the Medicine Bow Mountains in central Wyoming were discussed in detail by Romme & Knight (1981), who investigated and modeled the interactions of fire frequency and topographic position on vegetation dynamics in this part of the middle Rockies. Although much of the high country in the Medicine Bows has a potential for supporting climax forests dominated by *Picea engelmannii* and *Abies lasiocarpa*, such expressions of spruce-fir forests are primarily confined at this time to moist sites such as ravines and valley bottoms. Past occurrences of short-interval (less than 100 years) wildfires on open slopes and ridgetops favored development and maintenance of *Pinus contorta* forests (Lotan & Perry, 1983). Even though fire suppression has been in operation for more than a century, the slow rates of successional processes in these mountains have tended to impede the return of spruce-fir forests.

Romme & Knight (1981) included within their watershed study area a two-dimensional ordination of all major plant community types occurring between 2,250 and 3,000 m on sites ranging from moist valley bottoms to south slope ridgetops. *Salix*, *Alnus*, and *Populus* mixtures occur in the lower, moist habitats; *Pseudotsuga menziesii* forests occur on the mesic, lower north slopes; *Artemisia* communities occur on most xeric foothill elevations. At intermediate elevations of 2,500 to 2,700 m, combinations of *Pseudotsuga menziesii*, *Pinus contorta*, and *Populus tremuloides* prevail. Only moist sites above 2,700 m currently support mature spruce-fir forests.

The mountains in western Wyoming (Wind River, Salt River, and Wyoming ranges, as shown in Fig. 4) support an upper timberline of *Pinus albicaulis*, which achieves notable dominance in this part of the Rockies, and of *Picea engelmannii* and *Abies lasiocarpa* (Loope, 1971; Reed, 1976; Steele et al., 1983; Arno & Hammerly, 1984). A krummholz zone composed of these conifers is found at elevations near 3,050 m throughout these mountains. Much of the subalpine forest zone, however, is dominated by expansive stands of *Pinus contorta* except where limestone substrate prevails. This pine, together with *Pseudotsuga menziesii*, often forms the upper timberline forests at elevations above 2,700 m and then extends downward to the lower zones at or below 2,100 m (Moir, 1969; Arno & Hammerly, 1984). Loope & Gruell (1973) have described the natural role of fire in these northwestern Wyoming forests.

Near the lower timberline, *Populus tremuloides* groves comprise a broken belt separating *Pinus contorta* forests from the sagebrush communities in the lower valleys (Reed, 1971; Youngblood & Mueggler, 1981; Arno & Hammerly, 1984; Fig. 18). Although *Pseudotsuga menziesii* can be found in the western Wyoming mountain ranges, it does not form a distinctive forest zone as it does elsewhere in the northern Rockies, such as in western Montana (Arno, 1979). This is due to the importance of *Pinus contorta* as a seral species in zones where *Pseudotsuga menziesii* is the potential climax dominant. Many of the subalpine conifers can be found at lower timberline, often along mountain stream courses (Arno & Hammerly, 1984). The valleys in the western Wyoming mountain ranges are much cooler than comparable sites elsewhere in the northern Rockies; for this reason, *Populus tremuloides* and mesophytic conifers occupy the lower timberline zone (Steele et al., 1983). Pinyon-juniper and mountain chaparral are missing from the cold western Wyoming mountains (Arno & Hammerly, 1984).

The Absaroka Range and adjacent Beartooth Plateau (Montana–Wyoming border; Fig. 4) display an extensive alpine tundra zone with many ice fields at elevations over 3,000 m. Timberline parkland (open-canopied groves and scattered individuals) is also present, dominated by *Pinus albicaulis*, *Picea engelmannii*, and *Abies lasiocarpa*, similar to those in the Wind River and Teton ranges.

The Big Horn Mountains, spatially separated from the other middle Rocky Mountain units, are located east of the Big Horn Basin in west-central Wyoming and extend into adjacent parts of Montana (Fig. 4). Elevations in the Big Horns, which occupy an uplifted dome, exceed 4,000 m. Past and present glaciers are prominent land-shaping phenomena in this part of the middle Rockies. Annual precipitation is relatively low, reaching about 60 cm in the subalpine forest zone at 2,700 m. Soils derived from granite, shale,

FIGURE 18. Old growth *Populus tremuloides* forest near Scout Lake (3,100 m), Utah. Note conifer invasion in understory. USDA Forest Service.

limestone, and dolomite rocks play a major role in plant distribution patterns in many of the middle and northern Rockies east of the Continental Divide, including the Big Horns. A series of vegetation studies has been completed in the Big Horns (Hurd, 1961; Despain, 1973; Hoffman & Alexander, 1977).

Big Horn Mountain *Pinus contorta* forests occupy sites overlying the coarse and nutrient-poor granitic soils. Grasslands and shrublands generally occupy soils from shale and limestone, except where forests are supported in areas where moisture stress is lessened due to slope aspect (Arno & Hammerly, 1984). *Picea engelmannii* and *Abies lasiocarpa* occur in the subalpine-timberline zone of the Big Horn Range, but *Pinus albicaulis* is absent from this area. *Pinus contorta* is dominant on granitic soils at elevations below the subalpine zone which extends from 2,700 m to 2,100 m. The lower timberline is formed by *Pseudotsuga menziesii* near 1,800 m. Juniper woodlands (*Juniperus scopulorum* and *J. osteosperma*) are closely associated with the *Pseudotsuga menziesii* zone on the west slopes; *Pinus edulis* is replaced by *Pinus flexilis* in this juniper community type. *Pinus ponderosa* var. *scopulorum* becomes important only in this part of the middle Rocky Mountains (east face of Wyoming Big Horns and northward into Montana) but does not display the large growth forms seen among the *P. ponderosa* var. *ponderosa* occurring further west. Geographically, *P. ponderosa* var. *scopulorum* occurs eastward into the Black Hills of South Dakota, to the exclusion of Rocky Mountain conifers (Johnson & Pfister, 1982).

The middle Rockies support widespread sagebrush-grass; Tisdale & Hironaka (1981), Blaisdell et al. (1982), Hironaka et al. (1983), and West (1983) provided in-depth literature reviews of the major community types in the nonforested areas of this region. Where the Wyoming Basin and Great Plains meet, there exist sod-forming grasslands dominated by *Bouteloua gracilis* and *Agropyron smithii* intermixed with *Artemisia tridentata* and other sagebrush taxa. These communities are the products of the continental climate, with growth moisture arriving in early summer rainfall. Elsewhere in southern and central Idaho and southwestern Montana, bunchgrass prairies are present, dominated by *Agropyron spicatum*, *Festuca idahoensis*, *Stipa comata*, and *Poa sandbergii*. In these sagebrush-bunchgrass communities, moisture comes primarily in winter and spring, with droughty summers.

The middle Rockies sagebrush-bunchgrass community types recognized by Hurd (1961), Beetle & Johnson (1982), Johnson & Pfister (1982), and Hironaka et al. (1983) include the following, each named after the major dominant: a) *Festuca idahoensis*, b) *Agropyron spicatum*, c) *Bouteloua gracilis*, d) *Purshia tridentata*, e) *Symphoricarpos oreophilus*, f) *Artemisia tridentata*, g) *A. tripartita*, h) *A. nova*, i) *A. arbuscula*, j) *A. longiloba*, k) *A. cana*, l) *A. rigida*, m) *Atriplex canescens/A. confertifolia/A. nuttallii*, and n) *Sarcobatus vermiculatus*. Shrubland community types in the same region include a) *Quercus gambelii*, b) *Acer grandidentatum*, and c) *Cercocarpus ledifolius*.

Modern (post-1900) vegetation shifts in middle Rocky Mountain ecosystems, believed to be induced by fire suppression and domestic grazing (Sauer, 1950; Humphrey, 1962; Steele et al., 1981, 1983), also involve extensive invasion by *Juniperus occidentalis* into grassland and sagebrush communities. Tisdale & Hironaka (1981), pointing to the sensitivity of *Artemisia* to fire, suggested that fires in presettlement times must have been infrequent (long interval) in some parts of the sagebrush region, such as drier *Artemisia* habitat types where fuel loads were low.

The *Juniperus* woodland expansion in the Rocky Mountains and adjacent regions was described by Barney & Frischnecht (1974) and Young & Evans (1981). Problems attending these changes were described in a lengthy juniper management symposium (Martin et al., 1978). Through wood rat (*Neotoma*) midden and lake sediment analysis, Mehringer & Wigand (1986) documented that western juniper has had a long history of rapid geographic shifts in response to climate changes during the past 4,000 years. They stated, ". . . the spectacular and persistent expansion of western juniper over the last hundred years—despite chaining, bulldozing, cutting, poisoning and burning—is not an unusual event necessarily requiring explanations unique to the historic period. In fact, the rate and degree of change in the comings and goings of western juniper over the late Holocene are equal to or greater than those seen over the past hundred years" (Mehringer & Wigand, 1986: 118).

Plant communities historically used as sheep and cattle range throughout the middle Rockies have been severely altered as a result of abusive levels of grazing. Employing paired-stand analysis techniques, range ecologists have provided extensive documentation of compositional changes attributed to grazing. Native species of

FIGURE 19. *Abies lasiocarpa* (center) and *Pinus flexilis* (left & right) on King's Hill (2,200 m) in northern continental ranges, central Montana; Lewis and Clark National Forest, Montana. USDA Forest Service.

Agropyron, Festuca, Poa, and *Stipa* are classed as "decreasers" which are reduced in abundance. In their place, introduced grasses and forbs invaded and, for all practical purposes, have created new vegetational equilibria on the western rangelands. As an example, cheatgrass (*Bromus tectorum*), an introduced annual grass, has proven to be a superior competitor in western bunchgrass communities (Harris, 1967; Mueggler & Harris, 1969; Daubenmire, 1970; Mueggler & Stewart, 1980) and has come to dominate large areas in the middle and northern Rockies.

Other invaders that have become widespread on rangelands include *Poa pratensis, Centaurea maculosa, Cirsium vulgare, Tragopogon dubius, Euphorbia esula,* and *Hypericum perforatum.* Many of these species, along with *Rudbeckia occidentalis,* have also become established in conifer forests severely disturbed by logging and/or domestic grazing. Man's present-day penchant for working land on higher and steeper slopes is contributing to an acceleration of vegetation change. Furthermore, conflicts between agriculture and livestock, and winter foraging by big game, frustrate efforts to reverse the loss of native plant components.

OTHER ROCKY MOUNTAIN VEGETATION TYPES

Other vegetation types occurring within the northern Rockies are described below. Some of these are distributed throughout the northern Rocky Mountains, i.e., timberline/alpine tundra and wetland/riparian types, while others are confined to single mountain ranges or unique localized habitats.

TIMBERLINE AND ALPINE TUNDRA

Upper treeline reaches 2,275 m in southern Alberta and nearly 3,650 m in southern Colorado. Treeline zones in the interior continental mountains are subject to cold polar air and high winds (Fig. 19). Dry powdery snow accumulates at moderate to great depths but melts away during summer. Sharp temperature fluctuations also create severe winter stresses. In contrast, inland maritime timberline/alpine tundra is more moist

FIGURE 20. Alpine and nival life zones in vicinity of Beartooth Pass (3,300 m), Custer National Forest, Montana. USDA Forest Service.

than the continental areas and experiences less extreme winter temperatures.

Common northern Rocky Mountain timberline tree species have been identified earlier; these intermix islandlike within the lower alpine tundra zone. Slope aspect, microtopography, patterned ground (resulting from cryopedogenesis), soil chemistry, soil water potential, and wind exposure combine to form an environmental complex (Fig. 20) that dictates the arrays of low shrubs, perennial herbs, and graminoids forming the northern Rockies timberline/tundra ecosystems (Griggs, 1938; Choate & Habeck, 1967; Bamberg & Major, 1968; Habeck, 1969; Billings, 1969, 1978; Smith, 1969; Johnson & Billings, 1962; Arno & Hammerly, 1984; Bliss, 1985; Spence, 1985; Peet, 1987).

Alpine permafrost occurs in some northern Rocky Mountain ranges, where mean annual air temperature is at or below 0°C and may, according to Pewe (1983), date back to Wisconsin time when such frozen soil was widespread 1,000 m below present-day elevations. Such permafrost areas coincide with modern treeless areas where alpine vegetation may favor maintenance of the frozen soil conditions. Vegetation dynamics on sites that have experienced recent ice retreat have been described in detail by Spence (1985) for parts of Wyoming's Teton Range. He investigated plant invasions on moraines fronting glaciers. Continual disturbances take place on the moraines, and compositional differences among his study areas do not seem closely related to a successional chronosequence.

Bliss (1985) reviewed the physiological ecology of alpine and timberline plant communities in North America, adding to earlier efforts that emphasized floristic phytogeography. He stated that complexities of community structure and composition in the alpine zone, including spatial discontinuities between mountain ranges, have permitted only generalized classification units. Growth and survival in the alpine are closely related to growth forms. Bliss (1985) listed and discussed the following major growth form categories: 1) annuals (uncommon), 2) cushion and rosette-forming species occurring on exposed ridges, 3) graminoids found in all alpine habitats, 4) forbs, and 5) deciduous and evergreen shrubs, many of which are low mat-forming types.

Based on an extensive literature review, Johnson & Pfister (1981, 1982) listed the following alpine tundra community types typical of the Rocky Mountains. The common dominants are listed for each type:

1. Shrub Communities: *Salix rotundifolia, S. reticulata, S. arctica, Betula glandulosa, Dryas octopetala, Kalmia microphylla, Phyllodoce empetriformis, P. glanduliflora,* and *Vaccinium scoparium.*
2. Meadow and Turf Communities: *Geum rossii, Deschampsia caespitosum, Carex tolmiei, C. nigricans, Juncus* spp., *Poa alpina, Phleum alpinum, Polygonum bistortoides,* and *Oxyria digyna.*
3. Bog and Fen Communities: *Sphagnum* spp., *Carex aquatilis, C. rostrata, C. simulata, Eriophorum* spp., *Juncus* spp., *Pedicularis groenlandica, P. contorta, Kalmia microphylla, Ranunculus* spp., *Calamagrostis canadensis,* and *Eleocharis* spp.
4. Cushion Plant and Fellfield Communities: *Silene acaulis, Dryas octopetala, Trifolium nanum, Luzula spicata,* and *Selaginella densa.*
5. Boulder Field Communities: *Geum rossii, Mertensia* spp., *Ribes cereum, Polemonium* spp., *Aquilegia* spp., *Penstemon fruticosus,* and *Sibbaldia procumbens.*
6. Snowpack Communities: *Carex nigricans, Juncus drummondii, Erythronium grandiflorum, Valeriana sitchensis, Luzula glabrata,* and *Senecio triangularis.*

The nival zones of the Rockies (Figs. 5, 6, and 20) exhibit snowfields that support cold-adapted floras composed predominantly of algae, but not vascular plants, although some fungi species may also be present (Garric, 1965; Vinyard & Wharton, 1978). Snow algae occur on the surfaces of glaciers and snowfields and may give the snow a reddish color (or even yellow, green, blue, black, or purple), depending on the species involved. These algae have enzyme systems that catalyze reactions most efficiently at lower temperatures (Hoham, 1975). In the Rockies, and elsewhere in western North America, one of the most common species is *Chlamydomonas nivalis,* which is known to cause the pink-red "watermelon snow." Red coloration on the snow surface in summer is caused by an accessory photosynthetic pigment called *astaxanthin,* which increases in abundance in intense sunlight. The cryophilic algae encyst during the four to eight months of winter and break dormancy in summer.

Other snow algae listed by Garric (1965) include *Scotiella nivalis, S. cryophila, Chodatella brevispina, C. granulosa, Raphidonema nivale, R. tatrae,* and *Romeria elegans* var. *nivicola.* Snow fungi that may be saprophytic on snow algae include *Chionaster nivalis* and *Selenotila nivalis,* while another group of fungi, the Chytridiales, has been reported to be parasitic on snow algae (Vinyard & Wharton, 1978). The snowfield ecosystems also support ciliated protozoans, rotifers, springtails, and snow worms.

WETLAND TYPES

Wetland ecosystems in the Rocky Mountains occupy landscape units such as marshes, swamps, bogs, fens, and other topographic depressions with high water tables. Water may cover the sites ephemerally or intermittently and may be shallow or deep (under or over 2 meters). The term "wetland" also embraces wet meadows, potholes, sloughs, riparian zones (along stream courses), and river-overflow areas. Permanently-filled, shallow lakes and ponds less than 2 meters in depth, supporting emergent vegetation, are also included in this term. Wetland site definitions and classifications have been the subject of thorough attention by Windell et al. (1986). Their review of Rocky Mountain wetlands represents a comprehensive treatment of the subject and is the primary source for my synthesis of Rocky Mountain vegetation.

Rocky Mountain wetlands do not exist as regional climaxes, as in some high latitude arctic areas, because of the continental climate which prevails over much of the region. Snowmelt runoff is rapid, much of the northern Rockies do not receive high amounts of precipitation, and evaporation rates are high in many areas. Thus, wetland communities are formed only in certain topographic settings where an abundance of water occurs seasonally or permanently.

In their ecology of Rocky Mountain wetlands, Windell et al. (1986) provide detailed information on community structure and a general classification of these ecosystems. Their literature review covers the entire Rocky Mountains. An overview of their findings is given below, supplemented with information taken from other regional studies (Pfister & Batchelor, 1984; Youngblood et al., 1985). An outline of wetland community types will be presented, together with a listing of plant dominants for each.

1. Permanent Shallow Standing Water (less than 2–4 m):
    a. Floating communities: open water surface dominated by *Lemna* spp.
    b. Rooted submergent communities: dominated by species of *Isoetes, Nitella, Potamogeton, Najas,* and *Myriophyllum.*
    c. Rooted floating-leaved communities: dominated by species of *Nuphar, Nymphaea, Sparganium,* and *Potamogeton.*
    d. Rooted emergent communities: dominated by species of *Carex, Eleocharis, Juncus, Glyceria, Phragmites, Sagittaria, Scripus, Sparangium, Typha, Menyanthes,* and *Petasites.*
2. Seasonal or Permanent High Water Tables, Without Permanent Standing Water:
    a. Herbaceous wetlands: floating mats dominated by species of *Carex* and *Sphagnum.* On mineral soils: marshes or wet meadows dominated by grasses, sedges and rushes, not forbs. On organic soils: species of *Caltha, Erigeron, Pedicularis,* and *Senecio.*
    b. Fen communities: herbaceous wetlands on organic soils and dominated by sedges (*Carex* spp.) and other graminoids such as species of *Juncus, Eleocharis, Deschampsia,* and *Calamagrostis.*
    c. Bog communities: Northern Hemisphere bogs are dominated floristically by a mat of *Sphagnum* spp. and members of the Ericaceae growing in the mat. Rocky Mountain regional bogs include species of *Kalmia, Drosera, Menyanthes, Eriophorum, Potentilla,* and *Gaultheria.*
    d. Marsh/wet meadow communities with fresh water: occur on mineral soils and are dominated by herbaceous species of the following genera: *Carex, Deschampsia, Danthonia, Juncus, Penstemon, Erigeron,* and *Calamagrostis.*
    e. Marsh/wet meadow communities with saline water: alkaline sites with sodium concentrations over 15%, supporting only salt-tolerant species such as *Sarcobatus, Distichlis, Sporobolus, Puccinellia, Triglochin,* and *Salicornia.*
3. Forested Wetlands: Rivers and streams in the Rocky Mountains that have well-developed floodplains supporting broadleaf deciduous forests and woodlands. The term "riparian wetlands" refers to plant communities occurring adjacent to running water. Rocky Mountain riparian forests are dominated by *Populus* (*P. trichocarpa, P. deltoides, P. angustifolia, P. balsamifera,* and *P. tremuloides*), as well as *Betula papyrifera, Fraxinus pennsylvanica, Ulmus americana,* and *Acer negundo.* Needle-leaved evergreens such as *Picea engelmannii, Pinus ponderosa, Pseudotsuga menziesii. Thuja plicata,* and *Abies grandis* also exhibit local dominance on riparian sites extending through elevational zones. Mixtures of *Populus* spp., *Juniperus scopulorum* and/or *Pinus ponderosa* are also found on floodplains. Such sites are subject to frequent disruptions by flooding and domestic grazing (and historically by fire), and communities are often in various stages of successional recovery.
4. Shrub-dominated Wetlands (Carrs): Some wetlands are dominated by shrub species rather than by forbs, grasses, or trees. Shrub species listed by Pfister & Batchelor (1984) as dominants in the northern Rockies are *Salix bebbiana, Cornus stolonifera, Alnus sinuata, A. tenuifolia, Betula occidentalis, B. glandulosa, Prunus virginiana, Sambucus melanocarpa, Crataegus douglasii, Elaeagnus commutata, Shepherdia argentea, Ribes* spp., *Rosa* spp., *Symphoricarpos* spp., *Rhamnus alnifolia,* and *Acer glabrum.*
5. Herbaceous Wetlands along Streams: Along fast-moving, steep-gradient streams are riparian communities that are dominated by mosses and/or a variety of herbaceous vascular plants that have high moisture requirements. Moss communities in the Rocky Mountain wetlands are dominated by species of *Plagiomnium, Cratoneuron, Fissidens, Dichelyma, Fontinalis, Funaria, Hygrophynum, Philonitis,* and *Oncophorus.* Streamside herb-dominated communities feature species of *Mertensia, Senecio, Mimulus, Heracleum, Delphinium, Aconitum, Primula, Saxifraga, Veratrum,* and *Athyrium.*

ASPEN COMMUNITIES

Trembling aspen (*Populus tremuloides*) forms clonal stands or continuous forests under various site conditions in all mountain vegetation zones from 900 m to 3,600 m throughout the Rocky Mountains. It intermixes with semiarid shrublands and with wet spruce-fir forests. It is the most widely distributed native North American tree; aspenlike trees appear to have been present in western North America since middle Miocene times (Harper et al., 1985). Aspen populations are variable, but no subspecies are recognized. The most expansive display of aspen in the Rocky Mountains occurs in the middle Rockies (Reed, 1971; Smith, 1985; Mueggler & Campbell, 1986), and it forms scattered grovelands in the northern Rockies (Lynch, 1955; Steele et al., 1981; Arno & Hammerly, 1984).

Biological and ecological attributes of aspen in the western United States have been recorded by DeByle & Winokur (1985). Aspens reproduce profusely by root shoots ("suckers"), especially following fire treatment. Establishment from seed is rare and may occur only during unusually wet years. As shown in Figure 18, aspen communities are often fire-induced pioneer or seral stages that become invaded and replaced by conifers (Lynch, 1955), while under other conditions—beyond conifer's limits—the groves may perpetuate themselves as local uneven-aged climax stands (Steele et al., 1983; DeByle & Winokur, 1985).

Aspen communities do not readily burn, but aspen's thin bark makes it extremely sensitive to fire. Although it is considered a fire-dependent community type, aspen stands have low flammability characteristics (Mutch, 1970). Modern fire suppression has led to an increase in mature aspen; young stands are not common (DeByle & Winokur, 1985).

Populus tremuloides communities have been subject to heavy use by domestic stock as well as by elk and moose, leading to replacement of the native understories by exotic weed species such as *Nemophilia brevifolia, Dactylis glomerata, Phleum pratense, Agrostis* spp., *Cerastium arvense, Rudbeckia occidentale, Poa pratensis,* and *Helianthella* spp. (Steele et al., 1983). Previous severe browsing of aspen shoots by elk and moose on the Yellowstone Park winter range, together with fungi and insect damage, led to the demise of aspen (Krebill, 1972). Recent browse pressure reduction has allowed vigorous aspen regrowth (Krebill, 1985, pers. comm.).

MINOR COMMUNITY TYPES

Pinus flexilis has been mentioned as a member of both the lower and upper timberlines within parts of the southern Canadian Rockies, northern Rockies (confined primarily to the East Fronts in Alberta and Montana), and middle Rockies. It also deserves mention as a dominant pioneering tree occupying volcanic deposits (cinder cones and lava flows) in and near the Craters of the Moon National Monument (Fig. 4, Area 22) in eastcentral Idaho (Eggler, 1941). Some *Pseudotsuga menziesii* is also found with *Pinus flexilis* on these extremely xeric sites, as are *Artemisia tridentata, Chrysothamnus nauseosus, Purshia tridentata,* and *Ribes cereum.*

Other communities occupying localized microsites, such as talus/scree, ponds, bogs, snow glades, rock outcrops, rock crevices, vernal pools, and sand dunes have been described by Chadwick & Dalke (1965), Daubenmire (1970, 1975, 1978, 1980), and by others. Throughout the Rocky Mountains, there are numerous specialized habitats that support minor communities often composed of rather unique combinations of plants. Some of these species have been identified by Rocky Mountain botanists as rare and/or endangered. Furthermore, some parts of the northern Rocky Mountain region support numerous geographic disjuncts and endemics, such as coastal *Cornus nuttallii* and *Alnus rubra* populations; these occur in the intermountain ranges in northern Idaho (Daubenmire, 1943, 1975; Johnson, 1968; Johnson & Steele, 1974).

CONCLUDING REMARKS

The Rocky Mountain vegetation exhibits variations in its local and regional distribution patterns as a result of the diversity associated with this region's physical setting and a variety of historical events related to mountain building, glaciation, climatic shifts, the presence or absence of fire, and anthropogenic influences. The dynamic nature of vegetation is the basis of its responses to changing environments spanning millions of years. Any modern description of the Rocky Mountain flora and plant communities is really only capturing a "moment" in an ever-changing phenomenon. We have every reason to believe that, within an historical context, the mountain vegetation zones described in this review have shifted altitudinally and latitudinally in response to climatic changes which are still taking place. Introduction of exotic plants by man adds to the diversity of the Rocky Mountain flora but may also contribute to the creation of new vegetation equilibria.

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COMPARATIVE AGE OF GRASSLAND AND STEPPE EAST AND WEST OF THE NORTHERN ROCKY MOUNTAINS[1]

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ABSTRACT

Given the taxonomic and biogeographic differences between dominant species in grasslands of the Great Plains and the palouse grasslands and steppe of the Pacific Northwest, it seems likely that the two biomes have had separate origins. Fossil leaf and seed floras and pollen data from east and west of the Rocky Mountain cordillera and pollen data from the cordillera area suggest that three distinct floristic provinces were in existence by the beginning of mid-Miocene (Barstovian) time. Montane conifer forest poor in genera typified the Rocky Mountain foothills and nearby basins, while mixed conifer-deciduous hardwood forest and *Taxodium* swamps rich in woody genera occurred in the Columbia Basin. On the Great Plains the Kilgore flora (Barstovian of Nebraska) indicates deciduous open forest and prairie dominated by species of eastern and southern affinities. Younger Neogene floras in the Pacific Northwest suggest that steppe and local grassland were beginning to be important in the Pliocene of the Pacific Northwest, while grasslands and open forest became widespread on the Great Plains somewhat earlier (late Miocene or Clarendonian–Hemphillian time). The persistence of mixed conifer and broad-leaved forest on the Columbia Plateaus suggests that this area was open to the west through about 8 Ma. Due to the increasing height of the Cascade Range and/or regional upwarping, the rain shadow east of the Cascades became increasingly effective after the Clarendonian. Many of the terrestrial herbaceous groups and some shrub taxa of xeric environments reported here from a variety of sites are unknown in the Paleogene and may have evolved during the Neogene. According to the regional pollen record, terrestrial herbs become more diverse in the late Neogene.

Recent fossil evidence has helped substantiate that the grasslands and steppe west of the Continental Divide in the Columbia Basin area are about three million years (Ma) old, about ten million years younger than similar vegetation types east of the Divide in the Rocky Mountain foothills and in the Great Plains. Biogeographic differences between the two areas are reflected in species composition and in the dominant habits of grasses. Some climatic differences between 'east' and 'west' exist, but they do not seem sufficient to account for the vegetation contrasts.

We propose that an examination of the Late Cenozoic history (Miocene to present) of the northern Rocky Mountains may help illuminate the nature of origins of the grassland and steppe east and west of the Divide. The region to the west of the Rocky Mountains, the Columbia Plateaus[3], is endowed with some of the finest and best-documented Miocene leaf floras in North America, while the region to the east, the Rocky Mountain foothills and the Great Plains, have Mio-Pliocene deposits for which pollen, leaf, and seed data are now available. To understand the history of grassland and steppe development, because they hinge on the present east/west contrasts, the following questions need to be answered: 1) When did grassland and/or steppe first develop in the northern Rocky Mountains area? 2) What were the regional patterns of climate during the time the grasslands developed? The general climatic regimes for the area can be revealed by the types of Neogene (Miocene and Pliocene) vegetation inferred from pollen or leaf data. Species identifications from the leaf and seed floras give an index of floristic patterns that can be compared with the perceived regimes.

It is our thesis that three distinct vegetation provinces had developed in the northern Rocky Mountain region by early mid-Miocene time (ca. 16 Ma): 1) a rich deciduous hardwood and montane conifer forest west of the Continental Divide and throughout the Columbia Plateaus; 2) a montane conifer forest, poor in tree genera, and with steppe elements in the Rocky Mountain foothills; and 3) a deciduous forest with ancestral grassland elements to the east and in the Great Plains.

If vegetation types east and west of the cordillera were basically different during the Mio-

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[1] We thank Daniel Axelrod, H. D. MacGinitie, Harold E. Malde, Jack A. Wolfe, and Robyn Burnham for their comments, and M. Kay Suiter for typing the manuscript.

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[3] "Columbia Plateaus" is the official physiographic usage by the U.S. Geological Survey (1981).

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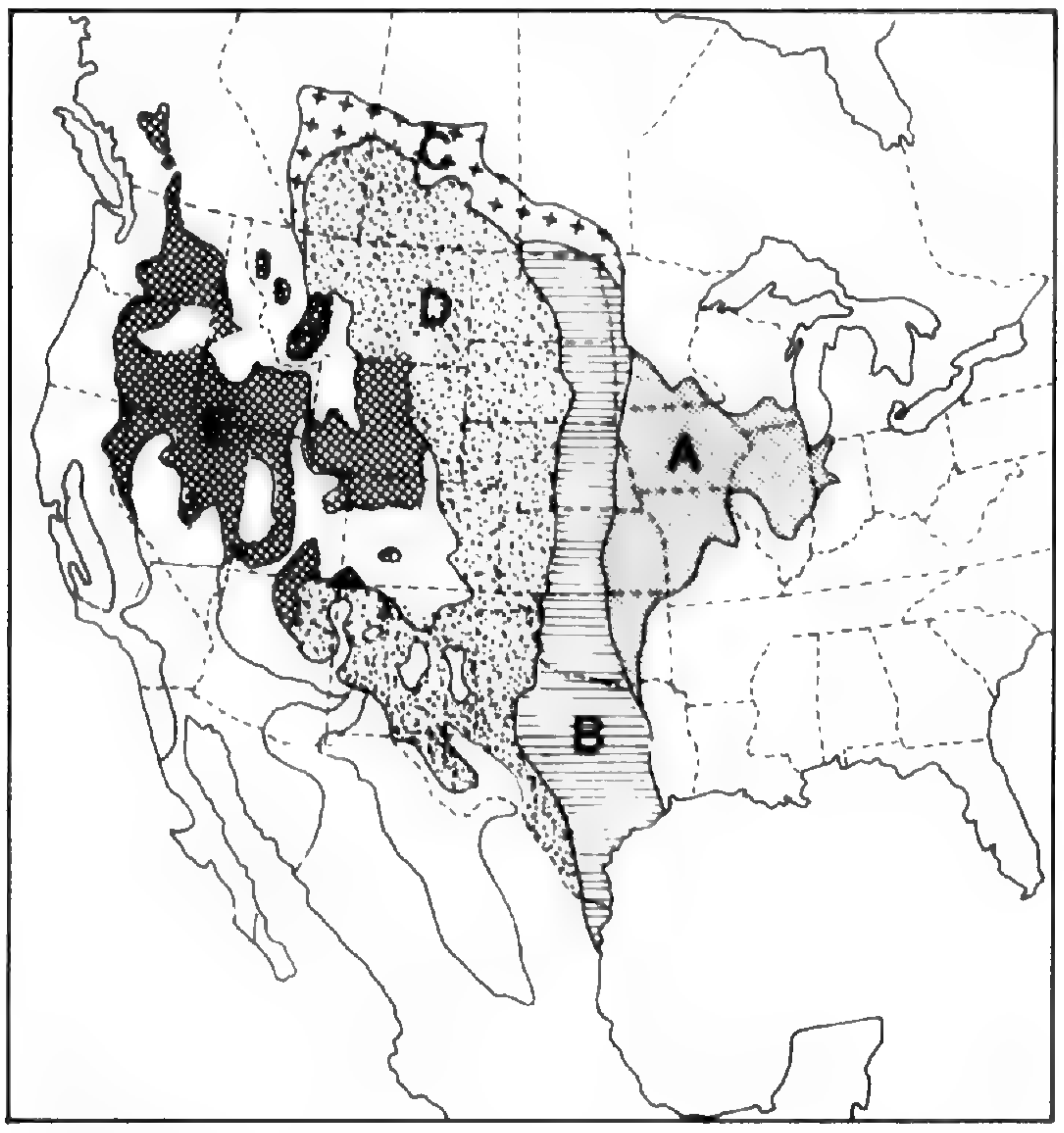

FIGURE 1. Present distribution of the chief grassland and steppe provinces in North America according to dominant taxa (from Daubenmire, 1978).—A, B. *Andropogon scoparius* province.—C. *Festuca scabrella* province.—D. *Bouteloua gracilis* province.—E. *Agropyron spicatum* province.

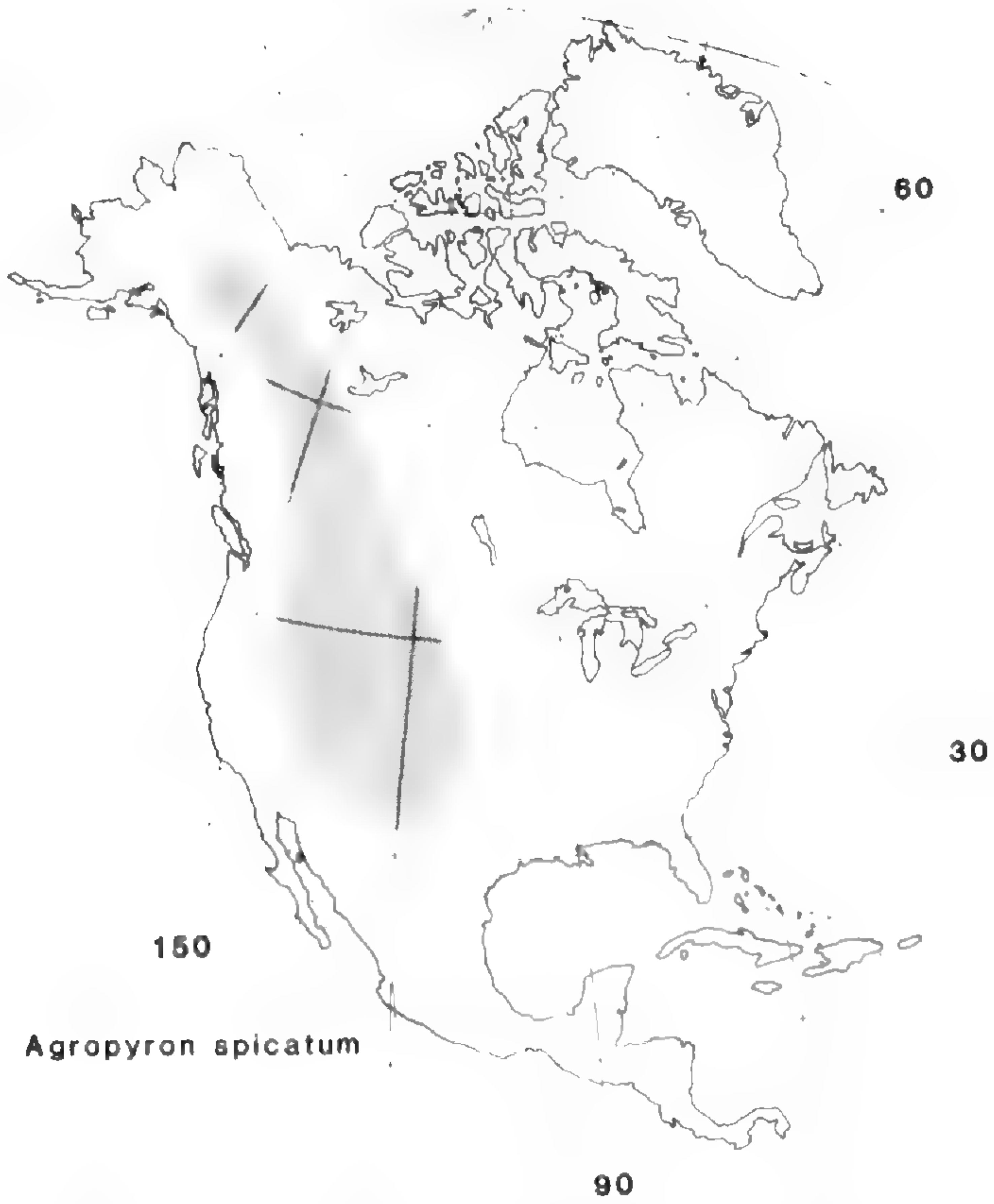

FIGURE 2. Present distribution of *Agropyron spicatum* (after Hultén, 1968; Hitchcock et al., 1969; Voss, 1972).

cene, the importance of this massif as a floristic barrier can be evaluated. Did the same species occur east and west of the divide or were they different? How do these vegetation patterns relate to the Neogene history of the region and to the development of grassland and steppe biomes?

PRESENT VEGETATIONAL PROVINCES

Figure 1 illustrates the outlines of existing grassland and steppe types in the U.S.A. On each side of the Rocky Mountain cordillera lie grasslands of different character. (1) At the eastern margin of the mid-continent grassland, there is the tall-grass prairie, a sod-forming grass association with rhizomatous root habit. The affinities of the dominant taxa, *Andropogon scoparius, Andropogon gerardii* (little and big bluestem), *Panicum* spp., and *Sorghastrum nutans* (Indian grass), lie to the south, in Central America, Mexico, and even South America. (2) The short-grass prairie immediately east of the cordillera, characterized by the dominance of *Bouteloua gracilis* (buffalo grass), *Aristida* spp., and others, is a province with rhizomatous and stoloniferous grasses. Most of the dominant taxa have their floristic affinities with the intermontane basins of the Rocky Mountain region. (3) To the west exists the palouse grassland and steppe of Idaho, eastern Washington, and eastern Oregon (Fig. 1), characterized by bunch grasses and steppic elements such as *Atriplex, Artemisia, Sarcobatus,* and other diverse desert-scrub genera. The biogeographic affinities of taxa in the palouse grassland and steppe are with areas to the north; for example, *Agropyron spicatum* ranges northward to Alaska and boreal regions (Fig. 2). *Festuca idahoensis* has its nearest relatives, the *F. ovina* complex, in the arctic and steppes of North America, Asia, and northern Europe (Fig. 3). *Artemisia cana* (Fig. 4) and other members of the *A. tridentata* group are mainly arctic or boreal.

Climates east and west of the Continental Divide differ significantly, chiefly with respect to the amount of summer precipitation. On the Great Plains summer rain emanates from tropical air masses moving northward from the Caribbean across this region during June and early July (Bryson & Hare, 1974). Along the southern cordillera summer rainfall occurs, especially during warm years, along the north–south path of the "Arizona Monsoon" (Neilson, 1986; Neilson & Wullstein, 1983). To the west, the palouse grassland and steppe region is characterized by a summer-dry climate, with even less summer precipitation than in the Great Plains region. The western area is dominated by the flow of dry Pacific air in summer and is in the rain shadow

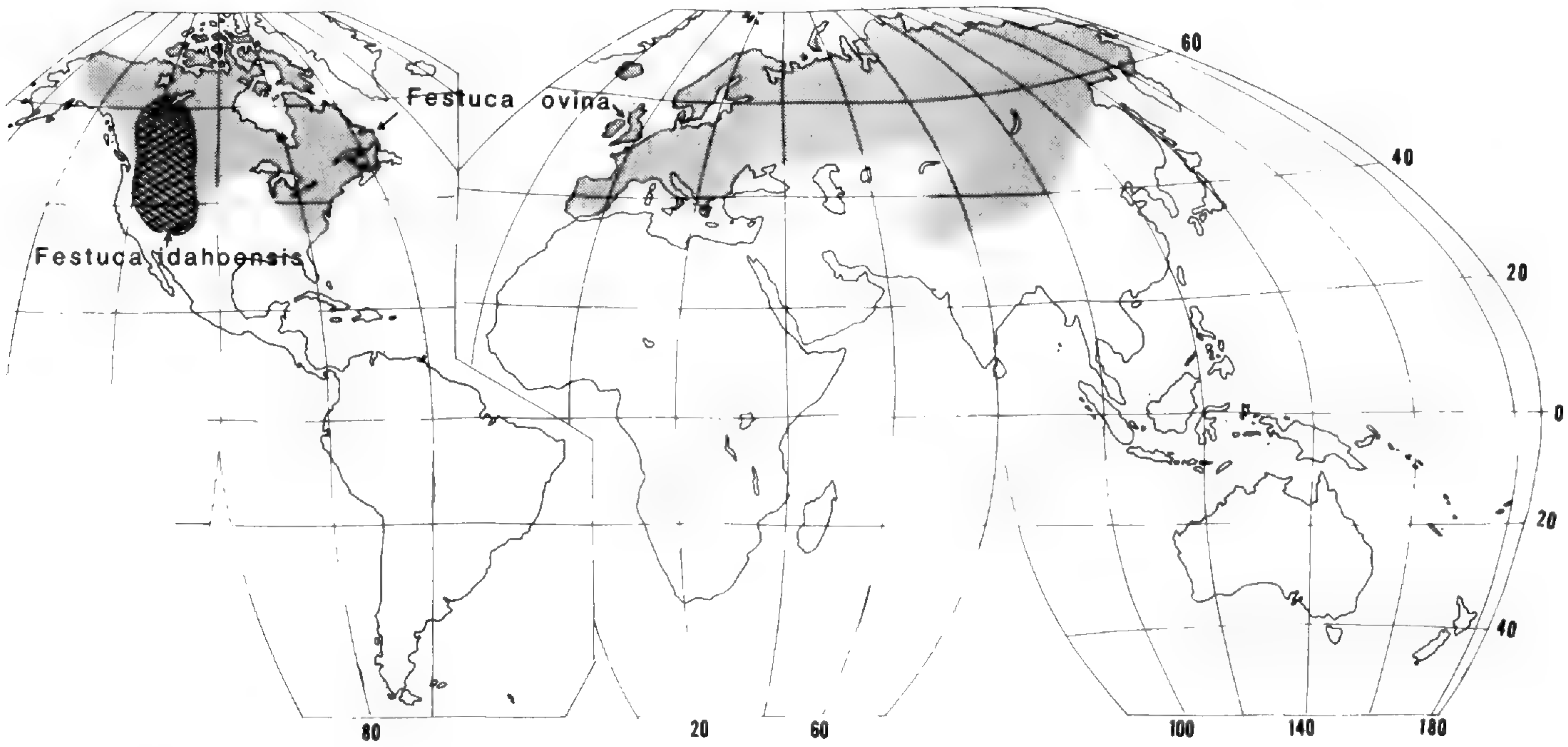

FIGURE 3. Present distribution of *Festuca idahoensis* and the closely related species *Festuca ovina* (after Hultén, 1968; Hitchcock et al., 1969).

of the Cascade Mountains; here, the distribution of grassland and steppe is limited to areas receiving less than 15–20 inches (380–500 mm) of annual precipitation, most of which falls in winter (Fig. 5).

The grassland provinces east and west of the Rockies are now dominated by separate taxa differing in geographic affinity and in growth habit (Table 1). These grasslands differ in distribution of C_4 (warm growing season) and C_3 (cool growing season) grasses. C_4 grasses are always of low frequency (less than 18%) west of the Rockies but may dominate in certain areas east of the Rockies (Mack & Thompson, 1982; Teeri & Stowe, 1976). In addition, there are fundamental differences between these two grassland provinces with respect to their carrying capacities for large, grazing ungulates; for example, the carrying capacity of the palouse grassland dominated by bunch grasses sensitive to trampling is much lower than that of grasslands east of the cordillera (Mack & Thompson, 1982). The biogeographic, physical, and climatic contrasts of these regions imply that their historical development must have been very different. This is the subject of the discussion that follows.

DATA BASE

Because our study concerns events after the early Miocene, we discuss data from sites younger than 18 Ma (Hemingfordian and younger stages). The sites are mapped in Figures 6 and 7 and are arranged according to geologic ages in Table 2.

West of the Rocky Mountain cordillera, the area of the Columbia Plateaus contains a wealth of well-documented fossil plant sites. We have studied data from 15 of these, of which four have yielded pollen data (Fig. 6). Dating is established by K/Ar isotope ratios for a few of these and by land-mammal evidence for others.

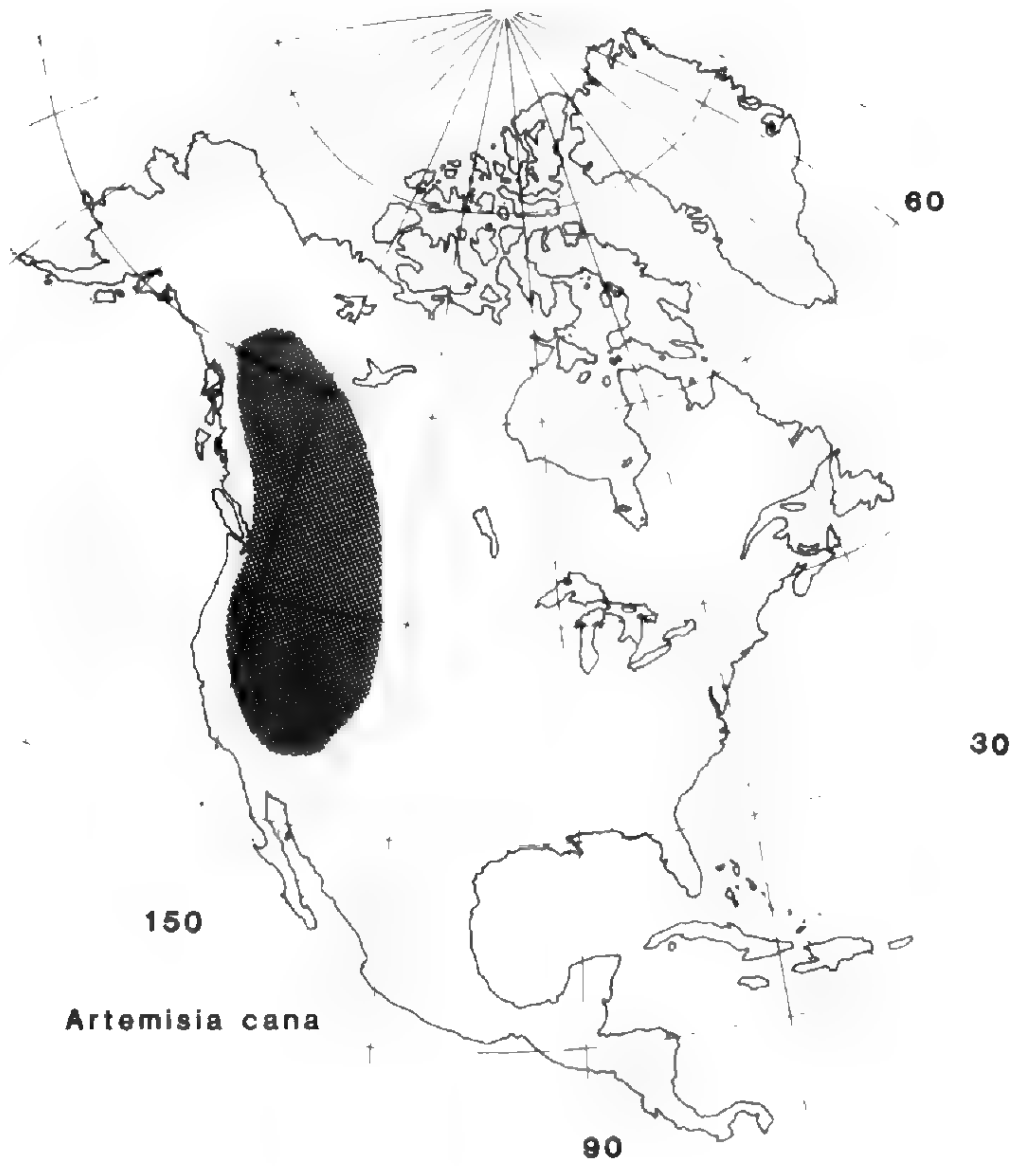

FIGURE 4. Present distribution of *Artemisia cana* (after Hultén, 1968; Hitchcock et al., 1955).

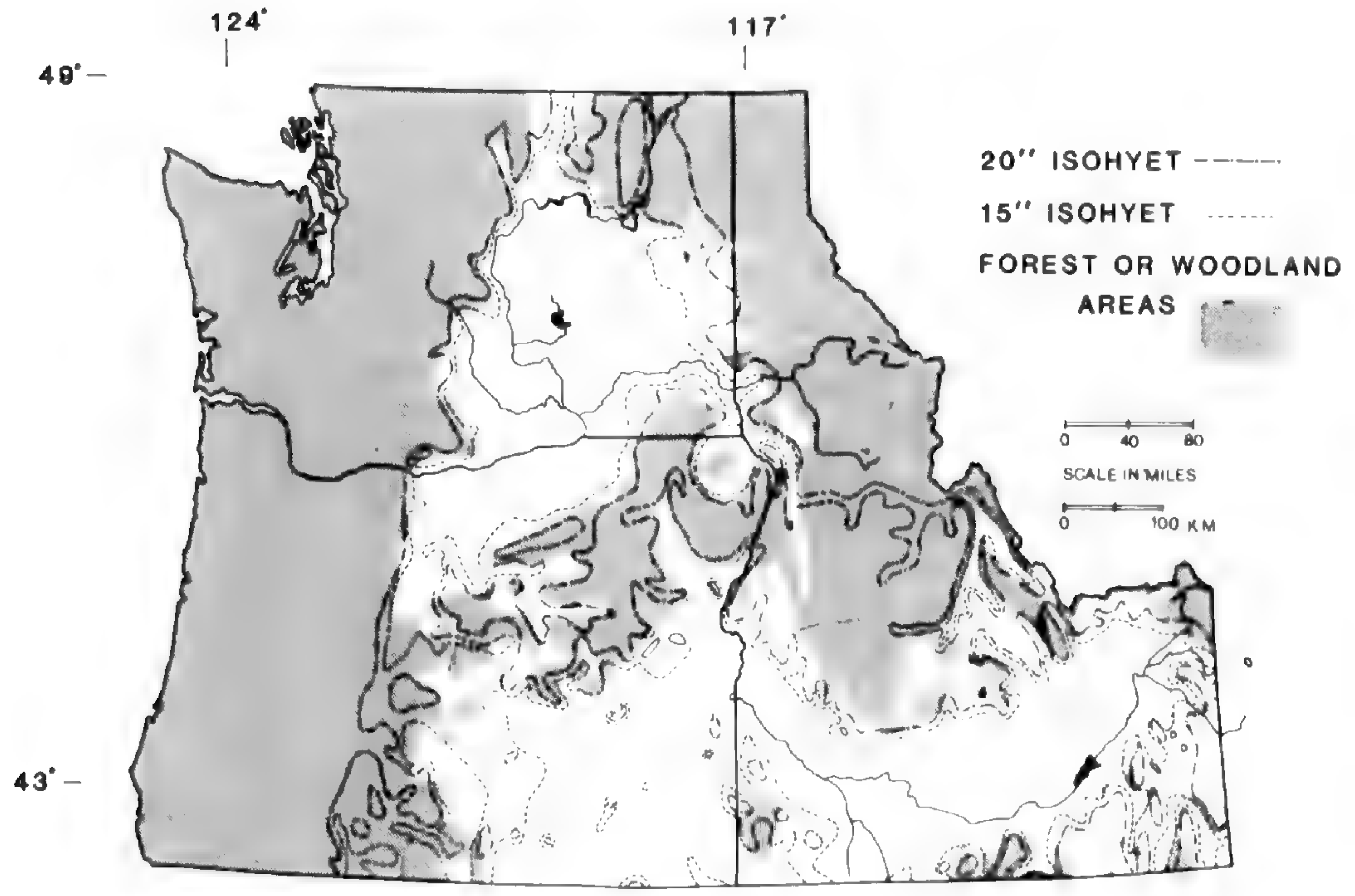

FIGURE 5. Relationship of the forest/steppe border to the 15- and 20-inch (380 and 500 mm) isohyets of annual rainfall in the Pacific Northwest (after Sherman, 1947, and U.S. Weather Bureau data).

In the foothills of the northern and central Rocky Mountains, we have four localities (Fig. 6) from which the main documentation is from fossil pollen, although some megafossil data exist (identification of taxa is on the generic level only). These floras are geographically scattered, but their relative ages were ascertained by land-mammal data.

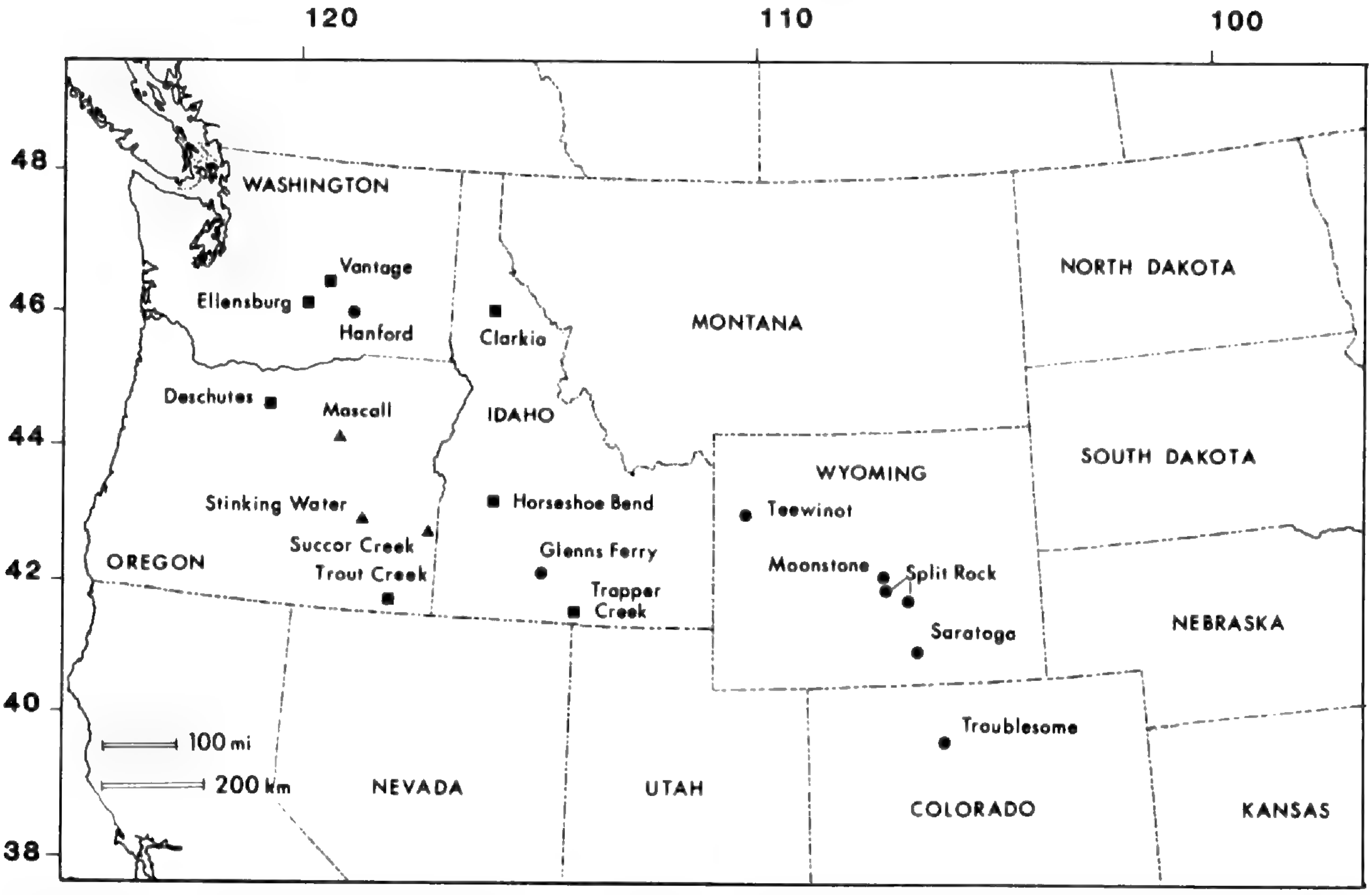

FIGURE 6. Locations of Miocene and Pliocene fossil flora sites in the northern and central Rocky Mountains and Columbia Plateaus. ■ = leaf localities; ● = pollen sites; ▲ indicate leaf and pollen data from the same site. Coal Mine Gulch (not shown) is 50 miles north of Succor Creek.

In the region east of the cordillera, there are several megafossil localities (Fig. 7) containing small leaf floras and there are abundant fruit and seed localities (Elias, 1942); recent work with pollen analysis and electron microscopy of fruiting parts, grass anthoecia, epidermal patterns, and phytoliths revealed the composition of many of these assemblages.

Miocene Vegetation Provinces of the Northern Rocky Mountain Region

Three vegetation provinces had developed by the mid Miocene in the northwestern and north-central mid-continent.

I. WEST OF THE ROCKY MOUNTAINS—THE COLUMBIA BASIN

A. MIOCENE FLORAS

Fifteen leaf floras of mid and late Miocene age demonstrate that mesic forest vegetation under a warm-temperate summer-wet climate existed in the Columbia Basin by about 18 Ma until Hemphillian time (about 8–4.5 Ma). Difference in warm- and cold-season average monthly temperature has been estimated at about 20°C (Wolfe, 1978). Even though important changes in climate and vegetation occurred through the main sweep of Miocene time, the major elements of the flora were not eliminated. Some chief features of the vegetation derived from the leaf flora are:

(1) Dominant vegetation (Trapper Creek[4] of Clarendonian age is an example; summary in Table 3) was deciduous hardwood forest and mixed montane conifer-deciduous forest, with some broad-leaved evergreen elements and diverse (8–26 genera) woody dicots. Shrubs were important (up to 30%), while herbaceous groups were few (only four taxa and these were generally rare aquatics).

(2) Species showed close relationships with modern elements of summer-wet areas in eastern Asia, eastern U.S.A., and/or western U.S.A. in about equal percentages. For example, at Trapper Creek modern affinities seem split between

TABLE 1. Chief characteristics of modern grassland types in the U.S.A.

	WEST	ROCKY MOUNTAINS	EAST
	Grassy steppe	Short-grass prairie	Tall-grass prairie
KEY SPECIES:	*Agropyron spicatum* *Poa* *Festuca idahoensis*	*Bouteloua gracilis* *Aristida* *Buchloë* *Muhlenbergia* *Sporobolus*	*Andropogon scoparius* *A. gerardii* *Panicum virgatum* *Sorghastrum nutans*
	(north temperate & boreal affinities)	(intermontane basin affinities)	(southern affinities)
DOMINATED MAINLY BY:	caespitose (bunch) grasses	rhizomatous/stoloniferous grasses	
CLIMATE:	summer dry	summer moist	

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[4] Axelrod (1964) considered the age of the Trapper Creek flora as 15–16 Ma. More recent evidence from K/Ar dating (Armstrong et al., 1975; Fields, 1983) suggests an age of 10.5–12 Ma.

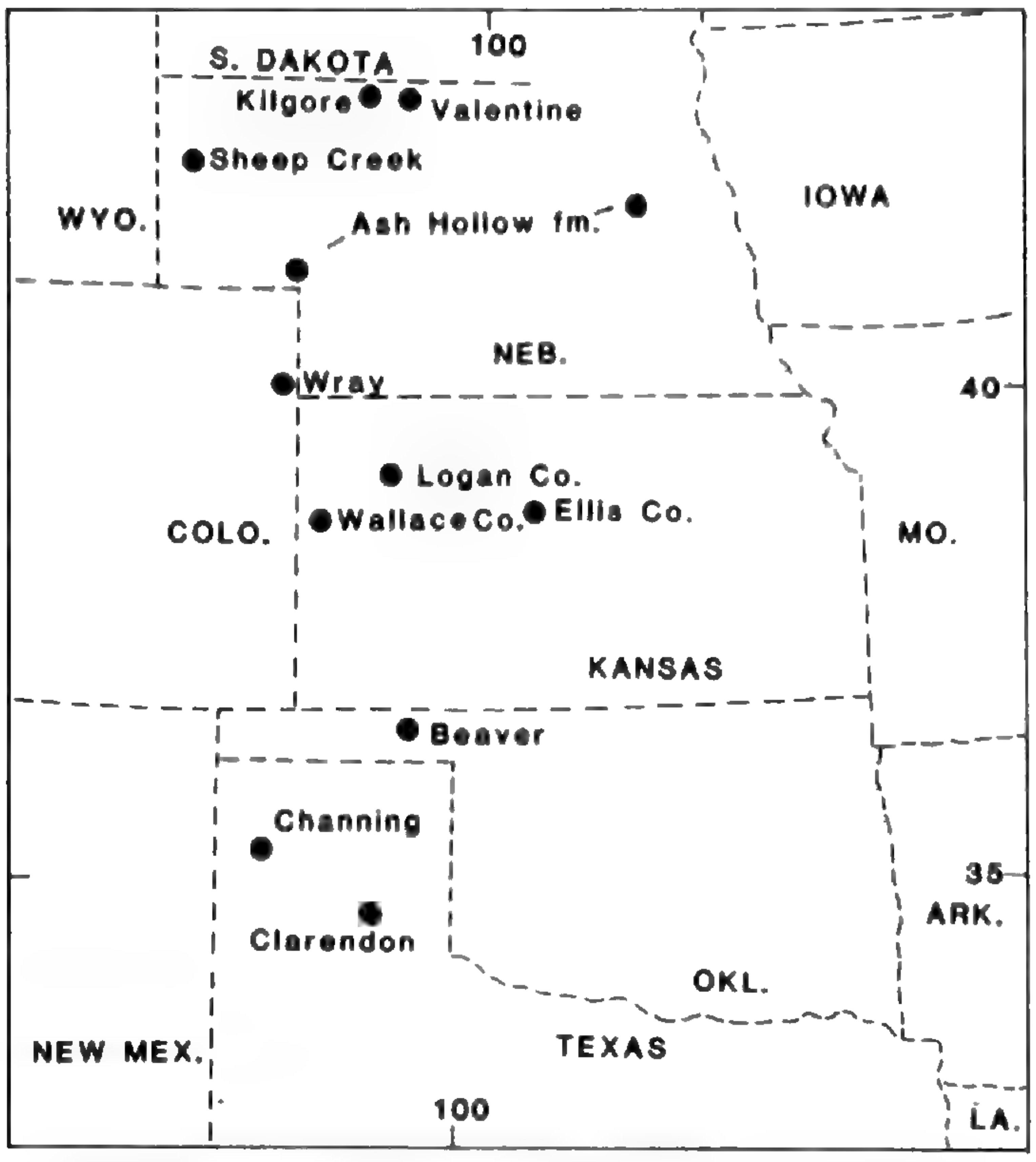


FIGURE 7. Location of Miocene and Pliocene fossil flora sites on the Great Plains (High Plains of Axelrod, 1979).

these three areas (Axelrod, 1964). There were only minor temporal changes in the role of these geographic elements through mid-Miocene time (Table 4).

(3) Vegetation was chiefly woody. Characteristic plant communities summarized for the mid-Miocene floras of southern Idaho included:

(a) Swamp forest, particularly *Taxodium* swamp with associated *Nyssa, Liquidambar, Persea, Salix,* and *Alnus.*

(b) Lake-border woodland, with *Quercus simulata* and species of *Acer, Betula,* and *Populus.*

(c) Valley forest, including some of the taxa mentioned above and a wide range of woody deciduous groups such as *Alnus, Amelanchier, Prunus, Parthenocissus, Cornus, Fraxinus, Ulmus, Pterocarya, Carya,* and *Sophora* as well as an important component of broad-leaved evergreens, such as *Quercus* (cf. *Q. chrysolepis*), *Sassafras, Berberis, Ilex,* and diverse conifers such as *Keteleeria, Picea* (cf. *P. breweriana*), *Pseudotsuga, Tsuga, Abies,* and *Sequoiadendron.*

(d) Mountain-slope forest, including many of the conifers and hardwoods mentioned in the valley forest, also *Garrya* (*G.* cf. *fremontii*), *Rhus, Ungnadia, Abies* (*A.* cf. *delavayi* or *A. recurvata*), *Abies concoloroides, Calocedrus* (*C.* cf. *decurrens*), and most importantly, *Pinus* (*P.* cf. *ponderosa, P.* cf. *monticola*), and *Cedrus.*

Some of the most frost-sensitive forms (*Liquidambar, Cedrela*) seem to disappear during the mid Miocene, especially in regions close to the Rocky Mountains. However, the occurrence of warm-temperate *Taxodium* swamp vegetation persisted in eastern Washington until ca. 8 Ma and in Idaho until ca. 12 Ma.

Although Miocene communities typically included species of eastern Asian and eastern American affinities, western American elements seem to dominate in the montane slope forest communities.

Chaney (see Chaney & Axelrod, 1959: 53) discussed the possibility that open savanna or prairie vegetation existed at some mid-Miocene sites where pollen and leaf data are available, e.g., Mascall and Stinking Water floras of eastern Oregon. Part of his rationale was based on the diverse fossil mammals whose modern relatives live in savanna habitats today (rhinoceros, horses, rodents, lagomorphs, camels, and most abun-

TABLE 2. Stratigraphic ages of Late Cenozoic floral localities of the Columbia Plateaus, northern Rocky Mountains, and Great Plains.

		Ma		EASTERN OREGON	EASTERN WASH.	SOUTHERN IDAHO	NORTHERN IDAHO	WYOMING COLORADO	NORTHERN NEBRASKA
Quaternary						Bruneau			
Pliocene		1.7	Blancan			Glenns Ferry			
Miocene	Late	4–5 8	Hemphillian Clarendonian	Deschutes	Hanford	Chalk Hills Banbury Basalt		Moonstone Teewinot	Ash Hollow
	Mid	12	Barstovian	Stinking Water Trout Creek Succor Creek Mascall	Ellensburg Vantage	Trapper Creek Poison Creek Payette	Clarkia	Saratoga	Kilgore Sheep Creek
	Early	16.5 18	Hemingfordian					Split Rock Troublesome	

TABLE 3. Dominant vegetation types in Late Cenozoic floras of the Columbia Plateaus (from Axelrod, 1964; Chaney & Axelrod, 1959; Graham, 1963; Leopold & Wright, 1985; MacGinitie, 1933; Smiley & Rember, 1985; Taggart et al., 1982).

	Barstovian							Clarendonian			Hemphillian			Blancan	Quaternary
	Trout Creek	Succor Creek	Clarkia	Horseshoe Bend	Vantage	Coal Mine Gulch	Mascall	Stinking Water	Lower Ellensburg	Trapper Creek	Chalk Hills	Hanford	Poison Creek	Glenns Ferry	Bruneau & Younger
Mixed deciduous evergreen hardwood forest							X		X				X		
Deciduous hardwood forest		X	X	X					X		X				
Ecotone		X			X		X								
Montane conifer–deciduous hardwood forest	X							X		X		X	X		
Ecotone										X					
Montane conifer forest										X					
Grassland and conifer forest														X	
Steppe and conifer forest														X	X
Steppe															X
Taxodium swamp forest		X	X	X		X			X			X			

dant, the oreodonts). Direct evidence, however, is limited. Herbaceous plants are an important element in modern savanna. Aside from aquatics and ferns, herbaceous groups are rare in the Miocene leaf record of the Columbia Plateaus. Even pollen evidence indicates that herbaceous groups were limited in diversity and abundance (Appendix I); in the Mascall only two nonaquatic herb types were identified by Jane Gray (in Chaney & Axelrod, 1959: 43): "Pollen of Gramineae are present but not numerous." The situation was similar in the Stinking Water and Blue Mountains floras. Some fossil seeds and fruits were found, but these, as in the leaf flora, were all from woody taxa.

The floristic role of herbs in mid Miocene of the region is illustrated in the pollen lists from the Succor Creek Formation (14–12 Ma at the type section; Fields, 1983) in southeastern Oregon (Taggart & Cross, 1980). Six probably terrestrial herbaceous groups are recorded: *Pachysandra, Ambrosia,* Onagraceae, Amaranthaceae, Gramineae, and Umbelliferae (Appendix I). Because the pollen diagrams summarize their abundance according to broad ecological groupings, the relative importance of herbs is not documented. In their discussion Taggart & Cross made it clear, however, that grass and Compositae pollen are sporadically abundant as part of a successional cycle (see below).

TABLE 4. Percentages of element representation in mid-Miocene floras and age groups, Columbia Plateaus region (from Chaney & Axelrod, 1959, table 32; Axelrod, 1964, table 5).

	Barstovian			Clarendonian		
Geographic Elements	Mascall	Succor Creek	Trout Creek	Stinking Water	Trapper Creek	Lower Ellensburg
Eastern American	65	61	50	58	58	70
Eastern Asian	50	50	50	53	69	45
Western American	37	37	56	60	62	58
Total taxa	64	46	46	38	61	32

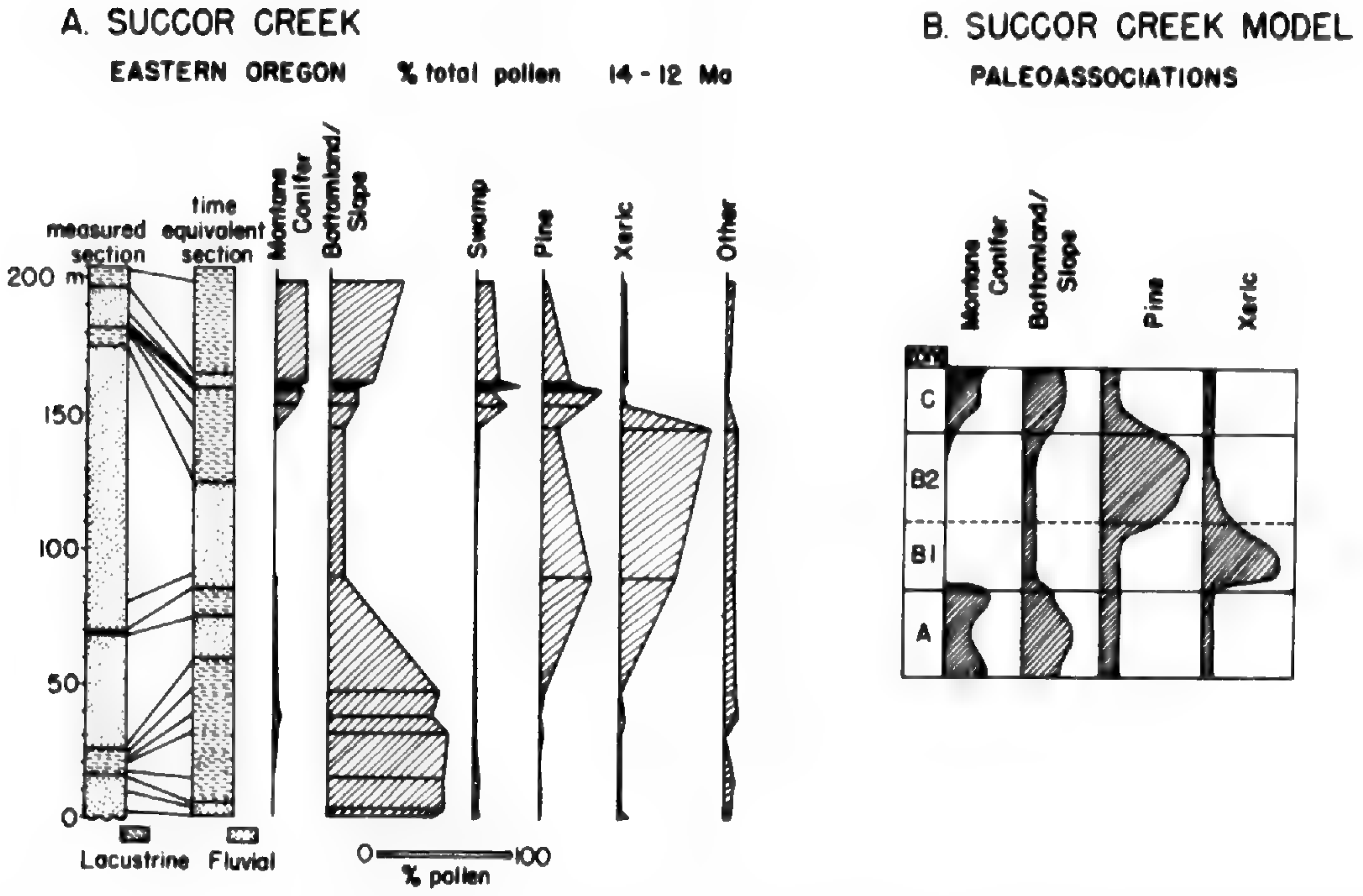


FIGURE 8. Generalized pollen diagram indicating vegetation phases in a 200-meter section at the Succor Creek flora type locality of mid Miocene age, eastern Oregon (A); a model of the successional sequence (B) is shown on right (from Cross & Taggart, 1982).

(4) Vertical arrangements of plant communities were suggested by pollen data. Many leaf floras do not demonstrate clearly that an altitudinal zonation occurred in the Miocene floras, yet pollen-stratigraphic evidence makes it certain indeed. At Succor Creek, Oregon, Taggart & Cross (1980) and Taggart et al. (1982) showed a repeated successional cycle of montane conifer forest, bottomland/slope associations, and xeric shrub with steppic elements followed by *Pinus* spp.; the sequence then reverts to swamp, bottomland/slope, and then to montane conifers. A single cycle in a 200-meter section is shown in Figure 8. The dramatic oscillations can readily be interpreted as elements from various altitudinal communities participating in an altitudinal succession caused by climatic changes. Taggart et al. (1982) believed the successional changes are related to disturbance episodes of volcanism, but it is also possible that these are forced by small oscillations of climate, or both.

At a much younger (ca. 8.5 Ma) site at Hanford in eastern Washington, floodplain sediments (lowest Ringold formation) of the ancestral Columbia River record a somewhat similar succession (Fig. 9a, b; Leopold & Nickmann, unpubl.). The sediments overlie the Upper Columbia River Basalts (10.5 Ma) and an unconformity dated at 8.5 Ma (Tallman et al., 1981; DOE, 1986: 3–40). The lithology indicates that local depositional environments were changing. In a series of cycles, fine-grained swamp deposits grade upward to increasingly coarse riparian sediments. Two pollen diagrams (core holes DC-3 and DC-7/8), each beginning in fine-grained sediments, register a rich Taxodiaceae-type (cf. *Taxodium*) swamp association. (We infer this identification because *Taxodium* is abundant in the underlying Ellensburg Formation.) This phase is followed by increases in bottomland/slope hardwoods, and finally *Cedrus* and *Pinus* dominate. Herbs and xeric elements are always present in trace amounts. Presumably in a floodplain area such as Hanford, the vegetation changes record either shifting riparian environments (edaphic factors) or changes wrought by climate. While the elevational relief of each of these forest types occupied is not clear at either site, it is possible that as much as 500–1,000 feet of relief existed at Succor Creek.

The Cascade Range was probably rising during Miocene time (McKee, 1972; Smiley, 1963), and its rain shadow eastward eventually changed the character of the vegetation from mesic and summer-wet to xeric and summer-dry. The lower Ellensburg and the Hanford floras suggest that eastern Washington was open to the west through ca. 8 Ma. This meant that the Cascades were not significant enough to block moisture from the westerlies until some time after the Clarendonian. In part this helps explain the general similarity of Pacific Northwest floras during the early and mid Miocene.

B. IMPLICATIONS FROM PLIO-PLEISTOCENE FLORAS

Given the data above concerning the characteristics of the Miocene forests of the Columbia Plateaus, when did forest vegetation diminish, allowing the development of grassland and steppe?

West of the Rocky Mountains, pollen data from Idaho demonstrate the decline and impoverishment of the Miocene forests and the development of local grassland and steppe. These changes that occurred from late Pliocene to Quaternary were surprisingly late. In lake and stream deposits of southwestern Idaho a unique and well-dated composite pollen sequence embraces parts of the last 11 million years, after Trapper Creek time through the early Quaternary (Fig. 10; Leopold & Wright, 1985). Fossil pollen in these deposits tends to be scarce, and pollen-bearing beds are hard to find (90% of our collections were barren). Some megafossils have been identified at certain sites.

In the sequence (Idaho Group) the lower sediment units are from the Poison Creek, Jenny Creek, and Chalk Hills formations and Banbury Basalt of mid and late Miocene age (Armstrong et al., 1975; Fields, 1983; Leopold & Wright, 1985; Appendix II). The floras record mixed deciduous and conifer forest with declining hardwoods; these were mainly *Ulmus* but also included *Pterocarya, Carya,* and *Juglans.* A holly-leaved oak (leaf evidence from the Poison Creek Formation) is reminiscent of that recorded at Trapper Creek (ca. 11 Ma). Wood from the Chalk Hills Formation records diverse hardwoods. Younger sediments of the Glenns Ferry Formation (ca. 3–2 Ma) containing the Hagerman lake beds record an impoverished pine and mixed conifer assemblage with rare pollen of exotic hardwoods. Steppe elements (*Sarcobatus* and other Chenopodiaceae, *Artemisia* and other Compositae) are consistently present and increase sporadically upward in this section. Peaks (up to 60%) of grass pollen are associated with the Hagerman fauna from which remains of about 100 horses (*Pleisippus*) have been found. In the upper Glenns Ferry, Chenopodiaceae and *Artemisia*/Compositae increase while tree pollen declines. Taxa of terrestrial herbs are more diverse than in the Miocene (Appendix I).

Miscellaneous Pleistocene samples from the area suggest that *Artemisia* and Chenopodiaceae are important, if not the dominant, pollen forms. Above an unconformity (see top of Fig. 10) Irvingtonian mammals including *Equus* plus K/Ar evidence date the Bruneau Formation as middle Pleistocene; a Bruneau pollen sample (D1694) shows *Artemisia* to be 50% of the count, suggesting a true *Artemisia* steppe had developed. Two other samples rich in *Artemisia* pollen (D1120 and D1698; Fig. 10), previously reported as Bruneau (Leopold & Wright, 1985), are now classified as Yahoo Clay of late Pleistocene age (Malde, 1982). The top fossil sample (D1697), showing 80% *Artemisia* and other Compositae pollen, is from a late Pleistocene soil above the King Hill Basalt.

In northern Oregon the Deschutes flora (ca. 4–5 Ma) suggests low-diversity riparian vegetation typical of unforested regions and is consistent with a decrease in summer precipitation in late Miocene time (Appendix III; Chaney, 1938).

Taken as a whole, the data indicate that steppe in the Columbia Basin probably did not develop as a major vegetation unit until after the Hemphillian (4.5 Ma). The Snake River Plain section places the change from rich (deciduous and) coniferous forests to montane conifer forest between 10 and 3 Ma. In this region steppe and palouse grassland probably became widespread for the first time in the Quaternary.

II. THE ROCKY MOUNTAIN FOOTHILLS

The lack of megafossil evidence for northern Rocky Mountain Neogene sites is unfortunate (the well-documented Clarkia flora of middle Miocene age lies in the Columbia Basin floristic province). Pollen records from the Rocky Mountains and eastern foothills demonstrate the comparatively modern aspect of plant communities there during the Miocene.

At Jackson Hole, Wyoming, the Teewinot lake deposits (predating the Teton Range) provide a long record of montane conifer forest with occasional bursts of lowland steppe and riparian types (Fig. 11; Barnosky, 1984). Presumed plant communities include:

(1) *Saline basins.* High percentages of *Sarcobatus* pollen accompany other Chenopodiineae, *Ephedra,* and sedges.

(2) *Presumed riparian* areas. These are characterized by pollen of probable phreatophytes,

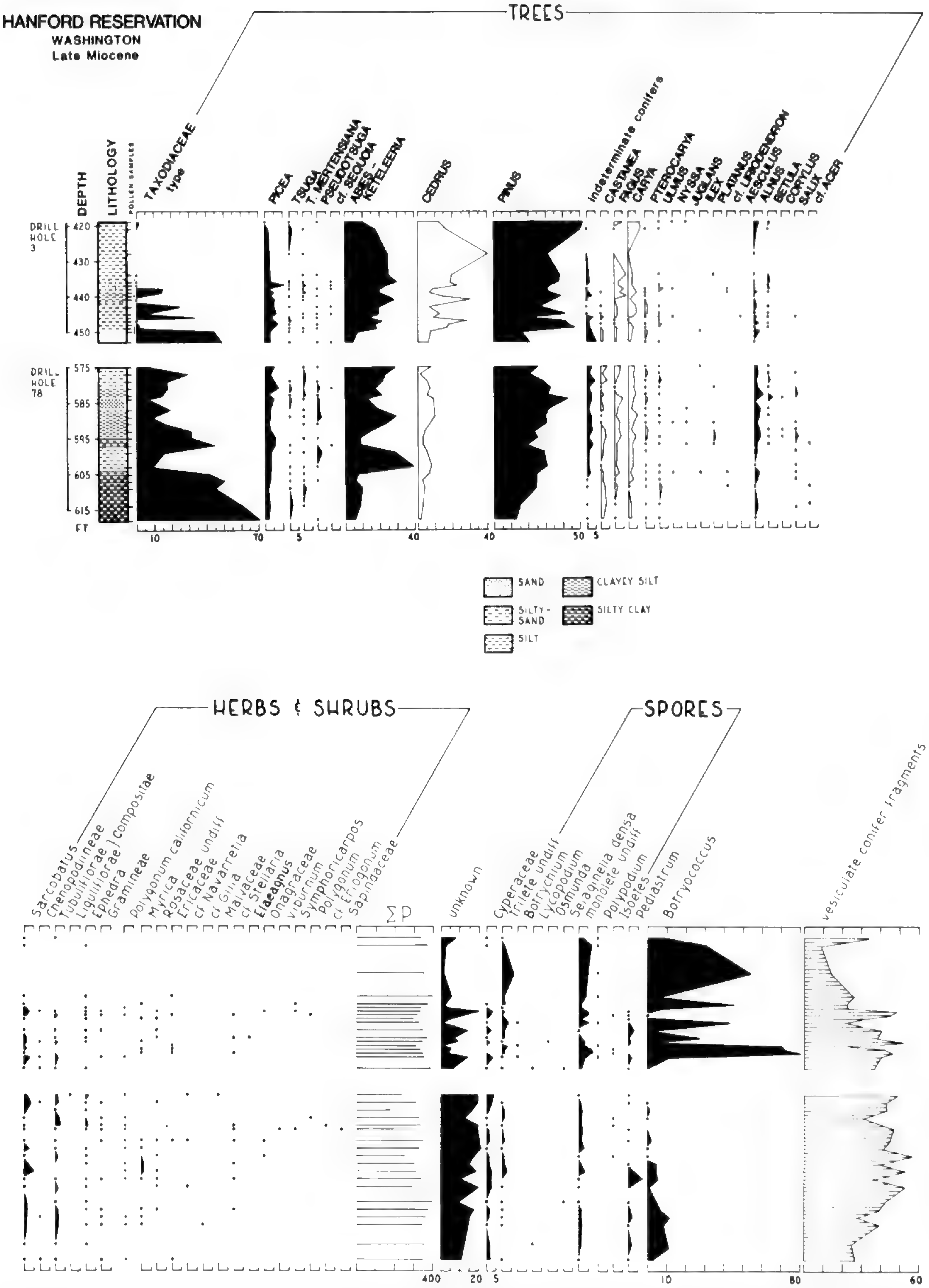


FIGURE 9A. Late Miocene pollen sequence, Hanford, Benton County, Washington. Two pollen diagrams from lowermost Ringold Formation, % total pollen (Leopold & Nickman, unpubl. data). Stratigraphic data are from Department of Energy (1986: 3–16) drill holes DC-3 and DC-78, which are correlative in age and about 12 miles apart. Depths below surface are given in feet. The sediments are dated at 5–10 Ma (probably 8.5 Ma).

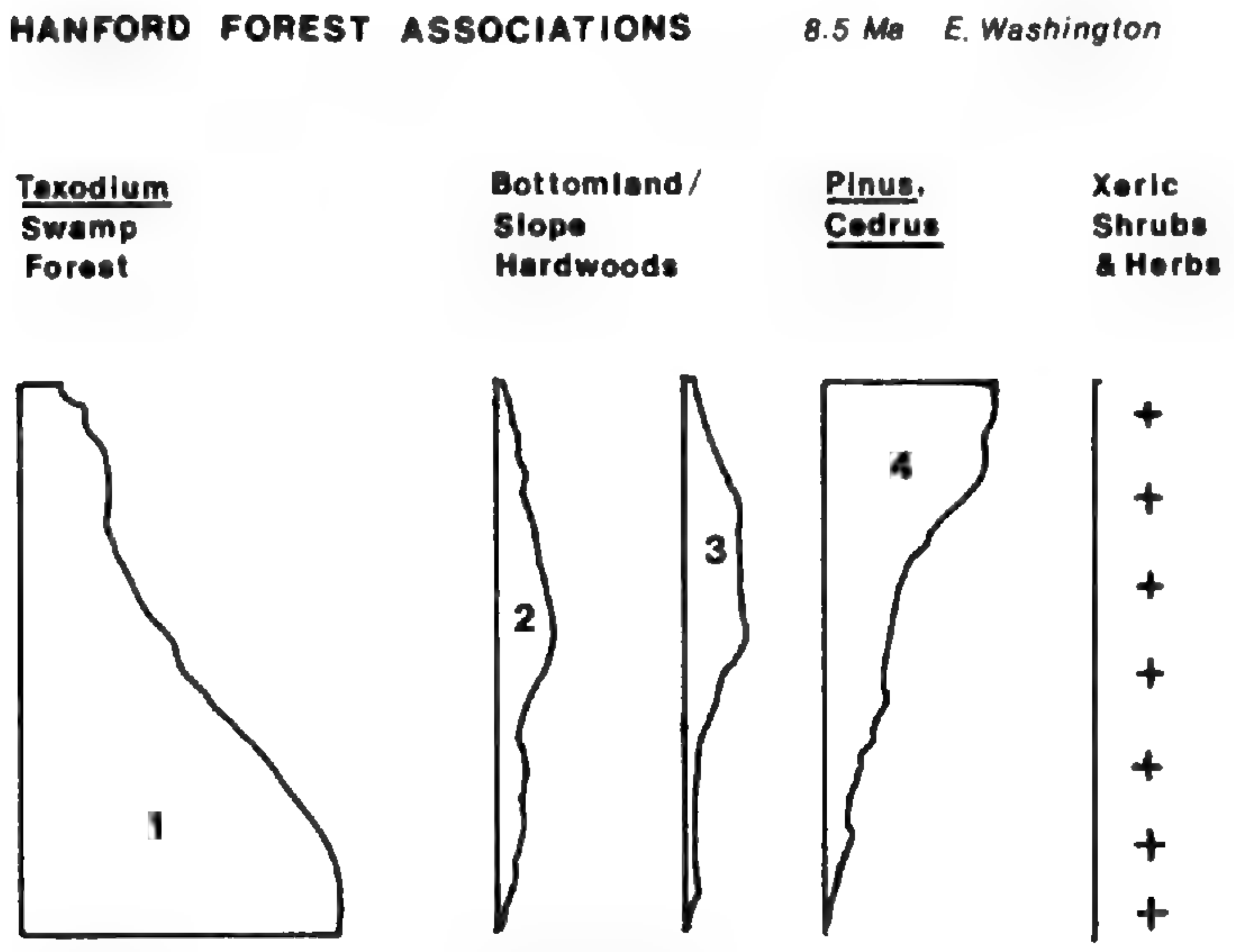


FIGURE 9B. Schematic phases of vegetation shown by Figure 9A pollen diagrams.

Carya, Ulmus-Zelkova, Pterocarya, Sapindaceae, and *Salix.*

(3) *Montane slope forest.* This assemblage is dominated by *Pinus* spp. with important amounts of *Abies, Picea,* and Cupressaceae pollen. *Tsuga, Quercus, Artemisia,* grasses, Onagraceae, and additional herbs may have been locally abundant (Leopold & MacGinitie, 1972: 198).

The proportion of broad-leaved Tertiary relict genera that are now exotic (eastern Asian and eastern American genera such as *Pterocarya, Carya,* and *Ulmus-Zelkova*) obviously is low compared with those in pollen and leaf assemblages of the same time period west of the Rockies (e.g., Hanford, Poison Creek, and Trapper Creek). Except for the "riparian" hardwoods, the flora has a modern aspect indeed, as it compares well with modern pollen rain (see top of Fig. 11).

Four other pollen sites from widely different times in the Miocene are in basins along foothills and in the eastern Rockies of Colorado and Wyoming (Fig. 12; localities in Appendix IV; selected pollen counts in Appendices V, VI; Leopold & MacGinitie, 1972). Early Miocene (Hemingfordian) sites are the Troublesome Formation from Grand County, Colorado (Izett,

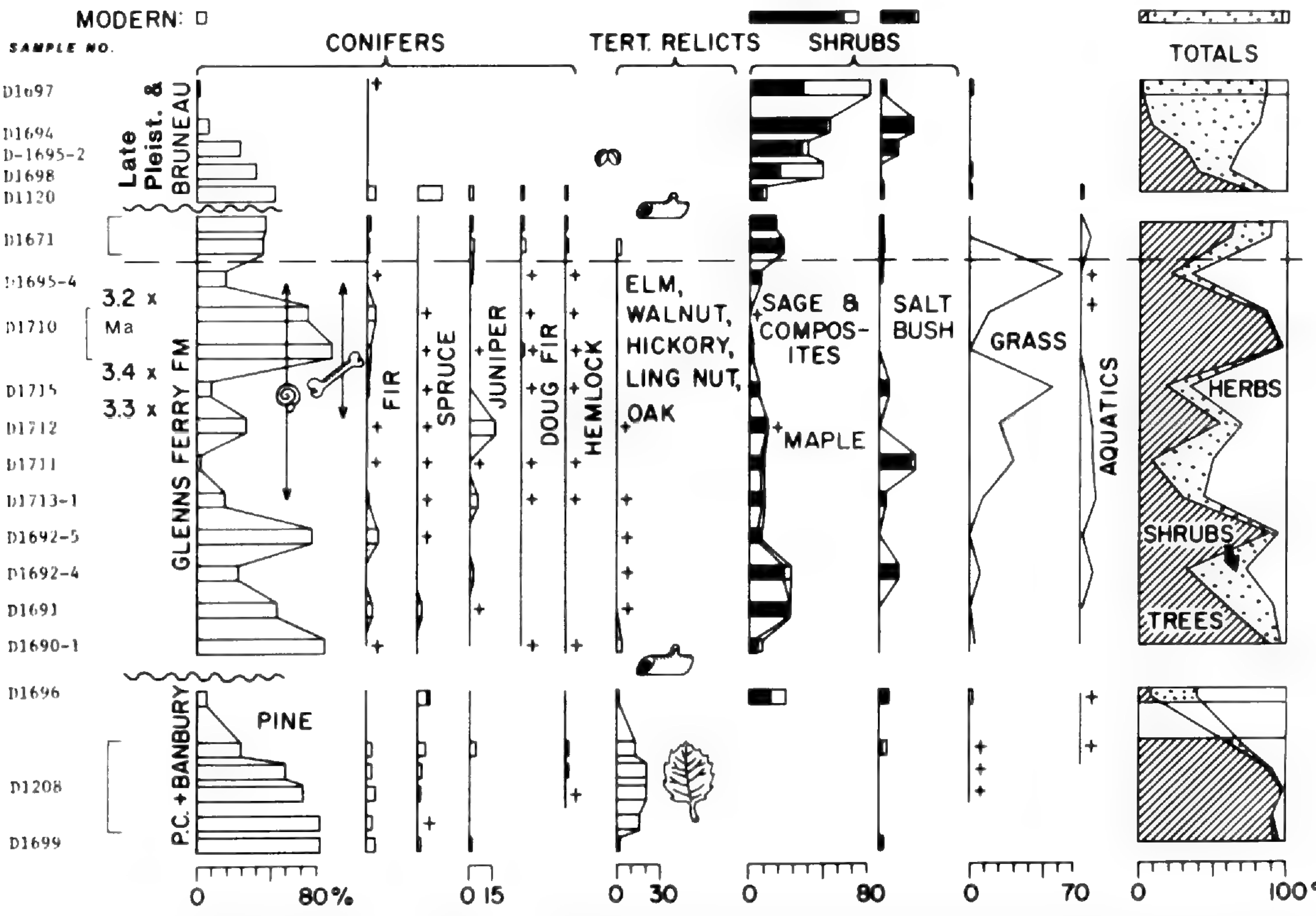


FIGURE 10. Composite pollen diagram, late Miocene to late Pleistocene, Hagerman area, southwestern Idaho. Modern pollen rain at Hagerman is shown at top (from Leopold & Wright, 1985). Fossil wood indicated along the unconformity at the top of the Glenns Ferry Formation is *Quercus,* white oak type (Malde & Powers, 1962). Note that Pleistocene samples D1120 and D1698 are now classified as from Yahoo Clay of late Pleistocene age. Sample D1695-2 is Glenns Ferry Formation (Malde, 1982). Sample D1697 is from a Late Pleistocene buried soil on the King Hill Basalt. Sample D1694 is of the Bruneau Formation of middle Pleistocene age. *Celtis* fruits (see symbol) are of Late Pleistocene age.

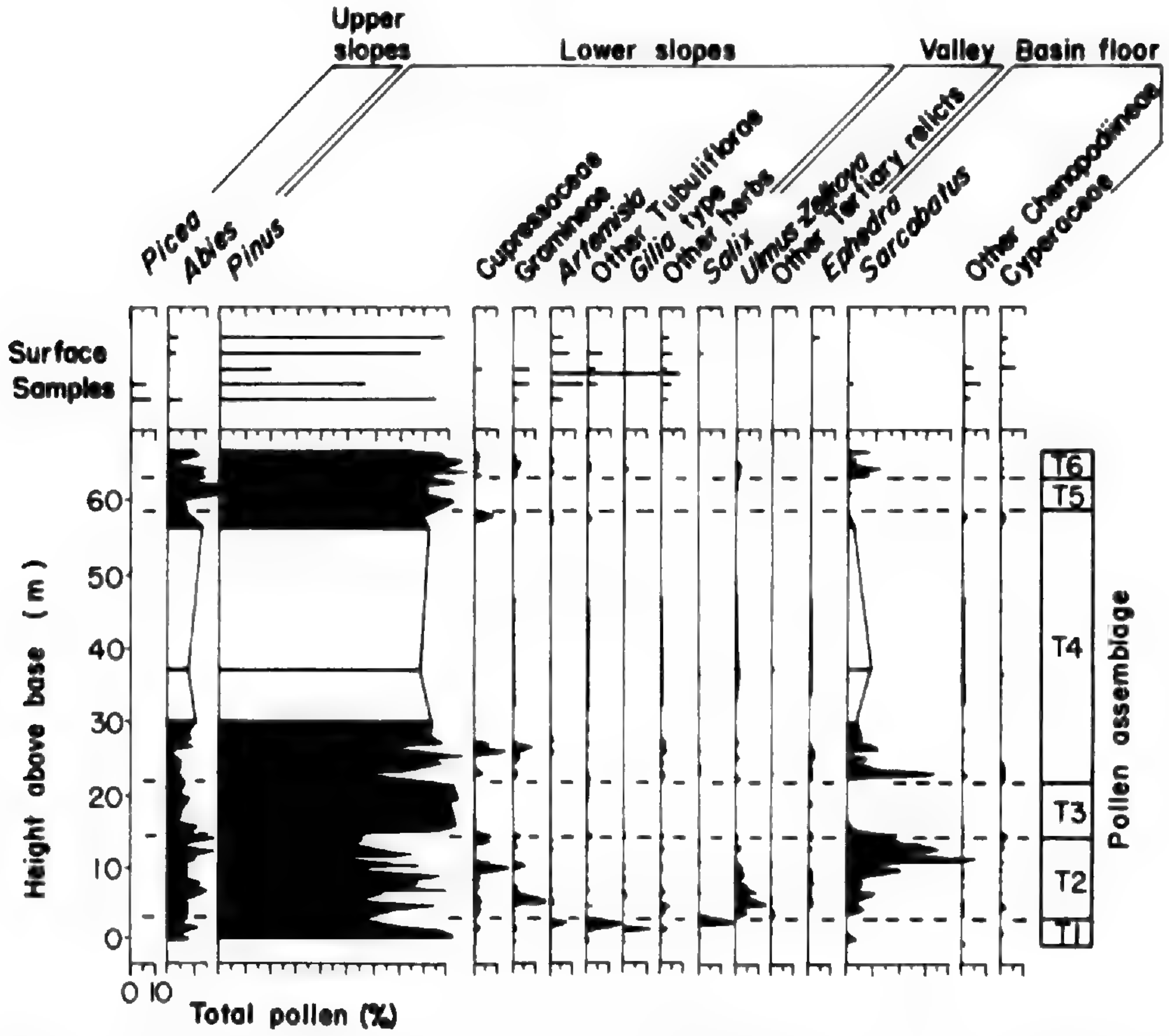


FIGURE 11. Pollen diagram, showing selected types and inferred habitat, upper Teewinot lake beds, Jackson Hole, Wyoming (% total pollen). K/Ar age is 9 Ma or late Miocene (from Barnosky, 1984).

1968), and the Split Rock Formation from the Sweetwater Basin, Natrona County, Wyoming (Love, 1961). A mid-Miocene (Barstovian) site is from the Saratoga Valley, Carbon County, Wyoming. The youngest site, the Moonstone Formation in the Sweetwater Basin, Wyoming, may be of Barstovian or younger age (Robinson, 1971; Love 1961). All are old lake beds near low rolling granite or bedrock hills that probably existed in the Miocene. Pollen is moderately abundant to rare and demonstrates impoverished floras similar to that evident at the Jackson Hole, Wyoming site. Only two types of communities can be conjectured from the data:

(1) *Open basin and lakeside environments* in which *Artemisia, Sarcobatus* and other Chenopodiineae, *Ephedra,* and *Eriogonum* suggest steppic and halophytic environments and in which *Salix,* Betulaceae, and aquatics imply lake-margin or riparian environments. Terrestrial herbs of the Polemoniaceae, Compositae, Onagraceae, Umbelliferae, and Polygonaceae may have grown in these basin environments (Appendix VII).

(2) *Mountain slopes* dominated by *Pinus* with lesser amounts of *Picea, Abies,* and *Juniperus.* Whether *Juglans, Carya, Quercus,* and *Ulmus-Zelkova* were associated with woodland or forest, or whether most of these were restricted to riparian environments cannot be deduced from the available information, though the latter is more probable.

Implications. The consistent presence of xeric and desert-scrub taxa that are sometimes abundant suggests the appearance of steppic vegetation with a diverse herb flora during widely separate times during the Miocene. Grass pollen grains are usually present but never abundant. They are probably associated with depauperate conifer forest or woodland. Several other basin sites in the central and southern Rockies are consistent with the modern aspects of these Miocene floras (Meyer, 1986; Leopold & MacGinitie, 1972).

The Rocky Mountain data stand in stark contrast to the Miocene basin sequences from Idaho westward to eastern Washington where pollen and leaf data alike point to rich forest vegetation containing abundant and diverse deciduous hardwoods. Broad-leaved evergreen trees are apparently absent in the Neogene of the Rocky Mountains.

III. GREAT PLAINS LOCALITIES

Megafossil floras from the Great Plains region (Fig. 7) suggest that prairie elements were present

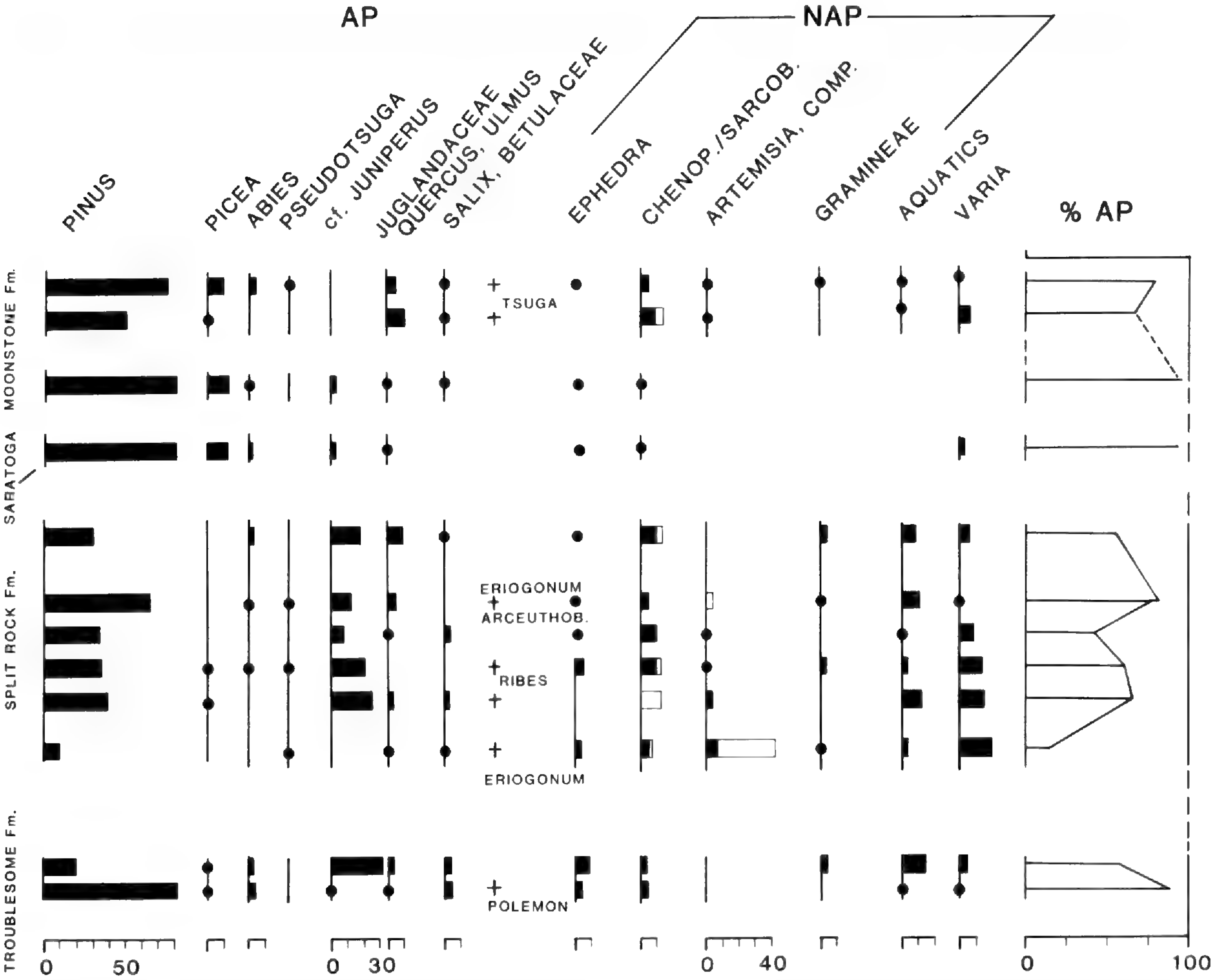


FIGURE 12. Pollen spectra from four Rocky Mountain sites: Troublesome Formation, Colorado, and Split Rock Formation, Wyoming, lower Miocene; Saratoga Valley, Wyoming, mid Miocene; Moonstone Formation, Wyoming, of younger Neogene age (Appendix V, VI).

and that grassland developed to various degrees during the Miocene (Elias, 1942; Chaney & Elias, 1938). An excellent summary by Axelrod (1985) portrays a sequence indicating a generally decreasing precipitation regime from about 16 Ma onward. The older sites are deciduous hardwood forest with prairie elements (Fig. 13). According to Axelrod, the younger sites suggest woodland or riparian border hardwoods with more extensive grassland (Fig. 13).

From the Neogene sediments of the upper Arikaree and Ogalalla groups on the Great Plains and High Plains, Elias (1932, 1935, 1942) made systematic fruit/seed and leaf collections at almost 100 localities from South Dakota to northern Texas. The widespread sediment layers with occasional volcanic ashes and vertebrate fossils provided stratigraphy. Elias undertook to define a sequence of fossil seed zones. Modern dating indicates that the main part of this sequence ranges from Hemingfordian through Hemphil-

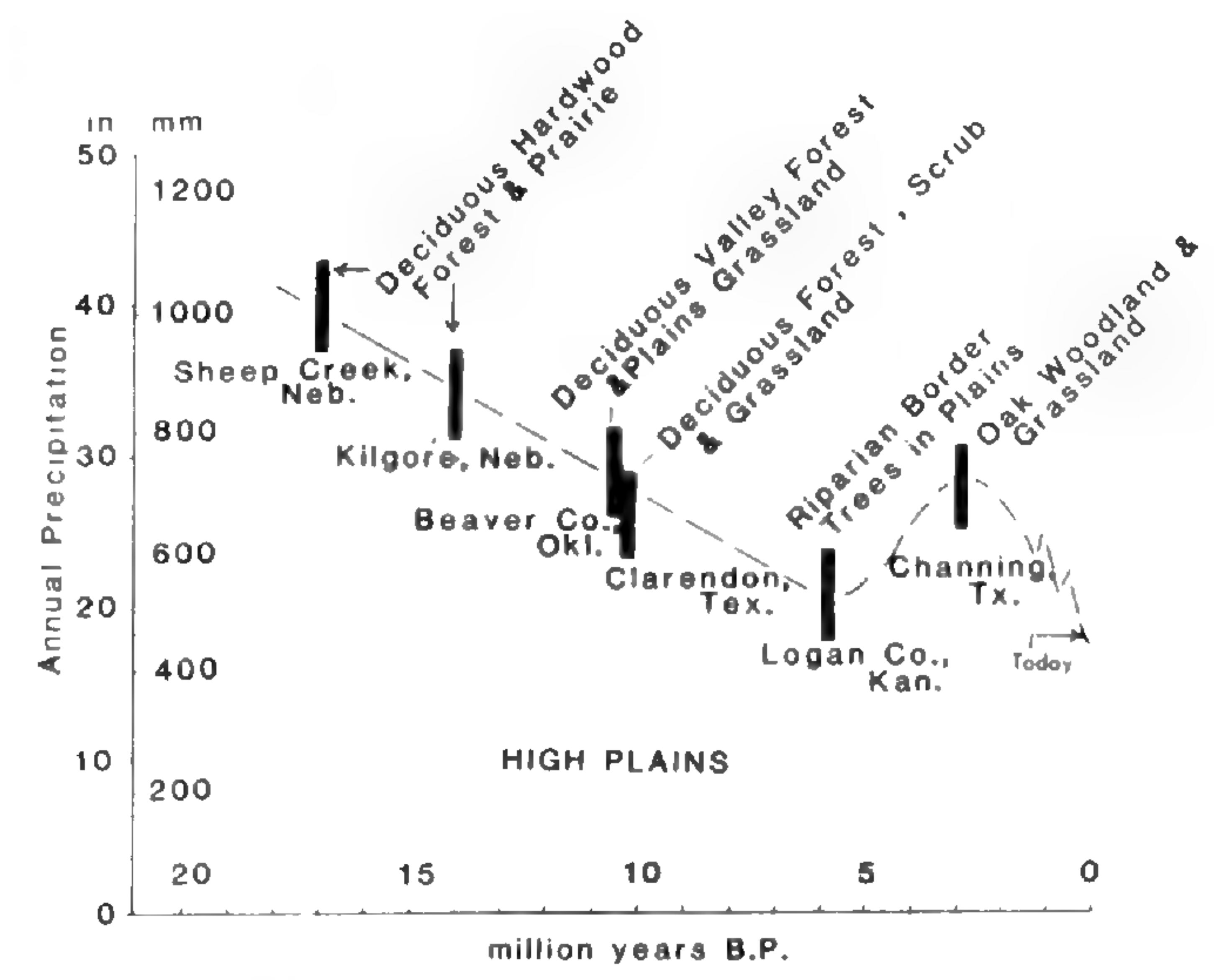


FIGURE 13. Fossil floras from the Great Plains (High Plains of Axelrod, 1979) suggest a gradual reduction in precipitation during the late Tertiary.

TABLE 5. Geographic affinities of the Kilgore flora, Nebraska (15–12 Ma, mid Miocene), showing the representation of its species in Miocene floras of the Columbia Plateaus (after MacGinitie, 1962).

Modern Distribution Groups	Number of Species in Kilgore Flora by Geographic Group	Number of These Species Occurring in Miocene of Columbia Plateaus
East of Rocky Mountains only	10	1
Mexico and southern Rocky Mountains	7	1
Rocky Mountains only	3	0
West of Rocky Mountains	2	0
Split affinities between distinctly eastern and distinctly western species	3	1?
Cosmopolitan	1?	1?
Eastern Asia	2	2
Total number of species:	27–28	4–6 or ca. 18–21%

lian (ca. 18–4 Ma). At most of his sites in the Ogalalla Group (Kilgore and younger age) fruiting parts of grasses and prairie herbs were the most common and in most cases the only fossils, although arboreal leaves were present at a few sites (most of the latter were summarized by Chaney & Elias, 1938, and by Axelrod, 1979, 1985).

Elias's identifications, corroborated in large part by the recent work of Thomasson, demonstrate that ancestral Stipeae appear in the earliest Hemingfordian strata or earlier, and that Boraginaceae (*Biorbia, Krynitzka*) and Paniceae appear consistently and abundantly in Clarendonian (Ash Hollow Formation) sites. Diversity of prairie taxa increases up section.

Perhaps the most surprising feature is the widespread nature of Elias's fossil fruit and seed zones. In Nebraska the following zones range from Kilgore age to Ash Hollow and younger units (Kimball Formation) of the Ogalalla Group (in stratigraphic order; Elias, 1942):

VI. Kimball Formation (calliche).
V. *Biorbia fossilia* with *Krynitzka coroniformis* and *Stipidium grande* (Ash Hollow Formation).
IV. *Krynitzka coroniformis* zone with *Stipidium tubus*.
III. *Stipidium commune* (Valentine Formation).

Elias found the same dominant species at the same zones in the Ogalalla at Wray, Yuma County, and at many other points in eastern Colorado. He found his *Krynitzka* zone underlying the *Biorbia* zone at Wallace County, Kansas (associated with fossil rhinoceros) and at other sites in Kansas. *Biorbia* subzones (not described here) were found in Beaver and Ellis counties, Oklahoma.

The presence of prairie elements during the Miocene has been documented by Thomasson using scanning electron microscopy to identify leaves, anthoecia (lemmas and paleas of grass

TABLE 6. Kilgore species occurring in Miocene floras of the Columbia Plateaus (from MacGinitie, 1962; Edwards, 1983). Question mark indicates probable fossil species, but affinity with modern taxon seems reasonably certain.

Species	Related to
Populus washoensis?	*P. grandidentata* (E U.S.A., SE Canada)
Pterocarya oregoniana	*P. insignis* (E Asia)
Mahonia marginata	*M. bealii* (China)
Cedrela trainii	*C. mexicana* (NW Mexico)
Acer minor?	*A. negundo* (W & E U.S.A. & S Canada)
Fraxinus coulteri?	*F. oregona* (W U.S.A.) *F. americana* (E & central U.S.A., S Canada) *F. pennsylvanica* (E & central U.S.A., S Canada)

spikelets), fruits, and seeds (Thomasson, 1978a, 1978b, 1979, 1980a, 1980b, 1980c, 1983, 1984, 1985; Voorhies & Thomasson, 1979). For assignment of fossil grasses, epidermal patterns and silica bodies (phytoliths) were particularly diagnostic. The plant fossils occurred frequently with vertebrate fossils (rhinoceros, elephantids, horse, and camel). The Ash Hollow Formation (Ogallala Group) in Nebraska, Clarendonian and Hemphillian in age, contains a rich assemblage of prairie plants and aquatics, including representatives of eight plant families (*Chara* sp., Characeae; *Equisetum* sp., Equisetaceae; *Potamogeton* sp., Potamogetonaceae; *Carex gracei* and two other *Carex* spp., *Cyperocarpus pulcherrima,* and *C. terrestris,* Cyperaceae; *Archaeoleersia nebraskensis,* 12 species of *Berriochloa, Nassella* sp., *Oryzopsis* sp., *Paleoeriocoma hitchcockii,* and *Panicum elegans,* Gramineae; *Biorbia, Cryptantha* spp., *Prolappula* sp., Boraginaceae; *Celtis willistonii,* Ulmaceae; and *Polygonum* sp., Polygonaceae). In addition, representatives of the Gramineae (species of *Berriochloa*) and Cyperaceae (*Cyperocarpus eliasii*) have been reported from the Sheep Creek Formation in Nebraska (late Hemingfordian), and new species of the Gramineae (*Berriochloa* spp.) and Boraginaceae (*Biorbia* sp., *Cryptantha* spp., and *Eliasiana* sp.) have been described from the Keller site in Ellis County, Kansas (Hemphillian or Clarendonian).

Although the affinities of most of the fossil species are speculative, those of the grasses appear to be rather straightforward. For example, the fossil grasses are classified in tribes Oryzeae, Stipeae, and Paniceae. *Archaeoleersia* appears to be the forerunner of *Leersia* (tribe Oryzeae) and is most similar to living *Leersia ligularis* and *L. monandra* of North, Central, and South America and to *L. triandra* of Africa (Thomassan, 1980b). *Berriochloa, Nassella, Oryzopsis,* and *Paleoeriocoma* are all classified in Stipeae. *Berriochloa* shows features that suggest it is ancestral in the evolutionary series: *Berriochloa–Piptochaetium–Stipa* (sect. *Hesperostipa*) (Thomasson, 1978a). *Paleoeriocoma,* likewise, belongs to an evolutionary series: *Nassella–Oryzopsis–Stipa*; this genus is found with *Nassella* in deposits and appears to be ancestral to species of *Oryzopsis* (sects. *Eriocoma* and *Oryzopsis*) and possibly to some species of *Stipa* (Thomasson, 1980c). *Panicum elegans* is most similar to extant species of *Dichanthelium* but has not been transferred to that genus due to inadequate sampling of the morphological characters of the many species of *Panicum* (Thomasson, 1980b). Tribes Oryzeae and Paniceae, especially, contain grasses of southern affinities; however, the relationships of tribe Stipeae remain uncertain (Barkworth, 1981) even though many extant species have southern affinities. The other families represented in the fossil deposits (Boraginaceae, Cyperaceae, and Ulmaceae) generally are best represented in subtropical or warm regions and, predictably, would have southern affinities.

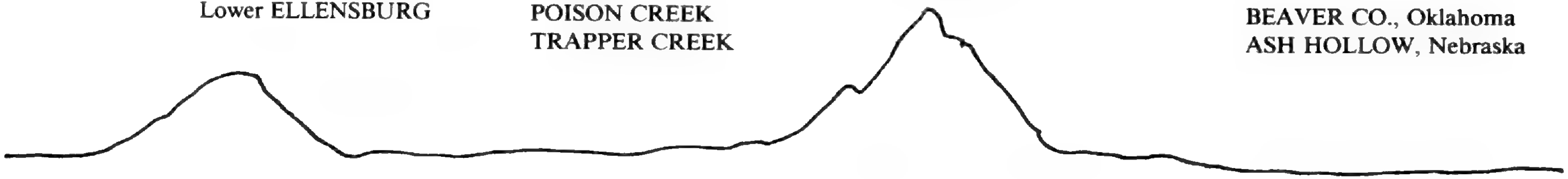
The Kilgore flora of Nebraska is central to our data base since the locality occurs at about the same latitude as the Columbia Plateaus floras. It is of mid-Miocene (Barstovian) age and was well documented by MacGinitie (1962), who provided leaf and pollen data. Hence it can be compared with sites of that age on the Columbia Plateaus. The 28 species MacGinitie identified show the strongest affinity (57%) with modern taxa that grow chiefly east of the Rocky Mountains; secondary affinity is with southerly taxa that now occur in Mexico and the southern Rocky Mountains (20%). Other relationships are minor and include a few species that occur west of the Rocky Mountains: two in eastern Asia, and one cosmopolitan group. Importantly, at least three species are intermediate between distinctly eastern and distinctly western North American taxa: *Fraxinus coulteri, Populus gallowayi,* and *Celtis kansana* (Table 5).

Only six Kilgore species (21%) occur as fossils in the Miocene floras of the Columbia Plateaus (Table 6). These include a mixture of geographic elements, and small east–west differences may occur according to more recent literature. For example, the Kilgore fossil of *Acer is A.* cf. *negundo* var. *negundo,* but the Columbia Plateaus species *Acer negundoides* is morphologically close to *A. negundo* var. *californicum* (J. A. Wolfe, pers. comm., 1986). In summary, the floristic relationship of the Kilgore with the Columbia Plateaus floras is slight.

Implications. The mid-Miocene grasses (e.g., Ash Hollow flora) include forms ancestral to those of the present Great Plains grasslands, many with southern affinity. Woody elements (e.g., Kilgore flora) are chiefly related to living taxa of the eastern U.S. The combined data suggest that the Great Plains flora of the mid Miocene was floristically distinct and had little in common with the Columbia Plateaus Miocene floristic province. The Kilgore flora of the Great Plains bears a stronger relationship to Miocene floras of the eastern sea-

TABLE 7. East–west transects of dominant vegetation types across the Rocky Mountain cordillera for two time intervals during the Miocene. Examples of floras are capitalized. Schematic mountain ranges are presumed to be somewhat higher during Clarendonian than before (regional uplift which probably occurred is not drawn here).

	Eastern Washington, Eastern Oregon	Idaho	Rocky Mountain Foothills	Great Plains
Clarendonian	Montane conifer & deciduous forest; *Taxodium* swamp	Montane conifer & deciduous forest	Montane conifer forest with steppe openings	Deciduous valley forest, plains & grassland
8–12 Ma	HANFORD Lower ELLENSBURG	BANBURY BASALT POISON CREEK TRAPPER CREEK	TEEWINOT, Wyoming	BEAVER CO., Oklahoma ASH HOLLOW, Nebraska



Barstovian/Late Hemingfordian	Deciduous hardwood forest & *Taxodium* swamp	Deciduous hardwood forest & *Taxodium* swamp	Montane conifer forest with steppe openings	Deciduous open forest & prairie
12–17 Ma	MASCALL	CLARKIA	TROUBLESOME, Colorado SPLIT ROCK, Wyoming	KILGORE, Nebraska

board, e.g., with Calvert Cliffs, than with floras of the Columbia Plateaus (J. A. Wolfe, pers. comm., 1987).

Kilgore vegetation was in Axelrod's (1985) view probably "a wooded grassland with semi-open grassy forests and woodlands on the interfluves as well as patchy grasslands." The fauna suggests a frost-free climate. This is consistent with MacGinitie's (1962) analysis.

In younger Miocene floras (Clarendonian and Hemphillian, e.g., from Ash Hollow, Nebraska and Beaver County, Oklahoma), seeds of prairie elements are much more abundant and more widespread. Leaf floras suggest that woody vegetation was confined chiefly to valley-bottom and riparian-border habitats. Together these data suggest "either parklands or grasslands" on the interfluves (Axelrod, 1985; 171). Pliocene floras indicate extensive grassland on the Great Plains, although, as Axelrod and MacGinitie pointed out, the evidence is not adequate to establish that pure grasslands occurred before the postglacial.

SYNTHESIS—CONTRASTS EAST AND WEST OF CORDILLERA

From the data presented, dominant vegetation types east and west of the cordillera can be compared for two times during the Miocene. Table 7 summarizes the general picture for the Barstovian/late Hemingfordian (ca. 17–12 Ma) and the Clarendonian (ca. 12–8 Ma). During these two intervals, the Columbia Plateaus west of the Continental Divide consistently maintained deciduous hardwood and montane conifer forests, both rich in woody genera, while evidence from the Great Plains east of the Rockies clearly indicated the existence of deciduous valley forest with grassland elements. Floristically the eastern floras bear little relation to those of the western area. During both of these times the eastern deciduous forest and grassland were separated from forests of the west (1) by the continued existence of the Rocky Mountain massif, which may have become more elevated during the Miocene (Trimble, 1980), and (2) by the continued presence of an impoverished montane conifer forest with steppe elements in the cordilleran area.

Through most of the Miocene there appear to have been floristic provinces distinct from each other:

(1) *The Great Plains province* had its primary affinity with species of the eastern U.S.A. and was floristically distinct from floras of the Columbia Plateaus. It contained elements that later became important forest species of riparian vallies (e.g., American elm) as well as extinct genera ancestral to modern grassland elements (*Berriochloa* and *Archaeoleersia*).

(2) *The Rocky Mountain province* was dominated by depauperate conifer forest or woodland with steppe. Except for infrequent pollen of Juglandaceae, Ulmaceae, and *Tsuga,* the spectra resemble modern pollen rain. The presence of *Tsuga* suggests that the "maritime conifer forest" (of Habeck, 1987) now found near the Canadian border may then have been in a more southerly position. We do not know what species may have been involved, but the impoverished generic list of Pinaceae alone places it in stark contrast with the rich conifer assemblages of the Columbia Plateaus region during the Miocene.

(3) *The Columbia Plateaus province* did not take on a relatively modern character on a generic basis until at least late Pliocene (Blancan) time or possibly even Pleistocene time. Although grassland and steppic elements (e.g., *Artemisia, Sarcobatus*) existed in this region throughout the Miocene, they were unimportant numerically during that period. Judging from the Snake River Plain data, grasses became sporadically abundant in Pliocene (Blancan) time—fully 10 Ma after grassland may have developed in the Great Plains region.

The late appearance of grassland west of the Rocky Mountains may mean that eastern and western grassland provinces are of different origins. Support for this tentative conclusion is derived from the following statement based on data presented earlier in the paper:

(1) Great Plains grassland taxa with southern affinities, now considered ancestral forms, appeared during the Miocene.

(2) The Great Plains floristic province was separated from the Columbia Plateaus during the Miocene by the orographic barrier and by the existence of an impoverished montane conifer forest with steppe on the Rocky Mountain cordillera.

(3) Grasses of northern affinities adapted to summer-dry conditions may have moved into the Columbia Plateaus from the north after the major shift from summer-wet to summer-dry climate about 6 Ma (Hemphillian)—during the demise of the rich Columbia Plateaus hardwood- and certain conifer-forest elements. Floristic evi-

dence confirms the strength of these barriers since Barstovian (mid Miocene) time.

Biogeographic Implications

The existence of montane conifer forest and steppe on the Rocky Mountain massif throughout the Miocene means that biogeographic connections between the deciduous forests of the Columbia Plateaus and those of eastern U.S.A. were cut off since at least the early Miocene.

Eastern hardwood and swamp elements coexisted on each side of the divide in the Miocene until they were eliminated in the west by the climatic deterioration during Pliocene time.

The important shift to a summer-dry climate came relatively rapidly to the Columbia Plateaus, diminishing a vast reservoir of genetic resources; this included many deciduous and coniferous taxa with affinities to modern taxa of eastern Asia and eastern U.S.A. that show adaptations to a summer-wet climatic regime. This basic change reduced the diversity of the montane coniferous forests of the interior in the Pacific Northwest except along the Pacific coast. It further established conditions in which steppic elements and grassland of northern distribution probably became established and prominent on the Columbia Plateaus.

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APPENDIX I. Pollen records showing occurrence of shrubs, terrestrial herbs?, and herbaceous aquatics in Late Cenozoic samples from Idaho, eastern Oregon, and eastern Washington. Numbers show maximum values in pollen/spore counts; + indicates presence.

	MIOCENE														
	Middle									Late			PLIOCENE	QUATERNARY	
	Mascall[1]	Blue Mountain[1]	Succor Creek[2]	Clarkia[3]	Stinking Water[1]	Miocene, Oregon[4]	Pliocene, Oregon[4]	Trapper Creek[5]	Poison Creek[6]	Jenny Creek[6]	Hanford[6]	Banbury Basalt[6]	Glenns Ferry[7]	Bruneau[6]	Late Pleistocene, Idaho[6]
SHRUBS															
Ephedra	+		+		+	+			+		1				
cf. *nevadensis*				+						+			2	4	+
cf. *torreyana*										+		+	+		
Alnus	+	+	+	5	+					+	4	+	1		1
Chenopodiineae		+	+	1	+?						+	7	20	20	3
Sarcobatus			+		+?			+	2	4	3	1	7		1
Compositae															
Artemisia			+							+	+	14	30	52	36
Elaeagnus											+	+			
Shepherdia			+	+		+									
Rosaceae											+		3		
Cercocarpus										+					
Ilex	+	+	+	+							+				
Rhus				+											
Corylus		+		1	+						+				
Myrica				+							+				
Malvaceae			+								+		+		
Myrtaceae													+		
Yucca type													+		
Ericales											+				
Vaccinium	?	?	+								+				
Caprifoliaceae			+												
Viburnum											+				
Symphoricarpos											+				
Sapindaceae											+				
Mahonia			+												
Cornus			+												
TERRESTRIAL HERBS?															
Compositae undet.			+		+							9	11	2	49
Liguliflorae							+				+		1		
Tubuliflorae											3		6		
Ambrosia			+								+		4		+

Appendix I. Continued.

	MIOCENE														
	Middle									Late					
	Mascall[1]	Blue Mountain[1]	Succor Creek[2]	Clarkia[3]	Stinking Water[1]	Miocene, Oregon[4]	Pliocene, Oregon[4]	Trapper Creek[5]	Poison Creek[6]	Jenny Creek[6]	Hanford[6]	Banbury Basalt[6]	PLIOCENE Glenns Ferry[7]	QUATERNARY Bruneau[6]	Late Pleistocene, Idaho[6]
Cruciferae												+	+	11	7
Acalypha type				+											
Onagraceae			+		+					+	+	+			
Polemoniaceae									1		+		4		1
Gilia type											+				
Navarretia											+				
Caryophyllaceae		+			+?										
Stellaria											+				
Gramineae	+	+	+	+	+					+	+	1	75		2
Polygonum cf. *californicum*							+				+				
Eriogonum										+	+		1		1
Anemone													+		
Aizoaceae type													+		
Pachysandra	+		+												
Umbelliferae	?		+												
Ferns	+	+		+	+				+		10	1	1		1
AQUATIC HERBS															
Typha	+	+	+	+	+								+		
Cyperaceae				+						+	10		4		
Scirpus													+		1
Potamogeton			+		+					1		+	1		1
Sparganium		+?			+?								+		
Lemna													5		
Nuphar													+		
Nymphaea													1		
Myriophyllum		+											+		

[1] Jane Gray in Chaney & Axelrod, 1959.
[2] Taggart & Cross, 1980; Graham, 1963.
[3] Gray, 1985.
[4] Gray, 1964.
[5] Leopold & MacGinitie, 1972.
[6] This paper.
[7] Leopold & Wright, 1985.

APPENDIX II. Selected pollen counts, Snake River Plain, Idaho (Fig. 10). Localities given in Leopold & Wright, 1985; the Jenny Creek Formation locality was previously considered as "Salt Lake Formation."

USGS Paleobot. Loc.:	Poison Creek Formation* D1699	Jenny Creek Formation D1208-3	Banbury Basalt D1696
Pinus	84.5	30.2	7.2
Picea	1.0	6.0	
Abies cf. *grandis*	5.4	3.6	
A. cf. *lasiocarpa*	1.0	+	
Pseudotsuga		1.2	
Juniperus	1.0	4.2	
Populus		1.8	
Betula		1.8	0.8
Quercus		4.8	
Alnus			+
Subtotal:	92.9	53.6	8.0
Cedrus-type	0.5		
Carya	0.5	1.8	
Juglans		1.8	+
Pterocarya		0.6	
Ulmus-Zelkova		10.1	0.8
Subtotal Tertiary relicts:	1.0	14.3	0.8
Acer			0.4
Ephedra cf. *torreyana*		0.6	0.8
Ephedra (White R. type)	0.5		
Sarcobatus	2.0	4.2	0.8
Other Chenopodiineae			6.8
Artemisia			14.0
Other Compositae			9.3
Cercocarpus type		0.6	
Elaeagnus			+
Subtotal shrubs:	2.5	5.4	32.1
Polemoniaceae	0.5		
Gramineae		0.6	1.3
Monocots	1.0	4.8	
Cruciferae			0.4
Dicots	2.0	11.9	0.8
Potamogeton		0.6	+
C3P3			56.4
Lycopodium			+
Onagraceae			+
cf. *Parthenocissus*			+
Fern spores	1.0	8.9	1.0
Subtotal NAP:	4.5	26.8	59.9
Total percent	100.9	100.1	100.8
Total tally	(202)	(336)	(236)
Cysts	0.5	1.2	
Botryococcus	12.0		

* Fossil leaves from the Poison Creek Formation identified by J. A. Wolfe (pers. comm., 1987) include *Quercus prelobata* Condit. and *Q.* cf. *chrysolepis* Liebm.

APPENDIX III. Revised list of the Deschutes flora, northern Oregon (after Chaney, 1938, with additions from J. A. Wolfe, pers. comm., 1987; Wolfe includes certain collections made by R. W. Brown from Chaney's floral horizon but a few miles away).

Acer negundoides
Quercus prelobata
Populus washoensis
Populus alexanderi (*P.* aff. *trichocarpa*)
Prunus irvingii (*P.* aff. *emarginata*)
Salix sp. (*S.* cf. *florissantii* of Chaney)
Salix aff. *caudata*
Ulmus affinis Tanai & Wolfe

APPENDIX IV. Localities of selected pollen samples from Wyoming and Colorado (Figs. 6, 12).

Formation	USGS Paleobotany Locality	Site Description
Split Rock	D1309	Type section: SE ¼ NE ¼ Sec. 25, T. 29 N, R. 89 W, Natrona Co., Wyoming. Limestone at top of pumicite, from unit 21 of J. D. Love (1961). Vertebrates from the Split Rock type area are of Hemingfordian age.
Split Rock	D3319	Upper part of formation, 2,650 ft. EWL 600 ft. SNL Sec. 36, T. 27 N, R. 85 W, Carbon Co., Wyoming. J. D. Love measured section L63-11. Sample B & C are 6 and 12 ft. above base of his unit 3. Sample D/E from his unit 4. Samples higher in this unit contain abundant reworked Cretaceous pollen.
Saratoga unit	D1540	Saratoga Valley, radioactive oil shale. SW ¼ NW ¼ Sec. 26, T. 18 N, R. 84 W, Carbon Co., Wyoming. J. D. Love locality L59-49. Associated with vertebrates of Barstovian age according to McGrew (1951).
Moonstone	D1308	Type section; white tuff and white laminated shale. Sec. 17, T. 30 N, R. 89 W, Natrona Co., Wyoming. Samples 1 and 2 are from Love's (1961) unit 16 and 17, respectively.
Troublesome	D3473	Rock Creek facies. NW ¼ SW ¼ Sec. 32, T. 2 N, R. 79 W, Kremmling quadrangle, Grand Co., Colorado. Glen Izett loc. G-63-303 and -304. Sample A is 18 ft. above sample B. Vertebrates from the lower and upper parts of the formation correlate respectively with the lower and upper Hemingfordian Group of Nebraska (Izett, 1968).
Troublesome	D1905	SW ¼ NE ¼ Sec. 29, T. 2 N, R. 79 W, Kremmling quadrangle, Grand Co., Colorado. Carbonaceous bed interbedded with silt lake facies containing mid Miocene vertebrates. Izett coll. G-0153-62.
Troublesome	D3493	NE ¼ SE ¼ Sec. 28, T. 3 N, R. 80 W, Gunsight Pass, Twin Peaks, Kremmling quadrangle, Grand Co., Colorado. Izett loc. G-63-305.

APPENDIX V. Pollen counts, Troublesome Formation, Grand County, Colorado (Figs. 6, 12). Percent pollen and spores. Small counts (shown in parentheses) indicate comparative abundance; + records taxa seen but not in tally.

USGS Paleobotany Locality:	D3473		D3493	D1905
	-b	-a		
Pinus	18.0	72.0	(105)	(62)
Abies sp.	1.3	1.3	(1)	
A. cf. *lasiocarpa*		0.7		
A. cf. *grandis*	+			(1)
Picea sp.	0.7	1.3	(6)	(12)
P. cf. *engelmannii*				(27)
Juniperus type	32.4	0.7		
Ephedra cf. *nevadensis*	8.0	2.7		(1)
Ephedra cf. *torreyana*	+	0.7	(1)	
Ephedra (short axis type)	+			
**Juglans*	+	0.7		
**Pterocarya*	1.3			
**Carya*	+	0.3		
**Ulmus-Zelkova* 4–5 pored	0.7	1.1		(1)
6 pored	+			
Acer	+			
cf. *Populus*	+			
Betula		0.7		
Subtotal trees:	62.4	82.2		
Elaeagnus	+	0.7		
Alnus	1.3	3.2		
Salix	1.3			
Sphaeralcea	0.3	0.7		
Caprifoliaceae				
Lonicera	0.3			
Symphoricarpos	0.3	0.7		
Chenopodiaceae	4.6	2.7	(3)	(1)
Sarcobatus				
cf. *vermiculatus*	0.7			(3)
Compositae	+		(1)	
Artemisia	+	0.7	(3)	
Xanthium type				(1)
Gramineae	1.3	1.1		(1)
Umbelliferae	0.7			
Polemoniaceae		0.3		
Dipsacaceae?	+			
Labiatae	0.3			
Arceuthobium		0.3		
Apocynaceae	+			
Claytonia type	+	0.7		
Sparganium		1.1		
Dicots	3.4	2.0		
Monocots	16.6		(4)	
Botrychium type			(4)	
Riccia type	+			
Trilete spores	7.4	2.7	(2)	
Total percent	100.9	99.1		
Total tally	(300)	(300)	(130)	(110)

* Genera now exotic to Colorado.

APPENDIX VI. Selected pollen counts, Natrona and Carbon counties, Wyoming (Figs. 6, 12). Percent pollen and spores: + records taxa seen but not in tally.

Stratigraphic Unit:	Split Rock				Saratoga	Moonstone	
USGS Paleobotany Locality:	D1309	D3319			D1540	D1308	
		-B	-C	-D/E		-1	-2
Pinus	8.3	39.5	35.3	51.5	80.0	53.0	72.0
Abies spp.				0.8			
cf. *concolor*							2.6
cf. *lasiocarpa*							2.0
cf. *grandis*			0.6		1.3		
Picea spp.		0.5	1.2			1.1	
cf. *engelmannii*					3.6		5.2
cf. *pungens*					7.6		4.6
**Tsuga*							
cf. *mertensiana*							0.4
cf. *heterophylla*							0.4
Pseudotsuga							
cf. *menziesii*	0.8			1.2		1.1	0.4
Juniperus type	0.4	20.5	20.7	7.4	1.8		
Quercus	1.2	1.0		0.4	0.4?		
Populus	+	0.5	0.6				
**Carya*		1.0					0.4?
**Juglans*		0.5					0.4
*cf. *Liquidambar*							1.2
**Ulmus-Zelkova*	0.4	1.0		1.6	0.9	12.5	3.1
Betula	0.4					3.2	
Salix		0.5		0.4			
**Ostrya-Carpinus*						0.5	3.2
Subtotal trees:	11.5	65.0	58.4	63.3	95.6	71.4	95.9
Alnus	0.4			0.4		1.1	0.8
Chenopodiineae	5.0	1.0	9.5	4.7		8.5	1.8
Chenopodium type	0.4						
Sarcobatus	2.1	6.0	1.8		0.9	7.4	1.2
Ephedra							
cf. *torreyana*		+	1.2	0.8	0.4		0.4
cf. *nevadensis*	0.4	1.5	4.1				
Compositae	7.5	0.5		1.2			
Liguliflorae		0.5	0.6				
Artemisia	42.4			1.2		1.1	
Ambrosia	0.8	0.5					
Sapindaceae		0.5					
Ribes		1.0					
cf. *Ptelea*	0.4						
Arceuthobium				0.4			
Caprifoliaceae type			0.6				
Eriogonum	0.4			0.4			
Gramineae	0.4	1.5	1.8	0.4			0.4
Umbelliferae		0.5					
Cruciferae				0.4			
Sparganium		1.5	0.6	0.8			
Cyperaceae	+	0.5	1.8	0.8			
Scirpus			2.4				
CP_3	4.5						
C_3	15.4	2.5		5.1			
Monocots		9.0	13.0	6.6		1.1	

Appendix VI. Continued.

Stratigraphic Unit:	Split Rock				Saratoga	Moonstone	
USGS Paleobotany Locality:	D1309	D3319			D1540	D1308	
		-B	-C	-D/E		-1	-2
Dicots	3.3	4.0		0.4		5.3	
Indeterminate	2.9	4.5	0.6	5.7	3.1	3.2	2.4
Fern spores	1.8	3.0	2.4	7.8		1.1	
Total percent	99.6	103.0	98.8	100.4	100.0	100.2	102.9
Total tally	(245)	(208)	(169)	(257)	(223)	(188)	(251)
Reworked pollen		21	3	28			
Botryococcus			++				

* Genera now exotic to Wyoming.

Appendix VII. Pollen records showing occurrence of shrubs, terrestrial herbs?, and herbaceous aquatics in pollen samples from the Mio-Pliocene of the central Rocky Mountains. Maximum values, % pollen and spores. + indicates presence or less than 1%.

	Troublesome	Split Rock	Teewinot	Saratoga	Moonstone
SHRUBS					
Ephedra					
cf. *nevadensis*	8	4	3		
cf. *torreyana*	1	1	1	1	1
Alnus	3	+	2		1
Sphaeralcea	1				
Chenopodiaceae	5	10	3		9
Sarcobatus	1	6	70	1	7
Compositae					
Artemisia	1	42	55		1
Elaeagnus	1				+
Caprifoliaceae		1			
Lonicera	+				
Symphoricarpos	1				
Ribes		1			
Ptelea type		+			
Yucca type			3		
TERRESTRIAL HERBS?					
Compositae					
Liguliflorae		1	4		
Tubuliflorae	1	8	15		
Ambrosia		1			+
Xanthium type	1				
Polemoniaceae	1				
Gilia type			11		
Cruciferae		+			
Claytonia type	1				
Onagraceae			+		
Polygonaceae			+		
Eriogonum		1			+
Umbelliferae	1	1			
Apocynaceae	+				
Labiatae	+				
Dipsacaceae	+				
Gramineae	1	2	15		+
Ferns	7	3			1
HERBACEOUS AQUATICS					
Cyperaceae		2	+		
Sparganium	1	2			
Scirpus		2	+		

FOSSIL POLLEN OF *SABICEA* (RUBIACEAE) FROM THE LOWER MIOCENE CULEBRA FORMATION OF PANAMA[1]

ALAN GRAHAM[2]

ABSTRACT

Fossil pollen of *Sabicea* (Rubiaceae) has been recovered from the lower Miocene Culebra Formation of Panama. The genus is presently widely distributed in Central and northern South America; it is well represented in the tropical moist and premontane wet forests of Panama. In the lower Miocene it was part of the low- to moderate-altitude insular vegetation characterizing the landscape between southern Mexico and northern Colombia. Its association with other members of the Culebra assemblage indicates tropical paleoclimates similar to those of the present. The genus has not been reported previously in the fossil record.

During studies on Tertiary vegetational history of the Gulf/Caribbean region, pollen and spores are frequently encountered representing genera with no previous fossil record, or whose stratigraphic and/or geographic range is considerably extended by the new records. Examples include *Pelliceria* (Theaceae/Pelliceriaceae; Graham, 1977), *Mortoniodendron* (Tiliaceae) and *Sphaeropteris/Trichipteris* (Cyatheaceae; Graham, 1979), *Micractinium* (Chlorophyta; Graham, 1981), and *Lisianthius* (Gentianaceae; Graham, 1984). Fossil pollen of *Sabicea* (Rubiaceae; Figs. 1–4) has recently been recovered from the lower Miocene Culebra formation of Panama, representing its first known occurrence in the geologic record.

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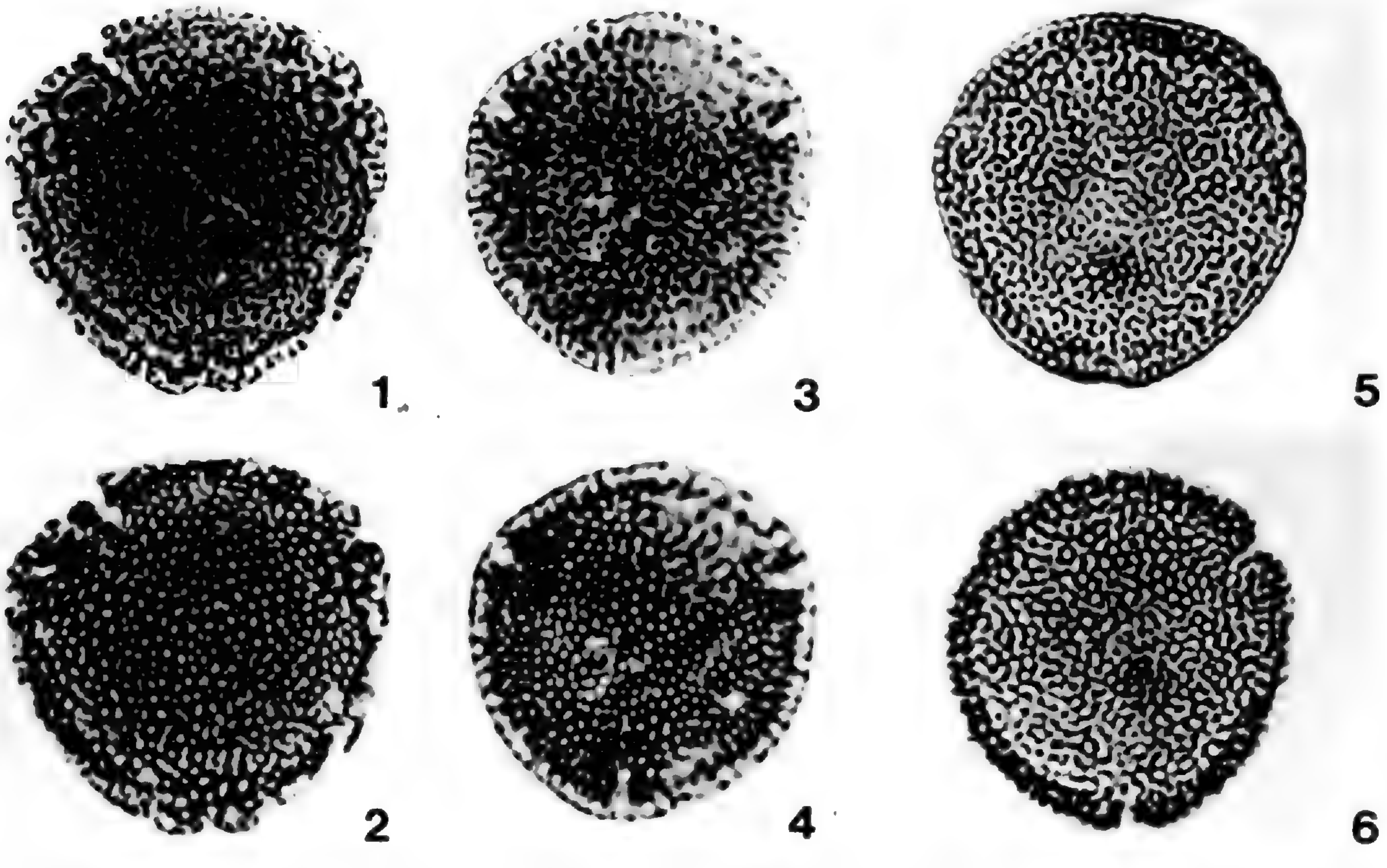

FIGURES 1–6. Fossil and modern pollen of *Sabicea* (Rubiaceae).—1, 2. Fossil pollen, Pan core 456, slide 1, ESF coordinates D-17.—3, 4. Fossil pollen, Pan core 470.6, slide 3a, ESF coordinates U-31,3.—5, 6. Modern pollen of *S. colombiana*. All taken at 400×, actual size in μm given in text. Fossil specimens and modern reference material are deposited in the palynology collections, Kent State University, Kent, Ohio.

ANN. MISSOURI BOT. GARD. 74: 868–870. 1987.

TABLE 1. Modern Rubiaceae pollen examined.

Taxon	Country	Voucher Collection	Herbarium where Voucher Deposited
Amphidaysa ambigua (Standley) Standley	Panama	*Busey 385*	MO
Coccocypselum guianense (Aublet) Schum.	Honduras	*Nelson & Romero 4263*	MO
C. herbaceum Lam.	Panama	*D'Arcy & D'Arcy 6731*	MO
C. lanceolatum (Ruiz & Pavón) Pers.	Panama	*Antonio 1425*	MO
Didymochlamys connellii N. E. Br.	Guyana	*Maguire et al. 32362*	MO
Gonzalagunia brenesii Standley	Costa Rica	*Croat 26591*	MO
G. bunchosioides Standley	Peru	*Ferreyra 1660*	US
G. panamensis (Cav.) Schum.	Panama	*Johnston 76*	GH
	Honduras	N. Mex. exch.	MO
G. rosea Standley	Panama	*White 7*	GH
Hippotis mollis Standley	Colombia	*Lawrence 505*	MO
H. tubiflora Spruce	Peru	*Klug 3084*	MO
Isertia deamii Bartlett	Guatemala	*Deam 6016*	MO
I. haenkeana A. DC.		Harvard exch.	GH
I. hypoleuca Benth.	Guyana	Shell Oil exch.	
	Costa Rica	*Jiménez 4127*	MO
	Panama	*Stimson 5062*	MO
I. pittieri (Standley) Standley	Colombia	*St. George Exped. 337*	US
Pentagonia brachyotis (Standley) Standley	Panama	*Dwyer 1385*	MO
P. macrophylla Benth.	Panama	STRI exch.	MO
	Panama	*Croat 4646*	MO
P. pubescens Standley	Panama	*Croat 4685*	MO
P. wendlandii Hook.	Panama	*von Wedel 2018*	GH
Raritebe palicoureoides Wernham subsp. *dwyerianum* Kirkb.	Panama	*Mori et al. 6617*	MO
Sabicea brasiliensis Wernham	Brazil	*Irwin et al. 24943*	MO
S. colombiana Wernham	Colombia	*Uribe 3041*	US
	Colombia	*Gentry et al. 47975*	MO
S. panamensis Wernham	Panama	*Dwyer 1831*	MO
S. paranensis (Schum.) Wernham	Peru	*Schunke V. 10548*	MO
S. villosa var. *adpressa* (Wernham) Standley		Harvard exch.	GH
S. villosa Rose & Standley var. *villosa*	Panama	*Luteyn et al. 1798*	MO
	Panama	*von Wedel 2889*	GH
	Panama	*Tyson 3437A*	MO
Schradera blumii Dwyer & Hayden	Panama	*Mori et al. 6625*	MO
Sommera grandis (Bartlett) Standley	Panama	*Allen 1575*	GH
	Panama	*Gentry et al. 13581*	MO

THE COLLECTING LOCALITY

In 1958 the Engineering and Construction Bureau of the Panama Canal Commission drilled a well through the Culebra Formation in front of Gold Hill on the west side of the Canal at latitude 9°02′N, longitude 79°38′W (Hole No. GH-9). Fifty-seven samples were taken from along the 124-meter core, and 21 contained well-preserved pollen and spores. The specimens of *Sabicea* were isolated from samples at the 456- and 470.6-foot depths. Other details on the Culebra Formation are provided by Graham et al. (1985) and Stewart & Stewart (1980). The materials and methods were as described in Graham (1985).

DESCRIPTION

Pollen oblate, amb oval-triangular to nearly circular; tricolpate/porate (apertures short, slit-like, ca. 2 : 1 length:width ratio), 4–6 × 2–3 μm, equatorially arranged, meridionally elongated, equidistant, inner margin faintly dentate (due to overlying sculpture elements), faint costae colpi;

wall 2–3 μm thick, tectate-perforate; finely reticulate, muri smooth, width about equal to diameter of lumen (ca. 0.5 μm); 32–36 μm.

DISCUSSION

Sabicea is a genus of about 125 species of climbing shrubs and vines widely distributed in tropical America and in Africa and Madagascar (Dwyer, 1980a, 1980b). In Panama it is represented by three species: *S. panamensis* (Guatemala to Colombia); *S. villosa* (with var. *villosa* widely distributed in Central and northern South America and with var. *adpressa* known from Panama, Colombia, and Peru); and *S. stellaris* (Panama). *Sabicea villosa* var. *adpressa* grows on Barro Colorado Island where it is "occasional in older clearings, on trails and at the margin of the forest along the lake; less commonly climbing to the top of the forest canopy and sometimes rooting in water," and it "is known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Panamá, and Darién, from premontane wet forest in the Canal Zone, and from premontane wet forest in Panamá and Darién" (Croat, 1978: 827).

Dwyer (1980a: 7) placed *Sabicea* in the tribe Mussaendeae with *Pentagonia, Sommera, Hippotis, Schradera, Amphidaysa, Gonzalagunia, Isertia, Raritebe, Coccocypselum,* and *Didymochlamys.* Pollen was examined from all of these (Table 1), and *Sabicea* can be distinguished on the basis of pollen characters. For example, grains of *Raritebe* examined were smaller (ca. 25 μm), thicker-walled, and tetra- to stephanocolporate. The pollen of *Coccocypselum* was considerably larger (45–50 μm), oblate-spheroidal, and scabrate to finely verrucate.

Three species of *Sabicea* were examined (Table 1), including all species and varieties reported from Panama except *S. stellaris* (holotype, MO, not sampled). The pollen showed only minor differences between the species (e.g., minute variations in wall thickness). The reticulum of the fossil specimens appears slightly more distinct than in the modern pollen examined. The modern forms (Figs. 5, 6) having slightly thicker walls darken more than those with thinner walls during acetolysis and more closely resemble the specimens in this respect. These are not inherent morphological differences or consistent characteristics of the pollen, however, and the specimens cannot be referred to any one modern species.

The specimens were part of a fossil assemblage that includes the following associates (Graham, in prep.; preliminary identifications): *Lycopodium, Selaginella, Alsophila/Cyathea, Pteris, Lygodium,* cf. *Antrophyum, Danaea,* Gramineae, Palmae, *Ilex,* Chenopodiaceae/Amaranthaceae, cf. *Rourea,* cf. *Doliocarpus, Dioscorea/Rajania* type, *Alchornea, Sapium* (*S. haematospermum* type), *Tetrorchidium, Casearia, Acacia,* Malpighiaceae, *Hampea/Hibiscus, Eugenia/Myrcia, Rhizophora, Allophyllus, Cupania, Matayba, Sideroxylon,* and cf. *Guazuma.* The landscape of present-day Central America consisted of low-lying volcanic islands at the time the Culebra assemblage was being deposited during the lower Miocene, ca. 25 Ma (e.g., Stehli & Webb, 1985). The association indicates that *Sabicea* grew in this physiographic setting and under paleoclimates not greatly different from those of the present.

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SYSTEMATICS OF THE AMPHI-ATLANTIC BAMBUSOID GENUS *STREPTOGYNA* (POACEAE)[1]

THOMAS R. SODERSTROM[2] AND EMMET J. JUDZIEWICZ[3]

ABSTRACT

Streptogyna is the only herbaceous bamboo genus with an amphi-Atlantic distribution. *Streptogyna crinita* occurs in tropical Africa, Sri Lanka, and India, and *S. americana* is found throughout the Neotropics. Although marked differences in habit and in morphology of lodicules and starch grains suggest segregation at the generic level, they are here retained in a single genus because they are quite similar in spikelet morphology and leaf anatomy. Multicellular microhairs are present on the lodicules of *S. crinita* and mark the first report of microhairs in the genus. Multicellular microhairs are otherwise well developed in the grasses only in the African herbaceous bamboo *Guaduella*, and they may be a primitive feature in the family as they are common in its putative outgroup, the Joinvilleaceae. *Streptogyna* shows strong bambusoid affinities in its ligule and leaf anatomy, spikelet structure, caryopsis and embryo morphology, and chromosome number, but differs from the core group of the subfamily in its seedling morphology and lack of epidermal papillae. Autapomorphies in the two species suggest that neither could have been derived directly from the other.

The grass genus *Streptogyna* was first brought to the attention of Western botanists in the late 18th century, when British and Swedish collectors brought back specimens of "rat-catching grass" from the forests of West Africa. A gathering from Nigeria by Palisot de Beauvois was used as the basis for *Streptogyna* in 1812, which he based on the only species known to him, *S. crinita.* The narrow leaves and many-flowered spikelets of *Streptogyna* were long taken as indications of pooid (festucoid) affinities. Thus, Bentham (1883), Hackel (1887), and Hubbard (1936) all considered that the proper disposition of this genus from the tropical rainforest lay with this large, temperate-region grass group. But there were dissenters, and Nees von Esenbeck (1835) and Steudel (1855), for example, suspected the bambusoid affinities of the genus. *Streptogyna* was briefly revised by Hubbard (1956), who indicated that the group deserved tribal status, but it was not until Tateoka (1958a) and Metcalfe (1960) examined its leaf anatomy that the bambusoid affinities of *Streptogyna* became clear. Recent workers agree that *Streptogyna* should be placed in its own tribe in the Bambusoideae (Calderón & Soderstrom, 1980; Clayton & Renvoize, 1986). In a treatment of the herbaceous bamboos of Sri Lanka, Soderstrom et al. (1987) offered a detailed descriptive account of the leaf-blade anatomy in the two taxa. The present study provides a revision of the genus and attempts to clarify the relationships of the two species by examining characters that have not yet been studied in detail, such as morphology of lodicules, starch grains, and embryos.

MATERIALS AND METHODS

Specimens of *Streptogyna* were examined from the following herbaria: AAU, B, BM, BR, CAY, CEPEC, F, G, ISC, K, M, MO, NA, NY, P, PDA, RB, S, US, W, and WIS. For anatomical studies, spikelets, leaves, and embryos (Table 1) were dehydrated in dimethoxypropane, infiltrated with tertiary butanol, embedded in wax, sectioned using a rotary microtome, and stained in chlorazol black E. Lodicules were rehydrated with Aerosol-OT before examination. Starch grains from caryopses were cut on a freezing microtome and stained with I_2KI. Observations of living plants of *Streptogyna* were made by Soderstrom in Brazil (March 1972, and May 1976) and by Jud-

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Table 1. Specimens of *Streptogyna* for which embryos (e), floret bases (using the scanning electron microscope) (f), lodicules (l), and starch grains (s) were examined.

S. crinita

Cameroon: *Buesgen 530* (l) (US). Gabon: *without collector,* Limbareni, May 1875 (l) (US). Guinea-Bissau: *Espirito Santo Expedition 3735* (l) (US). India: *Wight 2362* (l, s) (PDA). Ivory Coast: *Bamps 2175* (e, s) (BR). Liberia: *Baldwin 6305* (l) (US). Sierra Leone: *Fairchild s.n.,* Jan. 1927 (e, l, s) (US). Sri Lanka: *without collector,* 3 Jan. 1881, Henaratgoda (l) (PDA); *Senaratna 2700* (l) (PDA); *Gardner s.n.,* Dec. 1846 (l) (PDA). Zaire: *Gilbert 14213* (s) (BR); *Lebrun 605* (e, l, s) (P); *Mullenders 1226* (s) (BR); *Vanderyst 993* (l) (P).

S. americana

Brazil: *Eiten & Eiten 8903* (l) (US); *Prance et al. 6454* (l, e) (US); *Prance et al. 6527* (l, s) (US); *Swallen 5089* (l, s) (US); *Soderstrom 2193* (e, l, s) (US). Colombia: *Blydenstein 1687* (l) (US); *Idrobo & Schultes 608* (l, s) (US). French Guiana: *Broadway 771* (l) (US). Guatemala: *Weatherwax 104* (e, s) (US). Surinam: *Maguire 54093* (l) (US). Trinidad: *Hitchcock 10122* (l) (US). Venezuela: *Steyermark 86760* (l) (US).

ziewicz in Panama (March 1983). A Cambridge 35 scanning electron microscope was used to examine the lemmas of *Streptogyna* species.

RESULTS

Vegetative morphology. *Streptogyna* species are herbs of the rainforest understory and are less than one meter in height. *Streptogyna crinita* has long sympodial rhizomes that are densely covered with striate scale leaves, and the erect culms are leafy, bearing lanceolate leaves along most of their length (see figure in Soderstrom et al., 1987). *Streptogyna americana* is densely cespitose with the culms produced from short, nonscaly, sympodial rhizomes, and the linear leaves are all borne near the base of the plant (Fig. 6A). The leaves of *S. crinita* have glabrous sheaths while those of *S. americana* are hispid near the summit (Fig. 6B). At the summit of the sheath are borne membranous flanges that have been called lateral appendages (Tran Van Nam, 1972), as they appear to arise from a meristem independent of the sheath. These and the oral setae are moderately well developed in *S. crinita* but inconspicuous or absent in *S. americana.* Both species also have an indurate abaxial rim at the summit of the sheath (external ligule), and the leaf blades are deciduous above this structure. A short, membranous inner ligule is present in both taxa. The narrow leaf blades of *S. americana* are strictly glabrous, whereas the broader blades of *S. crinita* may have a scattering of long, delicate macrohairs on the adaxial epidermis.

Inflorescence. The panicle of *Streptogyna* species is spikelike, but in both species individual plants have been seen in which an additional floriferous branch is borne at the base of the main axis of the inflorescence. The inflorescence of *S. crinita* is generally shorter than that of *S. americana* and appears to be more densely flowered; this appearance is due in part to the larger glumes in *S. crinita.* Both species have loosely several-flowered spikelets (Fig. 6D) with the uppermost florets successively smaller and sterile and with a peculiar downward prolongation of the base of each floret, which, however, does not appear to be an elaisome, as no oil was detected within it. The glumes of *S. crinita* are broad, elliptic, and have many nerves, while those of *S. americana* have few nerves and are linear to lanceolate (Fig. 6E, F). The florets of both species are indurate and fall attached to a pointed, persistent rachilla internode (Fig. 6G) that presumably aids in external animal dispersal. In *S. crinita* the base of the floret is pilose and in the scanning electron microscope (SEM) the bulk of the epidermis, which appears granular through the light microscope, is composed of short prickles alternating with square to rectangular cells in a sharply defined pattern (Fig. 1a, b). The rectangular cells were observed to deflate when placed under the electron beam of the SEM. The lemmas of *S. americana* are glabrous and the epidermis is apparently covered by a thick cuticle that obscures the rounded prickles and intercalated rectangular cells (Fig. 1c, d). The lemmas of both species have long, antrorsely scabrous awns. The paleas are strongly bikeeled (Fig. 2a).

Flowers. The flowers of both species have three relatively large lodicules (Fig. 3). Those of *S. crinita* are spatulate, of firm texture throughout, and are strongly nerved until near the summit (Fig. 3A). Microscopically the epidermis of the upper portion of each lodicule consists of a uniform network of polygonal cells with moderately

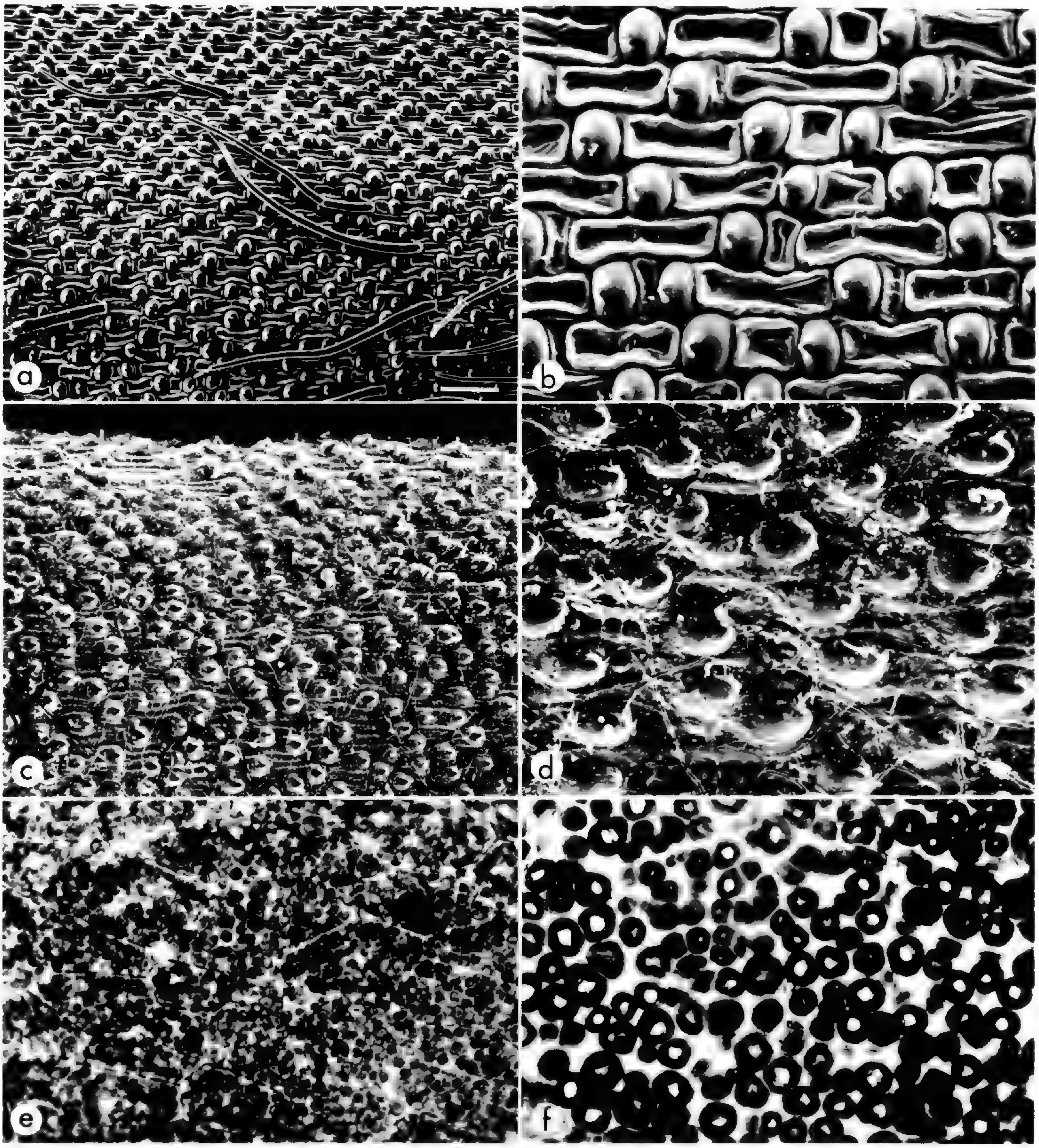

FIGURE 1. Scanning electron micrographs of the base of lemmas (a–d) and endosperm starch grains (e–f) of *Streptogyna*.—a, b. *S. crinita*, showing alternating prickles and deflated rectangular cells.—c, d. *S. americana*, showing prickles and intercalated cells obscured by thick cuticle.—e. *S. crinita*, showing small, moderately compound grains with few granules per grain.—f. *S. americana*, showing large, mostly simple grains. (a, b based on Sierra Leone, 20 Jan. 1927, *Fairchild s.n.* (US); c based on Mexico, *Orcutt 2933* (US); d based on Colombia, *Idrobo & Schultes 608* (US); e based on Sierra Leone, *Afzelius and Smeathman s.n.* (BM); f based on Brazil, *Soderstrom et al. 2193* (US). Scale bar in a = 100 μm for a, c; 20 μm for b, d–f.)

thickened walls (Fig. 3B). The apices of the lodicules are fringed with about 5–15 thin-walled microhairs, and each hair contains 4–8 cylindrical cells. The basal cell is slightly longer than the apical cells and does not collapse when dried as do the apical cells. The longer lodicules of *S. americana* are narrowly lanceolate or linear and often are widest just below the middle (Fig. 3C). In their lower portions they are strongly nerved and of firm texture, but at about the middle of their length the vascular bundles end and the lodicule tapers gradually to a very delicate, hyaline apex. Most specimens have the apices and uppermost margins of the lodicules fringed with

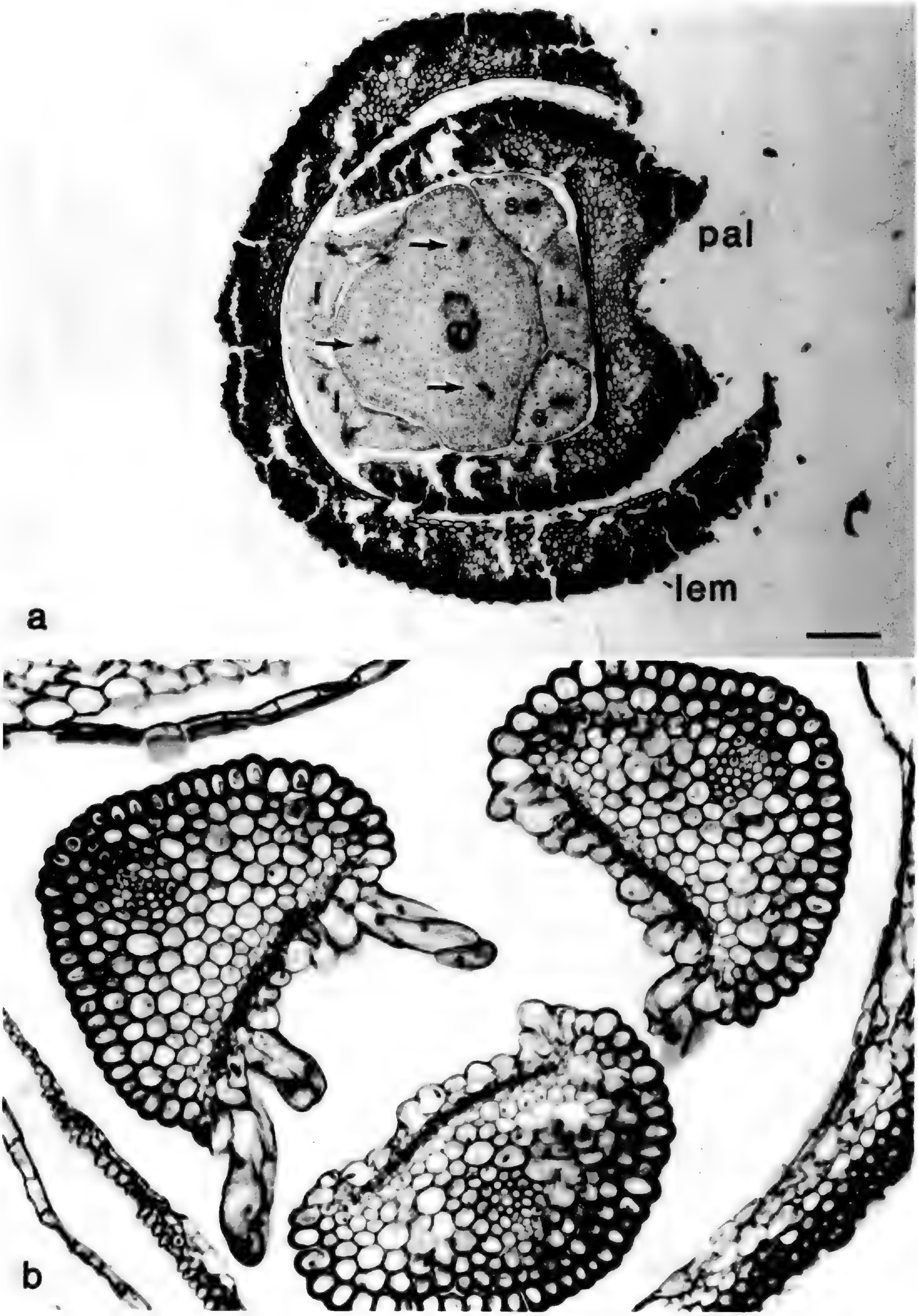

FIGURE 2. Floret anatomy of *Streptogyna americana*.—a. Transverse section through lower part showing lemma, palea, three lodicules (l), two stamens (s), and gynoecium (gy) with three stigmatic vascular bundles

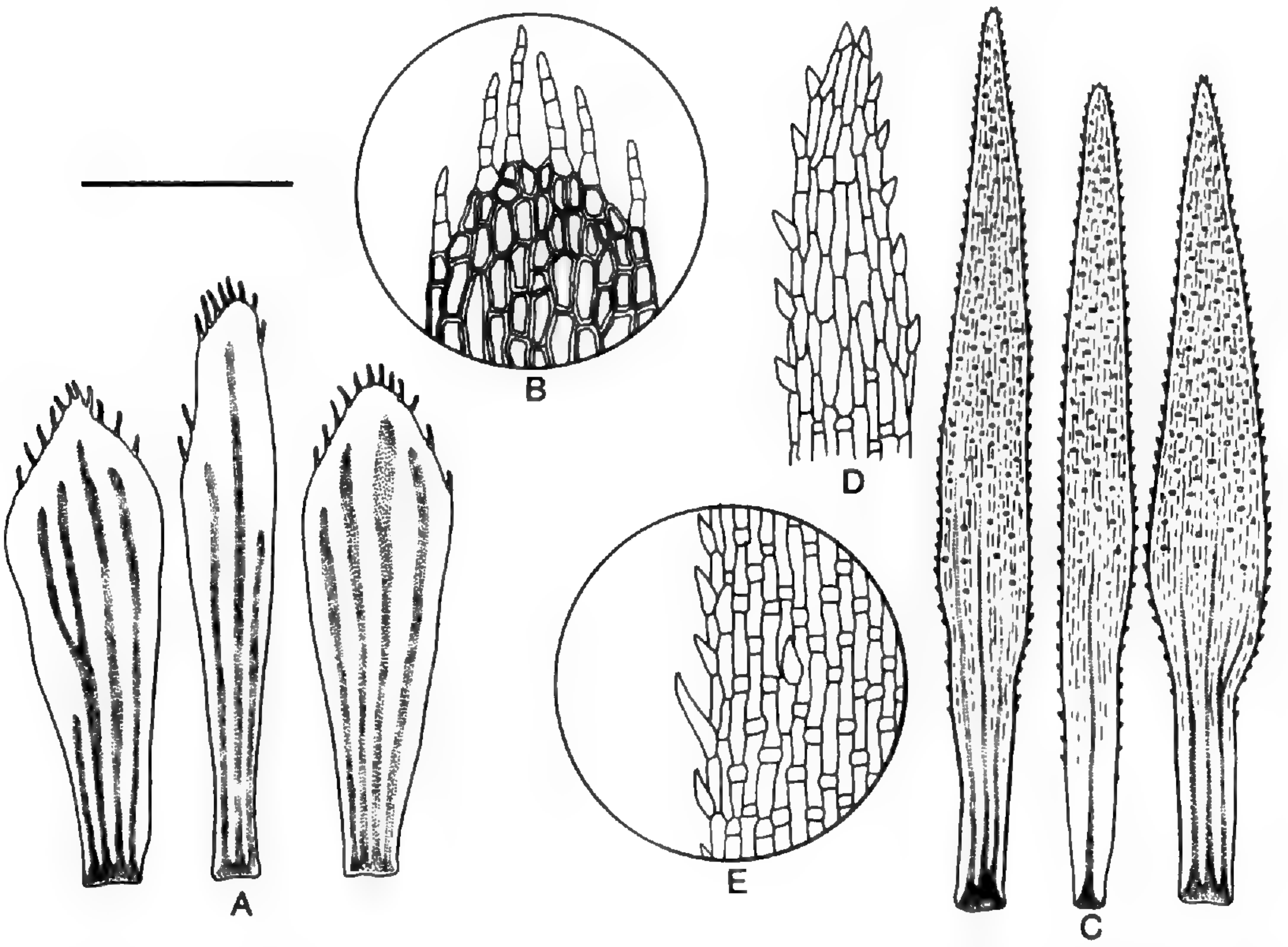

FIGURE 3. Lodicules of *Streptogyna crinita* (A, B) and *S. americana* (C–E).—A. Lodicules.—B. Detail of apex, showing multicellular microhairs and undifferentiated, thick-walled parenchyma cells on surface.—C. Lodicules.—D. Detail of apex.—E. Detail of upper portion of lodicule, showing prickles (mainly marginal) and short cells interspersed with long cells on surface. (*Streptogyna crinita* based on Cameroon, *Buesgen 530* (US); *S. americana* based on Trinidad, *Hitchcock 10122* (US). Scale bar = 1 mm for A, C; 0.2 mm for B, D, E.)

abundant prickles that occasionally grade into short cilia. The epidermis of the upper portion consists of alternating, thin-walled long and short cells, some of the latter modified into prickles (Fig. 3D, E). No bicellular or multicellular microhairs were observed on the lodicules of *S. americana.* The two stamens of both species are lateral anterior in position and are free to their bases (Figure 2a); the anthers are linear (Fig. 6M). The gynecium of *Streptogyna crinita* bears a single style branching into two stigmas, and the ovary is pilose near the summit. The stigmas, which are supplied by each of two lateral posterior vascular bundles in the ovary, are unusual in that they continue to grow after anthesis, elongating and producing stout retrorse barbs on their adaxial surfaces. *Streptogyna americana* has three stigmas (Fig. 6L) produced from three stigmatic bundles within the glabrous ovary (Fig. 2a). These stigmas also continue to grow after anthesis, elongating and producing short, papillate processes from a meristematic layer near the adaxial surface (Figs. 2b, 6N).

Fruit. Both species have a cylindrical, linear caryopsis with a linear hilum that extends the full length of the fruit (Fig. 6O, P). The mature endosperm starch granules of *S. crinita* are weakly to moderately coherent into masses of 3–6 that form individual grains 6–10 (rarely 15) μm in diameter (Fig. 1e). The starch grains of *S. americana* are nearly round, 10–30 μm in diameter, and are simple or rarely compounded into small masses (Fig. 1f). There is a prominent lacuna in the center of many of the grains. The embryo of *Streptogyna* species is small, basal, and when dissected out of the caryopsis is observed to be about one-half again as tall as it is wide. In median sagittal sections the embryos of *S. americana* (Fig. 4b) sampled had a prominent epiblast, no mesocotyledonary internode, and a small cleft between the scutellum and coleorhiza. In transverse sections the coleoptile had two lateral nerves and fused margins, the first embryonic leaf had five nerves and strongly overlapping margins, and the scutellum had three vascular traces (Fig. 4d). *Streptogyna crinita* had a similar embryonic

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(arrows).—b. Transverse section through upper part showing three stigmas with papillae arising from meristematic regions on adaxial surfaces. (Based on Brazil, *Soderstrom et al. 2193* (US). Scale bar: a = 100 μm; b = 25 μm.)

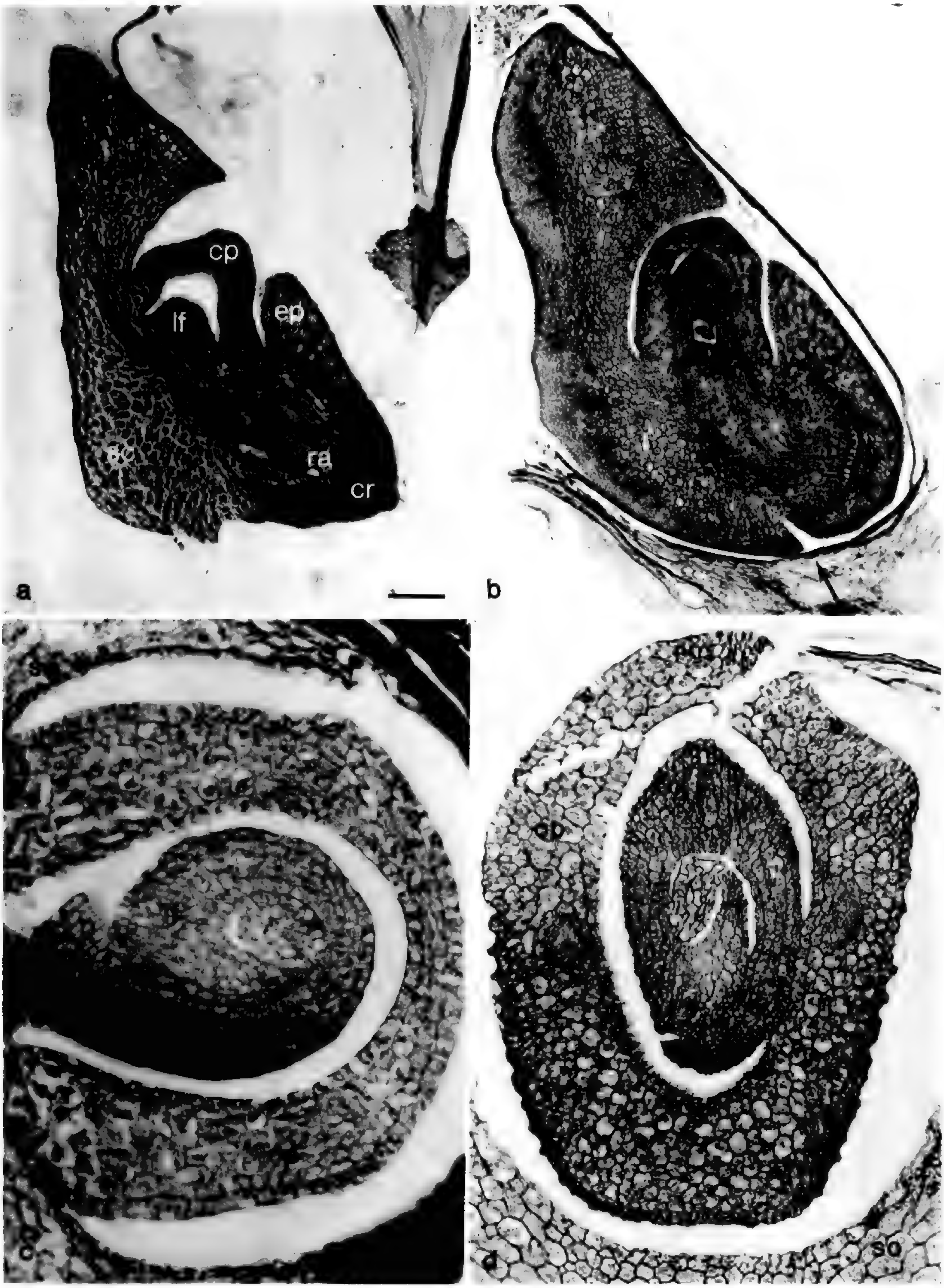

FIGURE 4. Embryo morphology of *Streptogyna* species.—a. *S. crinita,* median sagittal section showing inconspicuous cleft between scutellum and coleorhiza.—b. *S. americana,* median sagittal section showing small but distinct cleft (arrow) between scutellum and coleorhiza.—c. *S. crinita,* transverse section through plumule showing overlapping margins of first embryonic leaf; plumule is attached to scutellum on left.—d. *S. americana,* transverse section through plumule showing overlapping margins of first embryonic leaf; plumule is attached to scutellum on bottom. (a based on Zaire, *Lebrun 605* (US); b, d based on Brazil, *Soderstrom et al. 2193* (US); c

TABLE 2. Comparison of *Streptogyna crinita* with *S. americana*.

Character	*S. crinita*	*S. americana*
Distribution	Tropical Africa, Sri Lanka, India	Tropical America
Habit	Rhizomatous; leaves spaced along culm	Cespitose from short, knotty rhizomes; leaves clustered at plant base
Ligular area	Sheath summit glabrous; sheath auricles and oral setae conspicuous	Sheath summit hispid; sheath auricles and oral setae inconspicuous
Morphology of leaf blade	Lanceolate, 18–29(–40) cm long, 1–2.5 cm wide	Linear, 50–78 cm long, 0.8–1.6(–2.4) cm wide
Upper surface of leaf blade	Nerves slightly raised; glabrous or sparingly pilose	Nerves not raised; glabrous
Inflorescence	11–29 cm long, the spikelets overlapping	25–40(–67) cm long, the spikelets not overlapping
Glumes	Large; first glume 6–8 mm long, the second 17–26 mm long, 11–17-nerved	Small; first glume 3–12 mm long, the second 12–16 mm long, 7–9-nerved
Lemma	Base pilose; texture granular, the epidermal cells distinct in SEM	Base glabrous; texture smooth, the epidermal cells obscure in SEM
Lodicules	Oblanceolate, 1.5–3.5 mm long; multicellular microhairs present; prickles rare or absent; short cells absent; texture near apex firm	Linear, 3–6 mm long; multicellular microhairs absent; prickles abundant; short cells present; texture near apex hyaline
Ovary	Pilose near summit	Glabrous
Stigmas	2, retrorsely barbed	3, with soft, short hairs
Starch grains	Compound, individual granules 6–10(–15) μm in diameter	Simple, grains 10–30 μm in diameter
Embryo	Cleft between scutellum and coleorhiza not conspicuous	Cleft between scutellum and coleorhiza distinct
Seedling	Unknown	First leaf linear, erect
Chromosome number	$n = 12$	Unknown

structure except that the cleft between the scutellum and coleorhiza was less conspicuous, often present merely as an embayment on the lower side of the embryo (Fig. 4a).

DISCUSSION

Despite the statement of Jacques-Félix (1962) that there is little difference between the species, the Afro-Asian *Streptogyna crinita* and American *S. americana* are quite distinct from each other in a number of characters (Table 2). The long, scaly, flagelliform sympodial rhizomes of *S. crinita* are rare in herbaceous bamboos, a similar type being found only in some olyroids such as *Pariana parvispica.* The divergence in lodicule morphology (Fig. 3) between the species is great and in most grass taxa would imply separation at the genus level. Microhairs are not found on the foliage of either species (Tateoka, 1958a; Metcalfe, 1960; Jacques-Félix, 1962; Renvoize, 1985; Soderstrom et al., 1987), but this study has found them to be present on the lodicule apices of *S. crinita,* where they are multicellular and resemble those found on the foliage (Metcalfe, 1960; Jacques-Félix, 1962) and lodicules (pers. obs.) of the African herbaceous bamboo genus *Guaduella* (Guaduellae). Multicellular microhairs are also found on the foliage (Smithson, 1956) and floral bracts (pers. obs.) of species of *Joinvillea* (Joinvilleaceae), a group often considered to be among the closest relatives of the grasses (Stebbins, 1982; Dahlgren et al., 1985; Campbell & Kellogg, in press). Multicellular microhairs, consisting of three or more thin-walled cells, and with a blunt distal cell, have also been noted in the olyroid bamboos *Maclurolyra tecta* (Calderón & Soderstrom, 1973), *Diandrolyra tatianae*

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based on Ivory Coast, *Bamps 2175* (BR). Abbreviations: cp, coleoptile; cr, coleorhiza; ep, epiblast; lf, first embryonic leaf; ra, radicle; sc, scutellum. Scale bar: a, b = 100 μm; c, d = 25 μm.)

(pers. obs.), the woody bamboo *Arundinaria vagans* (Metcalfe, 1960), as well as in several other woody bamboo genera such as *Pleioblastus* and in several species of the arundinoid genus *Danthonia* (Tateoka & Takagi, 1967). The presence of microhairs on the lodicules but not on the foliage of *S. crinita* provides an exception to the generalization of these authors that only grasses with microhairs on their leaves also exhibit them on their lodicules. Tateoka & Takagi also illustrated a typical woody bamboo (*Sasa* species) lodicule with cilia, prickles, short and long cells, and bicellular microhairs that in many ways represents a composite of the features found in the two *Streptogyna* species. The lodicules of *S. americana* possess abundant marginal prickle hairs (which occasionally grade into short cilia) and have surfaces that are differentiated into long and short cells in the upper portions. In *S. crinita,* prickles are rare and cilia and short cells are absent on the lodicules, but microhairs are present.

The two species differ in stigma number and morphology. *Streptogyna americana* possesses three merely papillose stigmas, whereas *S. crinita* has two stigmas that are coarsely armed with retrorse barbs. However, in both taxa the stigmas elongate after anthesis, becoming entangled with each other and with the lemma awns. Reports of three stamens in at least some florets of both *Streptogyna* species (Doell, 1880; Bentham, 1883; Jacques-Félix, 1962) could not be confirmed in this study.

Streptogyna crinita consistently has small, weakly to moderately compound starch grains (Fig. 1e). This agrees with the descriptions of Jacques-Félix (1962) and also Yakovlev (1950), neither of whom cite specimens. The starch grains of *S. americana* are larger and essentially simple (Fig. 1f). Starch grain characters are not as reliable as anatomical or cytological data, but they have been considered to be taxonomically useful at the tribal level (Tateoka, 1962). Most bambusoids, as well as *Joinvillea* (pers. obs.), possess compound starch grains.

The two species of *Streptogyna* are similar in embryo structure (Fig. 4). Both possess typically bambusoid embryos with a formula of F+PP (see Reeder, 1962); that is, no internode is present between the divergence of the scutellar and coleoptilar vascular traces (F), an epiblast is present (+), a cleft between the lower part of the scutellum and the coleoptile is present (P), and the margins of the first embryonic leaf overlap (P). Jacques-Félix (1962) illustrated an embryo of *S. crinita* with no internode between the scutellar traces (F), an epiblast present (+), and lacking a cleft between the scutellum and coleorhiza (F), but in all individual embryos of the specimens that we examined a small embayment was present at the base of the embryo that could be interpreted as a cleft, although it was not as prominent as in *S. americana.* In transverse sections the embryos of both species had a first embryonic leaf with strongly overlapping margins (P). The embryo of both species is unusual among the Bambusoideae examined in that it is distinctly taller than it is wide.

CONCLUSIONS

Many grass genera occur in both the Old and the New World, but only very few tropical-forest Poaceae have this type of bihemispheric distribution pattern. Among the woody bamboos, *Arundinaria* and *Bambusa* (both Bambuseae), taken in their widest sense, have been considered to range across the Atlantic Ocean. However, studies of these groups by Soderstrom, Ellis, and collaborators are revealing them to be heterogeneous assemblages, and it appears *Bambusa* cannot be considered to exhibit a true amphi-Atlantic distribution. Among the herbaceous bamboos, only *Olyra* and *Streptogyna* occur both in South America and in the Old World, but *Olyra latifolia* is a widespread, weedy species that was almost certainly introduced by humans into Africa from South America quite early. Therefore the only bamboo genera with amphi-Atlantic distributions are *Streptogyna* and possibly *Arundinaria.*

Streptogyna differs from the bambusoid core group (Soderstrom & Ellis, in press) principally in details of seedling morphology (the first expanded blade of *S. americana* is narrow and vertical, not broad and horizontal as in all other bambusoids; Soderstrom, 1981) and lack of epidermal papillae, microhairs, and well-developed arm cells. Of these divergences, the distinctive seedling morphology is perhaps the most significant (see Kuwabara, 1960), but the seedling of *S. crinita* has not yet been examined. *Streptogyna* resembles the woody bamboos in possessing many-flowered spikelets, strongly developed fusoid cells, an adaxially projecting leaf blade midrib with complex vasculature, multicellular microhairs (as noted, present in *Guaduella* and several woody bambusoid genera), lateral appendages (Tran Van Nam, 1972), oral setae, and especially an external ligule and deciduous leaf blades. It may be noted that the multicellular microhairs of *Guaduella* species occur on both the leaf blades (throughout) and lodicules (on apices only) and that the basal cell is very long, about half the total length of the hair. *Streptogyna crinita*, in contrast, has uniseriate microhairs in which the basal cells are not conspicuously longer than the upper cells. Cytologically, *Streptogyna crinita* is similar to the bambusoids and has a basic chromosome number of $n = 12$, as reported by Veyret (1958), Tateoka (1958b, 1965), Kammacher et al. (1973), and Dujardin (1978), who studied material from Sri Lanka, Uganda, the Ivory Coast, and Zaire, respectively. *Streptogyna americana* has not been studied cytologically.

The generalization that microcharacters in the grass family are often more useful in generic, tribal, and subfamilial delimitations than are macrocharacters such as spikelet morphology because microcharacters are under less intense selective pressure thus finds an exception in the case of *Streptogyna*. In this genus, floret morphology, with its special adaptations to external animal dispersal (Ridley, 1930; van der Pijl, 1982; Soderstrom et al., 1987) is clearly a conservative feature. The leaf anatomy of the two species is quite similar, and one of the only consistent differences between the two is the presence of more prominent adaxial ribs over the veins in *S. crinita* (Soderstrom et al., 1987) and the occasional presence of adaxial ciliate macrohairs in the latter species.

We have shown that in the habit, lemma texture, starch grain morphology, and especially the lodicule structure the two *Streptogyna* species are quite different from each other, to the extent that segregation at the generic level might be seriously considered. Based on a comparison with *Joinvillea* and most Bambusoideae, it appears that the absence of multicellular microhairs on the lodicules of *S. americana* represents a more specialized condition than their presence in *S. crinita*, and conversely the two stigmas of *S. crinita* are probably derived from three, which *S. americana* retains. It seems likely that both species evolved from an extinct ancestor and that their separation is ancient. However, barring strong differences in leaf anatomy and cytology, grasses are traditionally segregated into genera on the basis of gross spikelet morphology, and the spikelet and floret structures of the two species of *Streptogyna* are quite similar, as is the leaf anatomy. It will be necessary to study the seedlings of *S. crinita* and the cytology of *S. americana* before a final decision can be made on the taxonomic level at which these two sibling species should be recognized.

TAXONOMIC TREATMENT

Streptogyna Palisot de Beauvois, Essai Agrost. 80. 1812. TYPE SPECIES: *S. crinita* P. Beauv.

Streptia Rich. ex Doell in Mart., Fl. Bras. 2(3): 171. 1880. Nomen nudum.

Perennial forest grasses; culms solid, unbranched above the base; leaf sheaths strongly ribbed, extending upward along both sides of the pseudopetiole and contiguous with the inner ligule; outer ligule present as a short, indurate rim; inner ligule short, membranous; lateral appendages and oral setae present at summit of leaf sheath; leaf blades deciduous, linear to lanceolate, narrowed below into a short pseudopetiole, the nerves parallel or very slightly oblique from the midvein at its base; midvein and primary nerves manifest only on the abaxial (lower) surface, the secondary lateral nerves and transverse veinlets inconspicuous; leaf margins antrorsely scabrous. Inflorescence pedunculate, a spikelike panicle, unbranched or occasionally with a spikelike branch at the base; rachis 3-angled, one side convex and the other sides concave and alternately bearing the spikelet pedicels. Spikelets short-pedicelled, greenish, several-flowered, the lower florets well developed, somewhat laterally compressed, hermaphrodite, the upper ones progressively smaller and sterile, disarticulation occurring between the fertile florets, each of these falling attached to the extended curved rachilla segment above it; glumes 2, membranous, persistent, many-nerved, the first shorter than the second and attached to the side of the thickened pedicel that supports the second glume; second glume convolute and enclosing the lowest floret at its base; lemmas narrow, elongate, awned, many-nerved, inrolled, indurate, the base extended beyond the attachment of the floret into a stipelike, oblique callus, the apex bearing a long, antrorsely scabrous awn; paleas strongly 2-keeled, sulcate between the keels; lodicules 3, elongate, strongly nerved; stamens 2, lateral anterior, the anthers basifixed; ovary with a long style; stigmas 2 or 3, becoming hardened and persistent, intertwined at maturity with the stigmas of other florets in the same spikelet and inflorescence; fruit a linear caryopsis, the hilum narrow, extending nearly the entire length of fruit, the embryo small, basal. Basic chromosome number, $n = 12$.

KEY TO THE SPECIES OF *STREPTOGYNA*

1a. Plant with long, scaly rhizomes; stigmas 2, retrorsely barbed; second glume 17–26 mm long; base of lemma pilose; leaf blades 10–25(–40) mm wide; paleotropical .... 1. *Streptogyna crinita*
1b. Plant cespitose from short, knotty rhizomes; stigmas 3, subglabrous; second glume 12–16 mm long; base of lemma glabrous; leaf blades 8–16(–24) mm wide; neotropical .... 2. *Streptogyna americana*

1. **Streptogyna crinita** P. Beauv., Essai Agrost. 80 + plate 16. 1812. TYPE: Nigeria: ["probably gathered in the forests of Oware or Benin" (Hubbard, 1956)] anno 1786–1788, *Palisot de Beauvois s.n.* (holotype, P, not seen).

Streptia crinita Rich., a herbarium name given as a synonym of *Streptogyna crinita* by Doell in Mart., Fl. Bras. 2(3): 172. 1880.
Streptia secunda Rich., a herbarium name given as a synonym of *Streptogyna crinita* by Doell in Mart., Fl. Bras. 2(3): 172. 1880.
Streptogyna gerontogaea Hook. f. in Trimen, Handb. Fl. Ceylon: 301–302. 1900. TYPE: Sri Lanka, without locality or collector, *C. P. [Ceylon Plants] 922* (holotype, K!).

Culms 55–100 cm tall, each representing the aerial extension of an upturned sympodial rhizome, the culm itself producing at its base 1–3 additional rhizomes to 25 cm long, these with short internodes about 1 cm long covered by the overlapping sheaths; sheaths bladeless, ovate-lanceolate, strongly striate, 7–10 mm long. Leaves evenly distributed on culm, not overlapping; sheaths finely ciliate on the margins, otherwise glabrous; outer ligule 0.4–0.9 mm long, tipped by a fringe of ciliate hairs ca. 1 mm long; inner ligule 1–2 mm long, the upper margin erose, ciliate on the abaxial (outer) surface, glabrous on the adaxial surface; sheath auricles 1–2 mm long; lateral appendages 0.3–1.2 mm long; oral setae sparse, delicate, less than 1 mm long; pseudopetioles 5–15(–25) mm long; leaf blades narrowly to broadly lanceolate, 18–29(–40) cm long, 1–2.5(–4) cm wide, acute at the tip, narrowed below to the pseudopetiole, primary lateral veins 4–8 on each side of the midrib; upper blade surface pale green, glabrous or occasionally with scattered spinelike hairs; lower surface lighter green than the upper surface, glabrous. Inflorescence 11–29 cm long, borne on a peduncle 2–10(–40) cm long, erect at first, becoming strongly pendent with age; spikelets (11–)20–30(–42), the glumes of adjacent spikelets strongly overlapping; rachis appressed-pubescent. Spikelets on pedicels 0.8–1.7 mm long, 4–5(–7)-flowered; first glume 6.5–10 mm long, linear-lanceolate, glabrous, 1–3-nerved, transversely veined; second glume (16–)20–23 mm long, 1.7–2.5 mm wide, elliptic-lanceolate, glabrous, 11–17-nerved, the nerves of various thicknesses, not all extending the length of the glume, with numerous transverse veinlets, the terminal awn up to 2 mm long, or occasionally the apex emarginate; lemma of lowest floret 18–25 mm long, lanceolate, indurate except for the broad, scarious margins, 7(–9)-nerved, the callus 1.5–2.5 mm long, pilose, the terminal awn (12–)15–26 mm long; rachilla internode attached to base of lowest floret 3–4 mm long; palea about as long as the lemma, not conspicuously protruding from it; lodicules firmly membranous, narrowly obovate or spatulate, with a fringe of multicellular microhairs at the apex (rarely glabrous), the anterior pair 1.5–3.5 mm long, 1–5-nerved, the posterior pair often slightly longer, narrowly oblanceolate, 1–3-nerved; filaments weak and ribbonlike, the anthers pale yellow, about 4 mm long; ovary fusiform, long-ciliate on the upper third and lower part of the style; style long, flattened, with sparse appressed hairs; stigmas 2, strongly retrorsely barbed above, the barbed portions elongating and coiling with age; caryopsis 12–16 mm long, 0.8–1.2 mm wide, slightly tapering to a persistent, ciliate beak at its summit.

Additional specimens examined. ANGOLA. CABINDA (MAIOMBE): Buco Zau, *Gossweiler 6557* (BM, K). BENIN: Djougou, *Chevalier 23891* (P.). CAMEROON: Without locality, anno 1908–1909, *Buesgen 530* (US); Mbamkin, *Letouzey 2652* (BR); S de Dimako, rive droite de la rivière Mbonda, *Letouzey 2682* (BR); 38 km ESE Djoum, pres Akoafim, *Letouzey 8400* (B, K); E de Yokadouma, *Meijer 15146* (MO); N'Kolbrisson, ca. 8 km W of Yaoundé, *de Wilde 1205* (B, BR, K, MO); Yaoundé, *Zenker 533* (US). CENTRAL AFRICAN REPUBLIC: Fort Crampel to the Koddo, *Chevalier 6407* (P); Fort de Possel, *Chevalier 10552* (P); Manovo-Gounda-St. Floris National Park, 8 km S of Camp Koumbala at confluence of Mbingou and Koumbala, 8°26'N, 21°15'E, *Fay 4087* (K); Mbaïki, *le Testu 3446* (BM), *Tisserant 3446* (K). CONGO: Brazaville a St. Joseph, *Chevalier 27341* (K). EQUATORIAL GUINEA. CAMPO DISTRICT: Bebady, route from Anio, *Tessmann 658* (K). FERNANDO PO: anno 1859, *Mann 108* (K, W). ETHIOPIA. ILLUBABOR: E of Abobo, 7°48'N, 34°37'E, *Chaffey 908* (K). GABON: without locality, *Griffon du Bellay s.n.* (K);

Limbareni, May 1875, collector's name illegible (US); Tchibanga, *le Testu 1336* (BM). Ghana: 6 chs. from Akudum, *Ankrah 405* (US); Amuni, *Chipp 53* (K); Ashanti, *Cummins 84-164*; Pra Suhien Forest Reserve, *Deaw 363* (F, MO); Kade, Agricultural Research Station, *Enti s.n., GC-42033* (MO), *Ankrah s.n.,* Ghana Herbarium No. 20190 (K); Sekodumasi, *Kitson 8* (BM); E of Anyaboni at S edge of Afram Plains, *Morton 6095* (K); Dawo Mato Kola, *Thomas D-28* (K); Akatri, *Thomas D-90* (K); Atuna, *Vigne 3522* (BR). Guinea: Bafing, *Adam 13795* (MO); 50 km de Kindia vers Mansu, *Roberty 10682* (G); Tèlimèlé nord, *Roberty 10775* (G). Guinea-Bissau: entre Sedengal e Ingone, *Espírito Santo Explorações Botânicas 3735* (US); Bedanda, *Pereira & Correia 2798* (K). India: without exact locality, *Wight 2362* (G, K, PDA). KERALA: South Travancore, 2,000 ft., *Beddome 290* (BM, K); Vetillapara forest, Cochin, *Fernandez 12* (K); Courtallum, Tinnevelly District, *Wight 1353* (K, W). Ivory Coast: Duékoué, *Adam 6398* (MO); Duékoué-Buyo, fôret N du Nzo, *Bamps 2175* (BR); near Issia, Daloa–Abidjan road, *Boughey 13609* (K); Bingerville, *Chevalier 16036* (P); Amatioré Forest Reserve, 10 km W of Tiassalé, *Fosberg 40539* (MO, US); Yalé, near Mt. Nimba, *Geerling & Bokdam 1828* (BR, MO); 5 km N of Sassandra, *Leeuwenborg 2261* (BR, MO); N of Sékré, ca. 15 km E of Béréby, *Oldeman 604* (BR, K, MO); 10 km N of N'Douci, *Oldeman 701* (BR, MO); N'Zidah, *Roberty 13683* (G, MO); Dabou, *Roberty 15528* (G); N'Zo, *Roberty 16049* (G); Adiopodoumé, *de Wilde 861* (BR). Liberia: Diebla, Webo District, *Baldwin 6305* (K, MO, NY, US); Gbawia, *Baldwin 6714* (MO, NY, US); Gretown, Tchien District, *Baldwin 6924* (MO); Sanokwele, *Baldwin 9550* (MO); Kle, Boporo District, *Baldwin 10570* (K, MO); Wohmen, Vonjama District, *Baldwin 12027* (MO); hinterland of Monrovia, *Dinklage 3375* (BR); Ganta, Sanokwele District, *Harley 959* (MO); Peahtah, *Bequaert in Hb. Linder 1012* (K, US). Nigeria: Itu, Cross River State, *Ariwaodo 83* (MO); Onitsha, *Barter 1814* (K, W); Obom Itiat, path to Atam Eki, Calabar Province, *Jones in F.H.I. 6870* (K); Olokemeji Forest Reserve, Abeokula Province, *Jones et al. in F.H.I. 14564* (MO, US); North-eastern: Ndoro District, Baissa Forest Reserve, *Latilo s.n.,* Forest Herbarium Ibadan No. 61439 (K); Ilaro Forest Reserve, 45 km SW of Abeokuta, *Lowe 4363* (K); Lagos, *Moloney s.n.* (K); Afi Forest Reserve, *Opara 836* (BR); Oban, *Talbot 856* (BM); Ibuzo, *Thomas 2010* (K). Senegal: Casamance, *Chevalier 2390* (P); Bignona, *Roberty 6424* (P). Sierra Leone: without exact locality, *Afzelius & Smeathman s.n.*; anno 1792–1796 (BM, S), *J. E. Smith s.n.*; anno 1791 ["Guinea"] (BM). Mt. Loma, *Adam 22422* (MO); Njala, *Dalziel 8420* (US); Kennema, *Deighton 397* (K), *Thomas 7822, 7903* (K); Kambia, *Deighton 838* (K); Heddle's Farm, *Elliot 3939* (BM, K, US); near Kambia, on Scarcies River, *Elliot 4389* (BM); Jola, 20 Jan. 1927, *Fairchild s.n.* (US); Zimi (Makpele), *Fisher 1* (K); Mabala, *Glanville 58* (K); Kambai Reserve, *Lane-Poole 344* (K); Kuntaia, *Thomas 441* (K); Yakala, *Thomas 2381* (K); Jigaya, *Thomas 2719* (K); Kanya, *Thomas 2983* (K). Sri Lanka: without definite locality, *C.P.* ["*Thwaites*"] *922* (BM, BR, G, K, W); Henaratgoda, 3 Jan. 1881, *Ferguson s.n.* (PDA, W); Matale, Dec. 1846, *Gardner s.n., C. P. 922* (PDA), Mar. 1883, *Lawson s.n.* (K); Buttala to Sirigala, 3 Mar. 1907, *Rock s.n.* (PDA); Dolukanda, *Senaratna 2700* (PDA); Dulva Kanda, *Tateoka 599* (B). Sudan. EQUATORIA: Talanga, Imatong Mountains, 4°01'N, 32°45'W, *Friis & Vollesen 484* (BR, K); Lotti forest, *Myers 9655* (BM); Sakure, Zande Land, *Wyld 334* (BM). Tanzania. ULANGA: Mangula to Kisawasawa, *Haerdi 624* (BR, G). Togo: Tomegbé, *Brunel & Heitz 5837* (B); Cascade de Tomegbé, S of Badou, *Ern 2096* (B); Plateau de Danyi, zwischen Adéta und Ndigbe-Apédomé, *Ern 2703* (B, K). Uganda: Damba Island, Kyagwe County, *Dawkins 459* (BM, K), *Maitland 801* (K); Gulu, Zoka forest, Acholi District, *Thomas 4031* (K). Zaire: Litendale, *Achten 485-A* (BR); Barumbu, *Bequaert 969* (BR); Avakubi, *Bequaert 1726* (BR); Mayumbe N'Benga, *Bittremieux 106* (BR); Menkao, *Breyne 918* (BR); Mabana, Maluku, *Breyne 3292* (BR, MO); Mayombi, *Brishe 31* (BR); Luni, *Brishe s.n.* (BM); Pansi, *Callens 2714* (BR); Lemba, route Luidi–Gombe Sud, *Compere 2077* (BR); M'Vuazi (Thysville), *Delhaye 24* (BR); Nkolo, M'Vuazi, *Devred 554* (BR); Lukolela, *Dewevre 544* (BR); Bas Uele, *Dewulf 331* (BR); INEAC, Luki, *Du Bois 333* (BR, K), *334* (BR); Zenge, Kasangula, *Dujardin 66* (BR); Mission de Kasinsi, Kwango, Bandunda, *Dujardin 183* (BR); Makamba, Bulungu, *Dujardin 491* (BR); Bingila, *Dupuis s.n.* (BR); Boyabokuda–Bogula (Badangabo), *Evrard 310* (BR); Djoa, Bolombo, *Evrard 4952* (BR); Tukpwo, *Gerard 2182, 4298* (BR); Ile Esali, Yangambe, *Germain 384* (BR, K), *Louis 6948* (B, BR), *7900, 13072* (BR); Panza, Inongo, *Gilbert 14213* (BR); Kisantu, anno 1900, *Gillet s.n.* (BR); Yambata, *de Giorgi 1669* (BR); Bolobo, env. Eala, *Goosens 2448* (BR); Karawa, Ubangi River, *Goosens 4123* (BR); Gatanga, *de Graer 294* (BR); Lisha, *Hens 156* (BR, G); Duma II, anno 1911, *van Keluom s.n.* (BR); Mutumbuta, 19 Apr. 1951, *Kimbau s.n.* (BR); Eiolo, 13 Nov. 1903, *Laurent s.n.* (BR); Lomkala, 26 Nov. 1903, *Laurent s.n.* (BR); Stanleyville, 15 Jan. 1904, *Laurent s.n.* (BR); Gimbi, *Laurent 600* (BR); Bolombo, *Lebrun 605* (BR, US); entre Businga et Banzyville, *Lebrun 2040* (BR, US); Moburasa, *Lemaire 193* (BR); Tambwe–Mwenza, Dibaya, *Liben 2694* (BR); Tuzule, riv. Lubi, *Liben 2976* (BR); Musoko, Luluabourg, *Liben 3507* (BM, BR); bord de la Lindi, 40 km N of Kisangani, *Lisowski 16480* (BR); Batiapanga, bord de la Mobi, 34 km SE of Kisangani, *Lisowski 17219* (BR); Lovanium, Kinshasa, *Lisowski 18349* (BR, K); 8 km N of Yakusu, *Lisowski 86435* (BR); Ile Booke wa Mbole, Yangambi, *Louis 10780* (BR, NY); entre Ngazi et l'Aruwimi, *Louis 12181* (BR); Tubeya Ilunga, rive droite de la Buchimaie SW de Kdakda Chefferie, *Luxen 369* (BR); Kisangani, *Mandango 3050* (BR); Loata, *Meurillon 23, 224* (BR); Yambata, *Montchal 136* (BR); Dundusana, *Mortehan 634* (BR); Kaniana–Haut Lomami, *Mullenders 472, 1226* (BR); Savane Makakumaka, Luki, *Nsimundele 57* (BR); Gimbi–Matadi, *Oldenhove 33* (BR); Kaparas, *Overlaet 418, 431* (BR); Mpangu, Kisantu, Terr. Popokabaka, *Pauwels 2360, 2388* (BR); Campus UNAZA (Lemba), Kinshasa, *Pauwels 6378* (BR); Epulu, *Putnam 50* (BR); Penge, *Putnam M-304* (BR); Mobwasa, *Reygaert 513, 1191* (BR); Nadibi–N'Iadinka, 28 June 1906, *Sapin s.n.* (BR); Boguge, près Mobwasa, *Thonner 138* (BR); Luki, vallée de la Minkudu, *Toussaint 2273* (BM, BR, M); Sonso, Kwango, *Vanderyst B-48* (BR); Kiala, Mar. 1907, *Vanderyst s.n.* (BR); Moyen-Kuolu, entre Yanda et Wemba, June 1907, *Vanderyst s.n.* (BR); Lazaret du Sacre-coeur, Kisantu, Apr. 1911, *Vanderyst s.n.* (BM, BR); Yindu, *Vanderyst 193* (BR); Kimuingu, *Vanderyst*

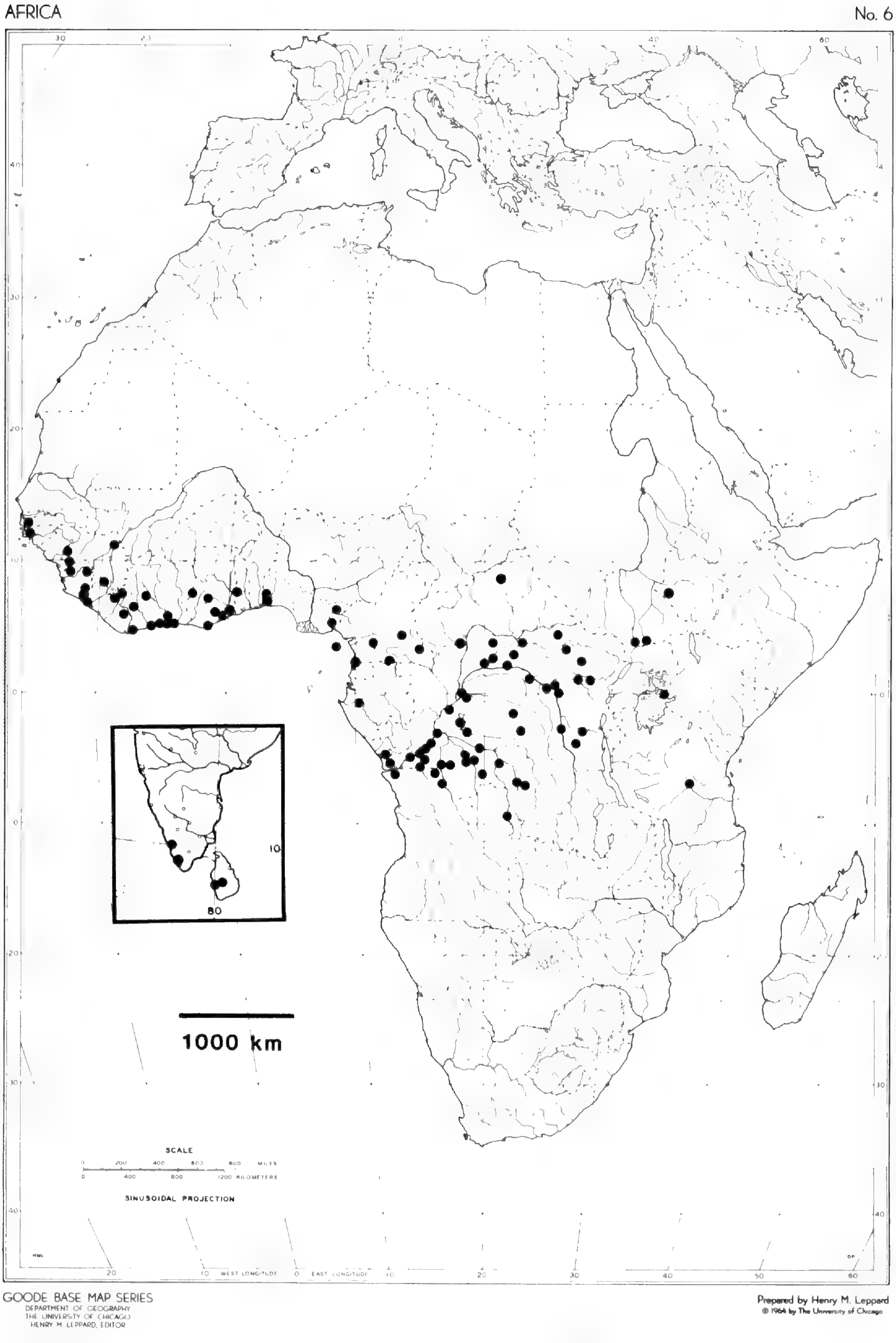

FIGURE 5. Distribution of *Streptogyna crinita* in Africa; inset, distribution in Sri Lanka and southern India.

313 (BR); Dima, *Vanderyst 862* (BR); Iles du Kasai, *Vanderyst 993* (BR, US); Mokaba, *Vanderyst 1693, 3606* (BR); Kikwit, *Vanderyst 2783* (BR), *2913* (BR, MO), *9235* (BR); Mukulu, *Vanderyst 3191* (BR); Chenal, *Vanderyst 4502* (BR); Yanga, Apr. 1915, *Vanderyst s.n.* (BR); Kimpako, *Vanderyst 5429* (BR); Kisantu, *Vanderyst 5924, 20399, 29971, 29979, 32082* (BR); Tangu, *Vanderyst B-3* (BR); Ipamu, *Vanderyst 8709, 12941* (BR); Benga, Kisantu–Kwango, *Vanderyst 14432* (BR); Vuaha?, *Vanderyst 20926* (BR); Iona Bata, *Vanderyst 25681* (BR); Tsanga, *Vanderyst 26986* (BR); Wutu, Kipako, *Vanderyst 30696* (BR); Bokoimkori, *Vanderyst 32624* (BR); Lemfu, Apr. 1907, *Vantolborg s.n.* (BR); Yaleko-Opala, *Vos 35* (BR); Luki, *Wasemans 1018* (BR); Kigombe, *Wellens 245* (BR); Bongollo, anno 1893, *Zenker s.n.* (F); Likimi, [*collector's name illegible*] *216* (BR).

Streptogyna crinita is widely distributed in wet to seasonally dry forests from sea level to 1,000 meters elevation in tropical Africa (Senegal to southwestern Ethiopia south to Fernando Po, northern Angola, and central Tanzania), southern India (Kerala), and Sri Lanka (Fig. 5). Based on abundant collection data from Africa, *S. crinita* appears to flower all year, with a maximum during October through January and slight minima (as denoted by a small decrease in the number of flowering collections and a considerable increase in the number of sterile gatherings) during August and September and to a lesser extent February and March, although *Hens 156* states that the species flowers "toute l'année" in Zaire. Several collectors note that *S. crinita* may be locally dominant, covering the forest floor in large rhizomatous clones. The species is used in western Africa to catch mice and rats, the animals becoming entangled in inflorescences that are placed outside their holes (Hubbard, 1956). *Afzelius & Smeathman s.n.*, anno 1792–1796, gave the herbarium name of "Aristidoides muricida" ["awned mouse-killer"] to the plant.

2. **Streptogyna americana** C. E. Hubb., Hook. Icon. Plant. 36(6): 1–6, tab. 3572. 1956. TYPE. Suriname: trail to Coppename River, rear of village of Paka-Paka, *Maguire 23975* (holotype, K, not seen; isotypes, F, MO, NY). Figure 6.

Plant cespitose or rarely from a series of short, knotty, horizontal sympodial rhizomes up to 2.5 cm long, the erect culms representing aerial extensions of very short sympodial rhizomes, sometimes becoming decumbent and rooting at the lower nodes. Leaves clustered at base of plant, strongly overlapping, usually concealing all the nodes, often displayed in a fan-shaped arrangement; leaf sheaths glabrous below, ciliate on the margins, hispid at the summit; outer ligule 0.6–1.1 mm long, erose or with a smaller apical fringe of cilia; inner ligule 1.1–2.7 mm long; sheath auricles not developed; lateral appendages usually inconspicuous; oral setae not evident, 1–2 mm long; pseudopetiole not well differentiated from remainder of blade; leaf blades linear, 50–78 cm long, 0.8–1.6(–2.4) cm wide, glabrous, oblique, the midrib noticeably excentric, flat but often becoming inrolled; primary lateral veins 3–5 on each side of the midrib; upper (adaxial) blade surface dark green, the lower surface lighter green; cross-veins inconspicuous. Inflorescence 25–40(–67) cm long, borne on a peduncle 1–8(–40) cm long; spikelets 14–25(–49), the glumes of adjacent spikelets not or only slightly overlapping; rachis subglabrous below, appressed-pubescent above. Spikelets 4–6 flowered, borne on pedicels 1–3 mm long; first glume 3–12 mm long, linear to lanceolate, glabrous, 1–3(–5)-nerved; second glume 10–16 mm long, 1.1–1.7 mm wide, ovate-lanceolate, (5–)7–9-nerved, with scattered inconspicuous transverse veinlets and an awn up to 3 mm long; lemma of lowest floret 19–24 mm long, narrowly lanceolate, completely glabrous, the (5–)7(–9)-nerves green, evident on the inner surface but not visible on the granular outer surface except near the summit of the body; calluslike prolongation of lemma 1–2 mm long, the terminal awn 12–21 mm long, arising from between 2 inconspicuous teeth at the summit of the body of the lemma; rachilla internode attached to lowest floret, persistent, 4–6 mm long; palea slightly longer than the lemma, usually protruding from it by 0.5–3 mm; lodicules narrowly lanceolate, firmly membranous and strongly nerved below, often abruptly widening about ⅓ of the way from the base, then tapering in the upper ⅔ to an attentuate, nerveless, hyaline apex, this usually fringed with prickles or occasionally with a few cilia, microhairs absent; anterior lodicules 3.2–6 mm long, 0.5–1 mm wide, 1–3(–5)-nerved, the posterior lodicule often slightly shorter and narrower, 1(–3)-nerved; anthers 2.5–3.5 mm long, narrowly linear; ovary glabrous; stigmas 3, lacking coarse barbs, glabrous below, at maturity hispidulous-papillose adaxially near the summits; caryopsis 14–17 mm long, 1–1.2 mm wide, glabrous.

Additional specimens examined. BELIZE: Cohune ridge, Sapon road, *Gentle 8121* (BM, F, G, NY, S, US); Cohune ridge, hill slope, Hummingbird Highway, *Gentle 8682* (BM, F, G, NY, S, US); 40 miles section

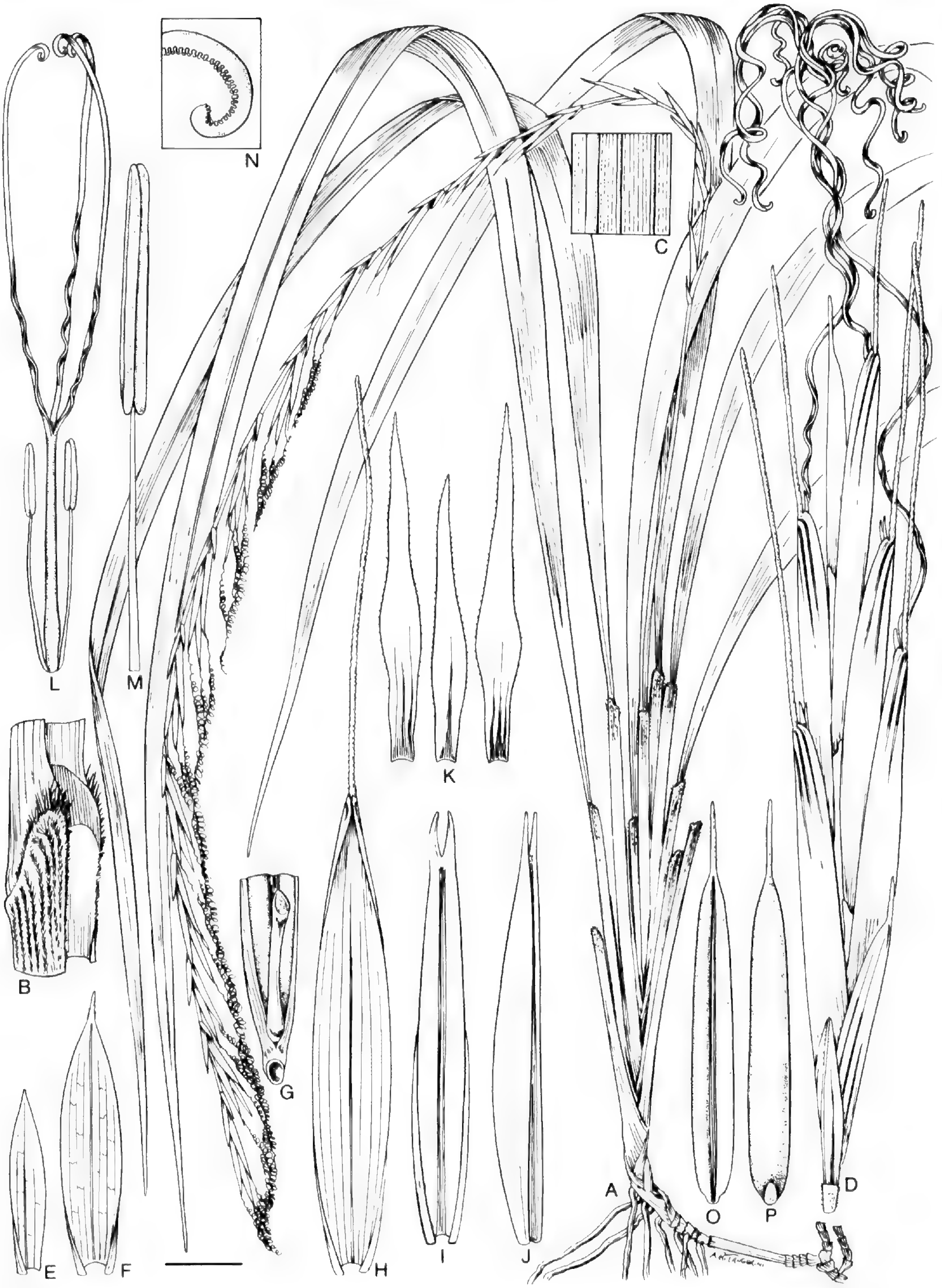

FIGURE 6. *Streptogyna americana.*—A. Habit of plant, showing deciduous leaf blades.—B. Ligular region, showing hispid sheath summit, outer ligule (left), and inner ligule and oral setae (right).—C. Section of abaxial surface of leaf blade, showing midrib (left) and absence of transverse veinlets.—D. Spikelet.—E. First glume.—F. Second glume.—G. Base of floret, showing basal prolongation of lemma and persistent rachilla internode.—H. Lemma, unrolled, showing inner surface.—I. Palea, ventral surface.—J. Palea, profile.—K. Lodicules, with posterior member in center.—L. Androecium of two stamens and gynoecium.—M. Stamen.—N. Stigma, showing

Hummingbird Highway, *Gentle 9005* (S, US). Bolivia. BENI: Alto Ivon, 11°45′S, 66°02′W, *Boom 4792* (NY), *4827* (MO, NY, US); 18 km E of Riberalta, 11°05′S, 65°50′W, *Solomon 6169, 7801* (MO). Brazil. ACRE: 125 km from Rio Branco on road to Pôrto Velho, 9°45′S, 66°20′W, *Calderón & Soderstrom 2301* (US). AMAPÁ: Rio Jari, near Cachoeiras das Guaribas, 0°24′N, 53°07′W, *Egler & Irwin 46417* (NY, US); road to Amapá, vicinity of km 108, Rio Pedreira, *Pires & Cavalcante 52222* (MO, NY, US); Serra de Tumac-Humac via Rio Cuminá, *Sampaio 5562* (US); Mitaraka S, crête W, 2.5 km sommet, *Sastre 1656* (CAY, P, US). BAHIA: Parque Nacional de Monte Pascoal, 16°54′S, 39°24′W, *Calderón & Pinheiro 2204* (CEPEC, US); 19 km N of Esplanada City on road to Jaquera, *Calderón et al. 2410* (B, NY, US); Monte Pascoal, 14 km E of BR-101 at point 13 km N of Itamarajú, *Soderstrom et al. 2193* (CEPEC, US). ESPÍRITO SANTO: Reserva Florestal de Linhares, 19°24′S, 40°04′W, *Martinelli & Soderstrom 9757* (RB), *Soderstrom & Sucre 1883* (CEPEC, US). MARANHÃO: Fazenda Bacaba, Doctor Haroldo, 5 km S of MA-119 from entrance 3 km NW of Lago do Junco, 4°26′S, 44°58′W, *Daly et al. 469* (MO, NY); Rio Pindaré, Monção, *Fróes 20312* (US); Caxias to Barra do Corda, before Curador [Pres. Dutra], *Swallen 3583* (US). MATO GROSSO: Fazenda Az de Ouro, 14°13′S, 57°02′W, *Amaral 9* (RB); 260 km along road NNE of Xavantina, a few miles W of base camp at 12°51′S, 51°45′W, *Eiten & Eiten 8903* (US); 5 km NW of base camp, 12°49′S, 51°46′W, *Harley & Souza 10271* (US); 8 km NE of base camp, *Ratter et al. 974* (NY, US); 4 km N of base camp, *Ratter et al. 1820* (K, NY, US); Serra do Itapirapuan, Alfonso, *Lindman A-3347*; Sararé, 15°05′S, 59°50′W, *Pires & Santos 16316* (MO, NY). PARÁ: Belterra, *Black 47-936* (NY); inter São João et Santa Anna, *Burchell 9201* (BR, US); Rio Parú de Oeste (TIRIOS), *Cavalcante 824* (US); Gorotire village at Rio Fresco, 7°47′S, 51°07′W, *Gottsberger & Posey 17-22183, 32-24183* (MO); Curuá Alemquer, *Kuhlmann 1725* (US); Maicurú, São Francisco, *Pires & Silva 4262* (NY, US); Serra Buritirama entre B-2 e B-3, Marabá, *Pires 12320-A* (US); range of low hills ca. 20 km W of Rendenção, near Côrrego São João and Troncamento Santa Teresa, 8°03′S, 50°10′W, *Plowman et al. 8645* (F, MO, NY, US); 100 km S of Rendenção on road to Barreiras dos Campos: Fazenda Inajapora between Rio Inajazinho and Rio Inajá, ca. 8°45′S, 50°25′W, *Plowman et al. 8883* (F, MO, NY, US); Belém–Brasília Highway 17 km S of Ligação do Pará, near km 1,509, ca. 4°17′S, 47°32′W, *Plowman et al. 9409* (F, MO, NY, US, WIS); 6 km N of Ligação do Pará, near km 1,532, 4°05′S, 47°32′W, *Plowman et al. 9522* (MO); 12 km E of Reprêsa Tucuruí (Rio Tocantins), 3°45′S, 49°40′W, *Plowman et al. 9799* (NY); Jari, estrada do Munguba, km 14, *Silva 2198* (MO, NY); Lageira, airstrip on Rio Maicurú, 0°55′S, 54°26′W, *Strudwick & Sobel 3109* (F, MO, NY); Sete Varas airstrip, Rio Curuá, 0°59′S, 54°29′W, *Strudwick & Sobel 4289, 4313* (F, MO, NY); Santarém, *Swallen 3281* (US); Japanese concession 35 km N of Monte Alegre, *Swallen 3411* (US); Óbidos, *Swallen 5089* (US). PERNAMBUCO: Escada, Eng. Conceição, *Andrade-Lima 67-5038* (F). RONDÔNIA: Guajará-Mirim, Ponto 19, *Cordeiro 924* (MO); 1 km N of Riberão, road Abunã–Guajará-Mirim, *Prance et al. 6454* (MO, NY, US), *6527* (F, MO, NY, S, US); in sylvis umbrosis ad flumen Guaporé, *Riedel 1248* (G, NY); Mineração Mibrasa, setor Alto Candeias, km 128, 10°35′S, 63°35′W, *Teixeira et al. 625* (MO). RORAIMA: Conceição, Rio Blanco, *Luetzelburg 21383* (M). Colombia. CAQUETÁ: Entre Puerto Rico y San Vicente del Caguán, hacienda Las Palmas, *Cabrera 3629* (F). META: E de San Martín, N del Caño Camoa, *Blydenstein 1687* (US); Monte de Caño Camoa, *Hermann 11186* (US); sabanas de San Juan de Arama, margen izquierda del Río Güejar, aterrizaje "Los Micos," *Idrobo & Schultes 608, 1217* (US); margen izquierda del Río Sansa, Sierra de la Macarena, *Idrobo 2160* (NY); Caño Ciervo, Sierra de la Macarena, *Philipson et al. 2023* (BM, S, US); margen derecha del Río Guayabero, Raudal de la Macarena (Angostura 1), *Pinto & Bischler 334* (US). VICHADA: ca. 35 km from Las Gaviotas on road to Santa Rita, *Davidse & Llanos 5211* (MO); Gualandayas, ca. 100 km E of Gaviotas, *Wood 4220* (K). Costa Rica. PUNTARENAS: Finca Los Helechales, between Buenos Aires and Cerro Pittier, *Hatheway 1686* (US); Los Tejares de Buenos Aires, *Pittier 10602* (BR, M, US, W); entre le Río del Convento et Buenos Aires, *Tonduz 3643* (BR, W). French Guiana: vicinity of Cayenne, hill above Grant's Road, *Broadway 771* (NY, US); Haut Tampoc: Saut Awali, *Cremers 4546* (CAY); Tumac-Humac, Koulimapopann-Mitaraka (frontière) P.K. 7.5, *Granville 1139, 1417* (CAY, US); versant N des Monts Galbao, 10 km WSW de Saül, 400 m, *Granville 1621* (CAY); 14 km de Dégrad Claude, *Granville 2267* (CAY); Sommet Tabulaire, ca. 50 km SE Saül, *Granville 3586* (CAY, MO, US); Chemin des Emérillons, 1 km de Saut Verdun, *Granville B-5037* (CAY); Cayenne, Chemin du Moulin Vidal, 13 July 1955, *Hoock 1187* (K, P); Saül, 30 June 1956, *Hoock s.n.* (NY); Cayenne, anno 1839, *Leprieur s.n.* (G), anno 1866, *Jelski s.n.* (W); Montabo, *Herb. L. C. Richard s.n.* (W); Karouany, *Sagot 1076* (BM, W). Guatemala. ALTA VERAPAZ: ca. 6 km E of Sebol on San Luis Road to Achiote, *Contreras 4486* (US). IZABAL: ridge N of Quiriguá, *Weatherwax 104* (US). Guyana: Wabuwak, *Wilson-Browne 476* (K, NY). Mexico. CHIAPAS: Javalinero, Palenque, *Matuda 3637* (F, US). VERACRUZ: Sanborn [ca. 17°34′N, 95°07′W], *Orcutt 2933* (K, MO, US). Nicaragua. ZELAYA: region of Braggman's Bluff, *Englesing 218* (F); Miguel Bikan, ca. 52 km SE of Waspám, *Pohl & Davidse 12310* (F, ISC). Panama. CANAL AREA: Barro Colorado Island, *Calderón 2098, 2148* (US), *Croat 4343, 8585, 8609, 8619* (MO), *9436* (MO, NY), *13214-A, 14019-A* (MO), *Foster 2305* (F), *Judziewicz 4436* (MO, WIS), *Shattuck 530* (F, MO), *Standley 41159* (S, US); Indio, Madden Lake, *Miller 2045* (US); hills N of Frijoles, *Standley 27480* (MO, US); forest along telephone cable trail

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adaxial papillae near tip.—O. Caryopsis, ventral surface showing linear hilum.—P. Caryopsis, dorsal surface showing small, basal embryo. (Based on Brazil, *Soderstrom et al. 2193* (US). Scale bar = 24 mm for A; 4 mm for C–F, I, J, L, O, P; 2 mm for B, G, H; 1 mm for K, M; and 0.5 mm for N.)

FIGURE 7. Distribution of *Streptogyna americana.*

between S-16 and S-49, Río Indio, *Steyermark & Allen 17459* (BR, G, MO, S, US). DARIÉN: Cerro Pirre, *Gentry & Clewell 7147* (MO), *Mori & Kallunki 5374* (MO, US); 0.5–2.5 km NE of Manené, *Hartman 12175* (MO). PANAMÁ: San José Island, *Johnston 433* (BM, US), *728, 1115* (US). PERU. MADRE DE DIOS: Río Tambopata, Lago 3 Chimbadas, ca. 65–70 river km SSW of Puerto Maldonado, ca. 10–15 km air SW effl. Río La Torre, 12°49'S, 69°17'W, *Barbour 5762* (MO). SURINAM: without locality, *Weigelt s.n.* (W); Zuid River, 3 km above confluence with Lucie River, *Irwin et al. 55900* (B, MO, NY, US); ab Wia wia-bank ad Grote Zwiebelzwamp, *Lanjouw & Lindeman 1153* (NY); Rikanau prope Moengo, *Lindeman 6090* (F); Brownsberg, near Irene fall, *Lindeman 12084* (K, NY); Lucie River, ca. 2 km below affluence of Oost River, *Maguire et al. 54093* (NY, US); Avanavero oever, *Stahel & Boonacker 4579* (US). TRINIDAD: without locality, *Botanical Garden Herbarium No. 3367* (US), *Crueger 362* (US fragment), *Finlay 3* (K, W); Caparo forests, *Broadway 4932* (US); Tabaquite, edge of High Woods, *Hitchcock 10122* (BM, US). VENEZUELA: Alto Orinoco, *Rusby & Squires 349* (K, NY). AMAZONAS: vicinity of Culebra, Río Cunucunuma, 3°40'N, 65°45'W, *Steyermark & Delascio 129185* (MO); Mavaca, Alto Orinoco, *Aristeguieta & Lizot 7380* (NY). BOLÍVAR: alrededores km 88, carretera El Dorado, *Aristeguieta 3713* (MO); 17 km W of Río Caura on road between Caicara and Ciudad Bolívar, *Davidse 4443* (MO, WIS); 10 km SW of Río Aro on road between Caicara and Ciudad Bolívar, *Davidse 4476* (MO); km 28, S of El Dorado, *Davidse 4966* (MO); 20–35 km SE of Monteco on road to San Pedro de las Dos Bocas, 7°10'N, 62°55'W, *Liesner & Gonzalez 5851* (MO); along pica 105, 40 km S of Tumeremo, 29 km N of El Dorado, *Steyermark 86572* (NY); Pica La Lira, at km 27 S of El Dorado, 1–6.5 km E of highway, *Steyermark 86638* (NY); woods bordering savannah by Río Asa, above raudal Cotua, S of La Paragua, *Steyermark 86760* (US). DELTA AMACURO: 3 km N of Piacoa [probably in the state of Delta Amacuro], *Steyermark 86277* (F, NY); E side Río Cuyubini, Cerro La Paloma, *Steyermark 87653* (NY). SUCRE: S slopes of Cerro Imposible, between Cedeño and Boca del Tataricual, along Quebrada Imposible, *Steyermark 62845* (F, US).

Streptogyna americana is found in shaded, well-drained sites in moist forests below 500

(–800) meters from Veracruz, Mexico, and Trinidad south to northern Bolivia and Espírito Santo, Brazil (Fig. 7). Most common on the margins of the Guyana Highlands and in easternmost and southernmost Amazonia, this species is rare or absent in the central portion of the Amazon Basin. Collectors in Panama (*Judziewicz 4440*), Venezuela (*Davidse 5211*), and Surinam (*Irwin 55900*) noted that the leaf blades become inrolled during hot dry weather or soon after collection. Most Central American collections were made November through April, indicating a dry season peak of bloom, while Guyanan and eastern Amazonian collections have been made principally June through August; the five Atlantic Brazilian gatherings were made from March to May. Common names of *S. americana* include "barba de paca" (*Ratter et al. 1820,* Brazil) and "barbatigre" (*Cabrera 3629,* Colombia), suggesting external animal dispersal.

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APPENDIX I.

LIST OF TAXA CITED

Arundinaria vagans Gamble
Bambuseae Kunth
Bambusoideae Nees
Danthonia DC
Diandrolyra tatianae Soderstrom & Zuloaga
Guaduella Franchet
Joinvillea Gaudich.
Joinvilleaceae Tomlinson
Maclurolyra tecta Calderón & Soderstrom
Olyra latifolia L.
Pariana parvispica R. Pohl
Pleioblastus Nakai
Sasa Makino & Shibata
Streptia crinita Rich. ex Doell
Streptia secunda Rich. ex Doell
Streptogyna P. Beauv.
S. americana C. E. Hubb.
S. crinita P. Beauv.
S. gerontogaea Hook. f. in Trimen
Streptogyneae C. E. Hubb. ex Soderstrom & Calderón

WOOD ANATOMY OF NOTEWORTHY SPECIES OF *LUDWIGIA* (ONAGRACEAE) WITH RELATION TO ECOLOGY AND SYSTEMATICS[1]

SHERWIN CARLQUIST[2]

ABSTRACT

Ludwigia anastomosans, a tree to 10 m, is studied because it is unusual in the genus in its arborescent habit. It proves to have unusually wide vessels; it also has interxylary phloem, hitherto reported for only one species of the genus. Wood anatomy of *Ludwigia peduncularis* and *L. torulosa* shows that they may be more closely related than so far indicated. Vestigial bars on perforation plates of *L. torulosa* are the first observed in Onagraceae and are believed to represent an instance of paedomorphosis, but also retention of a primitive feature. Other indicators of paedomorphosis in *Ludwigia* are abundance of erect ray cells and notably long vessel elements. The hypothesis that degree of vessel grouping is related to ecology in taxa having fiber-tracheids or libriform fibers is validated by *Ludwigia,* which has the lowest degree of vessel grouping for the family and is essentially aquatic. Other anatomical features reflective of ecology, combined in the Mesomorphy ratio, present a not dissimilar pattern that can be integrated with that given by vessel grouping if one takes into account probable transpiration rates and temperature regimes as well as water availability.

Data on wood anatomy of eight species of *Ludwigia* have been presented earlier (Carlquist, 1975, 1982a). That number seems small unless one takes into account the fact that *Ludwigia* is predominantly herbaceous; the most familiar species are nonwoody herbs of very wet habitats such as ponds, ditches, and streams. One of the species in the present study is a notable exception: *L. anastomosans* (DC.) Hara is a tree. The data on the collection studied here describe it as a tree 10 m tall with a trunk 15 cm dbh. Wood anatomy is of special interest because of this habit. In fact, the results obtained below demonstrate that the wood of *L. anastomosans* differs appreciably from that of other *Ludwigia* species.

Dr. Elsa Zardini, who collected the material of *L. anastomosans,* also kindly supplied material of two other species because she wished to see if wood anatomy demonstrated the degree of relationship between them. Dr. Zardini has contemplated the idea that *L. peduncularis* (Griseb.) Gómez may be closely related to *L. torulosa* (Arn.) Hara.

The wood anatomy of *Ludwigia* is of considerable interest with respect to ecology because *Ludwigia* characteristically grows in very wet places. *Ludwigia anastomosans* was collected in bamboo clumps by a blackwater stream in the Parque Natural de Caraca, Minas Geraes, Brazil. The material of *L. peduncularis* came from ditches near Havana, Cuba. The *L. torulosa* specimen was collected in a natural pond 17 km south of Tumeremo, Distrito Roscia, Estado Bolívar, Venezuela. In taxa with libriform fibers such as Onagraceae, Carlquist (1984a) hypothesized degree of vessel grouping to be in direct proportion to adaptation to dry conditions. In this case *Ludwigia* species ought to exhibit a low degree of vessel grouping. Although figures for vessels per group were developed in the earlier survey of woods of the family (Carlquist, 1975), no comparisons were made between those figures and ecological regimes occupied by the various species.

Ludwigia is a group of interest with relation to paedomorphosis in wood anatomy. This is, in turn, related to habit and ecology. The species in the present study were examined in this context to see if woodiness in *Ludwigia* is primary or secondary.

Although a study on wood anatomy can be expected to reveal new records for anatomical features, two in the present study proved of especial interest and worthy of discussion: occurrence of interxylary phloem and presence of vestigial bars on some perforation plates.

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ANN. MISSOURI BOT. GARD. 74: 889–896. 1987.

MATERIALS AND METHODS

Voucher specimens are located at the Missouri Botanical Garden. Appreciation is expressed to Dr. Elsa Zardini for providing dried wood samples suitable for study. For *L. peduncularis* and *L. torulosa,* samples represented basal portions, but diameter was small (2 and 4 mm, respectively). The material of *L. anastomosans* was from a branch about 1.5 cm in diameter. Although this is much less than the 15 cm diameter reported for trunks of this species, the branch material is considered here to represent an essentially mature pattern.

Woods were boiled in water, stored in 50% ethyl alcohol, and sectioned on a sliding microtome. Sections prepared in this way were, in part, satisfactory, but cell collapse on account of thinness of wood cells was excessive in some instances. Therefore an alternative method involving further softening, embedding in paraffin, and sectioning on a rotary microtome (Carlquist, 1982b) was employed. Sections prepared by both techniques were stained in a safranin–fast green combination. Macerations were prepared with Jeffrey's Fluid and stained with safranin.

Means are based upon 25 measurements (fewer if feature is scarce) except for vessel wall thickness, libriform fiber diameter, and libriform fiber wall thickness, in which a few typical cells were measured. Vessel diameter includes the wall, although lumen diameter may be preferable for some purposes and may be calculated by subtracting wall thickness from the data presented here. Mean values for vessel grouping are obtained on the following basis: a solitary vessel = 1.0, a pair of vessels in contact = 2.0, etc. Bark was not observed specifically in the present study, although sections of the stem of *L. torulosa* included portions of the spongy stem covering that proves to be aerenchyma like that figured for "*Jussiaea repens*" L. (now a *Ludwigia*) by Metcalfe & Chalk (1950), and studied in detail by Ellmore (1981) for *L. peploides* (HBK) Raven.

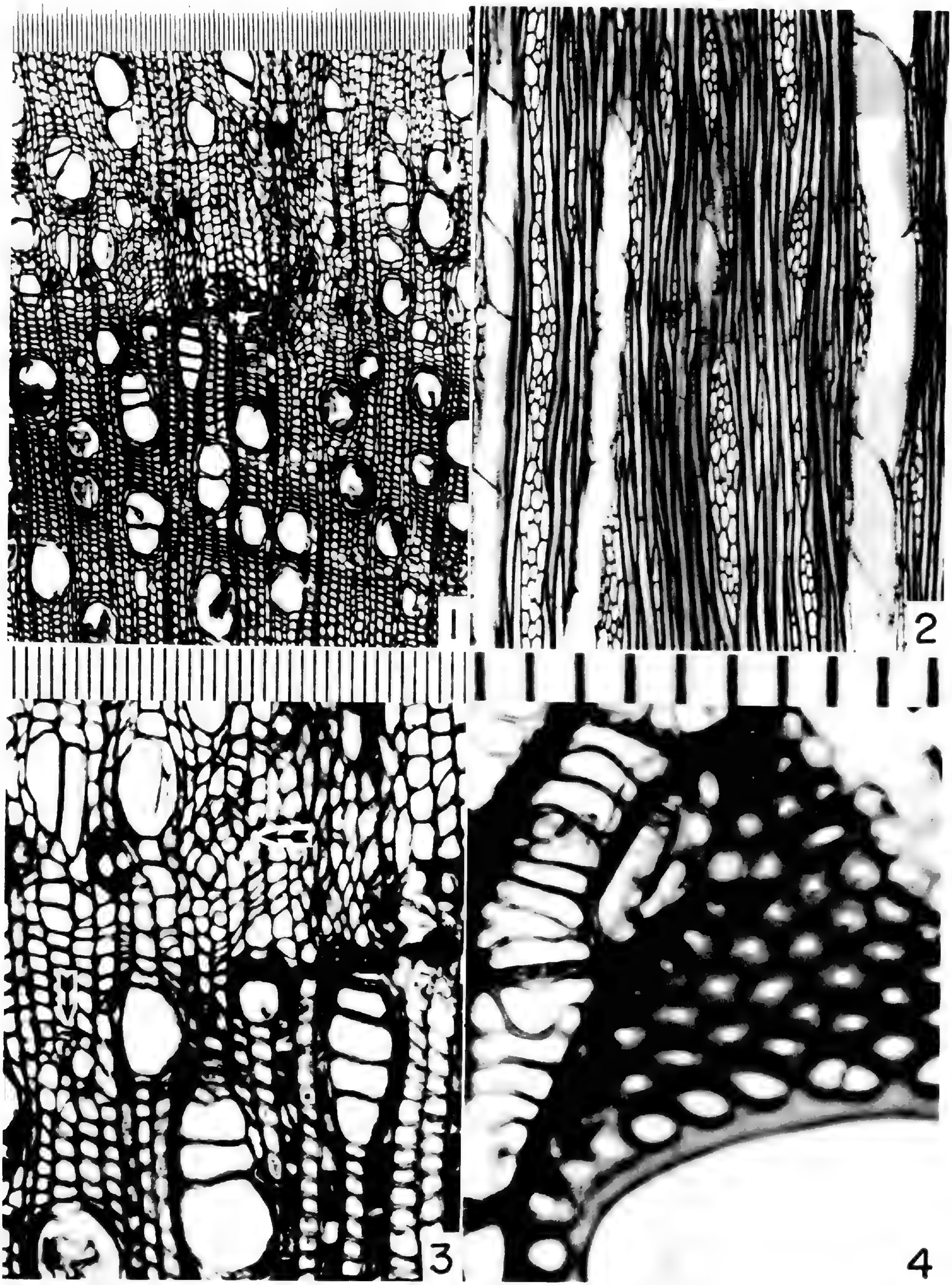
ANATOMICAL DESCRIPTIONS

Ludwigia anastomosans (DC.) Hara, *Zardini & Gentry 2175* (Figs. 1–6).

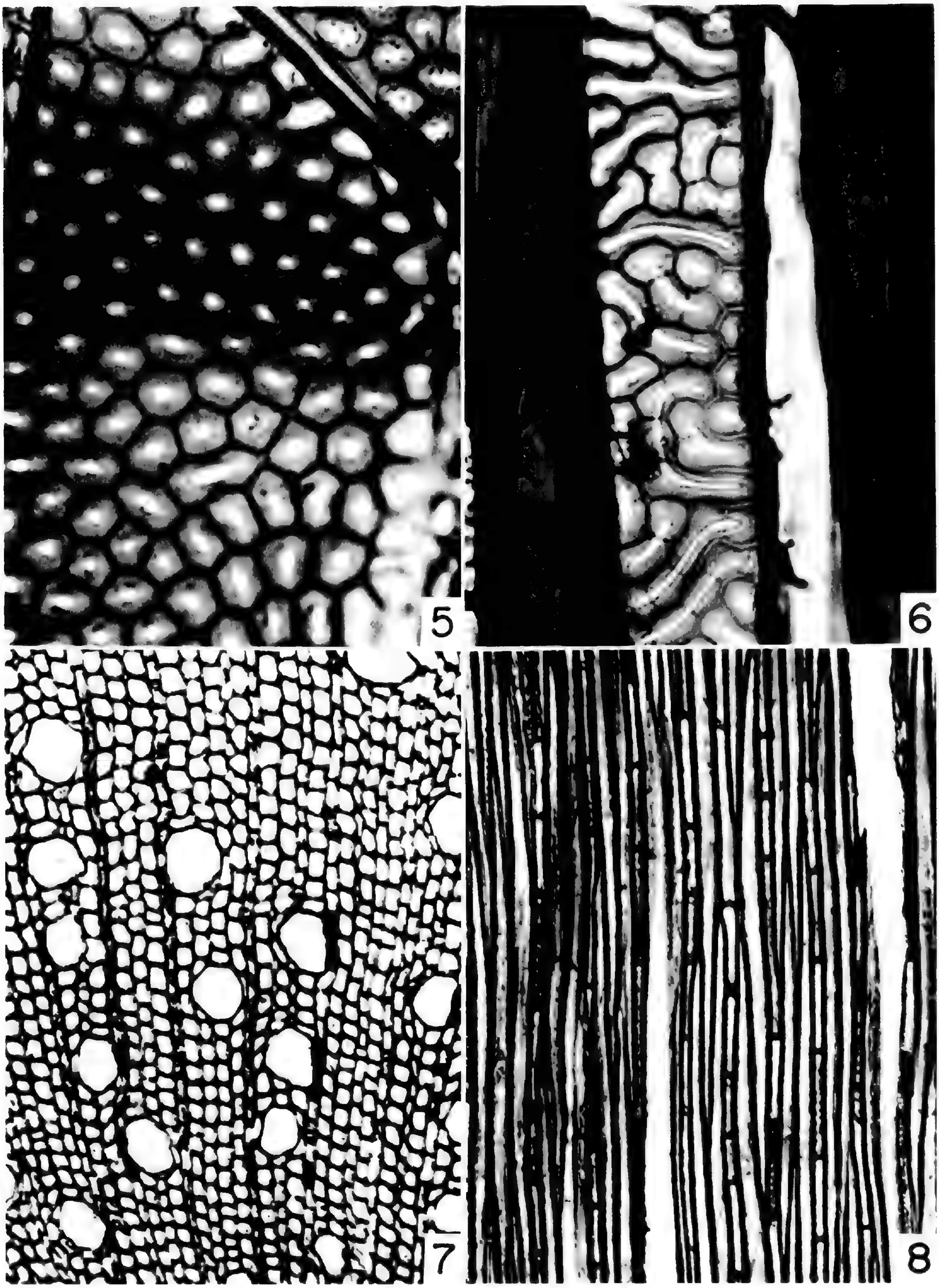
Growth rings inconspicuous, and probably related to water level of the riparian habitat (Fig. 1). Mean number of vessels per mm^2, 51. Mean number of vessels per group, 1.24; vessels tending to be grouped into radial multiples (Figs. 1, 3). Mean vessel diam., 109 μm. Mean vessel wall thickness, 2.5 μm. Mean vessel element length, 458 μm. Perforation plates simple (Figs. 2, 4). Lateral wall pitting of vessels alternate, pits crowded and circular to polygonal in outline, about 12 μm diam. on vessel–vessel interfaces (Figs. 4, 5). Vessel–axial parenchyma and vessel–ray pitting alternate to scalariform, pit apertures long (sometimes scalariform), pit apertures wide ("gaping"). Pitting with relatively conspicuous vesturing on vessel–vessel pits (Fig. 5, upper right), vesturing less pronounced on vessel–axial parenchyma and vessel–ray pits. Occasional vessel–vessel pits in aberrant patterns (Fig. 6). Tyloses abundant (Figs. 1, 3). Imperforate tracheary elements all libriform fibers because pits apparently simple, although a few exceptional pits with small borders also observed. Many libriform fibers septate. Mean libriform fiber diam., 28 μm. Mean libriform fiber wall thickness, 2.3 μm. Mean libriform fiber length, 588 μm. Numerous libriform fibers with gelatinous walls (Fig. 6) and therefore probably reaction wood. Axial parenchyma vasicentric scanty. Bands of phloem-containing axial parenchyma present in marginal positions (end of growth rings) or scattered without any relation to growth rings (Figs. 1, 3). Rays multiseriate and uniseriate, the former slightly more frequent (indicated by relative heights in Fig. 2). Ray cells predominantly erect and square (Fig. 2), a few procumbent cells present in multiseriate portions of multiseriate rays. Mean multiseriate ray height, 2,707 μm. Mean uniseriate ray height, 349 μm. Mean width multiseriate rays at widest point, 3.95 cells. Ray cell walls moderately thin, lignified. Wood nonstoried. Raphides present in phloem-containing axial parenchyma strands.

Ludwigia peduncularis (Griseb.) Gomez, *Ekman 13416* (Figs. 7, 8).

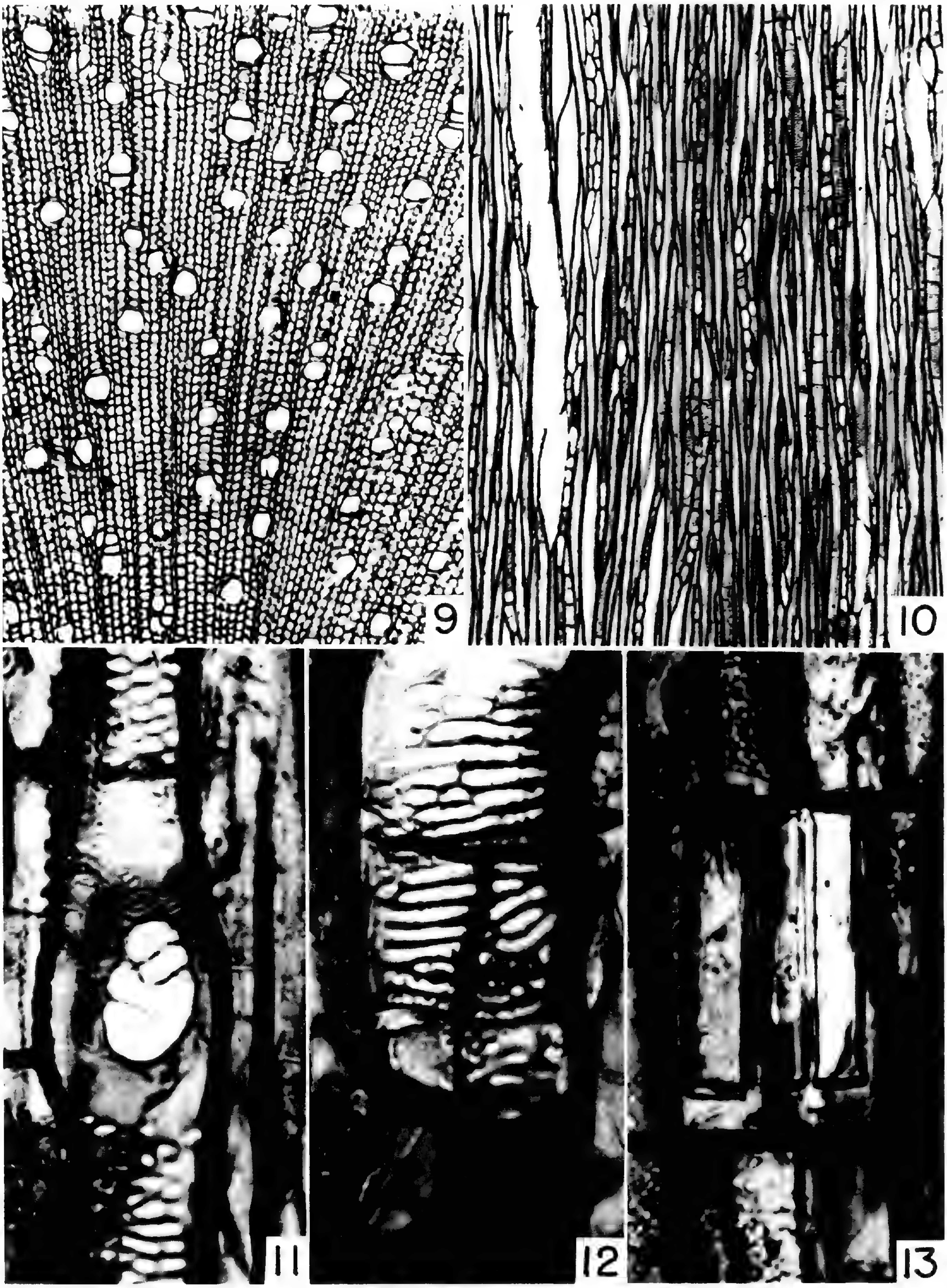
Growth rings absent (portion studied probably less than one year's accumulation). Mean number of vessels per mm^2, 62. Mean number of vessels per group, 1.30. Mean vessel diam., 50 μm. Mean vessel wall thickness, 1.8 μm. Mean vessel element length, 484 μm. Perforation plates simple. Lateral walls of vessels with crowded alternate elliptical pits (about 4 × 8 μm) with pointed ends and narrow apertures (vessel–vessel contacts). Vessel–axial parenchyma and vessel–ray pitting similar but with pits longer (appearing pseudoscalariform) and wider, and with wider



FIGURES 1–4. Wood sections of *Ludwigia anastomosans, Zardini & Gentry 2175.*—1. Transection; termination of growth ring occurs in the middle of the photograph.—2. Tangential section; multiseriate rays are wide, more numerous than uniseriate rays.—3. Portion of transection, showing strands of interxylary phloem (arrows) and vessels in radial multiples.—4. Portion of vessel wall from tangential section; intervascular pitting and perforation plate rim, below; axial parenchyma cells, upper left. Figures 1, 2, magnification scale above Figure 1 (finest divisions = 10 μm); Figure 3, divisions = 10 μm; Figure 4, divisions = 10 μm.



Figures 5–8. Wood sections of *Ludwigia*. 5, 6. *L. anastomosans, Zardini & Gentry 2175.*—5. Intervascular pitting from tangential section, showing transition between circular and polygonal pit shapes; vesturing evident in pits at upper right.—6. Portion of vessel and associated cells from tangential section; note aberrant pit and pit aperture configurations and splits in gelatinous fiber walls (right). 7, 8. *L. peduncularis, Ekman 13416.*—7. Transection; vessels solitary; dark-colored deposits in ray cells.—8. Tangential section; all rays are uniseriate. Figures 5, 6, magnification scale above Figure 4; Figures 7, 8, magnification scale above Figure 3.



FIGURES 9–13. Wood sections of *Ludwigia torulosa, Holst, Steyermark & Manara 2257.*—9. Transection; libriform fibers are thin-walled.—10. Tangential section; multiseriate rays are narrow, less frequent than uniseriate rays.—11. Portion of radial section showing vestigial bars on a perforation plate.—12. Portion of a radial section showing vessel–ray pitting.—13. Portion of a radial section showing rodlike crystals in two ray cells. Figures 9, 10, magnification scale above Figure 1; Figures 11–13, scale above Figure 4.

apertures. Pits of vessels vestured, less so in vessel–axial parenchyma and vessel–ray contacts than on vessel–vessel pitting. Imperforate tracheary elements all libriform fibers, the pits minute, apparently simple. Libriform fibers mostly septate. Mean libriform fiber diam., 18 μm. Mean libriform fiber wall thickness, 1.2 μm. Mean libriform fiber length, 778 μm. About half of the wood consisting of gelatinous fibers (Fig. 7), therefore apparently reaction wood. Axial parenchyma vasicentric scanty, very few strands adjacent to each vessel (or some vessels with no adjacent axial parenchyma). Interxylary phloem absent. Rays almost all uniseriate (Fig. 8). Ray cells all erect. Mean uniseriate ray height, 1,566 μm. Ray cells moderately thin-walled but lignified (Fig. 8). Wood nonstoried. No crystals observed. Axial parenchyma and ray cells containing droplets or massive accumulations of a brownish substance (Figs. 7, 8).

Ludwigia torulosa (Arn.) Hara, *Holst, Steyermark & Manara 2257* (Figs. 9–13).

Growth rings absent (portion studied probably less than a year's accumulation). Mean number of vessels per mm^2, 62. Mean number of vessels per group, 1.55. Mean vessel diam., 55 μm. Mean vessel wall thickness, 1.6 μm. Mean vessel element length, 374 μm. Perforation plates mostly simple, but some with modified or vestigial bars (Fig. 11). Lateral walls of vessels with alternate polygonal pits about 5 μm diam. on vessel–vessel contacts. Vessel–axial parenchyma and vessel–ray pits alternate, opposite, or scalariform, larger and with wider apertures than the vessel–vessel pits (Fig. 12). Vestures dense within cavities of vessel–vessel pits, somewhat less abundant on vessel–axial parenchyma and vessel–ray pits. Imperforate tracheary elements all libriform fibers, because the pits apparently simple. Libriform fibers nonseptate, but starch present in them. Mean libriform fiber diam., 25 μm. Mean libriform fiber wall thickness, 1.5 μm. Mean libriform fiber length, 538 μm. Libriform fiber walls somewhat gelatinous. Axial parenchyma vasicentric scanty, often only one strand adjacent to a vessel. Rays multiseriate and uniseriate, uniseriates more abundant (Fig. 10). Ray cells mostly erect, a few square cells present. Mean multiseriate ray height, 1,188 μm. Mean uniseriate ray height, 270 μm. Mean multiseriate ray width at widest point, 2.2 cells. Cell walls moderately thin but lignified. Wood nonstoried. Large rodlike crystals (one tip concave, the other convex, suggesting paired crystals) present in a few ray cells (Fig. 13).

CONCLUSIONS

HABIT AND ECOLOGY

In a given floristic area, wider vessels characterize trees as compared with shrubs and subshrubs (Carlquist & Hoekman, 1985). In a genus or family that ranges into diverse habitats, tropical tree species tend to have the widest vessels (e.g., Vliet, 1979). *Ludwigia anastomosans* has notably wide vessels for the family Onagraceae. Mean vessel diameter in this species equals the widest mean diameter reported in the earlier survey (Carlquist, 1975), a fact very likely related both to its arboreal nature and tropical habitat. The figure recorded for vessel diameter in *L. anastomosans* may be conservative, because the stem studied is relatively small compared with the large diameter of trunks of these trees. In trees, vessel diameter is greater at the periphery of older stems (e.g., Carlquist, 1984b).

The abundance of erect ray cells in comparison with procumbent ray cells in *Ludwigia,* even in *L. anastomosans,* suggests that *Ludwigia* may represent some degree of secondary woodiness. This idea was entertained for *Ludwigia* earlier (Carlquist, 1975). The presence of a few vestigial bars on perforation plates in *L. torulosa* (Fig. 11) is pertinent in this regard. Presence of a few such plates does suggest retention of primitive features in the primary xylem (the "refugium" theory of Bailey, 1944), but it also suggests that this feature is carried forward into the secondary xylem by virtue of paedomorphosis. Paedomorphosis is indicated by erect ray cells and the relatively long vessel elements (Carlquist, 1962), two features well displayed in *Ludwigia.* Presence of occasional scalariform perforation plates in otherwise specialized wood by virtue of paedomorphosis is illustrated in a few other predominantly herbaceous groups such as Campanulaceae (Shulkina & Zikov, 1980), *Crepidiastrum* of the Asteraceae (Carlquist, 1983a), or *Patrinia* of the Valerianaceae (Carlquist, 1983b). The presence of scalariform perforation plates is, however, more primitive than presence of simple plates exclusively.

In an earlier paper (Carlquist, 1984a), vessel grouping in taxa with libriform fibers (as in Onagraceae) or fiber-tracheids was held to be proportional to adaptation to dry conditions. This hypothesis is worth testing in Onagraceae, because of the wide range of ecological circumstances occupied by its members. Data on vessel grouping were prepared earlier for the family (Carlquist, 1975), and indices designed to enable comparison with ecological conditions were devised (Carlquist, 1977). These data can now be analyzed in the light of the vessel grouping hypothesis. Vessel grouping figures were not offered for six *Ludwigia* species studied earlier (Carlquist, 1982a), and so are presented here: *L. bullata* (Hassler) Hara, 1.08; *L. elegans* (Cambess.) Hara, 1.36; *L. peruviana* (L.) Hara, 1.10; *L. sericea* (Cambess.) Hara, 1.12; *L. tomentosa* (Cambess.) Hara, 1.04; *L.* sp. (aff. *L. longifolia*), 1.23.

The mean value for vessel grouping in the 12 collections of *Ludwigia,* sole genus of tribe Jussieeae, is 1.23. The next lowest value, by tribe, occurs in Hauyeae (1.67), followed by Fuchsieae (1.80) and Epilobieae (1.85); data for Lopezieae and Onagreae were subdivided into habit categories. If one considers that the aquatic habitats characteristic of *Ludwigia* species represent the most mesic ecological situations of the family, vessel grouping is a more accurate indicator of ecology within Onagraceae than the indices "Vulnerability" or "Mesomorphy." However, one should take into account that the Mesomorphy figure for Hauyeae (1,242), which seems high compared with that for 12 collections of *Ludwigia* (415), is related to the wide vessels in that tribe, which in turn is doubtless characteristic for a species transpiring large volumes of water in a warm, moist tropical forest. Both of these figures are much higher than for groups in the family occupying drier habitats, such as annuals of tribe Onagreae (161) or caudex perennials of Onagreae (48).

SYSTEMATICS

The data provided are consonant with the idea that *L. peduncularis* and *L. torulosa* may be closely related. These species have an unusual feature in common, the presence of rays exclusively or nearly uniseriate at the outset of secondary growth. The absence in *L. peduncularis* of the curious mirror-image crystals observed in *L. torulosa* is not considered decisive. Such crystals have been reported in *L. bullata, L. octovalvis,* and *L. peruviana* (Carlquist, 1975, 1982a). In turn, these crystals resemble the large, styloidlike crystals of *Hauya*; these latter crystals occur in axial parenchyma rather than in rays, as in *Ludwigia.* Data from wood anatomy should not be interpreted in too detailed a way here: variability within species is not known and not all species of all sections of *Ludwigia* have been studied. Wood anatomy is not often a decisive indicator of relationships at species and section (subgenus) levels.

The occurrence of interxylary phloem in *L. anastomosans* is noteworthy. Interxylary phloem has been reported previously for the genus only in *L. sericea* (Carlquist, 1982a), although it occurs elsewhere in the family (Carlquist, 1975). The significance of interxylary phloem seems to lie with seasonality in translocation of photosynthates, as noted earlier (Carlquist, 1975). Because *L. anastomosans* is a tree, presumably with an annual flowering season, production of interxylary phloem would be adaptive, whereas in an annual or short-lived perennial *Ludwigia* plant, the phloem from a single year, undiminished by crushing at the end of a season as in longer-lived plants, would probably suffice to channel photosynthates into flowers and developing fruits.

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THE ORIGAMI OF BOTANY: A GUIDE TO COLLECTING AND MOUNTING SPECIMENS OF CYCLANTHACEAE[1]

Barry E. Hammel[2]

Abstract

Guidelines for preparing and mounting specimens of Cyclanthaceae, as well as a key to the genera, are presented in order to facilitate collecting of a difficult and often neglected family. In general, specimens should be prepared so the depth of the leaf division is apparent and the lower surface of the basal part of the leaf is visible or accessible.

The family Cyclanthaceae has far fewer species than the other related families of large intractable monocots for which guides to the preparation of herbarium specimens have recently been published (Croat, 1985; Dransfield, 1986; Stone, 1983). Nevertheless, in much of the wet lowlands of the Neotropics the cyclanths form a very conspicuous element of the understory and epiphyte flora (Figs. 1, 2). Careful collecting in almost any area of wet primary forest often yields new species because the family is poorly represented in herbaria and many species are narrowly endemic. This paper is a call for more collections as well as a guide to help insure that they be properly prepared.

Specimen Selection and Preparation

How to find them. Cyclanths are often left uncollected due to their large size, epiphytic habit, ephemeral and seasonal flowering, and green fruits. Moreover, the fertile structures are born low on the plant and are overtopped by obscuring leaves (Fig. 3). However, even in a population that is out of season, examination of numerous plants will often reveal fertile structures. This effort is important. Both staminate and mature fruiting materials are essential for describing new species and often for identifying known species.

Dramatic—though nearly microscopic—differences in floral and fruit structure between vegetatively similar species are easily overlooked by the nonspecialist collector who may tend to "see" (and collect) only one common species of a genus in an area where three or four occur. Different species may occupy the same habitat on adjacent ridges or along different branches of a single stream. Differences in depth of lamina division, presence/absence and position of lateral costae, phyllotaxy, habit, and even subtle differences in lamina and petiole texture and color help reveal different taxa.

What to do to them. The artful folding (origami) of whole plants of large-leaved monocots may in itself be reward enough for a specialist in the particular family, but one can hardly expect specialists in other groups or even generalist collectors to spend so much time on one gathering. The final specimen is usually better for data recovery when redundant material has been removed and the essential properly folded. Thus, the first need in collecting large-leaved monocots is to know what parts of the plant to collect. Most of the following comments pertain to vegetative parts because most of the difficulties stem from them.

Since the leaves of cyclanths are bilaterally symmetrical, they can be split down the middle (Fig. 4). In general, the whole petiole and a piece of stem with attached inflorescence or infructescence should be included. Even when whole or half leaves are collected, two sources of information are often obscured or lost: the depth of division of the leaf and an abaxial view of the blade. It is not sufficient simply to press leaves so that the division is visible, since it often splits deeper on drying. On large leaves, which must be split to fit the press, the point of division can be indicated by cutting a notch at this point and folding the leaf so that the notch shows (Fig. 5). For leaves small enough to press entire, the best way to avoid ambiguity is to cut off one leaf lobe at the point of division (Fig. 6). The label should briefly record this notching and lopping of lobes,

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FIGURES 1, 2.—1. Dense understory of *Asplundia uncinata* Harl. in the wet lowlands of northeastern Costa Rica. Plants ca. 1.5 m tall.—2. *Evodianthus funifer* (Poit.) Lindman, a very widespread root-climbing epiphyte. Leaves ca. 50 cm long.

e.g., "notch marks point of division," or "lobe cut off at point of division."

The presence/absence and position of lateral costae is taxonomically meaningful at species and higher levels. Although these costae are very conspicuous on the lower surface, they are not visible at all from above. Thus, the blade should be folded to show at least the basal portion of the abaxial surface. This is true in all genera except *Carludovica*, and a few species of *Asplundia*, where features on the *upper* surface become important.

SPECIFIC (AND GENERIC) CONSIDERATIONS

The following key to the 10 genera of Cyclanthaceae is presented to facilitate discussion of generic characters and the requirements for collecting and mounting each genus. *Pseudoludovia*, no longer accepted, is not included in the key, nor are two new genera (R. Erikson, pers. comm.; Hammel & Wilder, in prep.), which require no special techniques.

FIGURE 3. The most conspicuous fertile stage, when the staminodia are exserted, is ephemeral and hidden among the leaves. Leaf blades ca. 65 cm long.

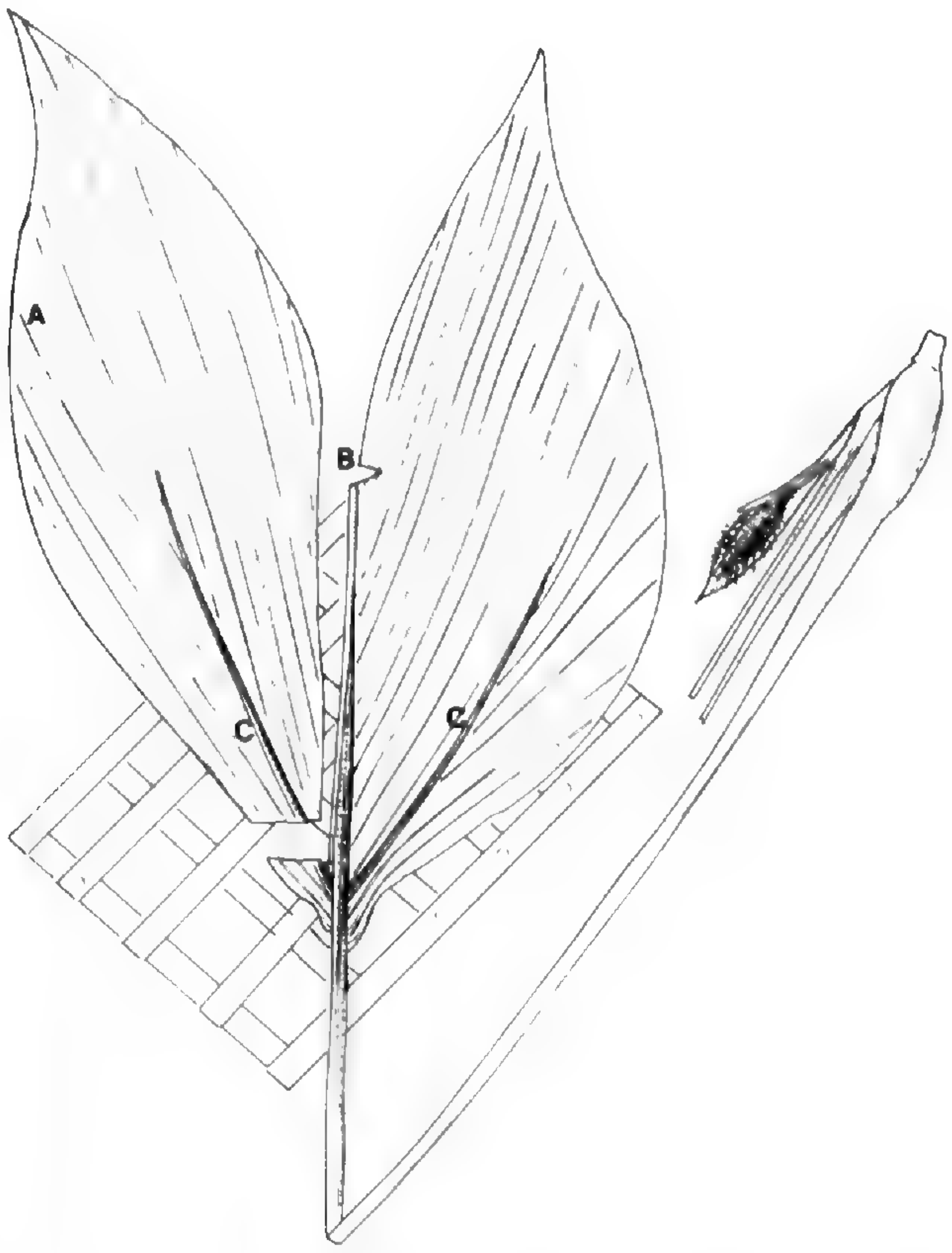

FIGURE 4. *Asplundia* specimen ready for pressing.—A. Section to be discarded.—B. Notch to mark depth of division.—C. Lateral costae.

KEY TO THE GENERA OF CYCLANTHACEAE WITH EMPHASIS ON VEGETATIVE CHARACTERS

1a. Leaf blades with the 2 major lateral costae running nearly the entire length of the blade, usually deeply bifid nearly to the base; spadix a cylinder of rings or spirals or both formed by alternating staminate and pistillate units; plants terrestrial, usually short-stemmed .... *Cyclanthus*

1b. Leaf blades with the 2 lateral costae (if present) always disappearing well below the tip of the blade, entire to deeply divided; spadix a cylinder or sphere of tightly packed and variously connate to free, but more typical staminate and pistillate flowers; plants epiphytic, lithophytic, or terrestrial, often long-stemmed.

  2a. Petioles mostly 1.5–3 m long; leaf blades palmately divided into 4 segments, the segments deeply toothed, the lateral costae short and far removed from the margin; plants terrestrial; surface of the mature spadix splitting irregularly to reveal the bright orange seed pulp and rachis; seeds angular .... *Carludovica*

  2b. Petioles mostly less than 1 m long; leaf blades usually entire or bifid, the segments rarely toothed but then the lateral costae long and running in the margin; plants terrestrial, epiphytic, or lithophytic; surface of mature spadix not splitting irregularly; seeds flat or terete.

   3a. Leaves with 2 conspicuous lateral costae about as thick as the median costa (often in *Asplundia*, rarely in *Dicranopygium*, always in the monotypic *Schultesiophytum*).

    4a. Spathes mostly dispersed along the peduncle; fruits dehiscent by apical caps, fused at the base .... *Asplundia*

    4b. Spathes clustered just below the spadix; fruits indehiscent.

     5a. Leaves bruising and drying black; fruits completely separate .... *Schultesiophytum*

     5b. Leaves remaining green; fruits connate in basal ½ or more .... *Dicranopygium*

   3b. Leaves without conspicuous lateral costae.

    6a. Spathes clustered immediately below the spadix.

     7a. Plants long-stemmed and openly branched, usually climbing; stems and dry leaves scabrous; fruits completely separate; seeds flat .... *Evodianthus*

     7b. Plants mostly short-stemmed and clumped, rarely climbing a short distance, usually growing on rocks along streams; stems and dry leaves smooth; fruits connate in basal ½ or more; seeds terete .... *Dicranopygium*

    6b. Spathes dispersed along the peduncle.

     8a. Leaves distichous.

      9a. Leaf blades crenate at most, never bifid; fruiting spadix nearly smooth, the pistillate flowers connate throughout; plants lianas or short-stemmed epiphytes .... *Ludovia*

      9b. Leaf blades of mature individuals bifid; fruiting spadix not smooth, the pistillate flowers completely or partly free; plants terrestrial or epiphytic, usually short-stemmed.

       10a. Seeds mostly rounded at both ends .... *Sphaeradenia*

       10b. Seeds with long appendages at both ends .... *Stelestylis*

     8b. Leaves spirally arranged.

      11a. Petioles lacking, the broadly channeled false petioles (sheaths) extending to the blade; leaves of climbing stems often undivided; mature fruits tan; spathes 8–11; plants lianalike canopy climbers .... *Thoracocarpus*

      11b. Petioles present in most species, the false petioles narrowly channeled when present; leaves of climbing stems divided; mature fruits usually orange or green; spathes 2–8; plants low trunk climbers or terrestrial .... *Asplundia*

Asplundia and *Dicranopygium* account for over half the species in the family, and it is within these two genera that variation in lateral costae is significant for distinguishing species. The requirement to show at least the basal portion of the lower leaf surface applies especially to these genera. For the small-leaved species of *Asplundia* it is important to insure that more than one leaf is preserved and that *both* surfaces of the basal part of the leaf are visible. This is necessary in order to see adaxial scars at the distal end of the false petioles, characteristic of several species in subgenus *Chaonopsis*. In *Asplundia* and *Dicranopygium*, whether or not the sheath splits up into fibers and the color and quality (dull vs. shiny) of its surface are necessary data points for identifying or characterizing species. Here, specimens should preserve a portion of the stem together with the leaf at its point of attachment.

Although *Sphaeradenia* consistently has only the median and no lateral costae, nothing is lost by preparing specimens of this genus (and of most others) as for *Asplundia* and *Dicranopygium*. In any case, for *Ludovia*, *Sphaeradenia*, and *Stelestylis* one should preserve part of the stem with attached sheaths in order to verify the distichous arrangement of the leaves and to show internode length (Fig. 6). *Asplundia*, *Dicranopygium*, and

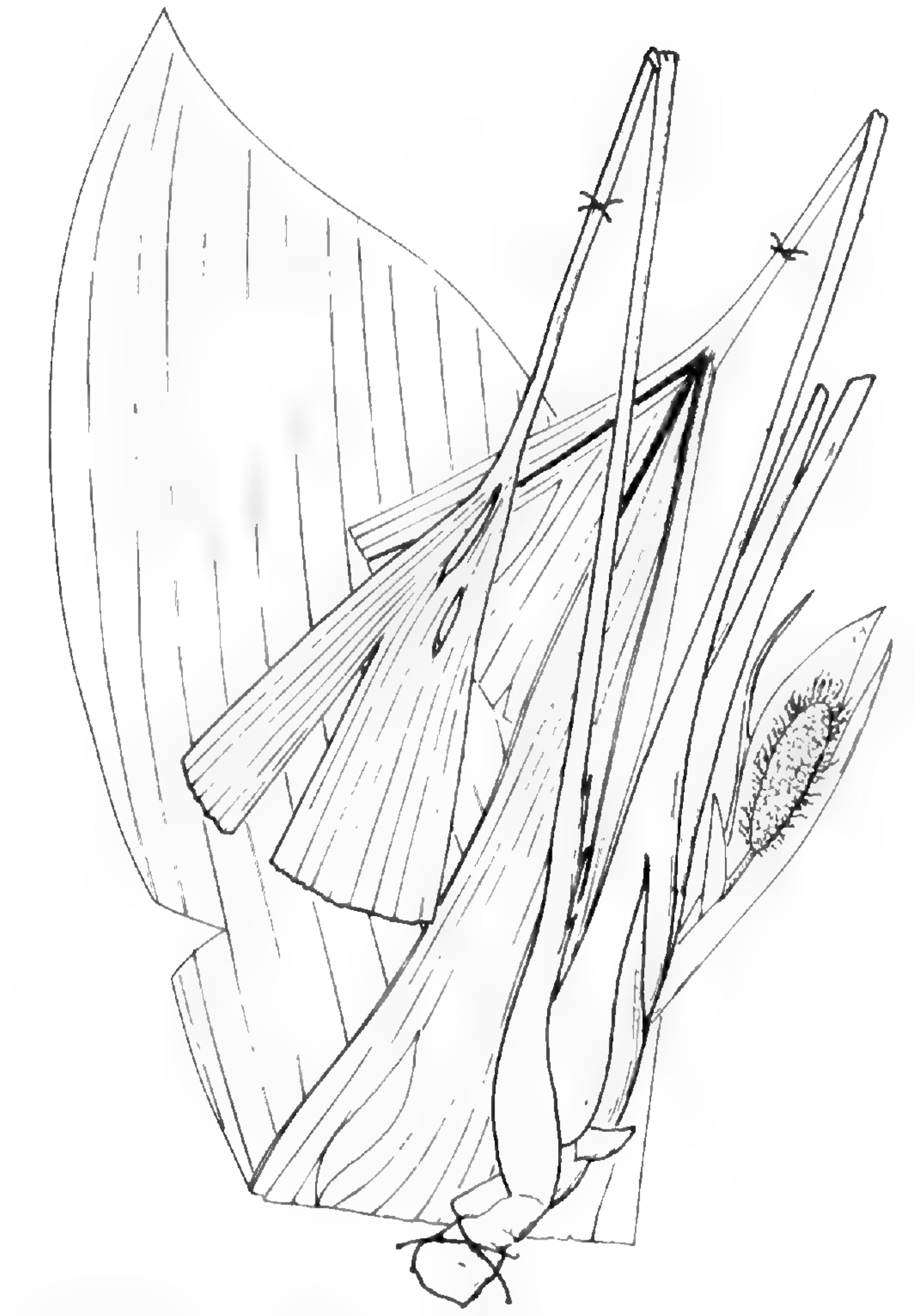

FIGURE 5. *Asplundia* specimen properly folded and mounted with string.

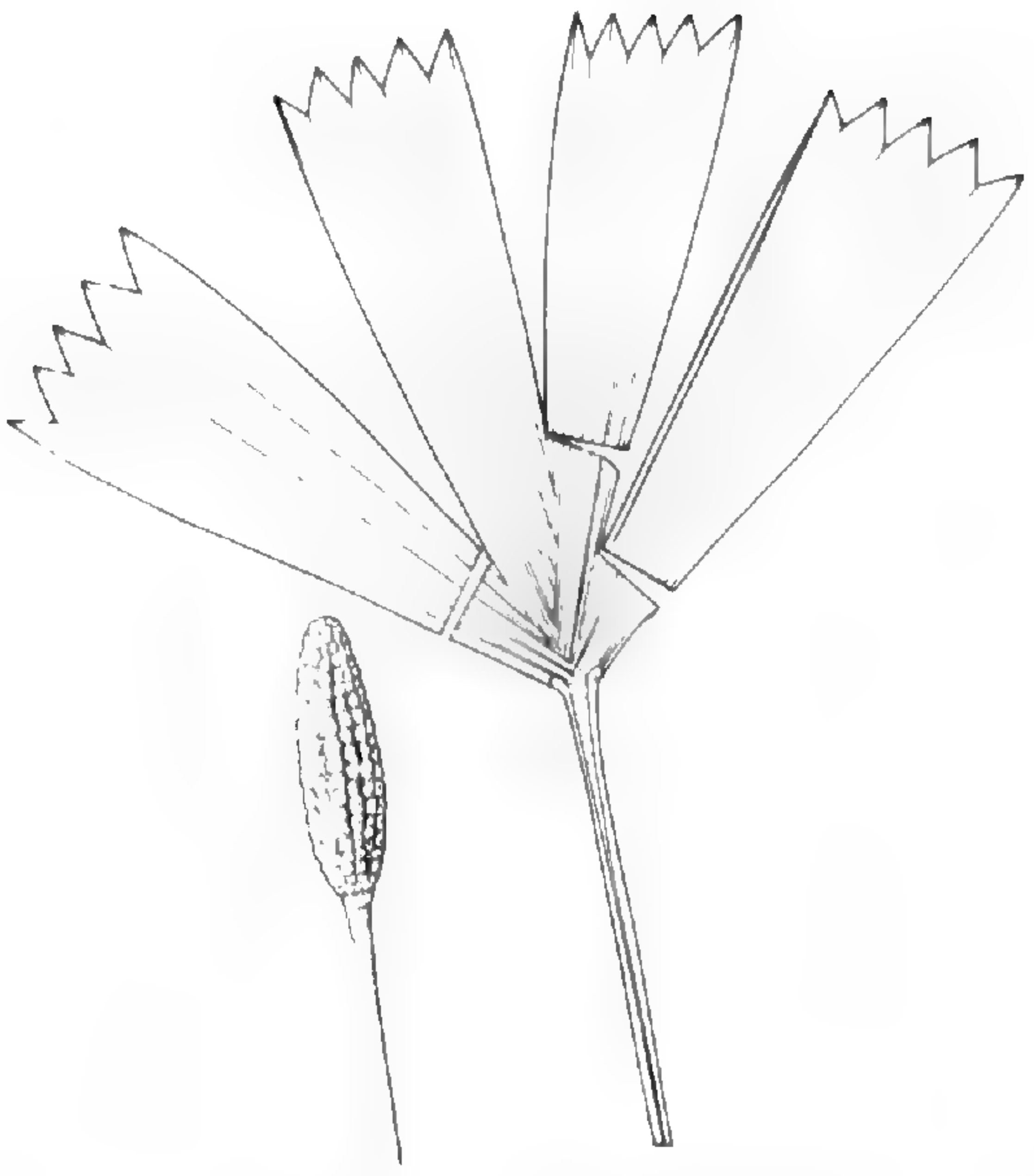

FIGURE 7. *Carludovica* specimen ready for pressing, showing sections to be discarded cut at point of division.

Sphaeradenia account for most of the species in the family so that the general rules for collecting these genera apply to most of the species one encounters.

Carludovica needs special attention in connection with the very large size and unusual shape of its mature leaves. In order to represent the essential features (the depth of the teeth and the

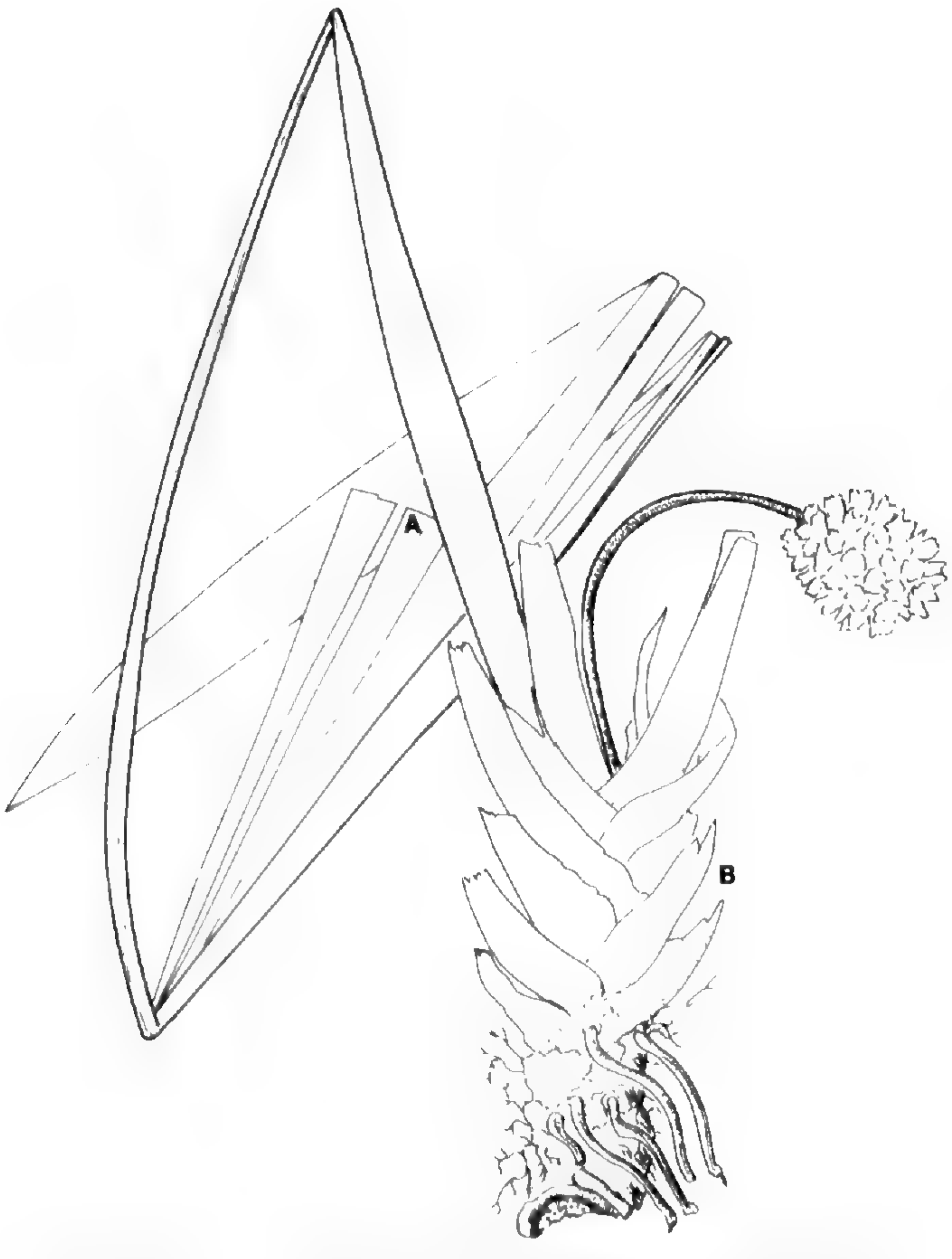

FIGURE 6. *Sphaeradenia* specimen showing blade cut off at point of division (A) and distichous phyllotaxy (B).

FIGURE 8. *Carludovica* specimen properly folded and mounted with string, showing hastulae (A) on upper surface.

depth of the divisions) only one of the four leaf segments need be preserved. The best approach is to cut off the two lateral segments and one of the central segments at the point of division and then fold the blade so that the teeth and the *adaxial* surface of the basal portion of the leaf are visible (Figs. 7, 8), thus showing the presence/absence of hastulae (Wilder, 1976). Sometimes even this reduced leaf must be split to fit on one sheet. Variation in petiole and peduncle length appears to be of little use for distinguishing species of *Carludovica,* but the length of these structures should at least be recorded in the field notes. Finally, for *Carludovica,* variation between species in shape of juvenile and immature foliage makes leaves from young plants worth preserving.

FIELD NOTES

Habit. Approximately 60% of the species of Cyclanthaceae are either strict epiphytes or root-climbers, which may eventually lose connection with the ground. Habit is quite diverse (and sometimes variable within species) in *Asplundia* and *Dicranopygium.* The longest-stemmed species are usually found only as climbers, some with shorter stems climb or grow free-standing, and the shortest-stemmed species never climb. Strict epiphytes occur only in *Ludovia, Sphaeradenia,* and *Stelestylis,* and terrestrial species occur in all of these genera. *Carludovica* is always terrestrial; *Cyclanthus* rarely climbs. Only species of *Dicranopygium* grow on rocks along streams. For these reasons one should always make careful note of the habit: epiphytic, lithophytic, terrestrial, or root-climbing. If the collector is certain that a species is both terrestrial and climbing, it is very useful to write that in the notes, e.g., "apparently same species also climber here but not fertile." If the stem is not preserved, the leaf arrangement should be noted. The approximate length of the stem or height above ground for climbers (e.g., "climbing to 10 m") should also be recorded.

Other vegetative characters. Even though care has been taken to record on the specimen the depth of the leaf division, it is also a good idea to record in the field notes the approximate range of this character based on the plant or population collected, e.g., "leaves divided from ½–⅔." The leaf segments of all species of *Carludovica* and a few species of *Asplundia* develop teeth in the unopened leaf. Unfortunately, with age, drying, or other trauma some large *Asplundia* leaves can split into teeth, which on herbarium sheets resemble those arising developmentally. Thus, for *Asplundia* one should indicate whether such teeth originate developmentally or by trauma.

As noted above, subtle differences in leaf and petiole surface textures and colors often separate species and should be recorded. In a few species of *Asplundia* and *Dicranopygium* the leaf folds are not adaxially keeled. Because all leaves on herbarium specimens appear to have variously keeled folds, it is best to record exceptions in the field notes.

The cross-sectional petiole shape is less variable in the Cyclanthaceae than in certain genera of Araceae (Croat, 1985), but again this feature is difficult to assess using dried herbarium material and should be described for unusual cases. Most petioles are basically terete and barely to obviously flattened above (D-shaped) and may have a small median adaxial groove. In *Thoracocarpus* and a few species of *Asplundia* the sheath reaches all the way to the base of the blade so the leaves lack a petiole. The petioles of *Schultesiophytum* are asymmetrically D-shaped with one margin rounded and the other sharply angled. The color of the stem cross section may also be taxonomically significant; in certain species of *Asplundia* and *Dicranopygium* cut stems rapidly turn reddish brown (perhaps indicating high concentrations of tannin).

Fertile structures. The infloresences of cyclanths are monoecious and protogynous. Their most conspicuous stage—when the staminodia are exserted—is also the most ephemeral. Varying in size and color, the vermicellilike staminodia may harbor taxonomic structure but have not been used because they are so seldom seen and poorly preserved on drying. When an inflorescence with mature staminodia is collected, field notes should include color and approximate length of staminodia. The number of spathes serves to distinguish taxa but is often difficult to count on herbarium material without damaging it. Field notes should mention the number, color, and texture of spathes. Most of these time-consuming measurements can be delayed (and many more characters accurately preserved) by preserving inflorescences in liquid. Dried material of these extremely succulent parts so misrepresents the living condition that, except for well-known species, collectors are strongly urged to preserve inflorescences or parts thereof in 70% EtOH.

The color of mature fruits is variable and should be noted. They may be white, red, yellow, or green at maturity. In *Sphaeradenia* the color of mature seeds is also variable and should be recorded.

MOUNTING THE SPECIMENS

All of the foregoing discussion, especially on artful folding, is to no avail if the dried material is mounted upside down. Collectors always assume that their material will be mounted the way they pressed it, with the numbered side of the newsprint equal to the up side of the specimen. However, once the connection between newspaper and plant is broken, as it can easily be with so many steps between collecting and mounting, and as it always is in the end, the decision must be made: which side is up? Responsibility for this final important step rests upon the mounter.

In the end, a liberal use of string and judicious use of glue can obviate even this decision. Generally, one need glue down only the first layer of leaf fold and then tie the stem and petiole(s) at appropriate places (see Figs. 5, 8). In this way the specimen can be unfolded partly or completely, and both sides of the leaf can be easily examined.

Mounters, of course, will continue to receive material gathered by those who have missed, ignored, or forgotten this guide, or who are not artists. If parts are missing, or no mark records the point of division, nothing can be done. But when the leaves have been folded improperly, this guide is especially for the mounters, who with a little care can salvage the specimen and enjoy the art.

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MESOAMERICAN *SISYRINCHIUM* (IRIDACEAE): NEW SPECIES AND RECORDS, AND NOTES ON TYPIFICATION[1]

JAMES E. HENRICH[2] AND PETER GOLDBLATT[3]

ABSTRACT

This paper supplements our treatment of *Sisyrinchium* for *Flora Mesoamericana* in which 13 species are recognized. One new species is described, *S. subalpinum,* from Mexico (only Chiapas), Guatemala, and Costa Rica. *Sisyrinchium trinerve,* previously known from Andean South America, *S. dimorphum* from Texas and northern Mexico, *S. longispathum* from Oaxaca, Mexico, and *S. subcernuum* from northern Mexico are reported in Mesoamerica for the first time. The type material for *S. convolutum, S. tenuifolium, S. mandonii, S. tinctorium,* and *S. bogotense* has been examined and a lectotype designated for each species.

In preparation for a treatment of Iridaceae for *Flora Mesoamericana* (Henrich & Goldblatt, in press), it has become clear that previous regional treatments of *Sisyrinchium* are to varying degrees inadequate or erroneous. The same species are treated under different names in some floras and few of the species have been matched with their types. Notes are thus presented here on the typification of several widely recognized species to supplement the formal treatment. There is also apparently one new species in Mesoamerica, *S. subalpinum,* a yellow-flowered species of section *Echthronema* Bentham. This is a dwarf, high-altitude relative of the common *S. tinctorium.* We also report for the first time the occurrence in Mesoamerica of the Andean *S. trinerve,* the northern Mexican *S. subcernuum,* the southern Mexican *S. longispathum,* and the predominantly Texan *S. dimorphum.* Finally, the species previously identified as *S. iridifolium* Kunth in Guatemala and Honduras corresponds closely to the Oaxacan *S. exalatum,* a tall, branched species with narrow leaves and thickened roots sometimes swollen terminally.

We recognize 13 species (Table 1) of *Sisyrinchium* in Mesoamerica, which is regarded for the *Flora* as including all the territory from the southern Mexican states of Yucatán, Campeche, Tabasco, Quintana Roo, and Chiapas southward to Panama. The species are numbered as they

TABLE 1. The species of *Sisyrinchium* recorded from Mesoamerica with their general distributions.

S. chiricanum Woodson	Mexico (Chiapas), Guatemala, El Salvador, Costa Rica, Panama
S. convolutum Nocca	Chiapas, Mexico to Panama, possibly the north coast of South America
S. dimorphum R. Oliver	U.S.A. (Texas), Mexico, Guatemala
S. exalatum Robinson & Greenman	southern Mexico (Oaxaca, Chiapas), Guatemala, Honduras
S. johnstonii Standley	Mexico (Chiapas), Guatemala, Costa Rica
S. longispathum Conzatti	Mexico (Oaxaca, Chiapas)
S. mandonii Baker	Guatemala, Costa Rica, Panama, Peru, Bolivia
S. micranthum Cav.	Mexico to South America, West Indies
S. subalpinum Henrich & Goldbl.	Mexico (Chiapas), Guatemala, Costa Rica
S. subcernuum (Bicknell) Henrich & Goldbl.	Mexico, Belize
S. tenuifolium Humb. & Bonpl. ex Willd.	Mexico, Guatemala, Panama
S. tinctorium Kunth	southern Mexico to Colombia and Venezuela
S. trinerve Baker	Costa Rica, Colombia, Venezuela, Ecuador to Bolivia

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appear in the *Flora* treatment. Species 1–3 belong to section *Sisyrinchium* (= section *Bermudiana* Bentham) and 4–12 to section *Echthronema* (Bentham, 1883).

KEY TO *SISYRINCHIUM* IN MESOAMERICA

1a. Flowering stems unbranched, consisting of 1 long internode without cauline leaves, but sometimes with a terminal bract subtending the opposed spathes of the 1–3 apical inflorescence units (rhipidia) (occasionally rhipidia with a short stalk, more often sessile).
  2a. Leaves filiform, to 1 mm wide; inflorescence units 1–3 .... 8. *S. longispathum*
  2b. Leaves linear to lanceolate, at least 1.5 mm wide; inflorescence units 1 or 2.
    3a. Roots tuberous, fleshy (Fig. 1A); flowers blue to white .... 3. *S. johnstonii*
    3b. Roots fibrous or thickened but not tuberous (Fig. 2B, D); flowers yellow.
      4a. Flowering stems subterete and not winged; ovary included in the upper part of the spathes .... 7. *S. trinerve*
      4b. Flowering stems flattened and winged; ovary exserted.
        5a. Spathes (20–)25–50 mm long, the outer longer (sometimes twice) than the inner .... 11. *S. tinctorium*
        5b. Spathes 11–16 mm long, usually subequal.
          6a. Plants 5–12 cm tall; roots slender but somewhat thickened (Fig. 3) .... 12. *S. subalpinum*
          6b. Plants 15–25 cm tall; roots fibrous (Fig. 2D) .... 13. *S. subcernuum*
1b. Flowering stems consisting of more than 1 internode, branched or at least with 1 or more cauline leaves.
  7a. Roots fibrous or thickened and cylindric, sometimes with persistent hairs (Fig. 1B, C).
    8a. Annuals 5–15(–25) cm tall; capsules 3 mm long, globose .... 2. *S. micranthum*
    8b. Perennials (15–)20–60 cm tall; capsules 4–5 mm long and globose, or 8–11 mm long and obovoid.
      9a. Flowers blue; spathes 14–18 mm long .... 1. *S. dimorphum*
      9b. Flowers yellow, spathes 26–32 mm long.
        10a. Roots with persistent hairs throughout or at least near the base (Fig. 1B) .... 5. *S. chiricanum*
        10b. Roots smooth, not bearing persistent hairs (Fig. 1C) .... 4. *S. exalatum*
  7b. Some roots tuberous and fleshy, either close to or remote from the stem base (Fig. 2A, C).
    11a. Basal leaves 3–8 mm wide, narrowly to broadly lanceolate to falcate.
      12a. Plants usually less than 30 cm high and with falcate leaves; capsules strongly 3-lobed; usually with swollen fusiform roots thickened from the base (Fig. 2A) .... 6. *S. convolutum*
      12b. Plants usually more than 30 cm high and with lanceolate leaves; capsules obscurely 3-lobed; roots thickened, if at all, distant from the base (Fig. 1C) .... 4. *S. exalatum*
    11b. Basal leaves 0.5–2 mm wide, linear; capsules not strongly 3-lobed.
      13a. Capsules globose, 5–7 mm long .... 9. *S. tenuifolium*
      13b. Capsules oblong, 12–16 mm long .... 10. *S. mandonii*

NOTES ON SELECTED SPECIES

1. **Sisyrinchium dimorphum** R. Oliver, Ann. Missouri Bot. Gard. 55: 397. 1969. TYPE: United States. Texas: Val Verde Co., San Felipe Springs, Del Rio, *Warnock & Cameron 9894* (holotype, SMU).

A species of *Sisyrinchium* from Chiapas and Guatemala sometimes identified as *S. scabrum* in herbaria appears to match *S. dimorphum*, which is recorded from Texas and Tamaulipas, Mexico. *Sisyrinchium dimorphum* is of moderate size with relatively short leaves 1–2 mm wide, a branched stem, and persistent fibrous leaf bases, distinctive in *Sisyrinchium*. It clearly belongs in section *Sisyrinchium* and has the blue (to white) campanulate perianth and connate (or nearly connate) filaments that characterize the group. The Mexican *S. scabrum*, typified by *Schiede 1020* (HAL), is similar in general morphology yet it is smaller in stature, has a smaller flower with an unusually small, sparsely pubescent ovary less than 1 mm long, and globose capsules ca. 2 mm in diameter, whereas *S. dimorphum* has a glabrous ovary ca. 2 mm long and larger, somewhat obovoid capsules 4–7 mm long.

4. **Sisyrinchium exalatum** Robinson & Greenman, Amer. J. Sci. 50: 166. 1895. TYPE: Mexico. Oaxaca: Cuilapan Mountains, 7,000 ft., *Smith 52* (not seen). Figure 1C.

When reported from Guatemala and Honduras (Standley & Steyermark, 1952; Molina, 1975), *Sisyrinchium exalatum* was treated as *S. iridifolium* Kunth. We concur in regarding it as different from all other Mesoamerican species but it does not correspond with *S. iridifolium*. This

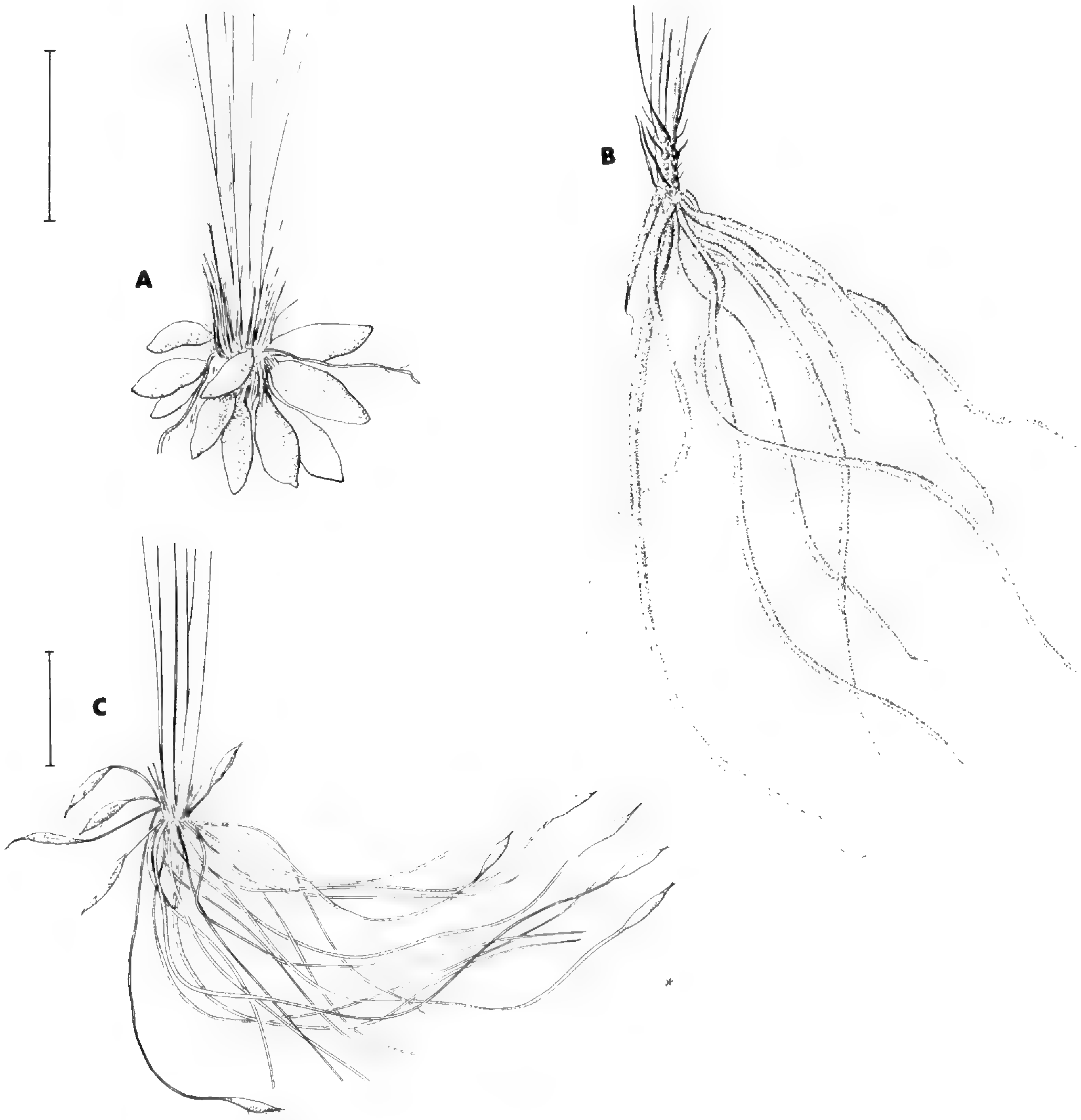


FIGURE 1. Root systems and stem bases.—A. *Sisyrinchium johnstonii.*—B. *S. chiricanum.*—C. *S. exalatum.* Scale bars = 2 cm; top bar for A, B.

is a South American species, the type from Caracas, Venezuela, which is similar to *S. exalatum* in leaf and stem morphology, but the roots are fibrous and not thickened as in the latter and the capsules are relatively small and nearly globose, rather than obovoid-ellipsoid and somewhat trigonous.

In Mesoamerica *Sisyrinchium exalatum* occurs in Mexico (Chiapas), Guatemala, El Salvador, and Honduras. It grows on grassy to lightly wooded slopes at elevations of 1,700–3,700 m.

Additional specimens examined. MEXICO. CHIAPAS: north end of San Cristóbal Las Casas, *Breedlove 6045* (F). EL SALVADOR. MORAZAN: slopes of La Montañita, 1,700 m, *Williams & Molina R. 10429* (F, MEXU, MICH, MO). GUATEMALA. HUEHUETENANGO: between Tojquiá and Caxín bluff, *Steyermark 50141* (F); Sierra Cuchumatanes, *Skutch 1243* (F). QUEZALTENANGO: Santo Tomás, *Steyermark 34825* (F). HONDURAS. COMAYAGUA: abierto de La Piramide, *Molina R. 14357* (F).

6. Sisyrinchium convolutum Nocca, Ticin, Hort. Pl. pl. 1. 1800. TYPE: Guiana "Cap. B. Spei," cultivated in "Hort. Parolin," collector unknown (lectotype, BASSA, here designated). Figure 2A.

Sisyrinchium guatemalense (Baker) Standley & Steyerm., Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 39. 1944; Flora of Guatemala, Fieldiana, Bot. 24:

173. 1952. *S. alatum* var. *guatemalense* Baker, Handbk. Irideae 180. 1892. TYPE: none cited nor located but authentic material at K, annotated by Baker.

Sisyrinchium convolutum is one of the more common Mesoamerican species of *Sisyrinchium*. It can generally be recognized by its moderate height, more or less falcate leaves, winged and branched stems, and large, inflated, trigonous capsules 8–10 mm in diameter. The capsules are glabrous, in contrast to the related and sometimes similar *S. tenuifolium*, in which they are sparsely pubescent. The flowers are yellow and relatively large with tepals to 15 mm long, and the spathes of the inflorescence are distinctively broad, giving it a somewhat inflated appearance. The roots are fleshy and tuberous (Fig. 2A).

Typification of *Sisyrinchium convolutum* has posed some difficulty. The illustration in the protologue matches the species to which the name has been applied here and elsewhere, except for the swollen, almost bulbous base and the roots figured as forming a fibrous mass. A specimen in the herbarium at Bassano del Grappa, Vicenza, where Nocca's types are believed to be housed, matches closely the illustration but lacks a base and roots. Given the stylized depiction of these organs, it seems likely that the artist drew them from imagination. We have chosen the specimen rather than the illustration as lectotype.

Sisyrinchium convolutum was confused with *S. alatum*, a strictly South American species, by Baker (1892) amongst others. Baker used the name *S. alatum* var. *guatemalense* for the plant, as did Standley & Steyermark (1952) in the *Flora of Guatemala* and Molina (1975) in an enumeration of the plants of Honduras. *Sisyrinchium alatum* is probably not closely related to *S. convolutum* and does not have fleshy tuberous roots as do the latter and related species.

7. **Sisyrinchium trinerve** Baker, J. Bot. 14: 267. 1876. *Sisyrinchium bakeri* Klatt, Abh. Naturf. Ges. Halle 15: 378. 1882, nom. superf. pro *S. trinerve*. TYPE: Bolivia. La Paz: vicinity of Sorata, *Mandon 1218* (lectotype, K, here designated); syntypes: *Mandon 1220* (K); *Pearce 87* (K). Figure 2B.

Known until recently only from the high Andes of Bolivia, Peru, Ecuador, Colombia, and Venezuela, *Sisyrinchium trinerve* has now been found in the páramo of Costa Rica above 3,000 m. It is readily recognized by its long, unbranched, nearly terete stem; rigid, narrow, predominantly three-veined leaves; yellow perianth; and ovary at least partly included in the spathes. A lectotype has been designated, since the protologue includes three collections, none designated as a type (Baker, 1876), and no herbarium is mentioned, although the Kew Herbarium is assumed to house the specimens seen by Baker. The collection *Mandon 1218* was chosen, since it comprises the best-preserved and most complete material.

Additional specimens examined. COSTA RICA. LIMON: Cordillera de Talamanca, Kámuk massif, 3,000–3,300 m, *Davidse & Herrera Ch. 29375* (MO). CARTAGO–SAN JOSÉ: Cerro de la Muerte, páramo, along stream, *Heithaus 239* (MO).

8. **Sisyrinchium longispathum** Conzatti, Flora Taxonomica Mexicana 2, 2: 124. 1947. TYPE: Mexico. Oaxaca: *Conzatti 4203* (not seen).

Known from only a handful of collections, all from mountainous areas of the southern Mexican state of Oaxaca, *Sisyrinchium longispathum* has been recorded from a single site in Chiapas, *Breedlove 27156*, 22 km north of Tuxtla Guttierrez. The species appears to be restricted to limestone outcrops and cliffs. *Sisyrinchium longispathum* is distinctive among the Mesoamerican species of *Sisyrinchium* in having filiform leaves and 2–3 inflorescence units per flowering stem, all crowded at the apex and each subtended by a short leaf. The yellow flowers are typical of section *Echthronema*. *Sisyrinchium longispathum* has no close relatives among the Mesoamerican species of *Sisyrinchium*.

9. **Sisyrinchium tenuifolium** Humb. & Bonpl. ex Willd., Enum. Pl. Hort. Berol. 2: 691. 1809, Hort. Berol. 2: 691. 1809. TYPE: Mexico. Without precise locality, *Humboldt & Bonpland s.n.* (lectotype here designated, B—Herb. Willdenow—only microfiche seen).

Sisyrinchium tenuifolium is one of the smaller species of the genus and can usually be recognized by its branched stems, narrow basal leaves 0.5–2 mm wide, and swollen tuberous roots. The bright yellow flowers are more or less typical for section *Echthronema*. It is particularly variable, with plants ranging from slender and unbranched with very narrow leaves to robust with broad leaves and many-branched stems. The latter forms resemble *S. convolutum* fairly closely and

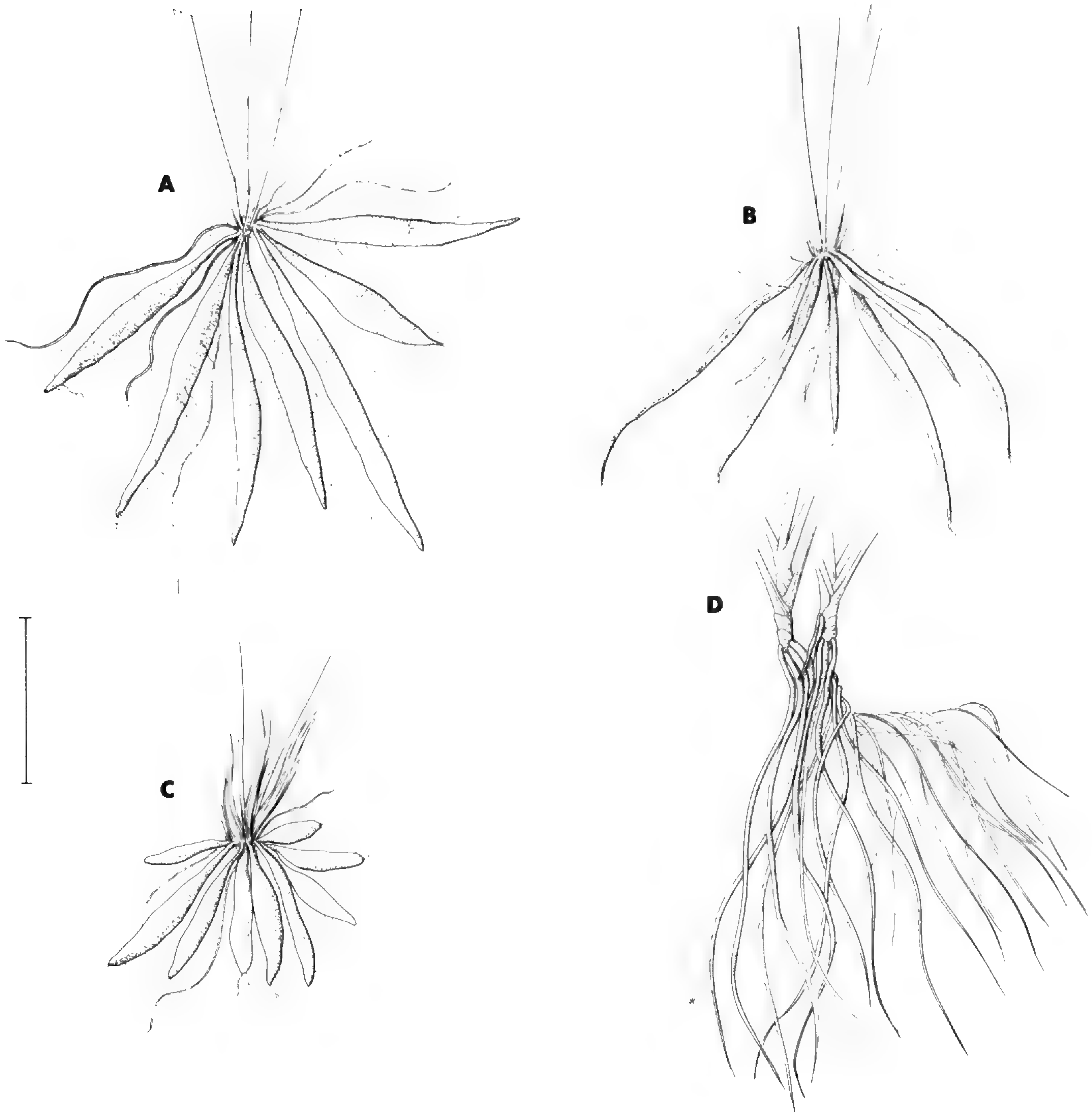


FIGURE 2. Root systems and stem bases.—A. *Sisyrinchium convolutum.*—B. *S. trinerve.*—C. *S. mandonii.*—D. *S. subcernuum.* Scale bar = 2 cm.

can be distinguished by their minutely pubescent ovary and smaller capsule.

The specimen in the Willdenow Herbarium at Berlin is chosen as the lectotype. Other Humboldt and Bonpland specimens of this species may be duplicates of the type collection and thus isolectotyes, as is the illustration in the *Hortus Berolinensis.*

10. Sisyrinchium mandonii Baker, J. Bot. 14: 269. 1876. TYPE: Bolivia. La Paz: vicinity of Sorata, Rancha de Cochipata, *Mandon 1217* (lectotype, K, here designated; isolectotypes, B, not seen, MO photo); syntypes: New Granada (Brazil), *Jurgensen 387* (K); New Granada, *Purdie s.n.* (K). Figure 2C.

Sisyrinchium mandonii has distinctive small, swollen, tuberous roots (Fig. 2C); branched stems; relatively narrow leaves 1–2 mm wide; and unusual large, ellipsoid capsules. It is predominantly Andean, represented by a few collections from Mesoamerica (*Steyermark 30513,* Guatemala; *Allen 698,* Costa Rica; *Woodson & Schery 427,* Panama), all from relatively high altitudes. It was first reported for Mesoamerica by Woodson (1945) from Panama.

Of the three collections cited by Baker in the protologue, *Mandon 1217* is selected as the lectotype as it is in good condition and Baker annotated it as the "Type." There is no indication whether Baker saw any duplicates of this collection but this is certainly possible. The two other collections cited, both at Kew, appear to be the same species, although they are from New Granada in eastern Brazil where *Sisyrinchium mandonii* does not grow. Mislabeling seems likely here.

11. **Sisyrinchium tinctorium** Kunth, Nov. Gen. Sp. 1: 324. 1815. TYPE: Venezuela. T.F. Amazonas: banks of the Orinoco near Esmeralda and the confluence of the Sodomonis, *Humboldt & Bonpland s.n.* (holotype, P).

Sisyrinchium bogotense Kunth, Nov. Gen. Sp. 1: 323. 1815. TYPE: Colombia. Cundinamarca: Bogotá, high plains between Suba and Suacha, *Humboldt & Bonpland s.n.* (holotype, P).

Sisyrinchium tinctorium is a common and well-known species in Mesoamerica. It also occurs in northern South America but is apparently less common there. It is distinguished by unbranched and often broadly winged flowering stems with terminal spathes, pale yellow flowers, and pendent, more or less pyriform capsules. Specimens in fruit are collected most often. The leaves have a characteristic thin, almost membranous texture when dry, and the roots are fibrous. Mesoamerican collections match the type of a second species, *S. bogotense,* particularly well. Our examination of the types of this and the Venezuelan *S. tinctorium* showed the two to be conspecific. The type specimens of *S. tinctorium* have comparatively narrowly winged stems and capsules smaller than most collections of the species. However, a few similar specimens have been collected in Mesoamerica, and variation is continuous from typical *S. tinctorium* to typical *S. bogotense.*

A diminutive species clearly allied to *Sisyrinchium tinctorium* is recognized here as *S. subalpinum,* which is shorter and has narrower leaves and smaller capsules than those of *S. tinctorium.*

12. **Sisyrinchium subalpinum** Henrich & Goldblatt, sp. nov. TYPE: Costa Rica. Limón: Cordillera de Talamanca, Atlantic slope, Kámuk massif, páramo northeast of the main Kámuk peak, elev. 3,000–3,300 m, *Davidse & Herrera Ch. 29294* (holotype, MO). Figure 3.

Plantae 5–12 cm altae, radicibus aliquantum incrassatis gracilibus sed non succulentis, foliis 1–2 mm latis ⅓ ad longius quam caule, floribus flavis stellatis, tepalis 4–5 mm longis subaequalibus, filamentis 1.5 mm longis infra liberis, antheris ca. 2 mm longis, ramis styli ca. 1.5 mm longis, capsulis nutantibus glabris.

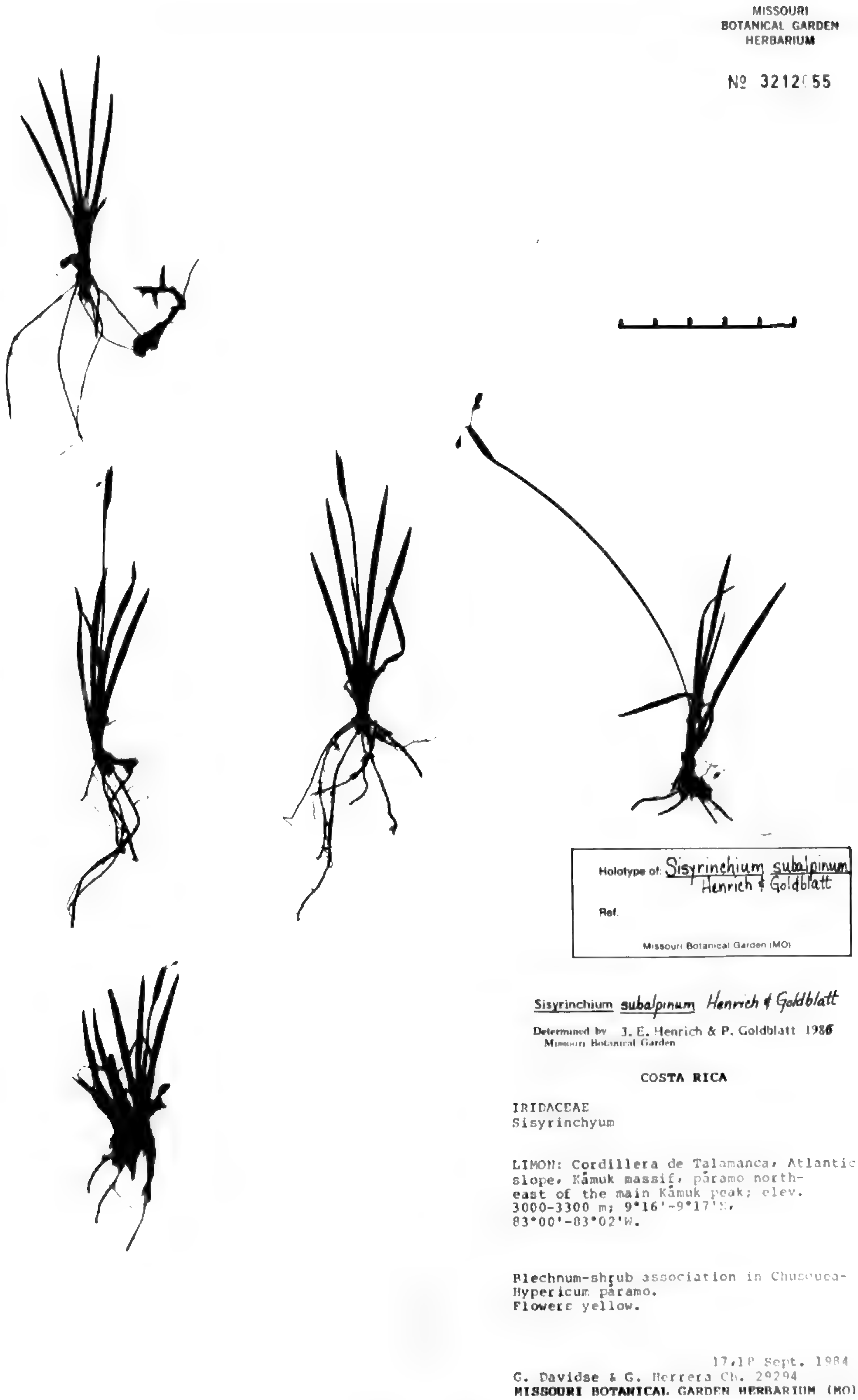
Plants 5–12 cm tall; the roots slender, somewhat thickened but cylindric, not fleshy or tuberous. Leaves several, all basal, ⅓ to as long as the flowering stems, 1–2 mm wide. Flowering stems less than 1 mm wide, unbranched, comprising 1 internode, flattened but barely winged; spathes 11–16 mm, subequal or the outer to ⅓ longer than the inner. Flowers small, yellow, stellate; tepals 4–5 mm long, subequal; filaments 1.5 mm long, free at least above (not seen below); anthers ca. 2 mm long. Ovary about 3 mm long; style branches ca. 1.5 mm long, slender, extending between the stamens. Capsules nodding, mature ones not seen, these probably somewhat pyriform and glabrous; seeds unknown.

Sisyrinchium subalpinum has been recorded at high elevations in Mexico (Chiapas) and in Guatemala and Costa Rica. It is restricted to páramos and moist, high, pine forests.

Additional specimens examined. MEXICO. CHIAPAS: Mt. Male near Porvenir, 3,200 m, *Matuda 4629* (MO). GUATEMALA. SAN MARCOS: along quebrada Canjula between Sibinal and Canjula, Volcán Tacana, 2,200–2,500, *Steyermark 35970* (F). COSTA RICA. CARTAGO: within 200 m of the summit of Cerro Chirriposillo, 3,400 m, *Weston 1574* (MO).

13. **Sisyrinchium subcernuum** (Bickn.) Henrich & Goldblatt, comb. nov. *Hydastylis subcernuus* Bickn., Bull. Torrey Bot. Club 27: 385. 1900. TYPE: Mexico. Baja California Sur: Sierra de Laguna, *Brandegee s.n.* (holotype, CAS). Figure 2D.

Sisyrinchium subcernuum belongs to what may be called the *S. tinctorium* complex, the species of which share similarly textured leaves, unbranched and winged flowering stems, and drooping capsules. The type is from Baja California Sur, and several more collections are known from higher elevations in Mexico. A few of the collections from Belize match the northern Mexico plants closely and must be treated as the same species. *Sisyrinchium subcernuum* can be recognized by its relatively narrowly winged stems, leaves 1–2 mm wide, small flowers with tepals about 6 mm long, and small capsules 6 mm long and 3 mm wide. The outer spathe of



MISSOURI
BOTANICAL GARDEN
HERBARIUM

№ 3212055

Holotype of: Sisyrinchium subalpinum Henrich & Goldblatt

Ref.

Missouri Botanical Garden (MO)

Sisyrinchium subalpinum Henrich & Goldblatt

Determined by J. E. Henrich & P. Goldblatt 1986
Missouri Botanical Garden

COSTA RICA

IRIDACEAE
Sisyrinchyum

LIMON: Cordillera de Talamanca, Atlantic
slope, Kåmuk massif, påramo north-
east of the main Kåmuk peak; elev.
3000-3300 m; 9°16'-9°17'N,
83°00'-83°02'W.

Blechnum-shrub association in Chusquea-
Hypericum påramo.
Flowers yellow.

17,18 Sept. 1984
G. Davidse & G. Herrera Ch. 29294
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

FIGURE 3. Type specimen of *Sisyrinchium subalpinum* (scale = 5 cm).

the inflorescence is longer than the inner, sometimes as much as twice as long.

Additional specimens examined. BELIZE. CAYO: near Millionario, 1,800 m, roadside, *Gentry 7694* (MO); between Millionario and Cuevas, *Dwyer 10821* (MO); vicinity of Cuevas, south of Millionario, ca. 1,900 m, *Croat 23602* (MO).

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NOTES

THE MESOAMERICAN *NEOMARICA* (IRIDACEAE), *N. VARIEGATA* HENRICH & GOLDBLATT, COMB. NOV.

The genus *Neomarica* (Sprague, 1928) comprises some 15 species of evergreen herbs of tropical forests and woodlands. Ravenna (1976) apparently merged it with *Trimezia* Herbert, a treatment we do not accept. The genus is distinctive in having a broadly winged flowering stem, the branches of the inflorescence often subsessile and crowded at the stem apices, and a single large cauline leaf subtending and extending well beyond the inflorescence. *Neomarica* is centered in eastern Brazil but occurs widely in South America, with a single species extending through Mesoamerica into southern Mexico. In several regional floristic treatments for countries in Mesoamerica the native *Neomarica* has been treated as *N. gracilis* (Herbert) Sprague. The type of *N. gracilis,* a figure in *Curtis' Botanical Magazine* (66: tab. 3713. 1839), is believed to have been found in Brazil and it matches an eastern Brazilian species. It does not correspond with the Mesoamerican species in morphology of inflorescence, flower, or seed.

The single Mesoamerican species of *Neomarica* was validly described in 1843 by Martens & Galeotti as *Marica variegata,* based on *Galeotti 5370,* collected in Veracruz, Mexico. The type at the Herbier du Jardin Botanique National de Belgique (BR) matches other collections of *Neomarica* from Mesoamerica in their subsessile inflorescence spathes and flower morphology. *Variegata* is the only epithet available for the Mesoamerican *Neomarica* and the combination is made below.

Neomarica variegata (Martens & Galeotti) Henrich & Goldblatt, comb. nov. *Marica variegata* Martens & Galeotti, Bull. Acad. Roy. Sci. Belgique 10: 112. 1843. TYPE: Mexico. Veracruz: Zacuapán, *Galeotti 5370* (BR, holotype).

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ANN. MISSOURI BOT. GARD. 74: 911. 1987.

TWO NEW *XYRIS* (XYRIDACEAE) FROM THE AMAZON BASIN OF BRAZIL

Among undetermined Xyridaceae sent to the senior author for definitive treatment during 1980–1982 are two from northern Brazil that we agree are new species to be added to the flora of Brazil.

Xyris pectinata Kral, Smith & Wanderley, sp. nov. TYPE: Brazil. Amazonas: Estrada Transamazônica, campina aberta, terreno arenoso, Proj. RADAM, 1 June 1976, *T. R. Bahia 35* (holotype, INPA; isotypes, US, VDB). Figure 1.

Herba perennis densicaespitosa, tenella, glabra; radices graciles. Folia linearia, 4–6 cm longa, erecta vel leviter expansa, vaginis scaporum longiora. Laminae planae vel leviter tortae, 0.9–1.2 mm latae, vaginis 3–5-plo longiores, longitudine distincte multinervosae, ferrugineae vel olivaceae; apices contracti, incurvato-acuti; margines incrassati, minute ciliati; vaginae carinatae, carinibus persaepe minute rufociliatis, incrassatis, lateribus valde longitudine multicostatae, pallide vel intense ferrugineae, marginibus in laminas gradatim convergentibus, ad apicem ligulam acutam 0.5 mm longam fascientes, infime gradatim dilatatae. Vaginae scaporum laxae, plerumque apertae, tortae, basin versus nitidae, a medio ad apicem carinatae, laminis aut similibus laminis foliorum aut brevibus. Scapi subteretes, filiformes, plus minusve spiraliter torti, 1.2–2 dm alti, ca. 0.4–0.5 mm crassi, olivacei, distaliter acute bicostati, costis laevibus. Spicae subglobosae vel late obovoideae, 4.5–6 mm longae, pluriflorae, breviter attenuatae; bracteae steriles 2(–4), pari infimo oblongo, 2–2.5 mm longae, areis dorsalibus linearibus bracteam aequantibus; bracteae fertiles arcte spiraliter imbricatae, late ovatae, obovatae, suborbiculatae, aut reniformes, ca. 3 mm longae, convexae et leviter carinatae, obtusae vel subtruncatae, ad apicem utrinque erosae et ciliatae, scariosae, minute tuberculato-rugulosae, a medio ad basim multo crassiores, nitidae, brunneolae, marginibus effuse et pectinate rigidofimbriatis; area dorsalis ovata, ca. 2–2.5 mm longa, glauca. Sepala lateralia ca. ½ connata, ca. 2 mm longa, inaequilateralia, lobis acutis scariosis, ala carinali angusta, integra. Laminae petalorum anguste obovatae, ca. 1.5 mm longae, ad apicem rotundatae, laceratae, luteolae. Staminodia aliquantum redacta, bibrachiata, brachiis ad apicem breviplumosis, pilis moniliformibus. Antherae oblongae, ca. 0.3–0.4 mm longae, loculis parallelis distinctis; filamenta ca. 0.5 mm longa. Capsula dorsaliventraliter compressa, oblongo-cylindrica, tenuissima, 1.2–1.3 mm longa; placenta basalis. Semen solitarium, lenticulariter oblongo-ellipsoideum, 1–1.2 mm longum, translucidum, pallide luteo-brunneolum, longitudine subtiliter striatum.

Delicate, smooth, cespitose perennial; roots slender. Leaves linear, 4–6 cm long, erect or somewhat spreading, longer than the scape sheaths; blades 3–5 times longer than the sheaths, plane or slightly twisted, 0.9–1.2 mm wide, longitudinally distinctly multinerved, strongly flattened, ferrugineous to olive-green; apices contracted, incurved-acute; margins thickened, minutely ciliate; sheaths carinate, with carinas minutely red ciliate, incrassate, the sides strongly longitudinally nerved, pale to deep red-brown, the margins gradually converging into the blade, at apex producing an acute ligule 0.5 mm long, below gradually dilating. Sheaths of scapes lax, mostly open, twisted, shining toward the base, carinate at the middle, with blades either similar to those of principal leaves or shorter. Scapes subterete, filiform, ± spirally twisted, 1.2–2 dm high, ca. 0.4–0.5 mm thick, olivaceous, distally with sharp, smooth costa. Spikes subglobose to broadly obovoid or short-cylindric, 4.5–6 mm long, several-flowered, short-attenuate; sterile bracts 2(–4), 2–2.5 mm long, with dorsal areas linear and as long as bract, the lowest pair oblong; fertile bracts tightly spirally imbricate, broadly ovate, obovate, suborbicular or reniform, ca. 3 mm long, convex and slightly carinate, obtuse to subtruncate at apex on either side, erose, scarious, minutely rugulose-tuberculate, much thicker from the middle to the base, shining, brownish, with margins effusely, pectinately, and rigidly fimbriate; dorsal area ovate, ca. 2–2.5 mm long, gray-green. Lateral sepals ca. ½ connate, ca. 2 mm long, inequilateral, the lobes acute, scarious, the carinal keel narrow, entire. Petal blades narrowly obovate, ca. 1.5 mm long, apically rounded, lacerate, yellow. Staminodia somewhat reduced, bibrachiate, the branches at apex short-plumose with moniliform hairs. Anthers oblong, ca. 0.3–0.4 mm long, the locules parallel, distinct; filaments ca. 0.5 mm long. Capsule dorsiventrally compressed, oblong-cylindric, very thin, 1.2–1.3 mm long; placenta basal. Seed solitary, lenticularly oblong-ellipsoid, 1–1.2 mm long, filling capsule, translucent, pale yellow-brown, finely longitudinally striate.

Additional material examined. BRAZIL. AMAZONAS: Transamazonas Highway, 53 km W of Aripuanã River; "campina" region, common in open campina of white sandy soil, 27 June 1979, *Cleofé E. Calderón, O. P. Monteiro & J. Guedes 2696* (INPA, US, VDB); Município de Borba, acima de Terra Preta, campina do rio

ANN. MISSOURI BOT. GARD. 74: 912–916. 1987.

Surubím, afluente do rio Abacaxis, 4°29′S, 58°33′W. Campina aberta, areia branca. Erva de 10 cm de altura; flores amarelas, 4 July 1983, *C. A. Cid 4026* (INPA, NY, VDB).

This species is easily distinguished by its fringe of strong though slenderly tapering rigid bristles on the margins of the fertile bracts, nearly separate anther locules, and reduced staminodial condition. It is unusual in its particularly small and thin-walled capsule, this tightly filled by a single large seed.

Xyris calderonii Kral, Smith & Wanderley, sp. nov. TYPE: Brazil. Amazonas: Transamazonas Highway, 9 km W of Rio dos Pombos, ca. 1.5 km E of Igarapé dos Pombos, and ca. 64 km E of the Aripuanã. Common in white sand campina, flowers yellow, 18 June 1979, *Cleofé E. Calderón, O. P. Monteiro & J. Guedes 2549* (holotype, INPA; isotypes, US, VDB). Figure 2.

Planta humilis, annua, praeter inflorescentiam glabra. Radices filiformes. Folia linearia, solum basalia, 3–7 cm longa, flabellate expansa, vulgo vaginis scaporum longiora. Laminae vaginis 2–4-plo longiores, 0.5–1 mm latae, planae, rectae, longitudine paucicostatae, a basi ad apicem compressae, porphyreae vel flavovirentes, apicibus abrupte contractis, incurvato-acutis, marginibus integris, non incrassatis; vaginae carinatae, porphyreae, pluricostatae, praeter costas scariosae, marginibus scariosis stramineis, in laminas gradatim convergentibus aut ad apicem ligulam scariosam curtam latam fascientibus, infime gradatim expansae, acies integrae. Vaginae scaporum laxae, plerumque apertae, rectae, carinatae, laminis aut similis laminis foliorum aut brevibus. Scapi subteretes, filiformes plus minusve spiraliter torti, 5–10 cm alti, 0.4–0.5 mm crassi, distaliter leviter multicostati, costis laevibus. Spicae subglobosae vel late ovoideae, 3–5 mm longae, pluriflorae, obtusae, involucratae. Bracteae steriles 2–4, subdecussatae, villosociliatae; par infimum foliaceum, rigidum, spica 2–5-plo longius, lanceolatum vel oblongum, 2–3 mm longum, carinatum, areis dorsalibus linearibus, viridibus et laminis similibus laminis foliorum sed triangulatis; par intimum ovatum, convexum, scariosum, acutum vel acuminatum, profunde villosociliatum, areis dorsalibus valde papillosis, vulgo sine laminis. Bracteae fertiles late ovatae vel suborbiculatae, 2.5–3 mm longae, valde rotundato-convexae, villosociliati, areis dorsalibus ovatis, valde granulato-papillosis. Sepala lateralia libera, oblonga vel ovata, 2–2.5 mm longa, valde inaequilatera, ala carinali lata, a basi ad medium integra, a medio distante ciliata, apicem versus lacerata. Laminae petalorum late obovatae, ca. 3 mm longae, luteolae, ad apicem late rotundatae et valde erosae. Staminodia bibrachiata, brachiis parce longipenicillatis. Antherae oblongae, sagittatae, ca. 0.5 mm longae; filamenta ca. 0.8–1 mm longa. Capsula matura late obovata, planoconvexa, ca. 1 mm longa, placenta basalia. Semina late ellipsoidea, ca. 0.3 mm longa, pallide brunneola, plus minusve reticulata.

Low annual, smooth except for the inflorescence. Roots filiform. Leaves linear, strictly basal, 3–7 cm long, spreading flabellately, commonly longer than the scape sheaths. Leaf blades 2–4 times longer than sheaths, 0.5–1 mm wide, flat, straight, longitudinally few-costate, flattened from base to apex, brown to yellow-green, the tips abruptly narrowed, incurved-acute, the margins entire, not thickened; sheaths carinate, brown, many-ribbed, scarious except for the ribs, with the thin edges stramineous, gradually narrowing into the blades or apically producing a short, scarious, broad ligule, gradually dilating toward base, the edges entire. Sheaths of scape lax, mostly open, straight, carinate, with blades similar to those of foliage leaves or shorter. Scapes subterete, filiform, ± spirally twisted, 5–10 cm high, 0.4–0.5 mm thick, distally with many low, smooth costae. Spikes subglobose to broadly ovoid, 3–5 mm long, several-flowered, obtuse, involucrate. Sterile bracts 2–4, subdecussate, villous-ciliate, the lowermost pair foliaceous, rigid, 2–5 times longer than the spike, lanceolate to oblong, 2–3 mm long, carinate, the dorsal areas linear, green, with blades similar to those of foliage leaves but triangulate; inner pair (if present) ovate, convex, scarious, acute, very villous-ciliate, the dorsal areas strongly papillate, without blades. Fertile bracts broadly ovate to suborbicular, 2.5–3 mm long, strongly rounded-convex, villous-ciliate, the dorsal areas ovate, strongly granular-papillose. Lateral sepals free, oblong to ovate, 2–2.5 mm long, very inequilateral, with keel broad, proximally entire, at middle distantly ciliate, toward apex lacerate. Petal blades broadly

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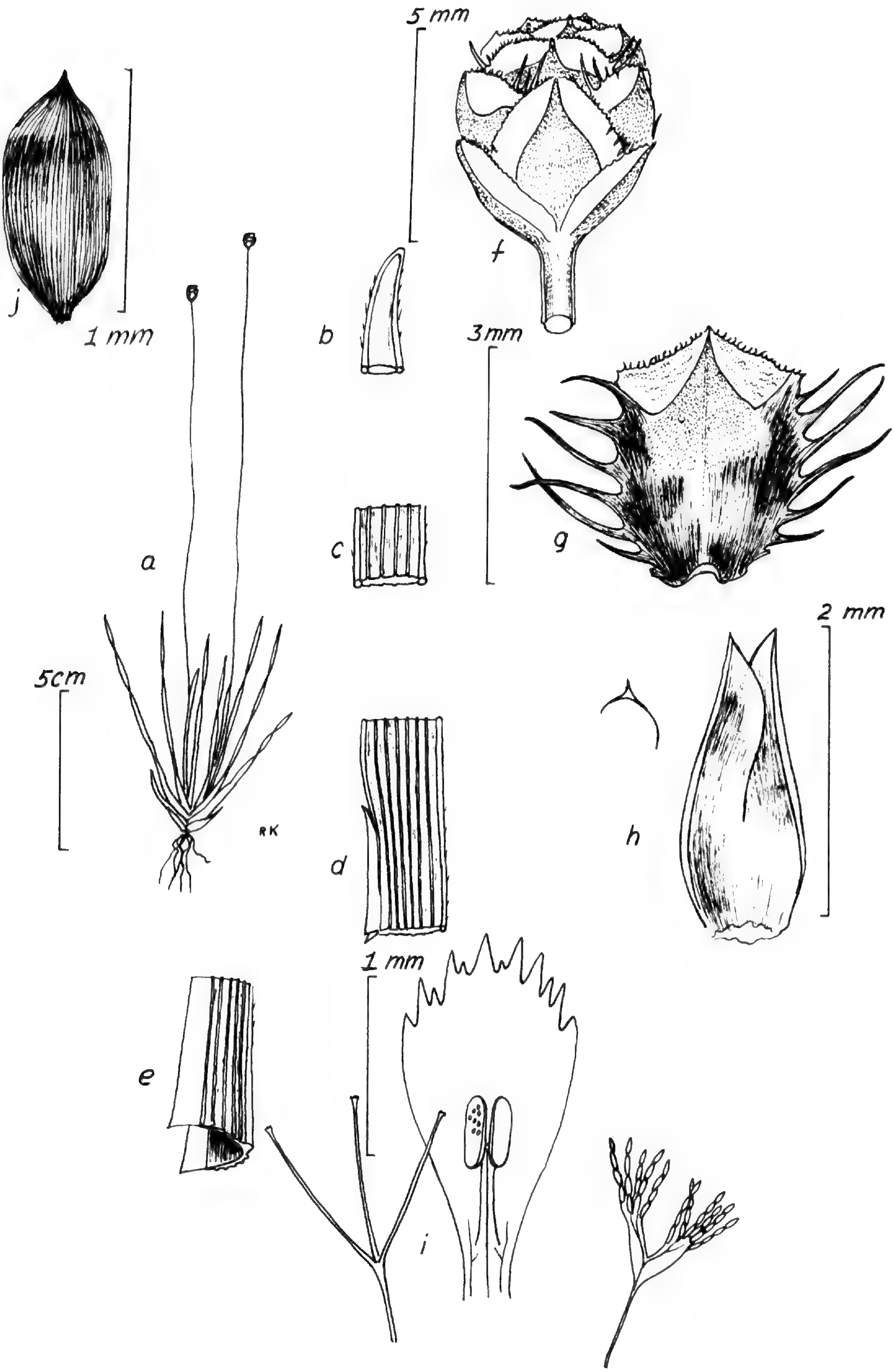
FIGURE 1. *Xyris pectinata* (*T. R. Bahia 35*).—a. Habit sketch.—b. Leaf tip.—c. Sector of mid blade.—d. Blade and sheath junction.—e. Leaf base.—f. Spike.—g. Fertile bract.—h. Lateral sepals.—i. Stylar apex, petal blade, stamen, staminodial apex.—j. Seed.

FIGURE 2. *Xyris calderonii* Kral, Smith & Wanderley (*Calderon et al. 2549*).—a. Habit sketch.—b. Leaf at mid blade.—c. Leaf blade–sheath junction, side (left) and ventral (right) views.—d. Mature spike.—e. Fertile bract.—f. Petal blade and stamen.—g. Stylar apex, staminode.—h. Lateral sepal, capsule.—i. Seed.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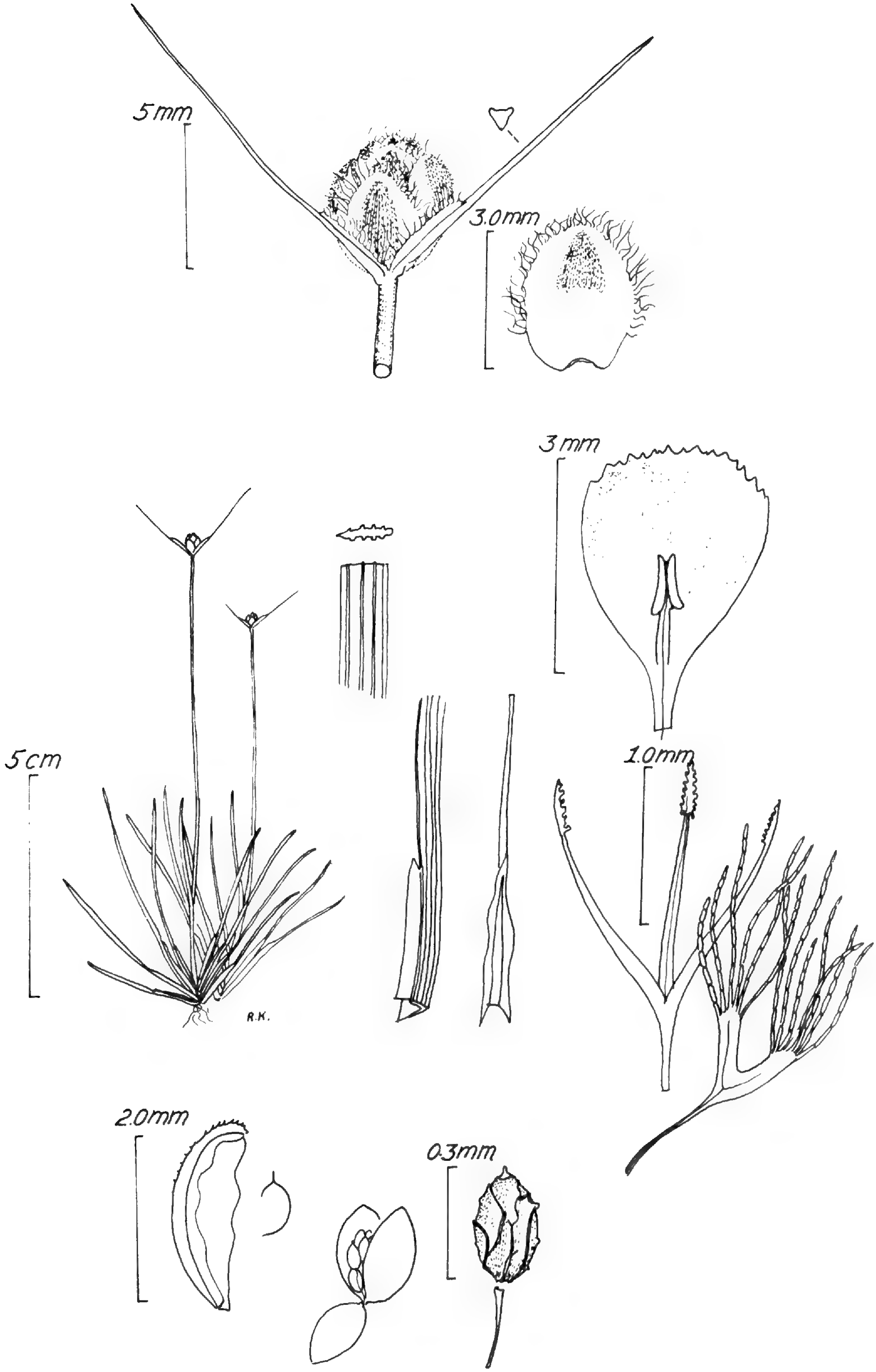
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obovate, ca. 3 mm long, yellowish, broadly rounded and strongly erose at apex. Staminodia bibrachiate, the branches sparsely long-penicillate. Anthers oblong, sagittate, ca. 0.5 mm long; filaments ca. 0.8–1 mm long. Mature capsule broadly obovoid, plano-convex, ca. 1 mm long, the placenta basal. Seed broadly ellipsoid, ca. 0.3 mm long, pale brown, ± reticulate.

There is no question that the affinities of this little plant are with *X. uleana* Malme; in the production of narrow leaf blades it is most similar to var. *angustifolia* Lanj., which also sometimes produces long-tipped basal bracts. However, the lateral sepals are smaller and show a somewhat different keel configuration; the dorsal areas are consistently long excurrent to produce acicular blades several times longer than the subtended spike. The scapes are uniformly terete.

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A NEW SPECIES OF *PIPER* (PIPERACEAE) FROM CENTRAL AMERICA

Piper calcariformis M. Tebbs, sp. nov. TYPE: Costa Rica. Alajuela: Finca Los Ensayos, NW of Zarcero, 850 m, *Croat 43546* (holotype, MO; isotype, BM). Figure 1.

Frutex 1–2 m altus. Folia oblongo-ovata apice acuta basin cordata lobis interdum inaequalibus. Petiolus vaginatus spica pendula, bracteis triangularibus, basin versus longe calcariformibus.

Shrub 1–2 m high, the stems shortly pubescent. Leaves 16–24(–28) cm long, 10–17(–21) cm wide, ovate-oblong, glabrous or with short sparse hairs on upper surface, pilose on veins beneath, the apex acute, the base cordate and sometimes with one lobe slightly longer than the other; secondary veins 4–6, arcuate-ascending towards apex; petiole sheathing, pubescent, 4–9 cm long. Inflorescence pendulous, 10–18 cm long, 7–10 mm wide in fruit, the peduncles 2–4 cm long. Floral bracts 2 mm long, triangular, sparsely to densely pubescent with lower part elongated into a long spurlike process. Anthers 0.8–1 mm long, dehiscing laterally; filaments 1–1.2 mm long. Style 3–4 mm long; stigmas 3, recurved. Fruit 1–1.5 mm long, round-oblong.

Additional specimens examined. PANAMA. BOCAS DEL TORO: *McPherson 7362, 8658* (MO). CHIRIQUÍ: *Knapp & Vodicka 5519* (MO); *Correa et al. 2113* (MO). VERAGUAS: *Croat 27695, 27726* (MO); *Mori & Kallunki 2586, 3891, 3896* (MO).

Distribution. In moist forest from 400 to 1,200 m in the Cordillera Central in Costa Rica and in the Serranía de Tabasara in Panama. Only one collection from Costa Rica, the majority of specimens coming from Panama.

Piper calcariformis is most closely related to *P. sagittifolium* C. DC. and shares similarities of inflorescence, bract and fruit shape. However, it can be separated easily from the latter by its ovate-oblong as opposed to sagittate leaves, its much longer, pendulous inflorescence, and by its styles with three stigmas rather than two as in *P. sagittifolium.* Both of these species can be separated from the rest of *Piper* by their distinctive inflorescences with unusually shaped bracts. They are related to the large-leaved pipers with long pendulous inflorescences of section *Macrostachys* Miquel.

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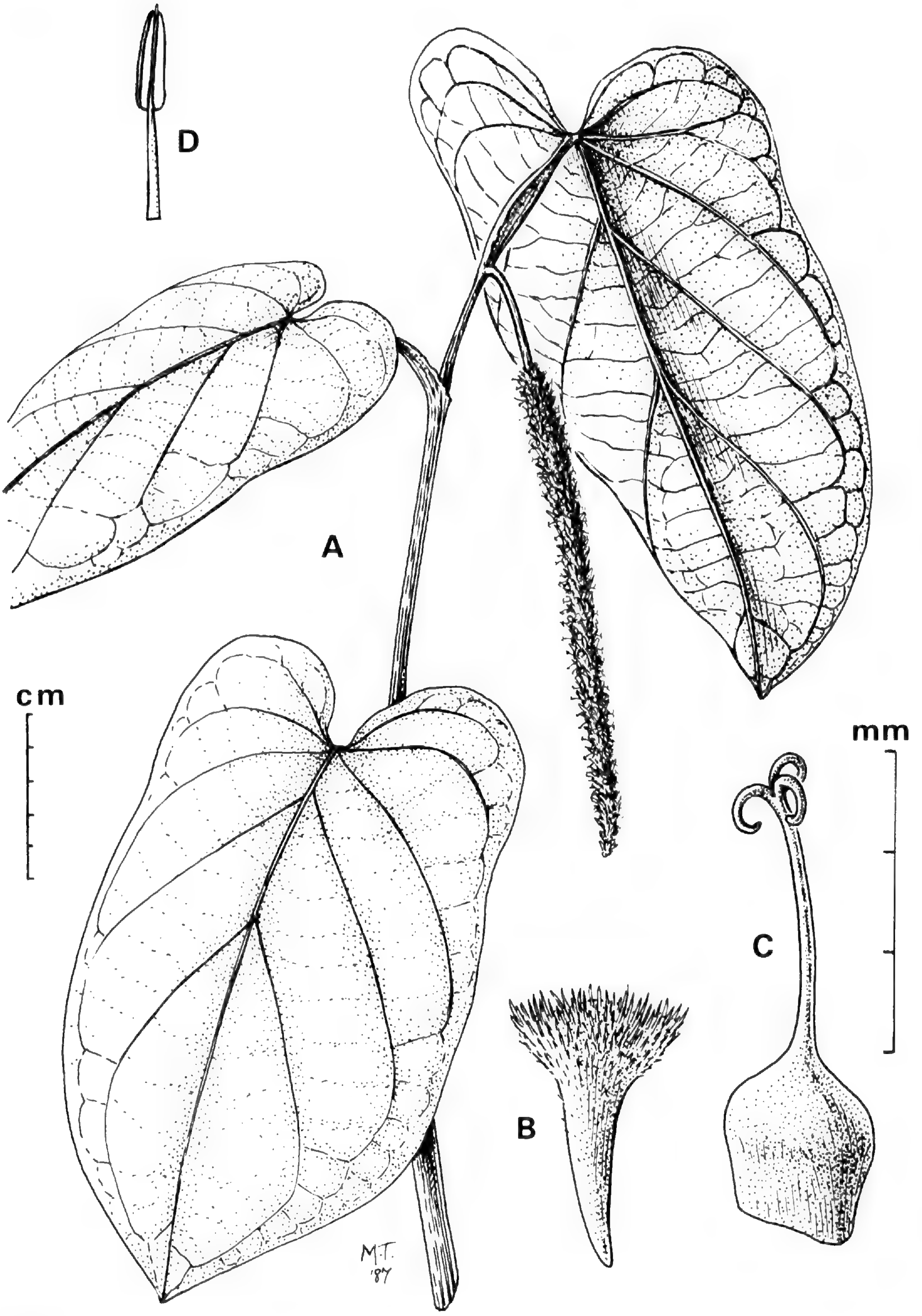

Figure 1. *Piper calcariformis* (*Croat 43546*).—A. Habit.—B. Bract.—C. Fruit.—D. Stamen.

A NEW SUBSPECIES OF *QUARARIBEA FUNEBRIS* (BOMBACACEAE) FROM NICARAGUA

Recent monographic work has clarified the relationships among members of *Quararibea* Aublet and *Matisia* Humb. & Bonpl. (Bombacaceae) in the northern Neotropics (Alverson, 1986). Taken together, these two genera consist of at least 60 species of trees found in wet or moist, primary forests from central Mexico to Brazil. Fieldwork in Mexico, Nicaragua, and Costa Rica has resolved the taxonomy of some of the more problematic species belonging to *Quararibea* sensu stricto (subgenera *Archiquararibea* and *Lexarza* of Vischer, 1920), including *Quararibea funebris* (Llave) Vischer. This widespread species, named from Mexican material (La Llave & Lexarza, 1825; Standley, 1923), includes two subspecies in Nicaragua, subsp. *funebris* and subsp. *nicaraguensis.* The typical subspecies occurs in moist to wet lowland and mid-altitude forests from central Mexico to northwestern Costa Rica, including forests at altitudes of 300–800 m within Nicaragua. The diminutive subspecies, first described here, occurs above 1,200 m in highland forests of a restricted area of northwestern Nicaragua.

Quararibea funebris (Llave) Vischer subsp. **nicaraguensis** Alverson, subsp. nov. TYPE: Nicaragua. Matagalpa: Finca Santa María de Ostuma, Cordillera Central de Nicaragua, 1,400 m, 18 Jan. 1965 (fr), *L. O. Williams, A. Molina R., T. P. Williams, D. N. Gibson & C. Laskowski 27978* (holotype, WIS; isotypes, F, NY, US). Figure 1.

Arbor, 5–25 m alta. Folia obovato-elliptica, 7–22 cm longa, 2–10 cm lata, pilorum caespitibus densis infra in venarum secundarium axillis exceptis glabrata vel sparsim pubescentia. Flores regulares, solitarii vel pauci consociati. Pedicellus 11–15 mm longus, 3 bracteolis triangularibus in medio. Petala spathulata, 15–16 mm longa, 5–6 mm lata, alba. Columna staminalis 16–22 mm longa, 24(–30?) thecis in apice fasciculatis. Stylus 17–26 mm longus. Fructus drupaceus, subglobosus, in sicco 20–25 mm longus et 14–18 mm diametro, calyce persistenti accrescenti in sicco rugoso et 11–13 mm longo per ⅓–½ longitudinis inclusus. Subspecies typicae similis sed praeter pedicellos saepius longiores in omnes partes minor.

Tree, 5–25 m tall, 25–30 cm dbh, monopodial; *trunk* smooth and slightly fluted; *branches* verticillate, diverging horizontally from trunk and drooping along distal half; *bark* pale and relatively smooth, not conspicuously peeling; *stipules* deciduous, narrowly triangular, 2–5 mm long, 1 mm wide, densely lepidote with fimbriate-peltate trichomes. *Leaves* simple (unifoliolate?), alternate, entire; *petioles* 7–18 mm long, including the inconspicuous proximal and distal pulvini, green, densely lepidote; *blades* entire, obovate to elliptic, the apex acute to acuminate, the base acute to rounded, 7–22 cm long, 2–10 cm wide, dark green, lustrous and glabrate above, medium green, duller, and glabrous to sparsely pubescent below, firm-chartaceous; *veins* prominent below; *secondary veins* 5–7 per side, pinnate, arched, loosely brochidodromous, bearing conspicuous domatia in their axils; *tertiary veins* reticulate. *Flowers* solitary or few together; *pedicels* 11–15 mm long, densely puberulent with pale yellowish-brown echinate-stellate trichomes, bearing 3 bracteoles, these broadly triangular, ca. 1.5 mm long, 1.5 mm broad at base; *calyx* infundibuliform, irregularly lobed at summit, 9–11 mm long, pale green, densely pubescent with pale stellate-echinate trichomes without, densely sericeous with long, pale, ascending trichomes within, the apical lobes bluntly triangular, to 3 mm long; *petals* spathulate, recurved at anthesis, 15–16 mm long, 5–6 mm wide, white when fresh, usually becoming sepia-brown when dried, moderately to densely pubescent with pale, lax, stellate trichomes on both sides; *staminal column* cylindric, dilated towards the toothed summit, 16–22 mm long, 1.5 mm diam., densely pubescent with pale, stellate trichomes for most of its length, becoming puberulent towards apex, bearing 24(–30?) thecae, the 5 apical teeth inconspicuous, ca. 0.5 mm long; *thecae* distinctly paired, ca. 2 mm long, 1 mm wide; *style* filiform, 17–26 mm long, exceeding the staminal column by 1–2 mm, tomentose; *stigma* capitate, ca. 2 mm diam. *Fruits* drupaceous, broadly elliptic to slightly obovate, bluntly mammillate and briefly apiculate with persistent style base, 20–25 mm long, 14–18 mm diam. when dry, 1- or 2-seeded; *exocarp* green, densely tomentose with appressed, pale, brown, stellate-echinate trichomes, these imparting a brown color when dried; *mesocarp* fibrous-fleshy, without conspicuous taste or odor in fresh, unripe fruits; *endocarp* bony-fibrous; *pedicels* of

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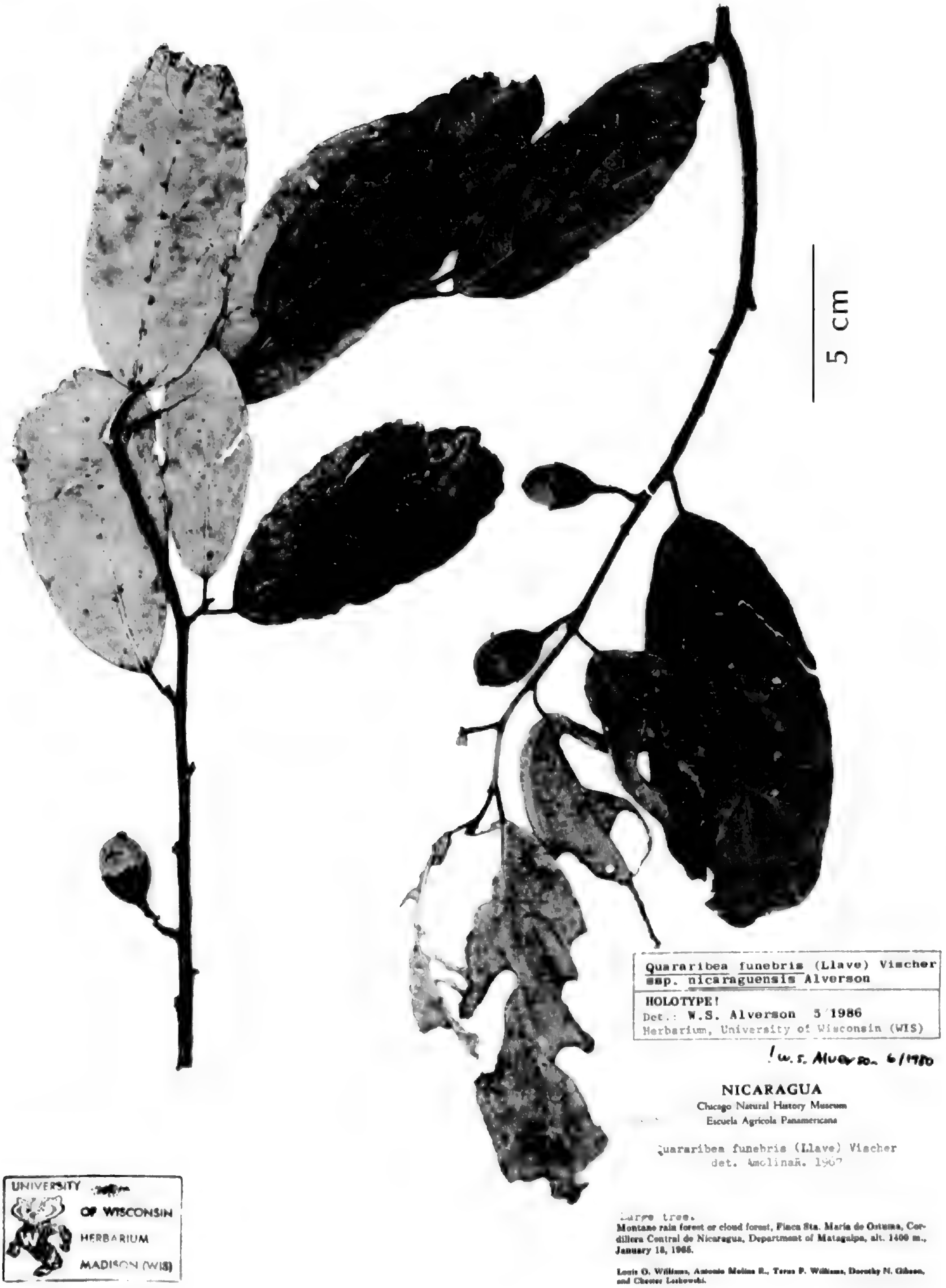

Quararibea funebris (Llave) Vischer
ssp. nicaraguensis Alverson

HOLOTYPE!
Det.: W.S. Alverson 5/1986
Herbarium, University of Wisconsin (WIS)

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NICARAGUA
Chicago Natural History Museum
Escuela Agricola Panamericana

Quararibea funebris (Llave) Vischer
det. AmolinaR. 1967

Large tree.
Montane rain forest or cloud forest, Finca Sta. Maria de Ostuma, Cordillera Central de Nicaragua, Department of Matagalpa, alt. 1400 m., January 18, 1966.

Louis O. Williams, Antonio Molina R., Terua P. Williams, Dorothy N. Gibson, and Chester Laskowski.

FIGURE 1. Holotype of *Quararibea funebris* subsp. *nicaraguensis*.

fruits slender, 10–19 mm long, bearing 2–3 persistent bracteoles near middle; *calyx* persistent, accrescent, cupulate, enclosing fruits for ⅓–½ their length, longitudinally finely rugose when dry, wingless, green, with vestiture as in flowering condition, the summit erose or irregularly toothed. *Seeds* 2, or 1 by abortion, ca. 13 mm long, 8 mm diam., consisting mostly of pale cotyledonal tissue; *testa* thin, dark brown. *Seedlings* unknown when young, probably hypogeal and cryptocotylar, when older bearing leaves smaller and more acuminate than those of mature plants.

Paratypes. NICARAGUA. ESTELÍ: El Zacatón, "El Delirio" camino a la laguna de Miraflor, 13°13′N, 86°14′W, 1,400 m, 11 Jan. 1984 (fr), *Moreno 22676* (MO, WIS). JINOTEGA: entre Santa Lastenia y entrada a Aranjuez, 13°02′N, 85°55′W, 1,200–1,250 m, 19 Jan. 1984 (fr), *Sandino 4704* (MO); Finca Aventina, in sierra east of Jinotega, 1,400–1,500 m, 23 June 1947 (st), *Standley 10002* (F); region of Las Mercedes, sierra east of Jinotega, 1,200–1,500 m, 3 July 1947 (st), *Standley 10746* (F); vicinity of Finca San Roque, sierra east of Jinotega, 1,300–1,500 m, 5 July 1947 (fr), *Standley 10856* (F, US). MADRIZ: Cerro Volcán Somoto (Volcán Tepesomoto), 13°26′N, 86°35′W, 25 Sep. 1980 (fl), *Moreno 2892* (MO). MATAGALPA: vicinity Santa María de Ostuma, on flanks of Cerro El Picacho, immediately east of Hwy. 3, ca. 9 km north (by air) of Matagalpa, 13°00′N, 85°55′W, ca. 1,500 m, 1 Dec. 1982 (fl buds, fr), *Alverson & Moreno 1982* (BR, CR, F, MEXU, MO, NY, PMA, US, WIS); (seedling), *1984* (MO, NY, WIS); (st), *1985* (WIS); 1,420 m, 5 Jan. 1984 (fr), *Gentry, Stevens & Moreno 44034* (MO); 1,350–1,585 m, 30 Aug. 1985 (fl), *Nee 27660* (MO, WIS); Fuente Pura a 11 km de Matagalpa carretera a Jinotega, 13°01′N, 85°56′W, 1,400–1,450 m, 7 Oct. 1980 (fr), *Moreno 3381* (MO, WIS); 13°00′N, 85°55′W, 1,400–1,480 m, 1 Dec. 1982 (fr), *18951* (MO) (same locality as *Alverson & Moreno 1982*); Cordillera Dariense, Santa María de Ostuma, 10 km N of Matagalpa, 1,500 m, 12 Aug. 1977 (fl), *Neill 2323* (MO); 26 Nov. 1977 (fr), *3005* (BM, MEXU, MO); 1,500 m, 15 Jan. 1963 (fr), *Williams, Molina R. & Williams 23952* (F, G, NY, S, US); between Hda. La Harmonía and Cerro La Carlota, ca. 12°59′N, 85°53′W, 1,200–1,300 m, 10 Dec. 1983 (fr), *Stevens 22574* (MO).

Quararibea funebris subsp. *nicaraguensis* is known only from the highlands of northwestern Nicaragua in the departments of Estelí, Jinotega, Matagalpa, and Madriz. It is common to locally extremely abundant (A. Gentry, pers. comm.) in primary, upland wet forests and cloud forests between 1,200 and 1,600 m. Flowering occurs during August and September, and fruiting takes place October through January, indicating a phenology similar to that of the typical lowland subspecies.

Although very similar, this new subspecies is morphologically distinct from *Quararibea funebris* subsp. *funebris*, being smaller in nearly all respects (Table 1). Its fruiting pedicels, however, tend to be longer than those of subsp. *funebris*. The two subspecies can be easily distinguished by their floral measurements. When in fruiting condition, the calyces provide the most obvious key character; they cover half or less of the mature fruit of subsp. *nicaraguensis*, as opposed to more than half in subsp. *funebris*.

TABLE 1. Comparison of the subspecies of *Quararibea funebris* in Nicaragua. Material is from Nicaragua with the exception of flowers of subsp. *funebris*, which are from northwestern Costa Rica.

	Subspecies	
Character	*nicaraguensis*	*funebris*
Leaf length	77–221	145–289
Leaf width	27–104	62–125
Petiole length	7–18	15–27
Floral pedicel length	11–15	13–14
Floral calyx length	9–11	18–20
Petal length	15–16	33–40
Staminal column length	16–22	33–34
Style length	17–26	35–36
Fruiting pedicel length	10–19	9–17
Fruiting calyx length	11–13	18–26
Fruit length	20–25	25–30

Measurements in mm.

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