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TAXONOMIC STUDIES IN THE PIPERACEAE—I. THE PEDICELLATE PIPERS OF MEXICO AND CENTRAL AMERICA (PIPER SUBG. ARCTOTTONIA)

ALLAN J. BORNSTEIN[1]

The taxon *Arctottonia,* originally proposed by Trelease as a new genus to accommodate the northern element of Neotropical pipers with pedicellate flowers (*Ottonia*), is recognized as a distinct subgenus within the highly heterogeneous *Piper.* The racemose inflorescence upon which *Arctottonia* and *Ottonia* were previously allied is considered to be a homoplasious character (Callejas, 1986) that occurs in three distinct evolutionary lineages. As currently circumscribed, *Piper* subg. *Arctottonia* is distinguished by its pedicellate flowers arranged in a loose raceme, its tendency toward adnation of the stamens to the ovary, its palmate-veined leaves, and its distribution from central Mexico to northern Central America. Fourteen species are recognized, of which five are described as new. A key is given for the subgenus; descriptions, illustrations, and specimen citations are provided for the species; and an argument is presented for recognizing *Arctottonia* and all other segregates from *Piper* sensu lato at the rank of subgenus.

The Piperaceae Agardh are a large pantropic family of well over 3000 described species, with major centers of diversity in northern South America and Central America in the New World, and Malaysia in the Old (Yuncker, 1958).

The family can be easily recognized on a gross morphological basis. The leaves are always simple and, with rare exceptions, entire; they are usually alternate, although the arrangement is somewhat variable. The flowers are minute, are perfect or unisexual (the plants then typically dioecious), and lack a perianth. The inflorescence (or infructescence) is a compact (or sometimes loose) spike or rarely a raceme. Each flower is subtended by a small, variable bract, and the ovary is unilocular with a single basal ovule. The fruit is a small drupe.

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Despite a considerable amount of attention during the past century and a half, the Piperaceae continue to be taxonomically difficult and enigmatic. The present chaotic taxonomic state of the family is largely a result of its unfortunate past treatment. Nowhere is this more true than for *Piper* L. sensu lato, which is perhaps the largest genus of flowering plants devoid of a natural classification.

The primary reason for this situation is the large number of described species, conservatively estimated at over 1500 for *Piper* alone. Many of these species, especially those established since the turn of the century, have been described without any reference to their putative position within the genus. Several factors have contributed to this artificially inflated species number. First, the flowers are small and the vegetative and floral morphology is uniform throughout the genus (Burger, 1972). Second, species descriptions have often been based on insignificant characters of little taxonomic value, or on fragmentary material often lacking flowers or fruits essential for identification. Third, new species are established based on their occurrence in a distinct political distributional unit, despite their similarity with previously described species. Both C. de Candolle and Trelease (two individuals who had a significant impact on the taxonomy of the family) were especially guilty in this respect, a situation that Standley and Steyermark (1952, p. 229) discussed as follows:

> In later years, however, [C. de Candolle], with more abundant material for study, became too enthusiastic in proposing new continental species, and named a very large number without apparent reference to West Indian species, presumably assuming that they must be new because of their remote occurrence. Trelease believed that the species of Piperaceae were extremely local, as many of them are. However, he went still further, and assumed that those of one country were distinct from all those (except a very few widespread and more or less "weedy" species) of the adjoining countries. Such narrow limits of distribution are not found in any other group of Central American plants, nor, in the opinion of the writers, does it exist in the Piperaceae. In his recognition of limiting geographic units, Trelease was scarcely consistent. He treated the whole of Mexico as one Piperaceous unit, and each of the Central American countries as a unit of equal standing. Now each of these Central American countries is about equal in area to one of the states of Mexico, obviously making such an alignment improbable.

Within the last 25 years there have been significant advances toward combating the nomenclatural problems created by this overabundance of names. Much of this progress has been achieved through floristic treatments of specific geographic and/or political units (e.g., in the Neotropics, Burger, 1971; Yuncker, 1972, 1973, 1974; Howard, 1973; Steyermark, 1984). Less frequent have been revisions of small segregates from *Piper* sensu lato (Steyermark, 1971; Smith, 1975). While the former method is perhaps more significant from a nomenclatural standpoint in that it tends to include far more taxa (and therefore more names), the latter can accomplish similar nomenclatural results while also addressing questions concerning evolutionary relationships within *Piper*. This paper, which treats the pedicellate pipers of Mexico and Central America, uses the latter approach. The goal is to provide a much-needed update of the taxonomy of this natural group of closely related species, with the ultimate intention of making progress toward a phylogenetic classification of *Piper* sensu lato.

TAXONOMIC HISTORY

Trelease (1921) considered the pedicellate pipers of Mexico and Central America as the North American counterpart to a group of primarily South American species known as *Ottonia* Sprengel or *Piper* subg. *Ottonia* (Sprengel) C. DC. In 1930 he segregated these same northern constituents as the new genus *Arctottonia* on the bases of their distinctive palmate leaf venation, their tendency toward adnation of the stamens to the ovary, and their disjunct distribution.

The first arctottonioid piper was described by Opiz (1828) as *Piper stipulaceum.* Kunth (1839), segregating genera from *Piper* sensu lato, transferred this species to his new genus *Enckea,* even though he characterized *Enckea,* in part, by sessile flowers and fruits.

Miquel (1843–1844), in his monographic treatment of the Piperaceae, shared Kunth's opinion that *Piper* should be divided into several small genera and consequently maintained the placement of *Enckea stipulacea* (Opiz) Kunth. Either Kunth and Miquel did not believe Opiz's original description to be correct with respect to the pedicellate fruits, or they simply chose to ignore this fact. The only other significant nomenclatural change before C. de Candolle assumed the mantle of authoritative monographer of the Piperaceae was Presl's (1851) first combination of an arctottonioid piper in the genus *Ottonia,* creating *Ottonia stipulacea* (Opiz) Presl.

In his monograph for the *Prodromus* (1869), De Candolle relegated all of Kunth's and Miquel's segregate genera to sectional status and/or submerged them in synonymy. His sect. *Enckea,* for example, comprised Kunth's genus *Enckea* and Miquel's genus *Callianira.* His circumscriptions allowed for the inclusion of both pedicellate- and sessile-flowered species in the same section, because he placed more emphasis on the number of stamens and the position of the inflorescence (axillary vs. terminal and leaf opposed). This resulted in the assignment of newly described arctottonioid pipers to his sects. *Enckea* (Kunth) C. DC. (*Piper muelleri* C. DC.) and *Steffensia* (Kunth) C. DC. (*P. neesianum* C. DC.). He also (p. 367) placed *P. stipulaceum* in his category of "species non satis notae, amenta oppositifolia, flores hermaphroditi, americanae," even though Presl's 1851 description of *Ottonia stipulacea* is rather extensive.

For the next 50 years little change in the taxonomy of *Piper* occurred with respect to taxon *Arctottonia.* During this period only one arctottonioid piper was described; *P. yucatanense* was established by De Candolle and assigned to his sect. *Enckea.* Indeed, since the taxonomy of *Piper* remained largely in the hands of De Candolle, his conservative viewpoint prevailed. Even in his later years, De Candolle's static views changed significantly only to the extent that he recognized *Ottonia* as a distinct section that combined the pedicellate members of his sects. *Enckea* and *Steffensia.*

With the influx of material collected in Mexico and Central America during the beginning of the twentieth century, new arctottonioid species were discovered. De Candolle described four such Mexican species, all of which were placed in section *Ottonia,* in 1920 (published posthumously). In his final treatise (De

Candolle, 1923), the key to all known piperaceous taxa, eight species referable to *Arctottonia* were included in *Ottonia,* which he now treated at the level of subgenus.

Trelease (1934, 1935), subsequent to his creation of *Arctottonia,* described three additional species of the genus, all supposedly new to science. Aside from *A. stipulacea* (Opiz) Trel., no other valid combinations have ever been published in *Arctottonia.* In fact, Lundell (1937) soon transferred two of the "new" species to *Piper* because he did not consider the characters used to distinguish *Arctottonia* significant enough to warrant its continuation as a distinct genus.

This sentiment regarding the status of *Arctottonia* has since prevailed. Yuncker (1950) eventually submerged *Arctottonia* under *Ottonia,* stating (p. 71) "it is not believed that the differences upon which Trelease based the genus *Arctottonia* are of generic status." Trelease and Standley (*in* Standley & Steyermark, 1952) did describe another arctottonioid piper as *Piper guazacapanense* but indicated in the key that it belonged, along with two other taxa, to subg. *Arctottonia.*

CLASSIFICATION OF PIPER SENSU LATO

A recent cladistic analysis of the tribe Pipereae (Callejas, 1986 and pers. comm.) confirmed the notions of Kunth and Miquel, among others, that *Piper* sensu lato is a highly heterogeneous assemblage from which segregate taxa should be recognized. One such group is the arctottonioid pipers of Mexico and Central America. Although they share a relatively unusual feature (pedicellate flowers) with *Ottonia,* which undoubtedly led De Candolle, Yuncker, and others to consider them as representatives of the same taxonomic unit, it is now apparent that the arctottonioid pipers are more closely related to another group of Neotropical pipers (i.e., sect. *Enckea*), with which they share the campylodromous or acrodromous leaf venation and a tendency toward adnation of the stamens to the ovary. The racemose inflorescence that had so influenced the thinking of previous monographers is apparently a parallel development that has arisen in three different lineages within *Piper* sensu lato (*Arctottonia, Ottonia,* and *Zippelia* Blume, a monotypic Old World taxon).

From the brief history presented in the previous section, it should be apparent that the hierarchical status of segregates from *Piper* sensu lato remains unresolved. The following comments constitute an argument for recognizing these groups at the level of subgenus.

On the one hand, all currently accepted segregates (i.e., *Lepianthes* Raf. (= *Pothomorphe* Miq.), *Macropiper* Miq., *Sarcorhachis* Trel., and *Trianaeopiper* Trel.; excluding, for the moment, *Ottonia,* which has recently been revised by Callejas (1986)) have been recognized at the generic level. This has served to emphasize the distinctiveness of their axillary (or seemingly axillary) inflorescences in contrast to the terminal, leaf-opposed inflorescences for the remaining taxa within *Piper.* However, if the development of axillary inflorescences is such an important evolutionary step, then one would expect these four taxa to be fairly closely related to one another, perhaps defining a distinct lineage within *Piper* sensu lato. To the contrary, current evidence (see Callejas, 1986) indicates that these groups are quite distantly related and that the development of an axillary inflorescence is another example of evolutionary parallelism, similar to the situation for pedicellate flowers. Therefore, if one recognizes these four groups as genera, then all other segregates from *Piper* sensu lato must be similarly treated. This, of course, is a valid option, but one that carries with it enormous nomenclatural consequences (hundreds of new combinations would be required) in a family already burdened by such problems.

A more practical option is to consider all segregates as subgenera within *Piper*. This system will not only be the most convenient but will also reflect the evolutionary relationships within *Piper* sensu lato as accurately as a classification at the generic level. The level of recognition here is not nearly as important as recognition itself. As long as the classification system is a relatively stable one with inherent meaning, the hierarchy within that system becomes merely a matter of choice. Therefore, I have chosen to recognize the pedicellate pipers of Mexico and Central America as *Piper* subg. *Arctottonia,* which agrees with the choice of Callejas (1986 and pers. comm.) for the ottonioid pipers (*Piper* subg. *Ottonia*) and thereby initiates what we hope will be the beginning of a more stable and meaningful infrageneric classification for the genus *Piper.*[2]

HABITAT AND GEOGRAPHIC DISTRIBUTION

Members of the genus *Piper* are common understory shrubs or small trees of various habitats but are best represented in lowland tropical rainforests. As such, most species prefer moist forest formations below 1000 m alt. Nevertheless, a considerable number of them, including the majority of species in *Piper* subg. *Arctottonia,* can tolerate the seasonally dry subdeciduous to deciduous tropical forests.

With a few notable exceptions the species in subg. *Arctottonia* occupy relatively open, often disturbed sites at the edge of primary forests, being frequent inhabitants of steep banks and stream sides. Because they are able to withstand these disturbed conditions, and with the increased destruction of the tropical forests by man, many of these species are able colonists of what would be considered second-growth forests.

The arctottonioid pipers can be subdivided geographically into two major groups. The vast majority of species occur in a zone between the coast and the foothills of the western Sierra Madre, from Sinaloa in the north to Chiapas and Guatemala in the south. The remaining three species occupy the eastern portions of Mexico, within or east of the Sierra Madre Oriental from central Veracruz to the Yucatán Peninsula, continuing into neighboring Honduras, with isolated collections from the lowlands of southeastern Nicaragua and central Panama. This geographic distinction is highly correlated with leaf shape: broadly ovate to suborbiculate and commonly cordate at the base in species from the "western assemblage," and narrowly ovate-lanceolate or narrowly elliptic with a long-acuminate apex in those of the "eastern assemblage" (see FIGURE 1).

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[2] For the four generic segregates mentioned, most of the ca. 40 species within these groups have been treated at one time or another as members of the genus *Piper*. Therefore, relatively few new combinations would be required to treat these groups appropriately at the rank of subgenus.

At low elevations near the coast in Nueva Galicia (see Rzedowski & McVaugh, 1966, for a definition of this area), several members of the "western assemblage" (*Piper brachypus* Trel., *P. brevipedicellatum* Bornstein, *P. rosei* C. DC., and *P. stipulaceum*) are common inhabitants of the palm forests dominated by *Orbignya cohune* (C. Martius) Dahlgren ex Standley. At slightly higher elevations and often farther inland, these same species are joined or replaced by other pedicellate pipers (*P. abalienatum* Trel. and *P. novogalicianum* Bornstein) and occupy sites in the disturbed semideciduous forests dominated by *Brosimum alicastrum* Sw., *Hura polyandra* Baillon, and species of *Ficus* L. and *Bursera* Jacq. ex L. Still other species in this group, including *P. colotlipanense* Bornstein from the state of Guerrero and *P. guazacapanense* from Chiapas and neighboring Guatemala, occur in seemingly stable and mesic environments in more remote localities.

Within the "eastern assemblage," the dominant and widely distributed *Piper neesianum* C. DC. and *P. yucatanense* are native to the "ramonales" forests of the Yucatán Peninsula, upland, climax, subdeciduous forests developing on calcareous soils and dominated by the breadnut tree, *Brosimum alicastrum*. However, the influence of man in these once relatively unoccupied regions has all but destroyed these primary forests, at least in Mexico. Fortunately, these two species (especially *P. neesianum*) have adapted as able colonizers of disturbed sites to remain fairly conspicuous elements of the second-growth forests that now dominate this area.

HABIT

With the single known exception of *Piper guazacapanense,* all members of *Piper* subg. *Arctottonia* are erect plants. They are 0.5–6.5(–9) m tall and 0.5–7.5 cm in diameter at the plant base; the most common forms are shrubs and slender treelike specimens. All of the species are woody with conspicuously nodose stems (a common feature for the genus), although the amount of wood developed in some species, especially the prostrate *P. guazacapanense,* is minimal. Since the inflorescences in subg. *Arctottonia* are terminal and leaf opposed, continued apical growth is assumed by the apical bud, resulting in a sympodial growth pattern.

MEASUREMENTS AND TERMINOLOGY

Information provided in the key and descriptions was obtained from the study of herbarium specimens, fluid-preserved materials (especially flowers and fruits), and notes made in the field. Voucher specimens of my own collections have been deposited at MICH, with complete or partial sets distributed to the following herbaria (cited according to Holmgren *et al.,* 1981, and in order of distribution): MEXU, CHAP, INIF, GH, NY, CAS, DUKE, F, and MO.

The terminology used to describe the various plant features generally follows that of Radford *et al.* (1974). With the exception of a few pickled fruits, all measurements have been taken directly from herbarium specimens. In some

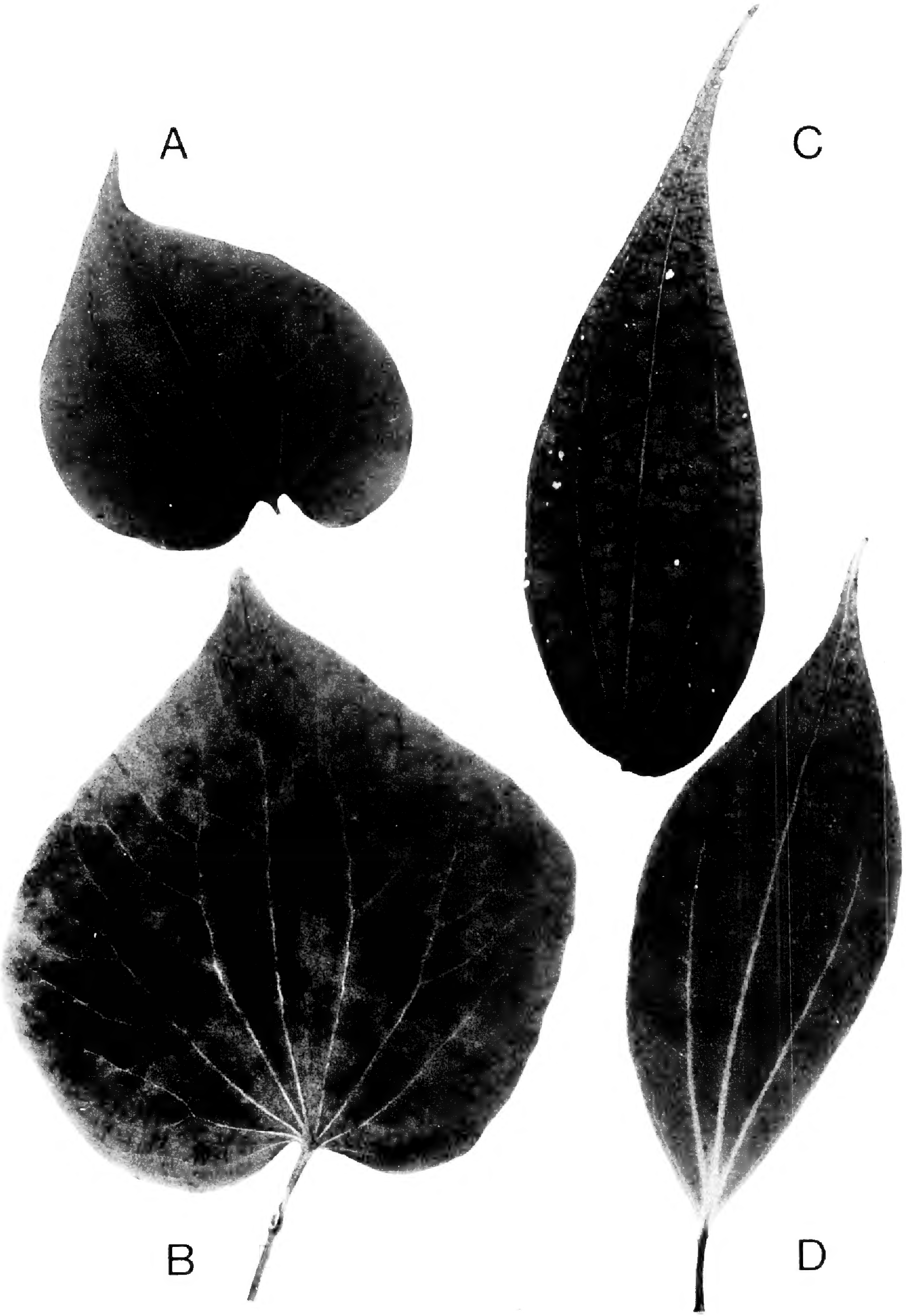

FIGURE 1. Major leaf shapes in *Piper* subg. *Arctottonia*. A, B, broadly ovate to suborbiculate, commonly cordate at base: A, *P. guazacapanense*; B, *P. abalienatum*. C, D, narrowly ovate-lanceolate or narrowly elliptic with long-acuminate apex: C, *P. yucatanense*; D, *P. neesianum*.

instances flowers were placed in a weak detergent mixture to soften them in order to count the number of stamens and stigma lobes more accurately.

Whenever possible, ten measurements were made from each collection number in an attempt to obtain a reasonable sample size and to document any variation that may exist within a single collection. Obviously immature or incomplete structures were avoided. Measurements of inflorescence length include the peduncle, since it was not always possible to separate the peduncle from the flowering rachis accurately.

A scanning electron microscope was used to observe details of the leaf surface (e.g., hair type) and various floral characteristics. This was facilitated by critical-point-drying the materials pickled in the field in order to retain their shape during the drying process.

Certain terms referring to the hairs and their overall appearance are used here in a relative manner:

puberulent—having very short (generally less than 0.1 mm), glandular or eglandular hairs barely visible at 10× magnification.

pubescent—similar to puberulent, but with the eglandular hairs noticeably longer (ca. 0.1–0.3 mm long) and generally visible to the unaided eye.

long-pubescent—similar to pubescent, but with the hairs 0.3–0.5 mm long.

densely pubescent—similar to pubescent, but with the hairs more numerous and therefore easily visible to the unaided eye. (This is obviously a subjective distinction. Quite often, densely pubescent and long-pubescent are correlated features.)

MORPHOLOGY

LEAVES

The leaves of *Piper* subg. *Arctottonia,* like those of the vast majority of pipers, are alternate, simple, and entire margined. As briefly discussed above, two distinct groups occur with respect to shape: those with leaves conspicuously longer than broad and lance-elliptic to elliptic-ovate, and those with leaves more nearly equal in length and width and broadly to very broadly ovate or suborbiculate (see FIGURE 1). The apex is predominantly acuminate, either long or short, while the base varies from cuneate to rounded or cordate. In some specimens of *P. yucatanense* and *P. neesianum,* the base is slightly oblique. Leaves are membranous in all species of subg. *Arctottonia* except *P. neesianum,* in which they are coriaceous, especially upon drying.

According to the terminology associated with Hickey's (1979) classification of the architecture of dicotyledonous leaves, the most prevalent venation pattern in subg. *Arctottonia* is acrodromous, with basal position and perfect development. In some species with cordate leaf bases, especially *Piper guazacapanense,* campylodromous venation is commonly found. The number of major veins varies from 3 to 9 (to 11), depending to a large degree on the width of the leaves, but only the three most central ones project into the acumen. The secondary veins are irregularly spaced, although in some species they form a series of interconnecting arches near the margin. Tertiary and higher-order veins form a random reticulation.

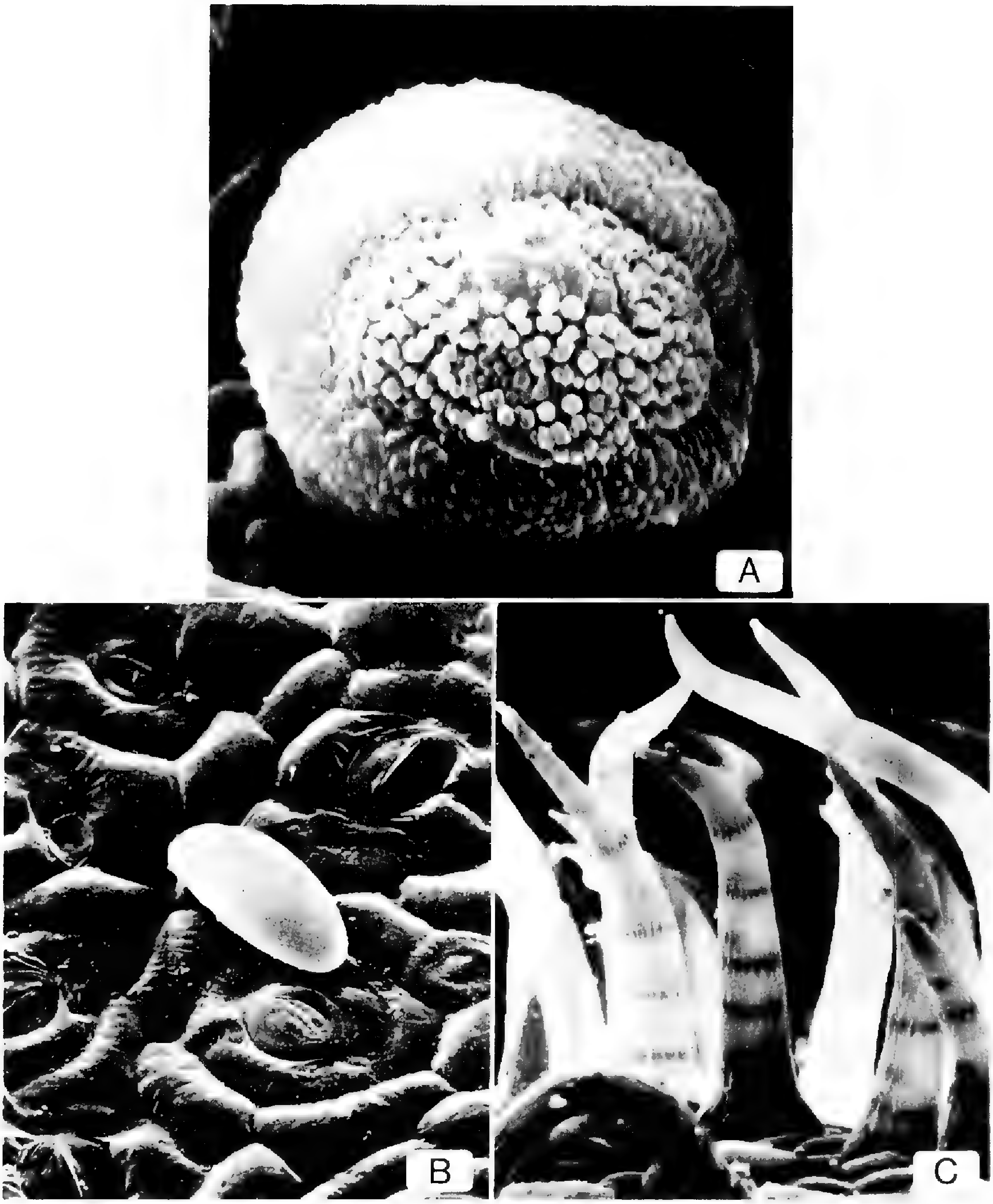

FIGURE 2. A, pollen grain of *Piper abalienatum*, representative of subg. *Arctottonia*, × 3850. B, C, hair types in *Piper* subg. *Arctottonia*: B, bicellular, glandular hair with short stalk cell and ellipsoid gland cell (*P. novogalicianum*), × 550; C, multicellular, uniseriate, eglandular hair (*P. stipulaceum*), × 275.

INDUMENTUM

Two hair types occur in subg. *Arctottonia* that I term glandular and eglandular. The glandular hairs are bicellular, with a small stalk cell subtending a larger, ellipsoid gland cell (see FIGURE 2B). These hairs are quite small (up to 35 μm) and are therefore easily overlooked. On mature leaves they are often absent or very sparse. They usually occur on both surfaces of the leaves, and

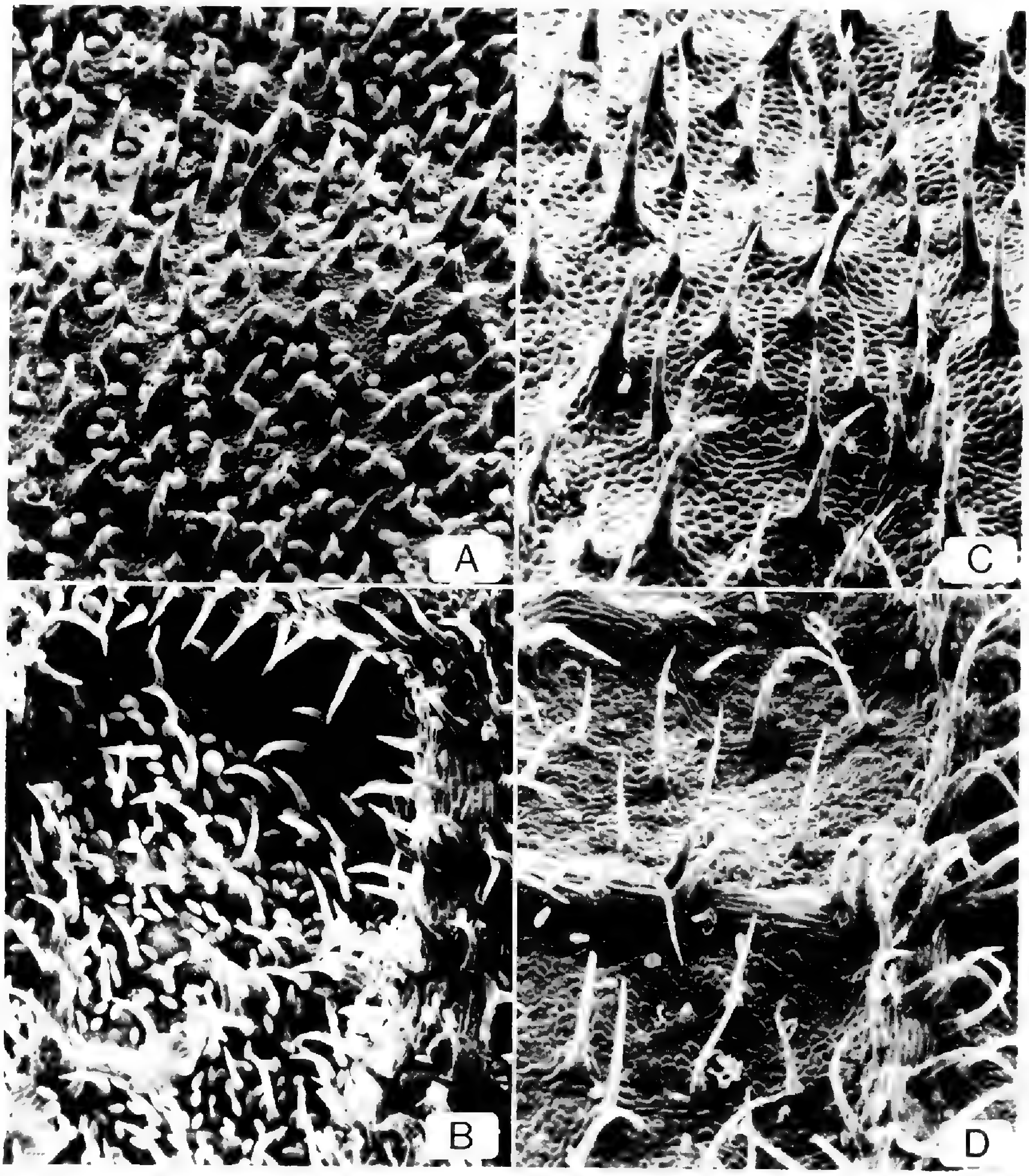

FIGURE 3. Distribution of hair types in *Piper* subg. *Arctottonia,* as seen on leaves of *P. stipulaceum*: A, upper surface, immature specimen, × 60; B, lower surface, immature specimen, × 60; C, upper surface, mature specimen, numerous eglandular hairs and sparse glandular ones (compare with A), × 55; D, lower surface, mature specimen, eglandular hairs mainly on veins, × 60.

they are quite commonly more numerous beneath, being especially concentrated in the regions between veins (see FIGURE 3).

The eglandular hairs are simple, unbranched structures. They are always multicellular, uniseriate, broadened at the base, and gradually tapered to an acute apex (see FIGURE 2C). The number of cells differs with hair length, which in turn is quite variable within a specimen. Hairs as long as 0.5 mm have been recorded in *Piper colotlipanense* and *P. abalienatum,* but approximately 0.1–0.3 mm is more normal. Like glandular hairs, eglandular ones are usually more abundant on the lower leaf surface; in contrast, however, they are more frequent on—and at times restricted to—the veins (see FIGURE 3).

On a gross level these hairs, especially the more conspicuous eglandular ones, produce surfaces ranging from sparsely puberulent to tomentose. The degree of pubescence and the distribution of hairs, in correlation with floral features, are quite useful in delimiting species (but see comments in the introduction to the taxonomic treatment).

PROPHYLLS

An interesting vegetative structure associated with the newly developing leaf and inflorescence is the prophyll. Technically, a prophyll is the "first leaf or one of two first leaves" of an axillary shoot (Esau, 1977, p. 522). In essence, prophylls are reduced leaves that subtend lateral branches, often occurring in odd positions and thus not conforming to the normal phyllotaxy of the shoot. In dicots there are usually two prophylls, whereas in monocots there is only one (Eames, 1961).

In *Piper* only one prophyll occurs, and according to Burger (1972), who has surveyed this character in several Costa Rican species, its development relative to the leaf base and axillary shoot is variable. On the basis of his study, he tentatively concluded that developmental differences, together with prophyll morphology and floral features, may suggest natural groupings in *Piper*.

In subg. *Arctottonia* the prophyll always functions to protect the developing axillary shoot by surrounding the new leaf (and inflorescence, if present) in a manner similar to the stipule in *Ficus* or the bud scale in *Magnolia* L. It is always apically acute and basally truncate, appearing triangular to widely deltate when laid flat. It may be glabrous (or appear so to the naked eye) but more often is abaxially pubescent.

Although this general characterization of the prophyll in subg. *Arctottonia* is consistent from one taxon to another, its similar occurrence in other taxa with different floral morphologies suggests, as Burger pointed out, that the apically acute prophyll has probably evolved independently along several distinct evolutionary lines. Nevertheless, it does help to define subg. *Arctottonia* since it correlates with other features such as racemose inflorescences and palmate leaf venation.

INFLORESCENCES

The inflorescence in subg. *Arctottonia* is unusual in that the flowers are borne on short pedicels. Therefore, the inflorescence is technically a raceme rather than a spike, as in the majority of pipers. As mentioned previously, this inflorescence type is shared with the South American–West Indian *Piper* subg. *Ottonia* and a single Old World species, *P. begoniaefolium* (Blume) Quis.

The length of the pedicel varies from commonly less than 0.5 mm in *Piper brachypus, P. brevipedicellatum,* and *P. mcvaughii* Bornstein to usually 1–3 mm in the remaining taxa. Within a specimen variation can be quite noticeable, especially when one compares flowering and fruiting pedicels. Apparently, in many cases, the pedicel continues to elongate as the flower matures. At the

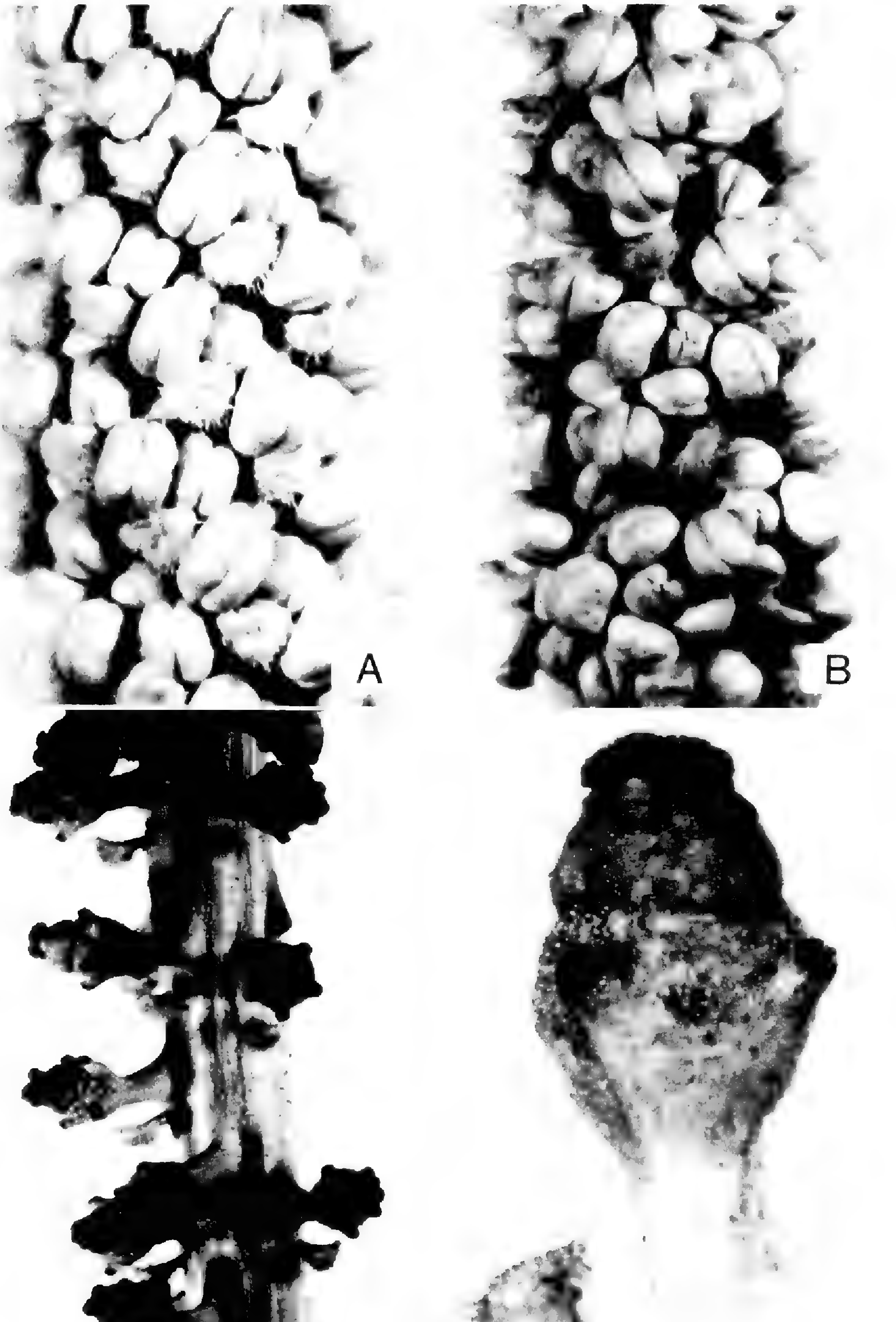

FIGURE 4. Basic floral features in *Piper* subg. *Arctottonia* and morphological changes occurring during development, as seen in *P. stipulaceum*: A, immature inflorescence,

same time, the maturing fruit expands and the receptacular portion of the pedicel swells, making it very difficult to determine the exact position of the pedicel-fruit junction. These developmental changes can create significant problems in identification, especially for material in early flower, since the pedicels are immature (see the developmental series in FIGURE 4). It is therefore more reliable, in my opinion, to examine young fruiting specimens for positive identification.

The inflorescence axis is rather narrow (rarely more than 2 mm) in all species. The peduncle is often slightly broader than the remaining rachis, but it is a gradual change of no apparent significance. The rachis is glabrous or, more commonly, puberulent to pubescent with eglandular and/or glandular hairs. This feature is useful in helping to delimit species.

FLORAL BRACTS

This character was an integral feature in Miquel's subdivision of *Piper* sensu lato into segregate genera. According to Callejas (1986), variation in bract shape is useful in helping to delimit taxonomic groups within *Piper.*

In subg. *Arctottonia* the floral bracts do not form a banded pattern. They are generally spatulate to spatulate-cupulate (otherwise described as conchaeform, shell-like, or conical at the expanded apical region). In some species the broadened apex narrows at the base to form a distinct petiole, whereas in others the bract is essentially sessile on the inflorescence rachis. The bracts may be completely glabrous (*Piper neesianum*), to sparsely puberulent (*P. mcvaughii*), to densely pubescent (*P. brachypus, P. colotlipanense,* and *P. brevipedicellatum*). Usually the hairs are present only on the abaxial surface or at the bract margin, and they may be eglandular (most common) and/or glandular. These variations prove useful at the species level.

FLOWERS

The flowers are very simple structures consisting only of the male and female reproductive parts (see FIGURE 4). A perianth is completely lacking. The androecium consists of (3 or) 4 to 6 (or 7 to 9) stamens, which may be attached immediately beneath the single ovary (hypogynous) or may, in a very few species (*Piper abalienatum, P. stipulaceum,* and *P. mcvaughii*), be adnate to it. In several taxa there appears to be a tendency toward adnation of the stamens to the lower portion of the ovary. This may simply be a developmental anomaly associated with fruit ripening and expansion, which involves the upper (receptacular) portion of the pedicel. In other cases the lower portion of the filaments appears to be fused to the ovary wall, with the free section therefore arising a

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bracts readily visible (note protandrous development of flowers), × 18; B, slightly more mature inflorescence, floral bracts becoming obscured by expanding flowers, gynoecium now evident, × 15; C, young infructescence, pedicels now conspicuous, bract shape more apparent, stamen position and number more readily determined, × 7; D, single young fruit and associated bract, adnation of stamens to ovary evident, × 21.

short distance from the apparent ovary base. For convenience I have chosen to refer to these stamens as hypogynous. When this tendency is especially strong, I have mentioned it in the species description or in the accompanying discussion.

The filaments vary but in most cases are less than 0.5 mm long. In *Piper abalienatum, P. colotlipanense,* and *P. muelleri* C. DC., the filaments are particularly long, often exceeding 1 mm. In all taxa the anthers dehisce by longitudinal slits. These are usually oriented laterally, a condition considered primitive by Burger (1972), although in several species there is often a slight change toward upward dehiscence. This is accomplished by an expansion of the connective at the base of the sporangial pairs, the anthers being tetrasporangiate. Burger (p. 360) has postulated that this change in anther orientation, in association with the congestion of the flowers and the compaction of the floral parts, is a response to "the activity of small pollen-collecting bees" (but see also comments by Callejas (1986) regarding floral ontogeny).

The pollen in subg. *Arctottonia* is constant within and between species. The following description employs Walker and Doyle's (1975) terminology. Scanning electron micrographs (FIGURE 2A) clearly indicate that the pollen grains are monosulcate. If the prevailing assumption is made, as Walker and Doyle (1975) suggested, that the aperture is distal-polar, then the grains would be more precisely classified as anasulcate. The exine sculpturing is verrucate, with the sulcus membrane appearing gemmate (described by Erdtman (1966) as granular). The pollen grains are minute to small (ca. 12.75 × 11.75 μm) and globose-subspheroidal. This description is in general agreement with that of Walker (1976) for the Piperaceae, providing further evidence that pollen morphology in the family is a relatively invariable feature and therefore of little or no taxonomic value at the level of species.

The gynoecium in all pipers is a single pistil with one locule and one basal orthotropous ovule. The number of carpels that form the gynoecium has long been a source of disagreement. Baillon (1872) interpreted the ovary as unicarpellate. Primarily on the basis of the number of stigmatic lobes, Rendle (1925), Lawrence (1951), and others have suggested that it is 2- to 5-carpellate. Evidence from carpellary vascular bundles indicates a tricarpellate derivation (Johnson, 1902; Murty, 1959). More recent developmental studies (Tucker, 1982) further substantiate the tricarpellate theory but do not eliminate the possibility of four carpels developing (e.g., *Piper amalago* L., a taxon within subg. *Enckea,* the sister group to subg. *Arctottonia*). Callejas (1986) has also shown that in *Piper* subg. *Ottonia,* four carpels per flower is the rule. Unfortunately, this feature was not critically examined in my study. Stigma branches—a fairly reliable criterion in *Piper* for judging the number of carpels—were counted, with values ranging from 3 to 5 (3 and 4 predominating). However, the number of stigmatic lobes varies within a single inflorescence, which strongly suggests that this feature is of little value in delimiting species. Its usefulness at higher taxonomic levels is still in question.

In the majority of *Arctottonia* species, the ovary is ovoid-ellipsoid, with prevailing tendencies toward globose. The most notable exception occurs in *Piper muelleri,* where the ovary is conspicuously depressed-ovoid, accentuated by the long staminal filaments and the elongate style. The style is a variable feature important in some cases in helping to distinguish between species. It is often depressed-ovoid but varies continuously to conical (*P. stipulaceum, P. colotlipanense, P. neesianum*) or columnar (*P. abalienatum, P. mcvaughii*). Associated with this change is an increase in the length ratio of style to ovary in the flowering condition from approximately 1 : 3 to 3 : 2. At maturity the stigma lobes are papillose, with numerous clavate or columnar hairs. With the exception of *P. muelleri* and the occasional specimen of *P. abalienatum*, where they are recurved, the stigma branches are short and flattened on the style.

FRUITS

The fruit in *Piper* is a small drupe with scant endosperm and abundant perisperm. It is most often globose, varying to ellipsoid (*P. yucatanense*), ovoid-ellipsoid (*P. neesianum*), and obloid (*P. stipulaceum*), and is small (2–3 × 1.5–2.5 mm). In most species the fruit is capped by the persistent style (see FIGURE 4), and glandular hairs are present to some degree. So far as is known, the fruit is opaque, either brown or black, except in *P. guazacapanense*, where it is a translucent pearl-white.

TAXONOMIC TREATMENT

The circumscription of taxa and the identification of specimens in *Piper* subg. *Arctottonia* have been complicated by changes that occur as a result of plant maturation. Vegetatively, this is usually manifested by a change in leaf and hair size, as well as the eventual loss of the hairs (especially the glandular ones) in the most mature specimens (see FIGURE 3). Florally, it involves the length of the inflorescence and the pedicels, the degree of pubescence on the bracts, the size and shape of the ovary, and the expansion of the ovary during fruit formation, which may, in turn, affect the position of the stamens and the appearance of the style (see FIGURE 4).

In the past the phenotypic differences caused by these changes were not linked to developmental phenomena, and some of them led to the misidentification of specimens or were considered significant enough to warrant the establishment of new species. In this study many of these developmentally induced variations have been discovered by collecting materials from the same individual at different stages of maturation. This has allowed me to observe these changes over time and thereby eliminate the confusion that often results when examining collections from different plants. I have thus been able to identify most specimens at a single, specific stage of maturation by comparing their appearance with "known" specimens. Unfortunately, this was not possible for all of the taxa that I have recognized. In these cases I have resorted to the standard practice of equating differences (discontinuities) with distinct species.

Piper subg. **Arctottonia** (Trel.) Standley & Steyerm. Fieldiana, Bot. **24**(3): 275. 1952.

Arctottonia Trel. Proc. Amer. Philos. Soc. **69:** 315. 1930. TYPE: *Piper muelleri* C. DC.

Shrubs or small trees, occasionally scandent or subherbaceous, terrestrial, the stems conspicuously nodose; plants glabrous or variously pubescent, the hairs bi- and/or multicellular, glandular or not. Prophyll single, lateral, triangular, forming cocoonlike structure enclosing and protecting developing shoot apex. Leaves alternate; petiole vaginate at base, without ligulate process; blade simple, entire, palmatinerved, acrodromous or campylodromous. Inflorescences terminal, leaf-opposed, more or less loosely flowered racemes, erect (or rarely pendent?); floral bracts petiolate or sessile, spatulate to strongly spatulate-cupulate, not forming bands at any stage of development. Flowers small, perfect; perianth absent; stamens 4 to 6 (to 9), the filaments to 1 mm long, rarely longer, the anthers ovoid to subglobose, bithecate, tetrasporangiate, dehiscent by longitudinal slits; ovary superior or with stamens variously adnate, unilocular with single, basal, orthotropous, bitegmic ovule, style present or absent, stigma lobes (2 or) 3 or 4 (to 6). Fruit a small drupe, fleshy or dry, ovoid to globose, smooth or distinctly ribbed or angled; seeds with much perisperm and little endosperm.

This subgenus constitutes a natural assemblage of 14 species confined to Mexico and Central America. The primary center of diversity is in west-central Mexico (Nueva Galicia); a second subgroup of three species, two of which are rather widespread, occurs from central Veracruz, Mexico, through the Yucatán Peninsula (Mexico, Guatemala, and Belize) to neighboring Honduras, with isolated plants in Nicaragua and Panama.

KEY TO THE SPECIES OF PIPER SUBG. ARCTOTTONIA[3]

1. Leaves 1.5–3 times longer than broad, lance-elliptic to narrowly ovate, the base cuneate-attenuate to rounded, very rarely slightly cordate.
    2. Rachis puberulent or densely pubescent with eglandular hairs; floral bracts pubescent to densely pubescent.
        3. Leaves pubescent beneath, especially along major veins; filaments 0.5–1 mm long; rachis puberulent; fruits depressed-ovoid to globose. . . 9. *P. muelleri.*
        3. Leaves glabrous to sparsely puberulent at petiole-blade junction; filaments < 0.25 mm long; rachis densely pubescent; fruits ellipsoid to obovoid to subglobose. . . . . 4. *P. cihuatlanense.*
    2. Rachis and floral bracts glabrous.
        4. Leaves chartaceous to coriaceous, shiny green above, gray-green to silvery beneath, nonrugulose; plant a dense shrub to 6.5 m tall; fruits ribbed; floral bracts < 0.5 mm long. . . . . 10. *P. neesianum.*
        4. Leaves membranous, dull green on both surfaces, generally drying rugulose; plant a loosely branched shrub to 3 m tall; fruits smooth; floral bracts 0.25–1.5 mm long. . . . . 14. *P. yucatanense.*
1. Leaves usually 1–1.5 times longer than broad, ovate to broadly ovate to suborbiculate, the base usually distinctly cordate, sometimes truncate to rounded.
    5. Stamens conspicuously adnate to ovary, often near middle.

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[3] Although it is possible to recognize two distinct lineages or subgroups within *Piper* subg. *Arctottonia,* interspecific relationships are more ambiguous since the polarity of certain character states is conjectural at best. For that reason, a formal phylogeny for subg. *Arctottonia* is not presented at this time, and the species in the following taxonomic treatment are arranged alphabetically. Comments concerning putative relationships can be found in the discussions that accompany each description.

6. Pedicels to 0.5 mm long, rarely longer; leaves 5.1–8 × 5.5–7.6 cm, sparsely puberulent beneath with short eglandular hairs. .... 7. *P. mcvaughii.*
6. Pedicels (0.5–)1–2(–3) mm long; leaves (4.5–)6.3–20.4 × (4.8–)6.5–19.8(–21) cm, puberulent to tomentose beneath.
    7. Style columnar to very long-conical, 0.5–2 mm long, as long as ovary in flower, ⅓–½ as long in fruit; filaments 0.5–1 mm long; ovary ovoid-ellipsoid; stamens occasionally in 2 whorls. .... 1. *P. abalienatum.*
    7. Style depressed-ovoid to short-conical, to 0.5 mm long, from ⅓ to equal ovary length in flower, ⅕–⅓ as long in fruit; filaments to 0.5 mm long; ovary ovoid to globose; stamens in single whorl. ... 13. *P. stipulaceum.*

5. Stamens hypogynous or sometimes appearing adnate to base of ovary due to its expansion in fruit.
    8. Plant a prostrate, creeping subshrub, periodically rooting at nodes; fruits pearl white, translucent; inflorescences < 4.5 cm long, few-flowered. .... 6. *P. guazacapanense.*
    8. Plant an erect shrub, never rooting at nodes; fruits green to black, opaque; inflorescences > 5 cm long, many-flowered.
        9. Prophylls, petioles, and leaf blades glabrous (to puberulent or very rarely sparsely pubescent).
            10. Rachis and floral bracts glabrous to sparsely puberulent, rarely with few scattered eglandular hairs; pedicels usually 1.5–2.5 mm long. ... . 8. *P. michelianum.*
            10. Rachis and floral bracts puberulent to more commonly pubescent or densely pubescent with eglandular hairs; pedicels 0.5–1.5 mm long, rarely longer, or flowers subsessile.
                11. Flowers subsessile, the pedicels to 0.5 mm long, rarely longer. ... . 2. *P. brachypus.*
                11. Flowers with pedicels 0.5–1.5 mm long. .... 12. *P. rosei.*
        9. Prophylls, petioles, and leaf blades pubescent to densely pubescent or tomentose (rarely only puberulent).
            12. Pedicels generally < 0.5 mm long, stout, about as long as broad. ... . 3. *P. brevipedicellatum.*
            12. Pedicels generally > 1 mm long, as long as—or, more commonly, distinctly longer than—broad.
                13. Filaments 0.5–1 mm long; young twigs, petioles, leaf blades, and prophyll densely long-pubescent to tomentose. .... 5. *P. colotlipanense.*
                13. Filaments to 0.5 mm long; young twigs, petioles, leaf blades, and prophylls puberulent to densely pubescent. .... 11. *P. novogalicianum.*

1. **Piper abalienatum** Trel. Amer. J. Bot. **8:** 216. *pl. 8, fig. 1.* 1921. TYPE: Mexico, Colima, Colima, July and Aug. 1897, *Palmer 100* (holotype, US!; isotypes, A!, MICH!, UC!). FIGURE 5.

Piper el-muletonum C. DC. Candollea **1:** 72, 246. 1923, *nomen nudum. Piper el-muletonum* C. DC. ex L. J. Schroeder, Candollea **3:** 137. 1926. TYPE: Mexico, Michoacán, El Muleto, 850 m, 30 June 1898, *Langlassé 215bis* (holotype, G!).

Medium-sized shrub, sparsely branched from base, appearing treelike, 1.5–4 m tall; youngest twigs lime green, densely pubescent, becoming glabrous, brown, and eventually light gray with warty lenticels; older stems with conspicuous swollen nodes, maximum diameter to 6 cm. Prophylls to 1.5 cm long at maturity, base truncate, apex acute, dorsally densely pubescent to tomentose. Leaves with petiole 1–4.5 cm long, stout, densely soft-pubescent with eglandular hairs; blade broadly ovate to orbiculate to occasionally depressed-ovate, 7.1–20.4 × (6.5–)7.6–19.8(–21) cm, rounded to distinctly cordate at base, gradually to abruptly acuminate at apex, (5- to) 7- to 9- (to 11-)nerved, puberulent to pubescent (rarely almost glabrous) above, densely soft-pubescent to tomentose (rarely glabrous to puberulent) beneath with eglandular hairs more prominent on slightly elevated major veins. Inflorescences (4.8–)5.7–15.2 cm long, green when young, turning yellow-white at maturity; peduncle stout, pubescent at base, remaining rachis glabrous or minutely puberulent with glandular hairs; bracts to 1.25 mm long (usually ca. 0.75 mm), narrow petiolate basal portion broadening gradually to abruptly into spatulate to spatulate-cupulate apical region, abaxially sparsely pubescent to pubescent. Flowers with pedicel (0.5–) 1–2(–3) mm long, to 1 mm in diameter, glabrous to sparsely puberulent with glandular hairs; stamens (4 or) 5 to 7 (or 8), adnate to near middle of ovary, occasionally appearing as if in 2 alternating whorls, the filaments elongate (to 1 mm), the anthers equal to or slightly shorter than filaments, dehiscing somewhat to conspicuously divergent upward from lateral; ovary ovoid-ellipsoid, 1–2 times as long as style, puberulent with glandular hairs, the style columnar to slightly conical, (0.5–)1–1.5(–2) mm long, persistent in fruit, the stigma 3- to 5-lobed. Fruits globose, to 2 mm in diameter, drying brown to black, with glandular hairs still present.

DISTRIBUTION. Confined to small area in west-central Mexico from southwestern Jalisco, along western side of Sierra Madre, through state of Michoacán (see MAP 1). Although not known from Guerrero, to be expected there, especially at mid-elevations in Sierra Madre del Sur.

HABITAT. Dense shade of mixed deciduous forests, 100–1000 m alt.; often associated with various Leguminosae, Moraceae (especially species of *Brosimum* Sw. and *Ficus*), Euphorbiaceae (*Hura* L.), *Bursera*, and *Malpighia* L. Always grows where water plentiful at some time of year; most abundant at edge of ravines above intermittent mountain streams.

PHENOLOGY. Flowering late May through July, most reliably in June. Young fruits beginning in late June; specimens with mature fruits collected as late as mid-October.

REPRESENTATIVE SPECIMENS.[4] **Mexico.** JALISCO: 1 km E of El Divisadero (1 km W of Villa Guerrero), 18 km ESE of Tomatlán, *Iltis & Nee 1650* (NY); Estación de Biología de Chamela, *Pérez & Sarukhán 1354* (MEXU, MICH); 15 mi SSE of Autlán on trail between Chante and Manantlán, *Wilbur 2105* (MICH). COLIMA: 2.3 km E on Hwy. 70 toward Ixtlahuacán, *Bornstein 90* (MICH); mountain trail S of Los Tepames, *Bornstein & Hensold 18* (MICH); 5.7 km S of Los Tepames on gravel road to Las Tinajas, *Bornstein & Hensold 21* (MICH); just beyond km 190 and before Río Tuxpan bridge on old Hwy. 110 between Colima and Pihuamo, *Bornstein 91* (MICH); ca. 18 road mi E of Colima, near bridge of Río Tuxpan, km 189, *McVaugh 15498* (MICH); ca. 11 mi SSW of Colima on Manzanillo road, *McVaugh 15564* (MICH); gorge of Río Cihuatlán, near bridge 13 mi N of Santiago, *McVaugh 15809* (MICH). MICHOACÁN: 3.5 mi N of San Juan de Lima on Hwy. 200,

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[4] A complete list of collectors for the entire study is given in the appendix.

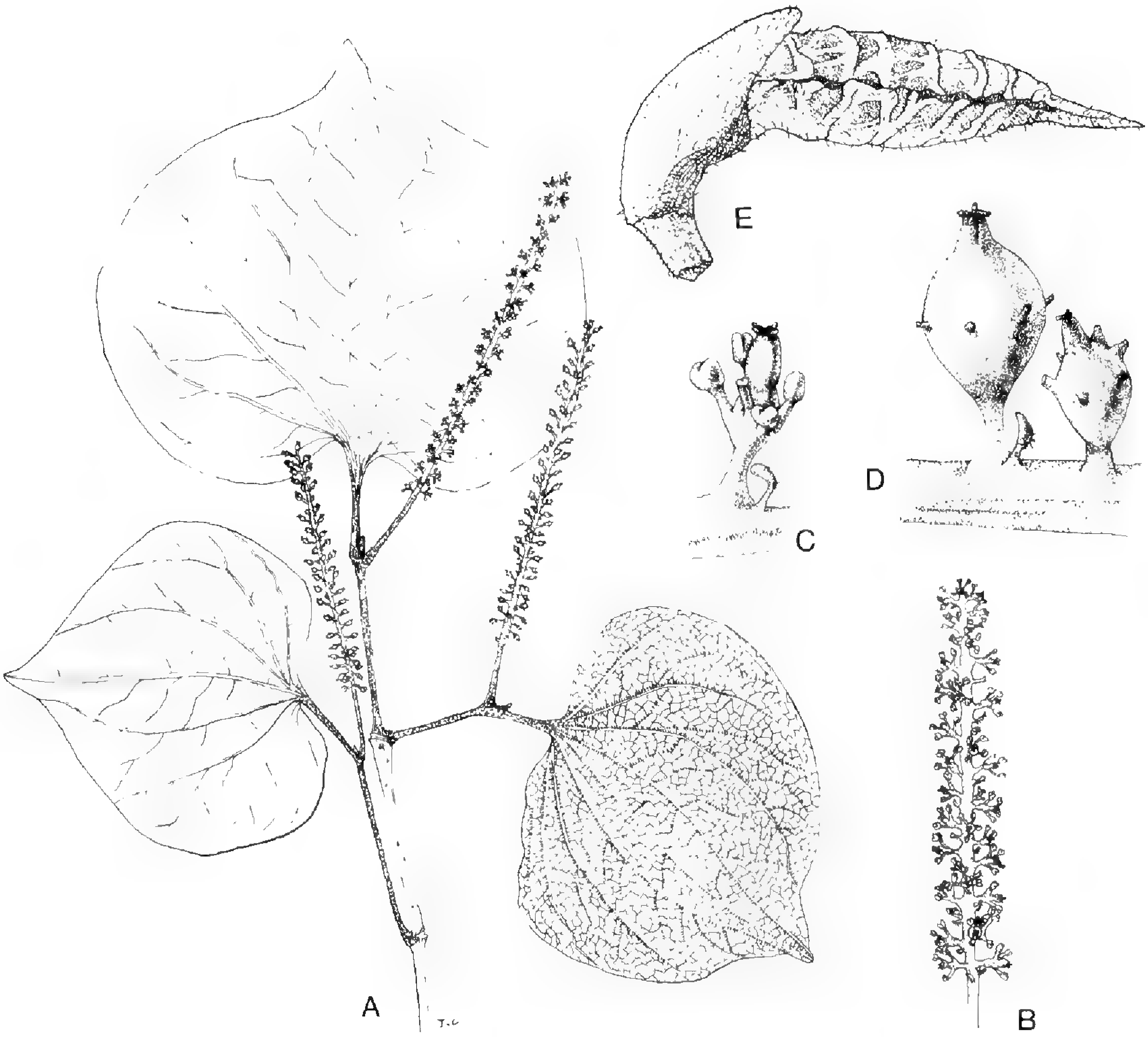


FIGURE 5. *Piper abalienatum*: A, flowering branch, × 0.2; B, inflorescence, × 0.8; C, flower with bract, × 12; D, fruits with bract, × 5; E, prophyll with emergent young leaf, × 3.5.

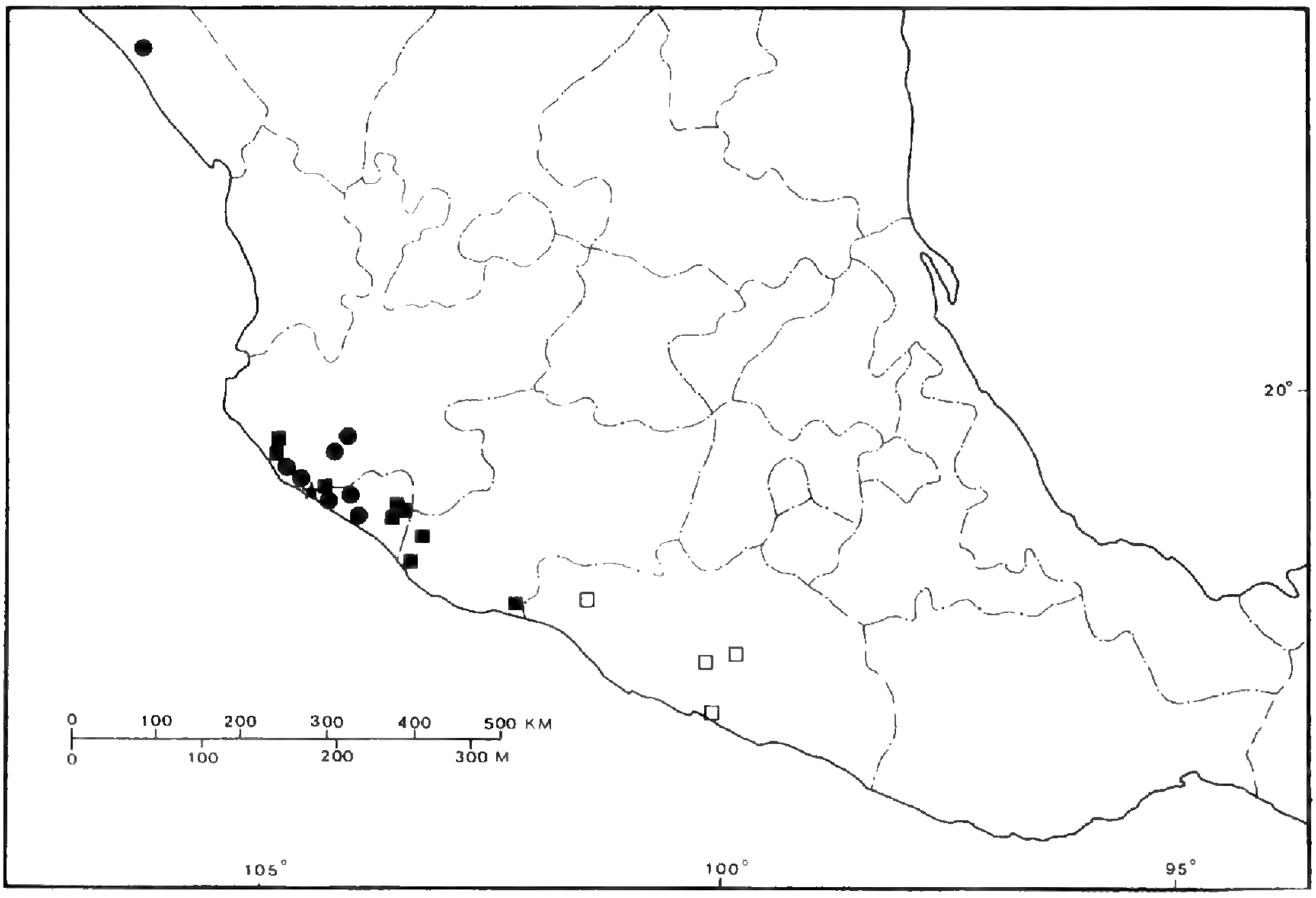
Bornstein & Chase 94 (MICH); Coalcomán, *Hinton 13855* (ENCB, ILL, NA, NY, PH, TEX, US); 32 km N of Playa Azul (region of Los Encinos), *King & Soderstrom 4929* (NY, TEX, US).

Piper abalienatum is most often confused with *P. stipulaceum,* because in both species the stamens are adnate to near the middle of the ovary. The differences between these two closely related taxa are discussed following the description of *P. stipulaceum* (and see TABLE).

Piper abalienatum also resembles *P. colotlipanense,* especially with respect to stylar features and filament length. It is distinguished from that species in having the stamens adnate to the middle of the ovary (vs. hypogynous or irregularly adnate to the lower portion of the ovary).

2. **Piper brachypus** Trel. Amer. J. Bot. **8:** 215. *pl. 6.* 1921. TYPE: Mexico, Colima, Manzanillo, 2–18 March 1891, *Palmer 1332* (holotype, US!; isotype, GH!). FIGURE 6.

Shrub to 4 m tall; twigs and older branches glabrous to very sparsely puberulent with glandular hairs. Prophylls to 0.7 cm long, base truncate, apex



MAP 1. Distribution of *Piper abalienatum* (solid squares), *P. brevipedicellatum* (circles), *P. colotlipanense* (open squares), and *P. mcvaughii* (star).

Characters used to distinguish between Piper abalienatum and Piper stipulaceum.

	SPECIES	
CHARACTER	*Piper abalienatum*	*Piper stipulaceum*
Leaves		
Average size (cm)	12.6 × 11.8	10 × 8.7
Surface	Pubescent to tomentose, especially beneath	Puberulent to pubescent, especially beneath
Stamens		
Arrangement	Irregular; occasionally in 2 whorls	In 1 whorl
Filament length (mm)	0.5–1; equal to or exceeding anthers	To 0.5; shorter than or nearly equal to anthers
Ovary shape (in flower)	Ovoid-ellipsoid	Ovoid to globose
Style		
Shape	Columnar to slightly conical	Depressed-ovoid to conical
Length (mm)	(0.5–)1–1.5(–2)	To 0.5, rarely slightly longer
To ovary ratio		
In flower	ca. 1 : 1	1 : 1–1 : 3
In fruit	1 : 2–1 : 3	1 : 3–1 : 5

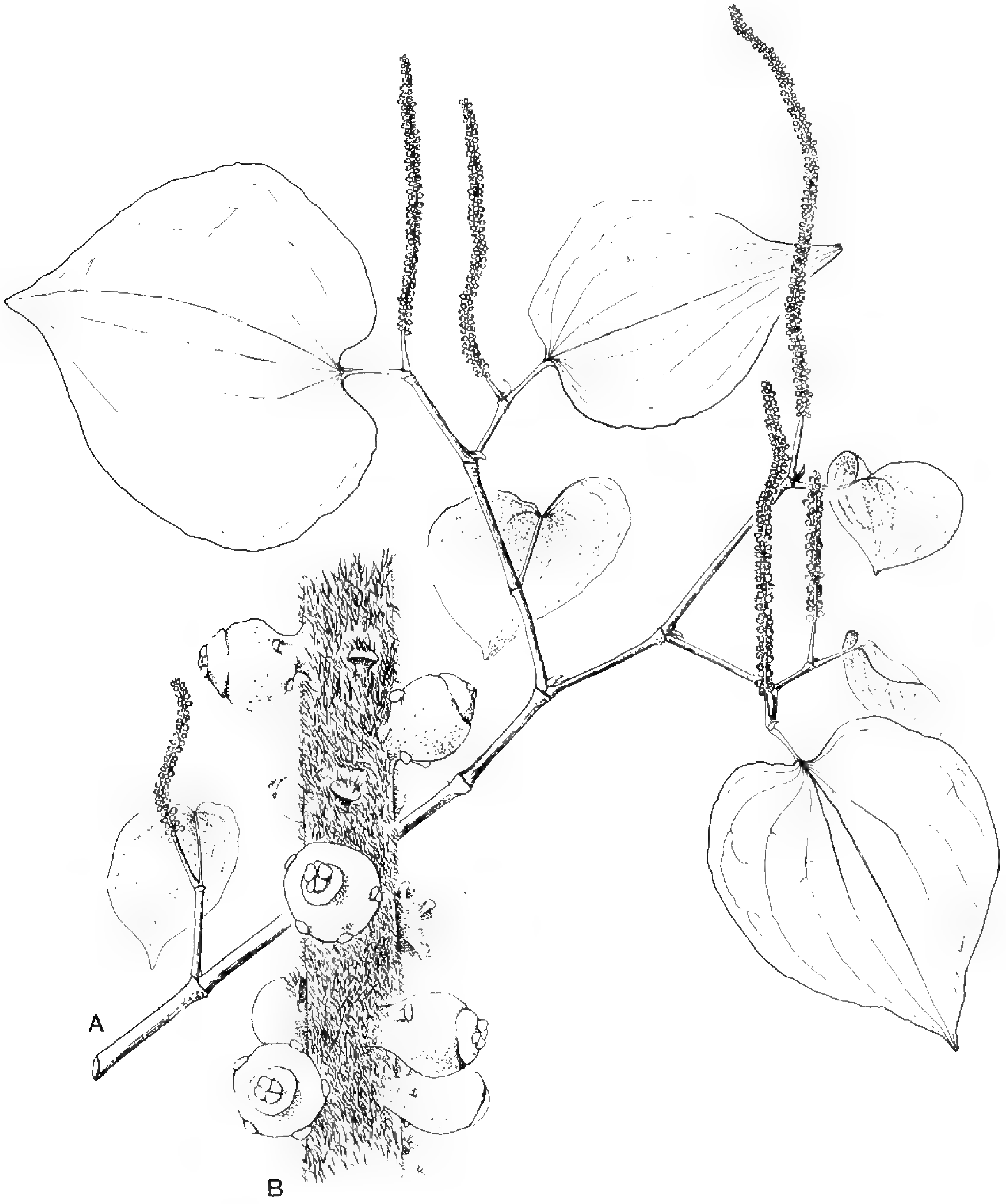
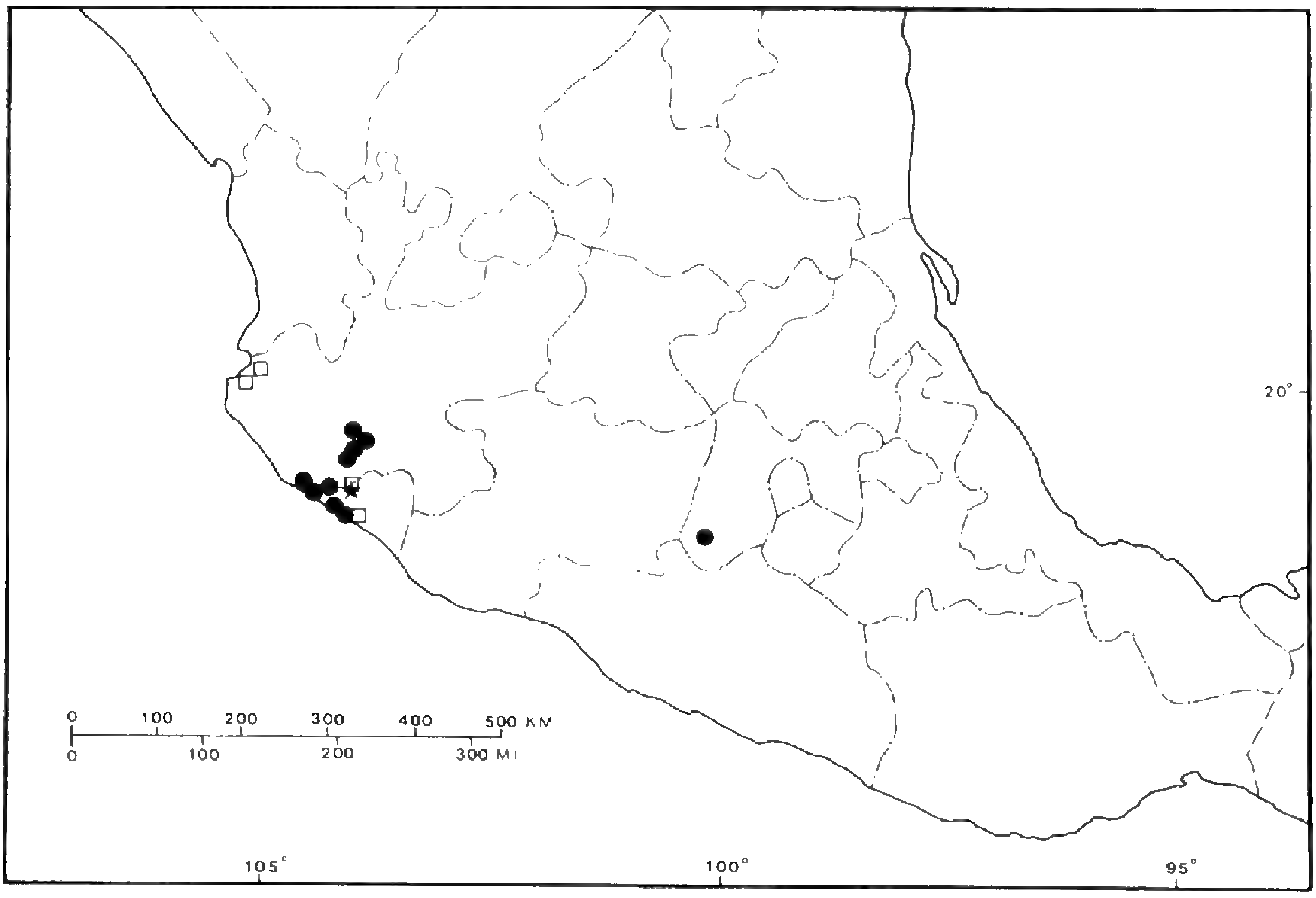


FIGURE 6. *Piper brachypus*: A, fruiting branch, × 0.4; B, portion of infructescence, × 6.

acute, glabrous or puberulent with short eglandular hairs. Leaves with petiole 0.7–1.6 cm long, narrow, glabrous or sparsely puberulent with glandular or short eglandular hairs; blade ovate to broadly ovate to occasionally suborbiculate, 4.4–8.6(–9.6) × 3.3–6.6(–9.1) cm, rounded to truncate to shallowly cordate at base, acuminate at apex, 5- to 7- (to 9-)nerved, glabrous to puberulent (especially at blade-petiole junction) with predominantly short eglandular hairs. Inflorescences (5.9–)6.8–11.6 cm long; peduncle glabrous to commonly puberulent to sparsely pubescent, remaining rachis pubescent to densely pubescent with long eglandular hairs; bracts sessile to subsessile, broadly spatulate to



MAP 2. Distribution of *Piper brachypus* (open squares), *P. cihuatlanense* (star), and *P. novogalicianum* (circles).

cupulate, to 0.5 mm long (rarely longer), pubescent to densely pubescent (especially abaxially) with eglandular hairs. Flowers with pedicel to 0.5(–1) mm long and in diameter, glabrous to puberulent with eglandular hairs; stamens 4 or 5 (or 6), hypogynous, to 1 mm long, the filaments to 0.5 mm long, the anthers small, dehiscing laterally; ovary ellipsoid to ovoid, puberulent with glandular hairs, the style depressed-ovoid to very short-conical, to 0.5 mm long, usually quite conspicuous in both flower and fruit, the stigma 3- to 5-lobed. Fruits ellipsoid to more commonly ovoid to globose, 1–1.75 × 1–1.75 mm, puberulent, style persistent but sometimes obscured by expanding ovary.

DISTRIBUTION. Growing in narrow band from Manzanillo, Colima, north to just south of Puerto Vallarta, Jalisco (see MAP 2).

HABITAT. Essentially unknown (*Mexia* and *Koelz* collections from wooded slopes, *Delgado et al.* from an oak forest). Near sea level to 450 m alt.

PHENOLOGY. Presumably follows phenological pattern of piper relatives in Nueva Galicia, therefore flowering May to July; specimens with fruits collected in March, mid to late July, November, and December.

SPECIMENS EXAMINED. **Mexico.** JALISCO: crossing puente of Río Las Juntas, on road to Puerto Vallarta, near El Tuito, *Delgado, Hernández, & Trejo 204* (MICH); Quimixto, *Mexia 1177* (A, GH, MO, NA, UC). COLIMA: vic. of Manzanillo, SW edge of Cuyutlán lagoon, *Ferris 6186* (A); dry slope near Río Cihuatlán, N of Playa de Santiago, *Koelz 34228* (ENCB, MICH).

Piper brachypus is distinguished by the combination of broadly ovate, glabrous leaves; pubescent rachises; densely pubescent bracts; subsessile flowers; hypogynous stamens; and small, usually ovoid to globose, conspicuously short-styled (= stylopodium, as described by Trelease) fruits.

3. **Piper brevipedicellatum** Bornstein, sp. nov. FIGURE 7.

Frutex 2.5–5(–9) m altus, ramunculis pubescentibus; prophyllum 5–10(–13) mm longum, dorsaliter pubescens; folia laminis late ovatis vel orbiculatis, (6–) 7.3–12.7 × (4.7–)5.6–12.8 cm, breviacuminatis vel acuminatis, basi cordatis, utrinque pubescentibus; inflorescentia 6–11.5(–13.4) cm longa, rhachidi puberula vel pubescenti pilis elongatis; bracteae usque ad 1 mm longae, spathulatae vel spathulicupulatae, abaxialiter pubescentes; pedicelli raro usque ad 1 mm longi; stamina hypogyna, ut videtur basi ovarii adnata, praecipue in fructu; stylus depresso-ovoideus vel breviconicus, usque ad 0.5 mm longus; fructus globosus, 2 × 2 mm, puberulus pilis glandulosis, stylo disciformi instructus.

TYPE. Mexico, Jalisco, 7.9 km WNW of Hwy. 80 along Hwy. 200 toward Puerto Vallarta, 250 m alt., 27 June 1983, *Bornstein & Weber-Bornstein 80* (holotype, MICH; isotypes, CHAP, GH, INIF, MEXU, NY).

Medium-sized treelike shrub, moderately branched from base, 2.5–5(–9) m tall; youngest twigs pubescent with eglandular hairs; older stems gray-brown with swollen nodes and warty lenticels, glabrous, maximum diameter to 5 cm. Prophylls 5–10(–13) mm long, base truncate, apex acute, abaxially puberulent to densely pubescent with eglandular hairs. Leaves with petiole 0.7–2.5 cm long, stout, puberulent to pubescent with eglandular hairs; blade broadly ovate to orbiculate, (6–)7.3–12.7 × (4.7–)5.6–12.8 cm, cordate at base, short-acuminate to acuminate at apex, 5- to 7-nerved, puberulent to more commonly pubescent above with predominantly eglandular hairs, pubescent beneath with both hair types (eglandular more abundant and conspicuous on major veins, glandular more predominant in areolar regions). Inflorescences 6–11.5(–13.4) cm long, green becoming yellow-white to white; peduncle stout, puberulent to pubescent with eglandular hairs, remaining rachis sparsely puberulent or subglabrous to pubescent with eglandular hairs; bracts to 1 mm long, sessile or subsessile, broadly spatulate to broadly spatulate-cupulate, 0.5–1 mm long, sparsely pubescent to pubescent with eglandular hairs abaxially, occasionally with some pubescence adaxially. Flowers with pedicel rarely to 1 mm long and wide, glabrous to puberulent with glandular and eglandular hairs; stamens 4 to 6 (or 7), hypogynous although often (especially in fruit) appearing as if adnate to base of ovary, filaments and anthers ± equal in length, anthers occasionally dehiscing slightly upward from lateral; ovary ovoid to globose, puberulent with glandular hairs, the style depressed-ovoid to short-conical, to 0.5 mm long, persistent in fruit, the stigma 3- to 5-lobed. Fruits globose at maturity, to 2 mm in diameter, puberulent.

DISTRIBUTION. Central Colima north to southwestern Jalisco from near sea level to ca. 1200 m alt. (see MAP 1). Also known from a single disjunct collection

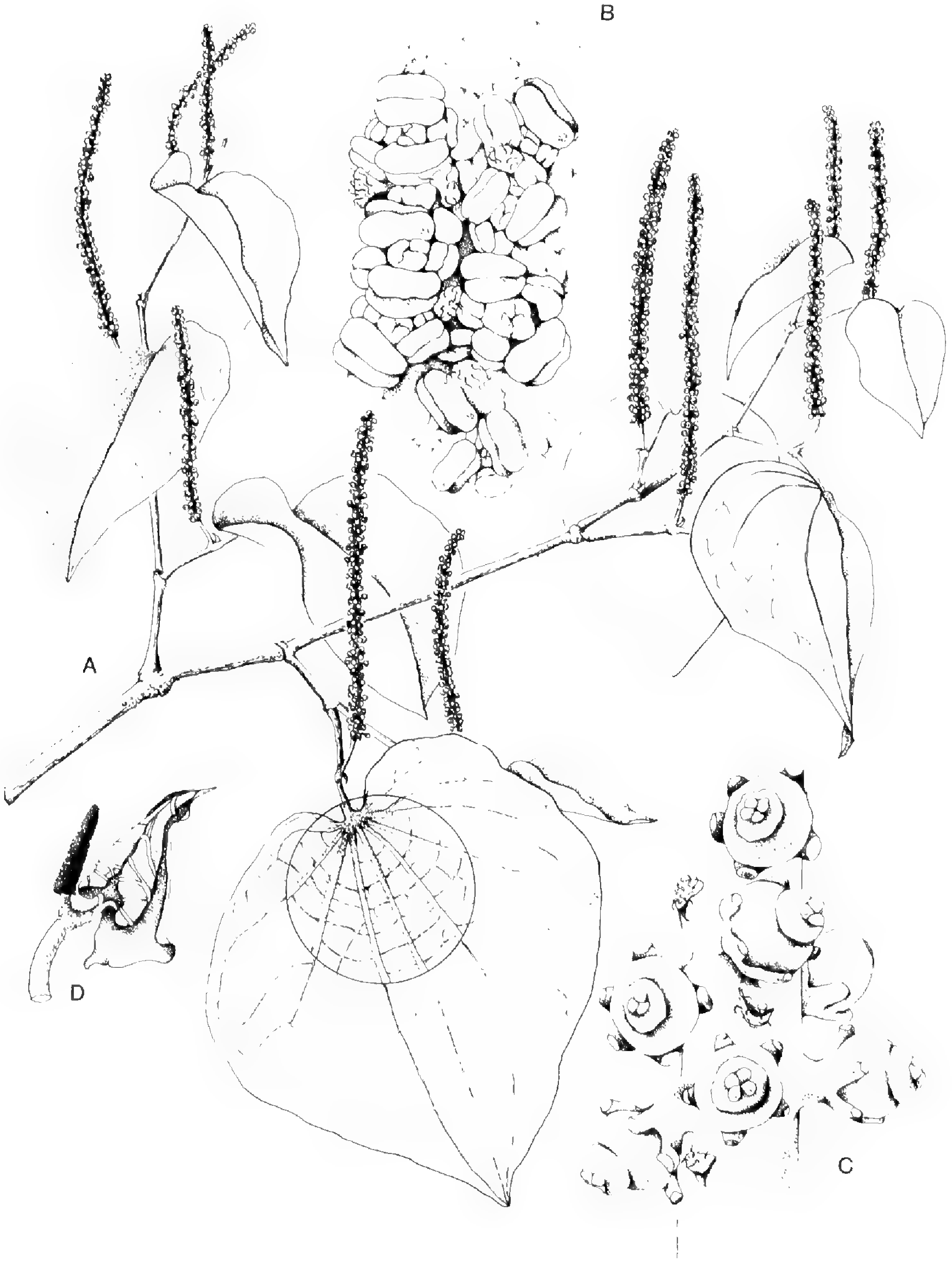


FIGURE 7. *Piper brevipedicellatum*: A, fruiting branch, × 0.4, with detailed inset of petiole-blade junction showing indument; B, portion of young inflorescence, × 5.6; C, portion of infructescence, × 5.6; D, prophyll with emergent young leaf and inflorescence, × 1.9.

ca. 500 km north in Sinaloa, which represents the northernmost extent of subg. *Arctottonia.*

HABITAT. Tolerant of a variety of conditions, including shaded, low-elevation palm forests dominated by *Orbignya cohune,* deciduous to subdeciduous, low-elevation forests near intermittent mountain streams, and deciduous, mid-elevation forests probably dominated by *Quercus* spp. The only potential common denominator of these sites is disturbance, which indicates that this species colonizes second-growth forests.

PHENOLOGY. Flowering late May through June and possibly early July. Fruits appear in late June; collected as late as December.

SPECIMENS EXAMINED. **Mexico.** SINALOA: Sierra de Pinal, just E of El Espinal, *Kimnach & Mejorada 2266* (MEXU, US). JALISCO: along Hwy. 80 between Autlán and Melaque, 4 km N of side road to Casimir Castillo, *Bornstein 75* (MICH); 7.9 km WNW of Hwy. 80 along Hwy. 200 toward Puerto Vallarta, *Bornstein & Weber-Bornstein 81* (MICH); 0.9 km de la carretera Puerto Vallarta–Barra de Navidad, ca. 7 km al SE de la Estación de Biología Chamela, sobre el camino a "El 25" (IMSS communidad), *Lott & Magallanes 611* (MICH); Estación de Biología, Los Pozos, Arroyo Colorado, *Lott 719* (MICH); ca. 8 mi S of Autlán toward La Resolana, *Wilbur 1625* (MICH). COLIMA: 0.5 km S of Comatlán on Hwy. 98 to Minatitlán, *Bornstein 87* (MICH); ca. 16 mi WNW of Santiago, road to Cihuatlán, *McVaugh 14983* (MICH); km 293, ca. 15 mi SE of Manzanillo, *McVaugh & Koelz 1623* (MICH).

Piper brevipedicellatum and *P. brachypus* both have flowers with hypogynous stamens and fruits crowned by a "stylopodial disk." However, in the former species there is a strong tendency toward adnation of the stamens to the ovary and the rachis appears less pubescent than in *P. brachypus*. Unfortunately, neither of these features is consistently different. On the other hand, the two species are quite distinct vegetatively since *P. brachypus* is essentially glabrous, whereas *P. brevipedicellatum* has pubescent twigs, prophylls, and leaves.

4. **Piper cihuatlanense** Bornstein, sp. nov. FIGURE 8.

Frutex usque ad 6 m altus, ramunculis et ramis glabris; prophyllum usque ad 6 mm longum, glabrum vel puberulum; folia laminis ellipticis vel anguste ovatis, 4.9–7.3 × 2.7–3.9 cm, acuminatis, basi rotundatis, glabris vel sparsim puberulis; inflorescentia 6.5–9.1 cm longa, rhachidi dense pubescenti pilis eglandulatis longis; bracteae 0.25–0.5 mm longae, spathulatae vel cupulatae, dense pubescentes pilis eglandulatis longissimis; pedicelli (0.5–)1(–1.5) mm longi, pubescentes; stamina hypogyna; stylus usque ad 0.25 mm longus, depresso-ovoideus, inconspicuus; ovarium et fructus ellipsoideus vel obovoideus vel globosus, 1–1.5 × 0.75–1.25 mm, puberulus.

TYPE. Mexico, Colima, steep, heavily wooded, moist ravines in gorge of Río Cihuatlán, near bridge 13 mi N of Santiago, 200–300 m alt., 27 July 1957, *McVaugh 15838* (holotype, MICH).

Treelike shrub to 6 m tall; twigs and older branches brown (occasionally silvery due to detaching epidermis), glabrous or with few locally concentrated eglandular hairs, especially at branch points, with inconspicuous round, pale brown lenticels. Prophylls to 0.6 cm long, base unknown, apex acute, glabrous to puberulent with very short eglandular hairs. Leaves with petiole 0.4–1.1 cm long, appearing glabrous but usually sparsely puberulent with glandular or very short eglandular hairs; blade elliptic to narrowly ovate, 4.9–7.3 × 2.7–3.9 cm, round at base, acuminate at apex, 5-nerved, glabrous to sparsely puberulent

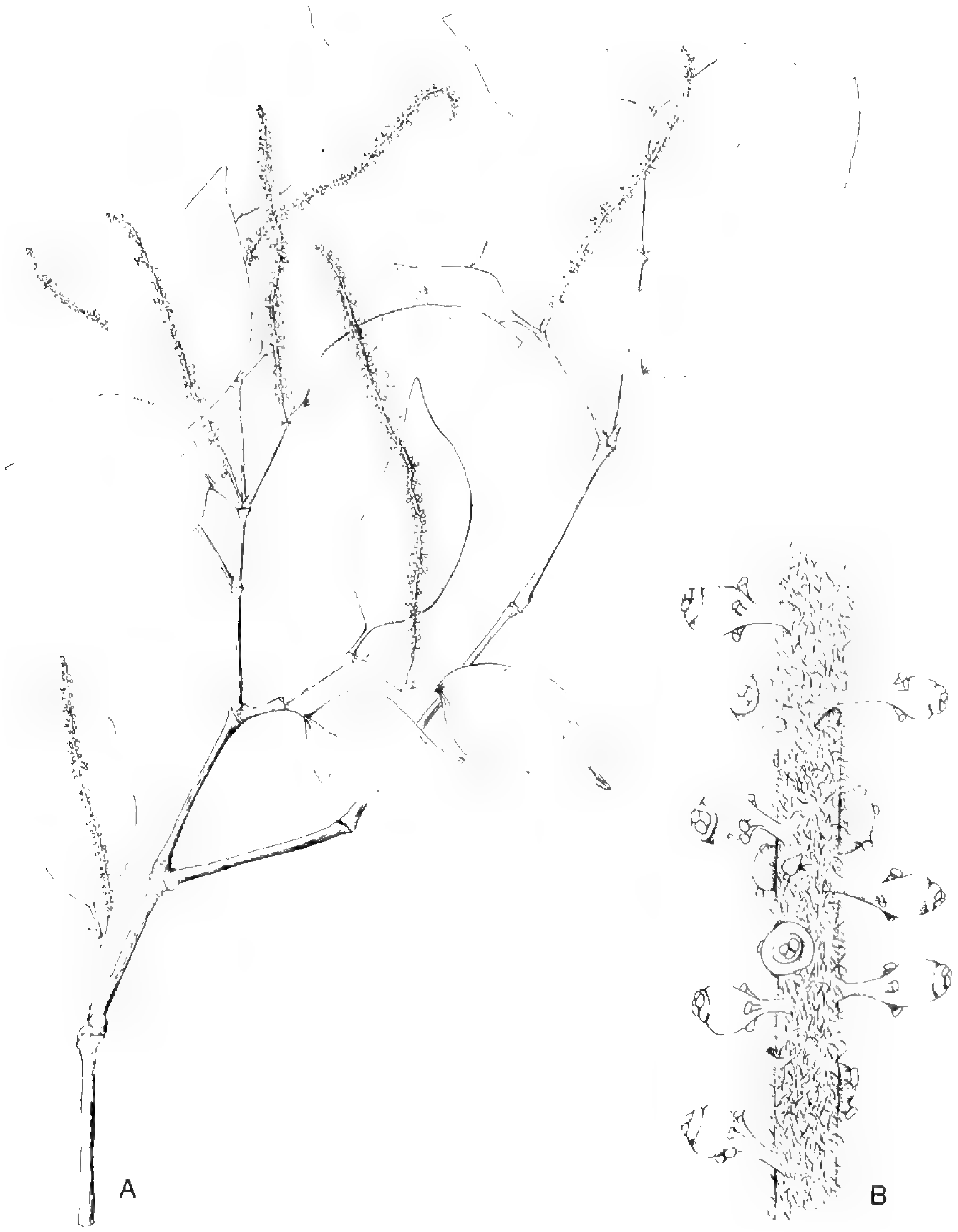


FIGURE 8. *Piper cihuatlanense*: A, fruiting branch, × 0.45; B, portion of infructescence, × 6.8.

(especially at blade-petiole junction) with short eglandular hairs. Inflorescences drooping, 6.5–9.1 cm long, color unknown; peduncle puberulent, passing abruptly into rachis, this densely pubescent with elongate eglandular hairs; bracts broadly spatulate to cupulate, < 0.5 mm long, usually ca. 0.25 mm, densely pubescent with very long eglandular hairs on both surfaces. Flowers with pedicel (0.5–) 1(–1.5) mm long, narrow, usually 1.5–2 times as long as broad, puberulent to distinctly pubescent with eglandular hairs; stamens 4 to 6, hypogynous, the filaments < 0.25 mm long, the anthers subglobose, to 0.5 mm long, dehiscing laterally; ovary ellipsoid to obovoid to subglobose, puberulent with glandular hairs, the style depressed-ovoid, < 0.25 mm long, inconspicuous in flower, totally obscured in fruit, the stigma 3- or 4- (or 5-)lobed. Fruits similar to ovary in shape, 1–1.5 × 0.75–1.25 mm, puberulent.

DISTRIBUTION. Known from two localities in northwestern Colima (see MAP 2).

HABITAT. Apparently restricted to barrancas of Río Cihuatlán at 200–300 m alt. (This area is quite moist during the rainy season and supports a dense tropical subdeciduous vegetation.)

PHENOLOGY. The McVaugh and Koelz collections suggest a flowering period that lasts through the rainy season (mid-May through October). More direct evidence is needed.

SPECIMENS EXAMINED. **Mexico.** COLIMA: barranca of Río Cihuatlán, N of Playa Santiago, *Koelz 34223* (ENCB, MICH).

Piper cihuatlanense is easily distinguished by its small, elliptic to narrowly ovate, subglabrous leaves, its very densely pubescent rachis and bracts with relatively long eglandular hairs, its often-pubescent pedicels, and its virtually nonexistent style (especially in fruit). If it is true that the racemes droop, as is indicated on the label of the type specimen, then this would also be a unique feature (for the entire subgenus).

5. **Piper colotlipanense** Bornstein, sp. nov. FIGURE 9.

Frutex usque ad 2.1 m altus, ramunculis fulvis dense tomentosis; prophyllum usque ad 0.8 cm longum, dorsaliter dense pubescens vel tomentosum; folia laminis late ovatis vel fere orbiculatis, (5.3–)6.6–13.1 × 4.6–11.6 cm, breviacuminatis vel acuminatis, basi rotundatis vel leviter cordatis, supra pubescentibus, subter pubescentibus vel tomentosis; inflorescentia 8.1–10.1 cm longa, rhachidi pubescenti vel sparsim pubescenti; bracteae 0.5–1 mm longae, spathulatae vel spathulicupulatae et breviter vel longe petiolatae, pubescentes vel dense pubescentes; pedicelli (0.5–)1.5(–2.5) mm longi; stamina hypogyna filamentis elongatis, 0.5–1 mm longis; stylus depresso-ovoideus vel conicus; ovarium et fructus ovoideus vel globosus, puberulus.

TYPE. Mexico, Guerrero, 2 mi W of Colotlipa, 2700 ft alt., 22 June 1953, *Rowell & Kubicek 3666* (holotype, MICH).

Medium-sized treelike shrub to 2.1 m tall; youngest twigs densely tawny-tomentose with eglandular hairs, becoming silvery and glabrous; older stems drying brown to gray, with swollen nodes and warty lenticels. Prophylls to 0.8 cm long, base truncate, apex acute, abaxially densely pubescent to tomentose with eglandular hairs. Leaves with petiole 1.1–2.3 cm long, narrow, vaginate at base or occasionally for nearly ½ length of petiole, densely soft-pubescent to tomentose with eglandular hairs; blade broadly ovate to nearly orbiculate, (5.3–)6.6–13.1 × 4.6–11.6 cm, rounded to shallowly cordate at base, short-acuminate to acuminate at apex, 5- to 7- (to 9-)nerved, pubescent above (especially along major veins), densely pubescent to tomentose beneath (especially along major veins), the hairs long, eglandular. Inflorescences 8.1–10.1 cm long, color unknown; peduncle pubescent to tomentose at base with eglandular hairs,

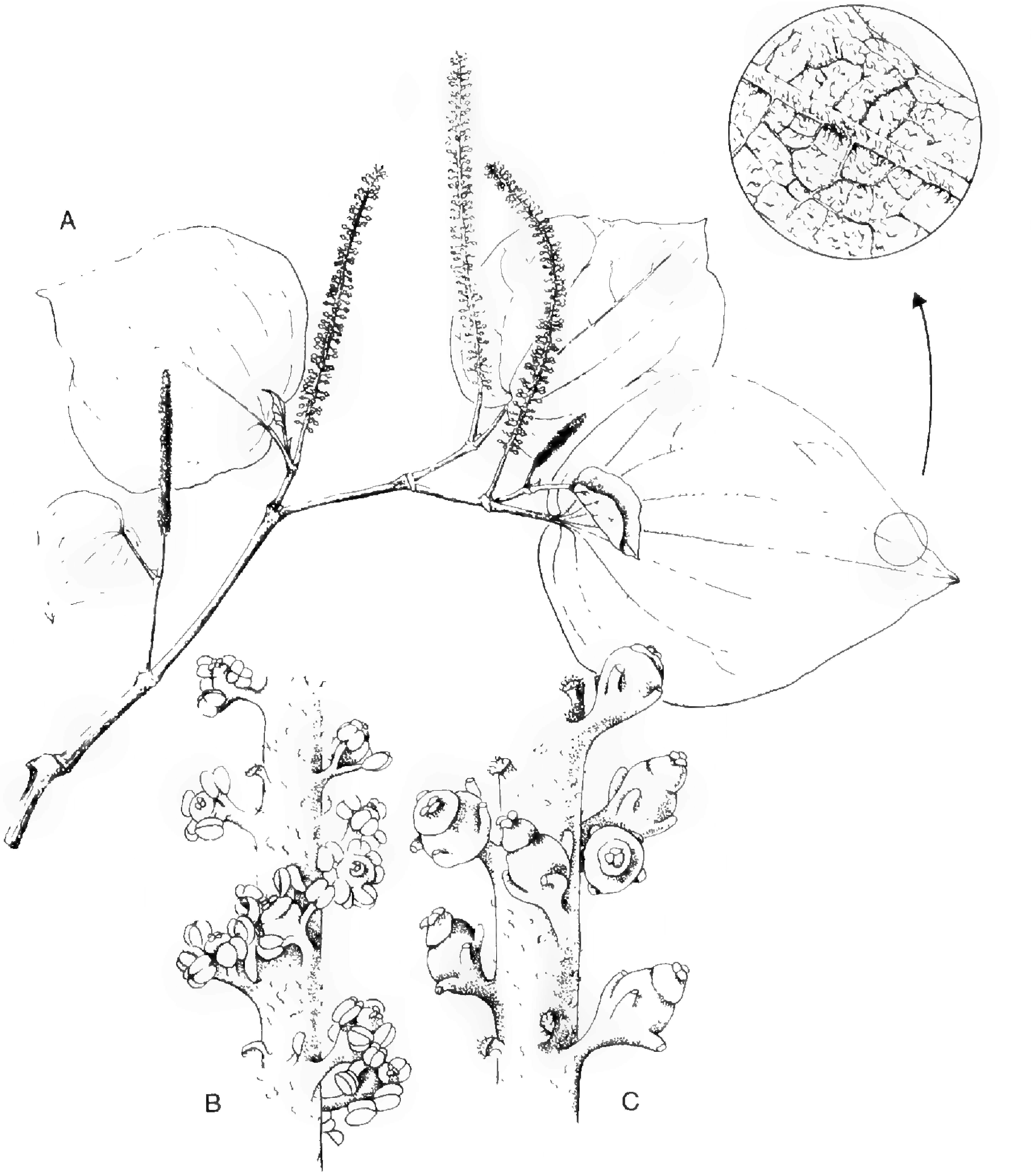


FIGURE 9. *Piper colotlipanense*: A, flowering branch, × 0.42, with detailed inset of lower leaf surface showing indument; B, portion of inflorescence, × 6.3; C, portion of semimature infructescence, × 6.3.

gradually transitional to sparsely pubescent for remaining rachis; bracts sessile or subsessile to distinctly long-petiolate, spatulate to spatulate-cupulate at apex, 0.5–1 mm long, pubescent to densely pubescent with eglandular hairs, most often on abaxial surface. Flowers with pedicel (0.5–)1.5(–2.5) mm long, up to 0.5 mm in diameter, glabrous to puberulent with glandular hairs, occasionally sparsely pubescent with eglandular hairs; stamens (4 or) 5 or 6, hypogynous, the filaments 0.5–1 mm long, the anthers to 0.5 mm long, rarely slightly longer, dehiscing laterally to slightly divergent upward from lateral; ovary ovoid to globose, puberulent with glandular hairs, the style depressed-ovoid to conical, in young fruit ⅓–¾ length of ovary, the stigma 3- or 4-lobed. Fruits (when submature) ovoid to globose, style very evident.

DISTRIBUTION. Guerrero, in low mountains of Sierra Madre del Sur, south of Chilpancingo de los Bravos (see MAP 1).

HABITAT. Herbarium label data indicate that this species occurs near edges of streams or rivers, or on hillsides on rocky soil at 150–850 m alt.

PHENOLOGY. Flowering May through June, possibly into early July. Young fruits in early June, expected into July and August.

REPRESENTATIVE SPECIMENS. **Mexico.** GUERRERO: S of Chilpancingo, *Clark 7141* (MO, NY); Vallecitos, Montes de Oca, *Hinton 10261* (ILL, K, NA, NY, PH, TEX, US); Pie de la Cuesta, 10 mi N of Acapulco, *MacDaniels 201* (F); 1 mi W of Achuitzotla, *Rowell & E. H. Cooper 2507* (MICH); 1 mi W of Colotlipa, *Rowell & Irby 3523* (MICH). LOCALITY UNKNOWN: *Sessé & Mociño 318* (F), *328* (F), *329* (F), *339* (ILL), *348* (F, ILL).

Piper colotlipanense is distinguished by its densely long-pubescent prophylls and leaves and its hypogynous stamens with long filaments.

6. **Piper guazacapanense** Trel. & Standley, Fieldiana, Bot. **24:** 301. 1952. TYPE: Guatemala, Santa Rosa, along Avellana road, S of Guazacapán, 150 m alt., 12 June 1940, *Standley 79461* (holotype, F!; isotype, NY!). FIGURE 10.

Procumbent perennial, occasionally rooting at nodes; stems largely herbaceous, becoming woody with age, glabrous. Prophylls to 8 mm long, base truncate, apex acute, abaxially puberulent to hirtellous. Leaves with petiole 4–17 mm long, slender, hirtellous with both glandular and eglandular hairs; blade broadly ovate to orbiculate-ovate, (3.5–)5–9 × 4–8 cm, cordate with rounded lobes at base, gradually to abruptly acuminate or long-acuminate at apex, 5-nerved (3 principal veins persistent almost to apex), dark green above and sparsely puberulent, paler beneath and puberulent to hirtellous with eglandular hairs ± restricted to veins and glandular ones to areoles. Inflorescences 1–3 (–4.2) cm long, yellow-green when young, turning white at maturity; peduncle and rachis glabrous to more commonly puberulent; bracts spatulate-cupulate to broadly cupulate, rarely to 1 mm long, abaxially puberulent with eglandular hairs (rarely glabrous). Flowers with pedicels 1–2.5 mm long, glabrous or occasionally minutely puberulent; stamens 4 to 7, hypogynous, filaments 0.25 mm long, anthers dehiscing laterally; ovary ovoid to globose, minutely puberulent with glandular hairs, the style ½ to equal the ovary in length, becoming obliterated in fruit, the stigma 3- or 4-lobed. Fruits globose, 2–2.5 mm in diameter, green when young, translucent pearl white at maturity, puberulent.

DISTRIBUTION. Southwestern Chiapas on northwestern edge of Sierra Madre de Chiapas, the north-central plateau in Chiapas, and southeastern Guatemala on southern edge of Sierra Madre (see MAP 3).

HABITAT. Moist, shaded ravines. Commonly found as dense groundcover along banks above small streams in tropical subdeciduous forests at 150–1000 m alt.

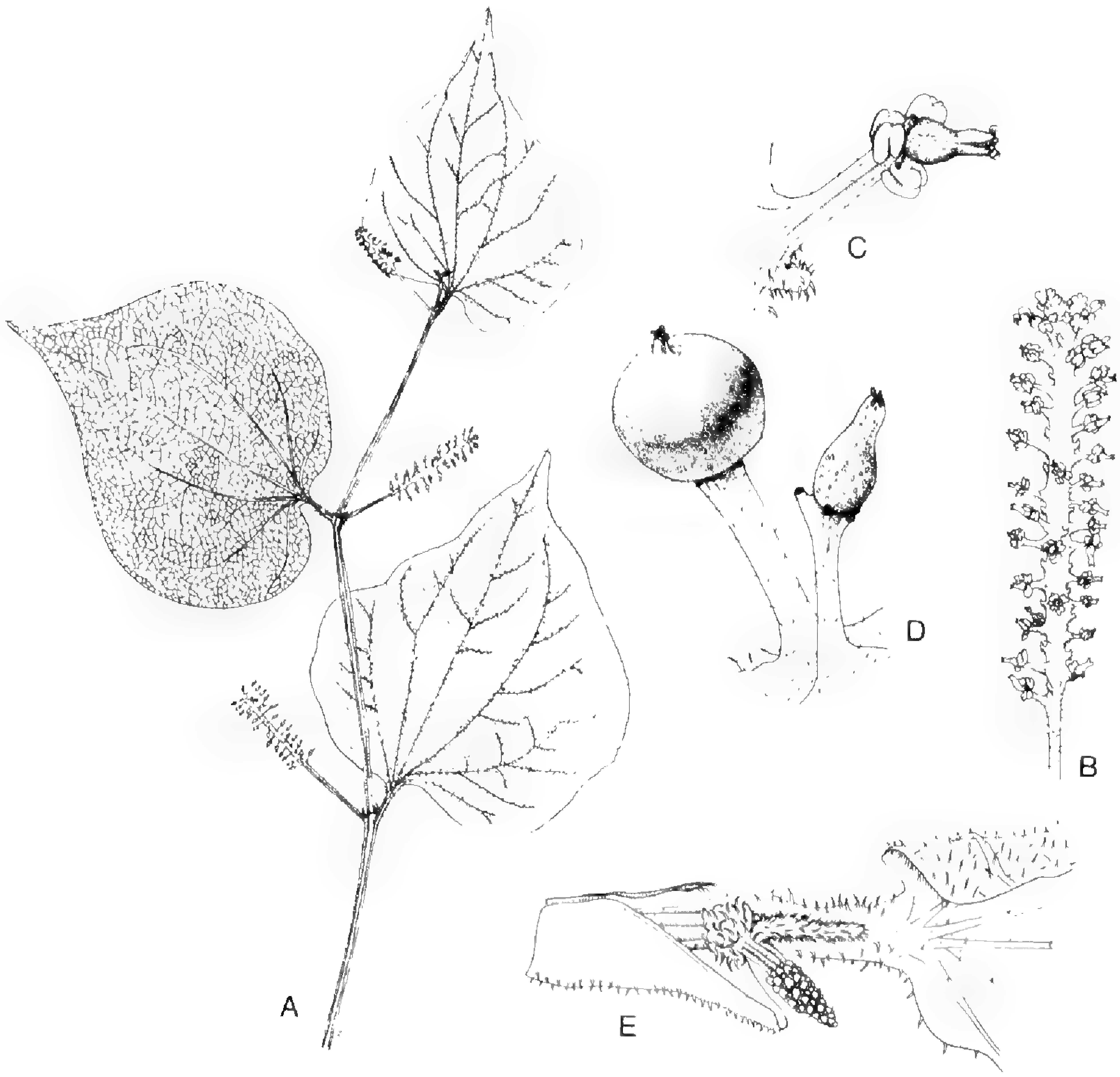


FIGURE 10. *Piper guazacapanense*: A, flowering branch, × 0.4; B, inflorescence, × 1.6; C, flower with bract, × 13; D, immature and mature fruits, × 8.6; E, prophyll with young leaf, young inflorescence, and succeeding prophyll, × 13.

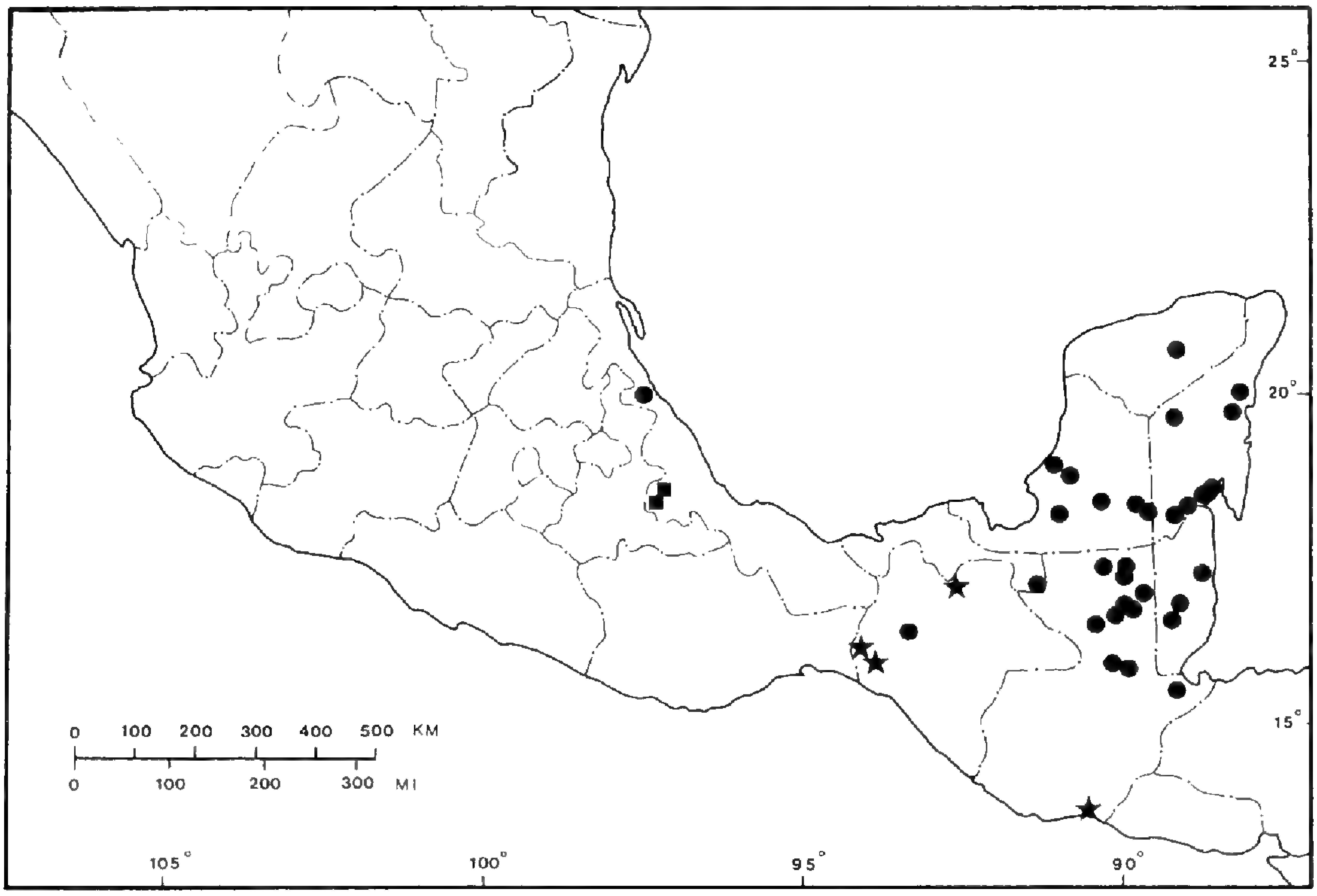
PHENOLOGY. Flowering mid-February to late May or early June, predominantly in April and May. Fruits collected in October, December, and February.

REPRESENTATIVE SPECIMENS. **Mexico.** CHIAPAS: 12 km S of Hwy. 190 near Rizo de Oro, behind microwave tower of La Mina in moist shaded ravine, *Bornstein, Chase, & Bornstein 59* (MICH); 13 mi N of Arriaga along Hwy. 195 on steep slopes along ravines, *Breedlove 25520* (ENCB, F, MEXU, MICH, MO, NY, TEX); along river below Huitiupan, *Breedlove & A. C. Smith 32576* (MEXU).

Piper guazacapanense is easily recognized by its prostrate habit, its small, heart-shaped leaves, its short, few-flowered inflorescences, and its globose, translucent fruits.

7. **Piper mcvaughii** Bornstein, sp. nov. FIGURE 11.

Frutex ramunculis fere glabris; prophyllum usque ad 0.3 cm longum, puberulum vel brevipubescens; folia laminis late ovatis, 5.1–8 × 5.5–7.6 cm, breviacuminatis, basi cordatis, supra puberulis, subter sparsim puberulis; in-



MAP 3. Distribution of *Piper guazacapanense* (stars), *P. muelleri* (squares), and *P. neesianum* (circles).

florescentia 6.7–8.8 cm longa, rhachidi sparsim puberula pilis glandulosis; bracteae usque ad 0.75 mm longae, late spathulatae vel valde cupulatae, sparsim puberulae vel puberulae; pedicelli 0.5(–0.75) mm longi, sparsim pubuleri, pilis glandulosis; stamina ovario adnata; stylus depresso-ovoideus vel brevicolumnaris, usque ad 0.75 mm longus; ovarium ovoideum-ellipsoideum; fructus globosus, usque ad 2 mm diametro, puberulus.

TYPE. Mexico, Jalisco, coastal plain near hwy. to Autlán, 4 mi N of Bahía Navidad, 40 m alt., 8 Nov. 1960, *McVaugh 20817* (holotype, MICH).

Shrub of unknown dimensions; youngest twigs drying brown, with sparse glandular hairs; older branches silvery, with brown, warty lenticels, glabrous. Prophylls to 3 mm long, base truncate, apex acute, abaxially puberulent to short-pubescent with glandular or short eglandular hairs. Leaves with petiole 1.1–1.8 cm long, narrow, appearing glabrous but sparsely puberulent with glandular hairs; blade broadly ovate, 5.1–8 × 5.5–7.6 cm, cordate at base, short-acuminate at apex, 5- (to 7-)nerved, puberulent above with predominantly glandular hairs (especially at petiole-blade junction and along blade margin), sparsely puberulent beneath on major veins, with mostly short eglandular hairs. Inflorescences 6.7–8.8 cm long, color unknown, with flowers widely spaced at maturity; peduncle and rachis sparsely puberulent with glandular hairs; bracts sessile or subsessile, broadly spatulate to occasionally strongly cupulate, to 0.75 mm long, sparsely puberulent to puberulent with glandular or short eglandular hairs. Flowers with pedicel ca. 0.5(–0.75) mm long and broad, sparsely puberulent with glandular hairs; stamens 4 or 5, adnate from

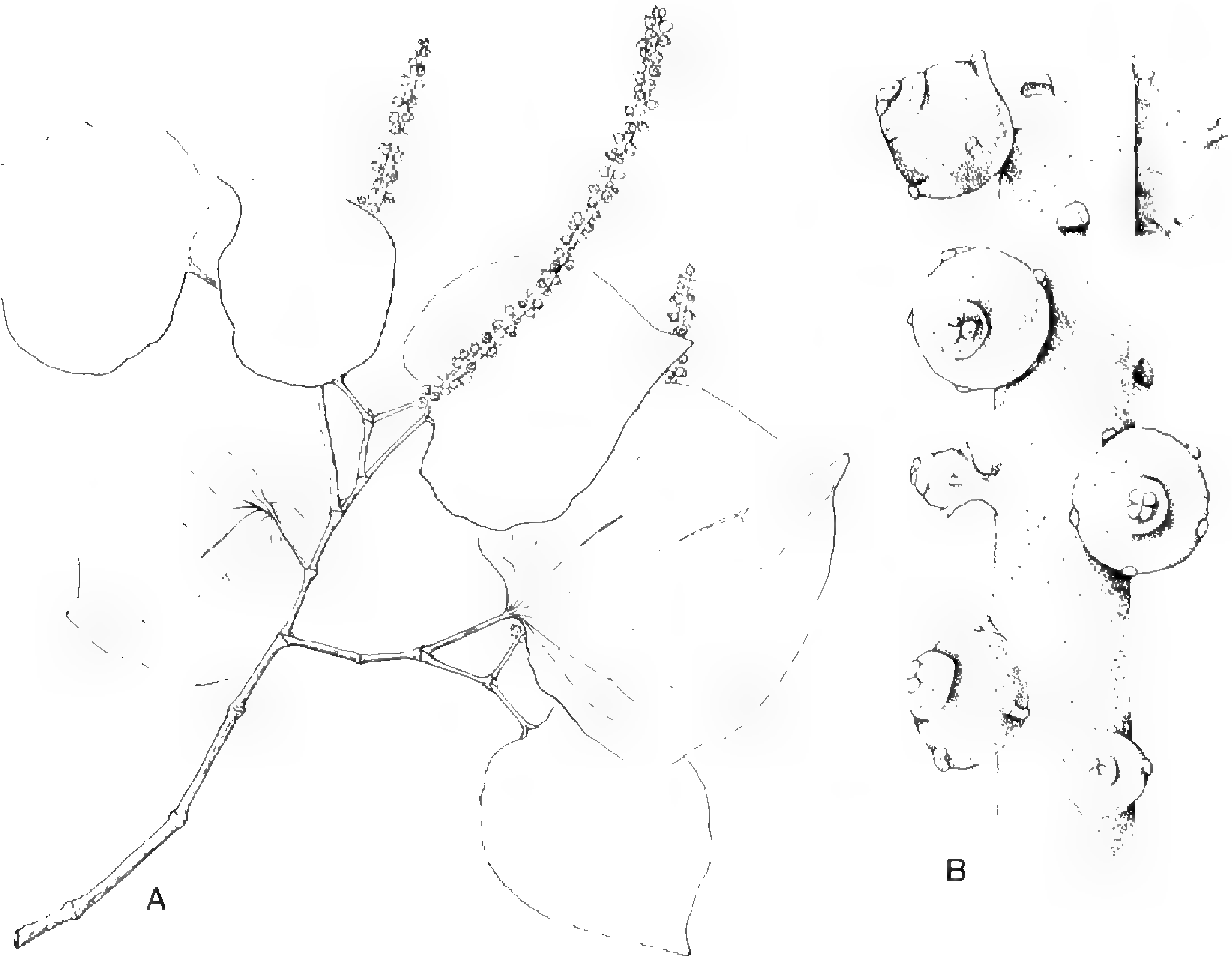


FIGURE 11. *Piper mcvaughii*: A, fruiting branch, × 0.4; B, portion of infructescence, × 6.

near base to middle of ovary, filaments ca. 0.25–0.5 mm long, anthers unknown; ovary ovoid-ellipsoid in late flower–early fruit, puberulent with glandular hairs, the style depressed-ovoid to short-columnar, to 0.75 mm long, the stigma (3- or) 4- or 5-lobed. Fruits globose at maturity, 2 mm in diameter, puberulent, style persistent and conspicuous.

DISTRIBUTION. Known only from type locality, southwestern Jalisco near Colima border (see MAP 1).

HABITAT. Type collection from second-growth deciduous forest with associated species of *Cordia* L., *Trichilia* P. Browne, and *Sideroxylon* L.

PHENOLOGY. Relatively unknown. Holotype, collected in November, has predominantly mature fruits. Based on flowering times of neighboring pipers, this species probably flowers from late May through June, at the beginning of the rainy season.

EPONYMY. Named in honor of Rogers McVaugh, Professor Emeritus at the University of Michigan, for his contributions that have increased our knowledge of botany in Mexico, and especially for his work on the flora of Nueva Galicia.

Superficially similar to *Piper brachypus*, *P. mcvaughii* differs in having stamens adnate to the ovary (vs. hypogynous) and the rachis and bracts puberulent

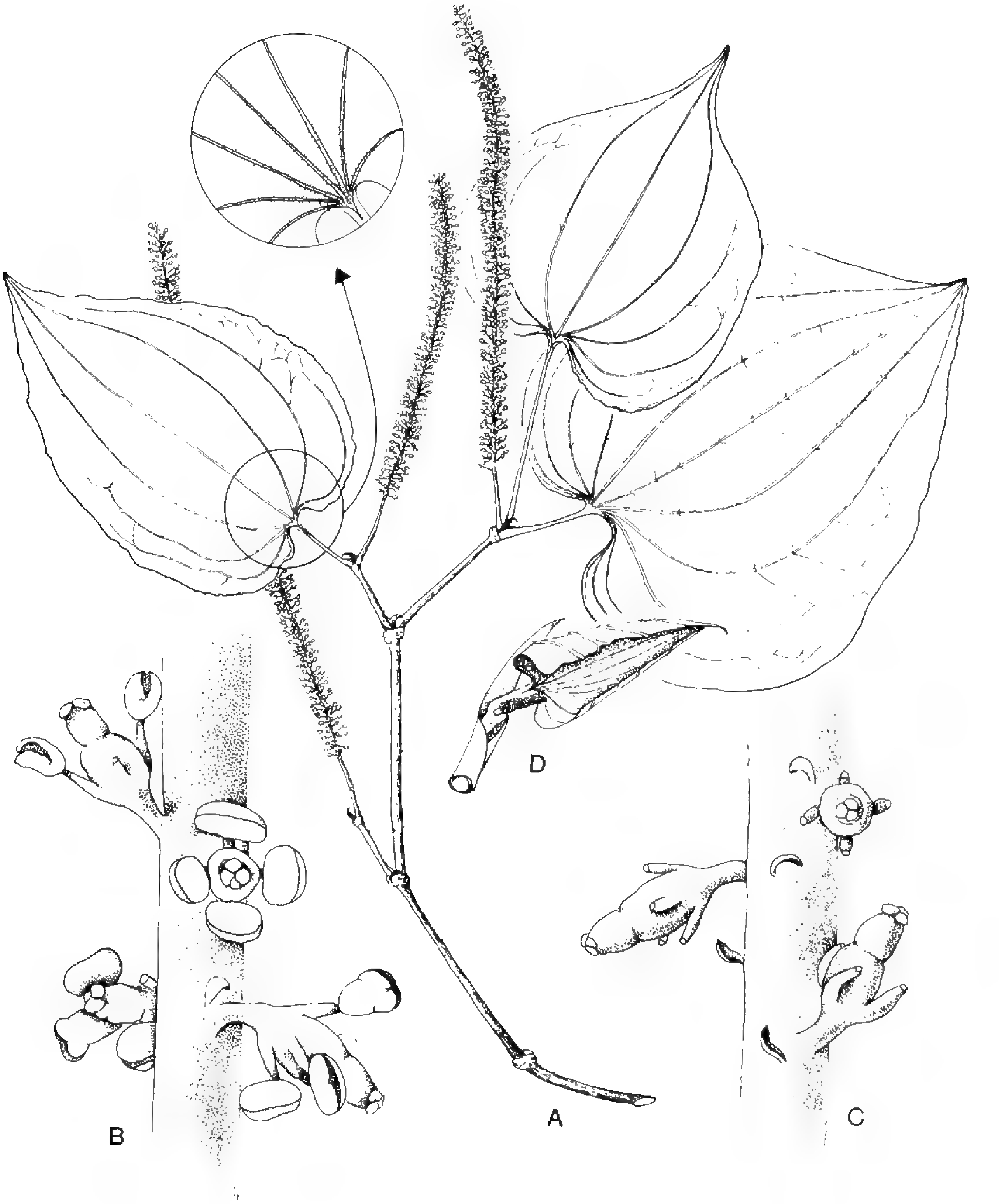


FIGURE 12. *Piper michelianum*: A, flowering branch, × 0.42, with detailed inset of petiole-blade junction to show puberulence; B, portion of inflorescence in late flower–early fruit, × 6.3; C, portion of young infructescence, × 6.3; D, prophyll with emergent young leaf and inflorescence, × 2.1.

with predominantly glandular hairs (vs. pubescent to densely pubescent with eglandular ones).

8. **Piper michelianum** C. DC. Annuaire Conserv. Jard. Bot. Genève **21:** 317. 1920. TYPE: Mexico, Michoacán, El Muleto, 850 m alt., 30 June 1898, *Langlassé 215* (holotype, G!; isotypes, GH!, K!, US!). FIGURE 12.

Piper mas Trel. Amer. J. Bot. **8:** 215. *pl. 7, fig. 2.* 1921. TYPE: Mexico, Michoacán, El Muleto, 850 m alt., 30 June 1898, *Langlassé 215* (holotype, US!; isotypes, G!, GH!, K!).

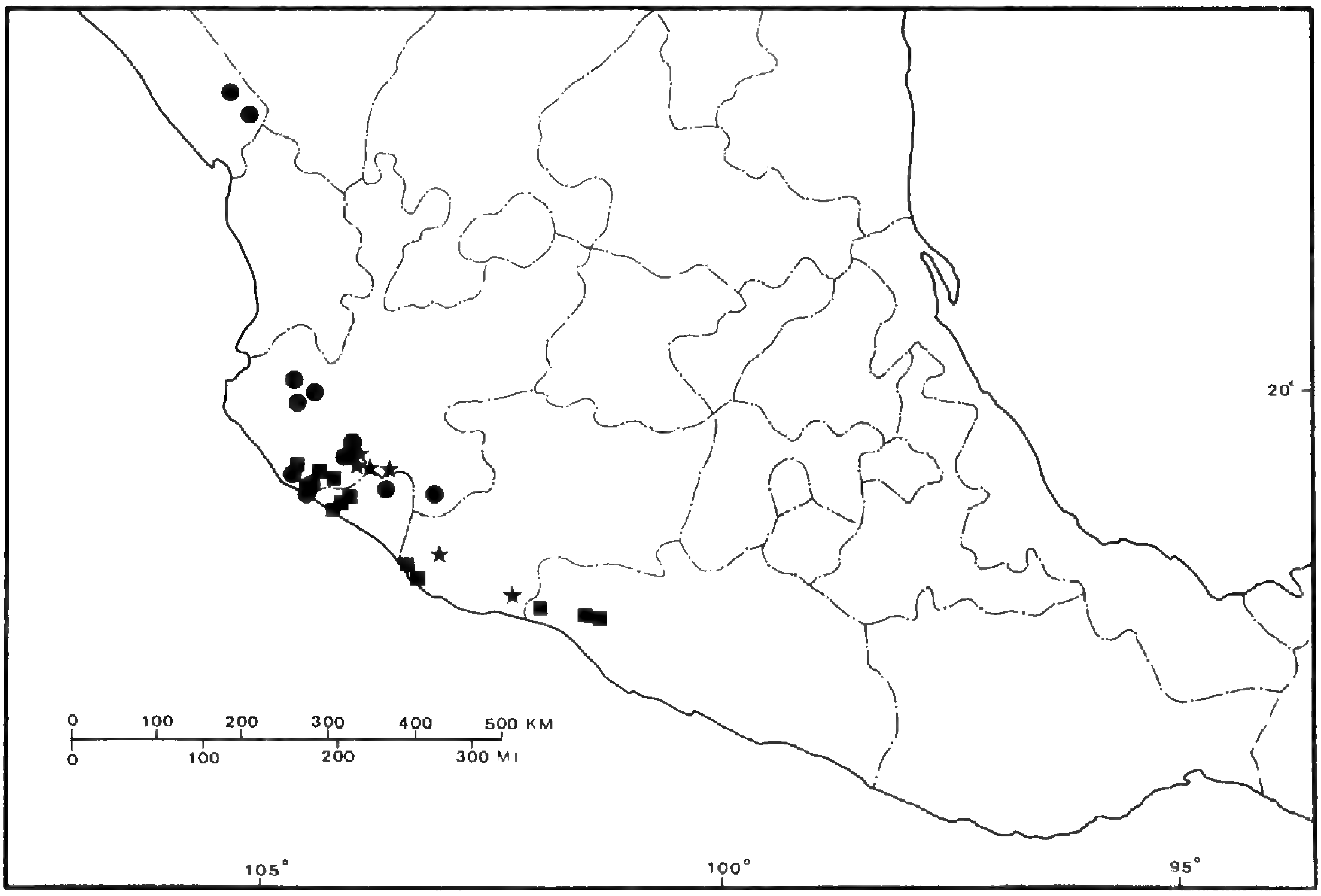
Medium-sized shrub, sparsely branched from base, appearing treelike, 2–5 m tall; youngest twigs very minutely and sparsely puberulent, predominantly with glandular hairs, soon glabrescent; older branches brownish, with warty lenticels; stems ash-gray, with swollen nodes, maximum diameter 6 cm. Prophylls to 1.2 cm long, base truncate, apex narrow and acuminate, both surfaces glabrous. Leaves with petiole 0.9–2 cm long, narrow, glabrous to puberulent (especially near blade junction) with eglandular hairs; blade round-ovate, (6–) 7.2–10.9(–13.4) × 6.1–8.6(–12.3) cm, shallow to moderately cordate at base, acuminate at apex, (5- to) 7-nerved, puberulent above with glandular and eglandular hairs (the latter generally restricted to veins), puberulent to sparsely and transiently pubescent beneath (especially on proximal ½) with glandular and eglandular hairs. Inflorescences 8.5–15.7 cm long, greenish when young, cream colored and fragrant at maturity; peduncle stout, glabrous to very minutely puberulent with mostly glandular hairs, remaining rachis glabrous to puberulent with glandular or very short eglandular hairs; bracts variable, ranging from sessile and strongly cupulate to distinctly petiolate with petiole gradually to abruptly expanding into spatulate to spatulate-cupulate apex, 0.25–1 mm long, abaxially glabrous to puberulent to very sparsely pubescent with eglandular hairs. Flowers with pedicel 0.5–2.5 mm long (depending on maturity), rarely to 0.5 mm wide, glabrous to puberulent with glandular hairs; stamens 4 (or 5), hypogynous, the filaments to 0.5 mm long, the anthers broadly obovoid, 1–3 times length of filaments, dehiscing slightly to conspicuously divergent upward from lateral; ovary ovoid to subglobose, puberulent with glandular hairs, the style conical to short-columnar, to 0.75 mm long, equaling to slightly exceeding ovary in length when in flower, the stigma 3- or 4-lobed. Fruits ovoid to subglobose at submaturity, 1.5–2 × 1–1.5 mm, style persistent but somewhat obscured by expanding ovary.

DISTRIBUTION. Foothills of Sierra Madre, from southeastern Jalisco through northern Colima to southwestern Michoacán, 800–1800 m alt. (see MAP 4).

HABITAT. Collected on steep hillsides above coffee plantations in association with species of *Juglans* L. and *Ficus*; in "precipitous wooded ferny barrancas"; in densely wooded arroyos with *Ficus* and various lianas; and on more open rocky slopes and ledges with *Bursera*, *Acacia* Miller, *Agave* L., woody Umbelliferae, and various orchids and bromeliads. All of these habitats feature steep terrain in an area where water is generally abundant during the rainy season but limited or absent during the dry season (mid-elevation subdeciduous forest).

PHENOLOGY. Flowering late May through June. Semimature fruits collected in mid-August.

REPRESENTATIVE SPECIMENS. **Mexico.** JALISCO: 1 km ESE of Ayotitlán (27 km por camino al E de Cuautitlán), *Cochrane et al. 10877* (NY); 3.3 km SSE of El Chante, halfway to Tecopatlán Valley, *Iltis & Nee 1416* (NY); 0.5–1 km NW of Rincón de Manantlán (13 km S of El Chante), *Iltis et al. 2559* (NY). COLIMA: just S of San Antonio on road to Comala, *Bornstein & Chase 95* (MICH); dirt road 3.5 mi N of San Antonio, *Chase 83112* (MICH); 1–1.5 mi S of Hacienda San Antonio, SW foothills of Nevado de Colima, *McVaugh*



Map 4. Distribution of *Piper michelianum* (stars), *P. rosei* (circles), and *P. stipulaceum* (squares).

16107 (MICH). MICHOACÁN: San José, in distr. of Coalcomán, *Hinton 13836* (ENCB, ILL, NA, NY, US).

TAXONOMIC NOTE. *Piper michelianum* and *Piper mas* were described on the basis of the same type material and are therefore nomenclatural synonyms.

Piper michelianum is distinguished by the combination of shallowly to moderately cordate leaf blades puberulent above and puberulent to transiently pubescent beneath, glabrous to puberulent rachis and floral bracts, narrow and elongate (usually 1.5–2.5 mm long) mature pedicels, and hypogynous stamens (usually 4).

Potentially confused with *Piper rosei* where their ranges overlap, *P. michelianum* lacks the conspicuous pubescence of the rachis and bracts and has narrower and slightly longer pedicels, as well as acuminate (vs. long-acuminate), basally cordate (vs. rounded) leaves that are more conspicuously pubescent beneath.

The Iltis collections from Jalisco are sterile and are therefore included here on a tentative basis. In sterile condition *Piper michelianum* resembles *P. brachypus* and *P. mcvaughii,* both of which are also glabrous to puberulent vegetatively. The only means for separating the three species morphologically is by examining the inflorescences. I have placed these two collections under *P. michelianum* on the basis of their habitat and distribution.

9. **Piper muelleri** C. DC. *in* A. DC. Prodr. **16**(1): 243. 1869. TYPE: Mexico, Veracruz, Orizaba, 1853, *Mueller 180* (holotype, BR!; isotypes, G!, GH!, ILL!, LE!, NY!). FIGURE 13.

FIGURE 13. *Piper muelleri*: A, fruiting branch, × 0.4, with detailed insets of lower leaf surface showing indument, and prophyll and young inflorescence emergent from next-oldest prophyll (absent); B, portion of semimature infructescence, × 6; C, portion of mature infructescence (note recurved stigmas), × 6.

Habit unknown, probably small to medium-sized shrub; young branches puberulent with eglandular hairs; older branches glabrous. Prophylls 0.5–1.2 mm long, slender, base truncate, apex acute, abaxially puberulent to pubescent with eglandular hairs. Leaves with petiole 0.6–1.8 cm long, stout, puberulent to densely pubescent with eglandular hairs; blade lance-elliptic to lance-ovate to rarely ovate, (7.3–)8.8–15.3 × 3.4–6 cm, rounded and symmetrical at base, acuminate to long-acuminate at apex, occasionally drying rugulose to bullate, 5- to 7-nerved (3 most central protracted to apex), glabrous above, densely pubescent beneath (especially along major veins) with eglandular hairs. Inflorescences 5–8.3 cm long; peduncle narrow, puberulent to pubescent, remaining rachis puberulent with eglandular hairs; bracts subsessile to minutely petiolate, 0.5–1.25 mm long, the apical region broadly spatulate-cupulate to cupulate, abaxially pubescent with eglandular hairs. Flowers with pedicel 0.5–2.5 mm long, sparsely puberulent to puberulent with eglandular hairs; stamens 5 to 7, hypogynous, the filaments to 1 mm long, equaling or slightly surpassing ovary length in flower or young fruit, the anthers subglobose, dehiscing laterally; ovary depressed-ovoid, glabrous, the style elongate, 1–1.5 times ovary length in flower, becoming largely obliterated during fruit maturation, the stigma (2- or) 3- or 4- (or 5-)lobed, with lobes recurved, persistent in fruit. Fruits depressed-ovoid when young, becoming globose at maturity, glabrous.

DISTRIBUTION. Eastern slopes of Sierra Madre Oriental, from Coscomatepec south to Orizaba in Veracruz (see MAP 3).

HABITAT. Essentially unknown, although two collections (*Matuda 1515* and *Seler & Seler 5172*) are from high elevations on mountains.

PHENOLOGY. Flowering in May, perhaps also in late April and early June. Fruits occurring from May until August or later.

SPECIMENS EXAMINED. **Mexico.** VERACRUZ: Orizaba, *Botteri 192 (= 1156)* (GH, K, US (2 sheets)); Cerro Punta Coscomat, *Matuda 1515* (A, MICH, MO, NY); Córdoba, Cerro de Chocamán, *Seler & Seler 5172* (GH, US).

Piper muelleri is distinguished from its closest relatives, *P. neesianum* and *P. yucatanense,* by its pubescent (vs. glabrous) plants, its comparatively long staminal filaments, and its uniquely shaped gynoecium.

Piper muelleri is perhaps the rarest species of the subgenus. It has not been collected since 1937, despite my efforts in recent years. With the continued destruction of tropical forests in many areas of Mexico, including the area surrounding Orizaba, it would not be surprising if this species were extinct. However, because I had very little information to guide me in my quest, it may simply be a matter of looking in the wrong place. I suspect that an exhaustive search of the region between Coscomatepec and Orizaba during the month of May could be rewarding and could thereby provide more detailed information concerning this species.

10. **Piper neesianum** C. DC. *in* A. DC. Prodr. **16**(1): 256. 1869. TYPE: Mexico, locality unknown, 1841–42, *Karwinski 823* (holotype, LE; isotypes, G!, H!). FIGURE 14.

Arctottonia sempervirens Trel. ex Lundell, Publ. Carnegie Inst. Wash. **436:** 302. 1934, *nomen nudum. Arctottonia sempervirens* Trel. ex Standley, Field Mus. Nat. Hist., Bot. Ser. **12:** 405. 1936. *Piper sempervirens* (Trel. ex Standley) Lundell, Publ. Carnegie Inst. Wash. **478:** 208. 1937. TYPE: Guatemala, Petén, Uaxactún, 16 April 1931, *Bartlett 12563* (holotype, MICH!; isotypes, ILL (2 sheets)!).

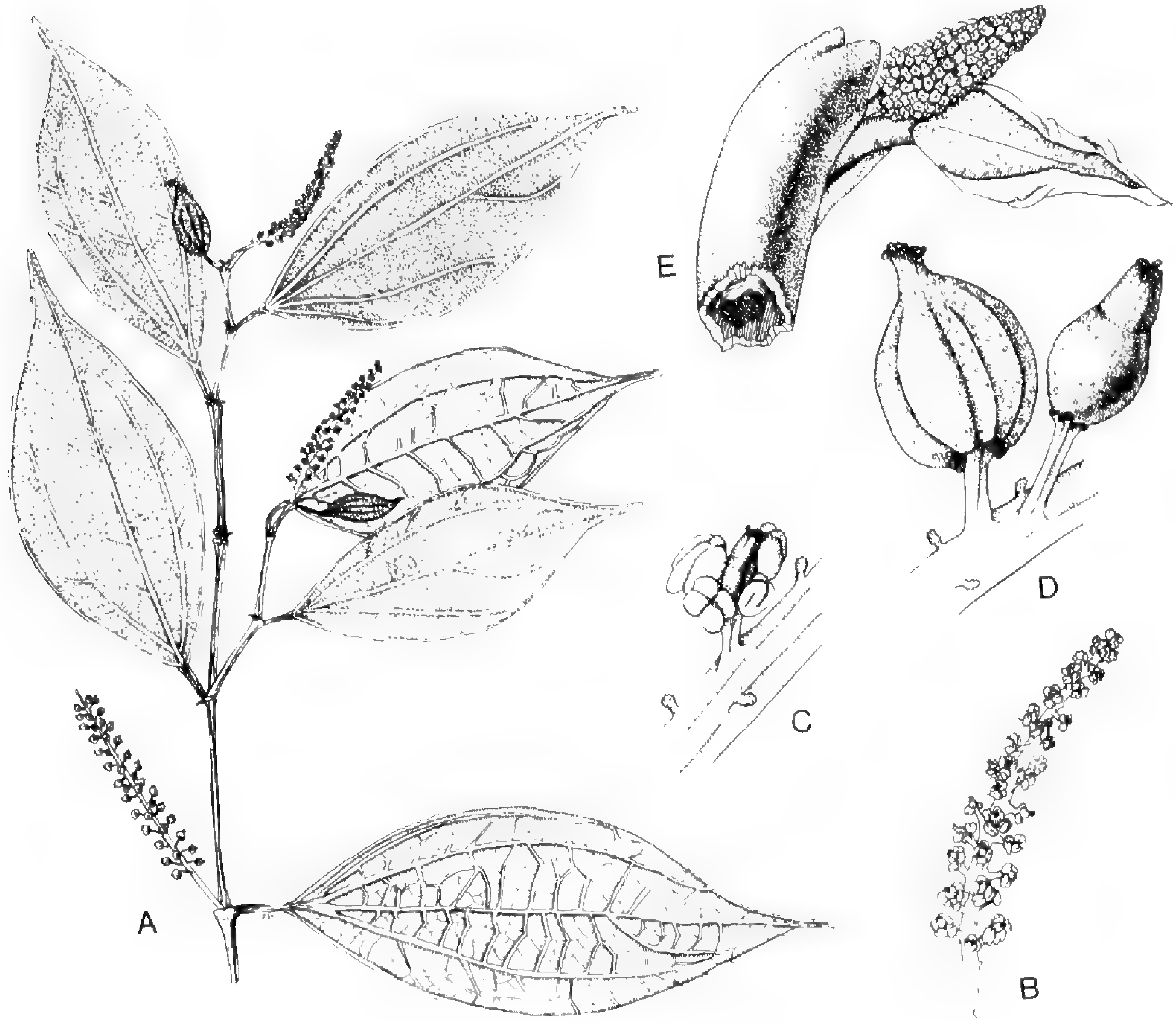


FIGURE 14. *Piper neesianum*: A, flowering branch, × 0.4; B, inflorescence, × 1.7; C, flower with bracts, × 10.5; D, immature and mature fruits with bracts, × 8.4; E, prophyll with emergent young leaf and inflorescence, × 8.4.

Slender shrub, multibranched from base, 1–6.5 m tall; bark green on young branches, becoming brown and warty with age. Prophylls to 0.5 mm long, base truncate, apex acute, appearing glabrous but with glandular hairs. Leaves with petiole 2–12 mm long, stout, with glabrescent glandular hairs; blade lance-elliptic to elliptic to ovate-elliptic, 5.2–12.6(–15.2) × 1.9–6.1 cm, rounded to more commonly acute, slightly unequal and occasionally auriculate at base, abruptly acuminate to long-acuminate at apex, stiff and coriaceous, 3-nerved (central nerve protracted to apex), dark shiny green above, gray-green to silvery beneath, both surfaces appearing glabrous but with glandular hairs (at least when young). Inflorescences (2.4–)3–6.9 cm long, white at maturity; peduncle slender, rachis appearing glabrous but with glandular hairs; bracts occasionally petiolate, narrowly spatulate to spatulate to rarely spatulate-cupulate, 0.25–0.5 mm long, glabrous. Flowers with pedicel 0.5–2.5(–3.5) mm long, lax, divaricate, appearing glabrous but with very sparse glandular hairs; stamens (3 or) 4 or 5 (or 6), the filaments ca. 0.25 mm long, the anthers subglobose, dehiscing laterally or occasionally slightly upward from lateral; ovary ovoid to rarely ellipsoid, puberulent with glandular hairs, the style conical, ¼ to equal ovary in length, indistinct when young, becoming more distinct with age, the stigma (2- or) 3- to 5- (or 6-)lobed, persistent in fruit. Fruits ovoid-ellipsoid to globose, 2–2.5 × 1.5–2 mm, conspicuously ribbed on drying, with sparse glandular hairs.

Distribution. Largely restricted to Yucatán Peninsula, especially central and southern portions; also extending into Chiapas and Veracruz (see Map 3).

Habitat. Originally occurring in "ramonales," upland climax subdeciduous forests developing on calcareous soils and dominated by the breadnut tree, *Brosimum alicastrum* (Moraceae). This vegetation type was typical of the Yucatán Peninsula until 20–25 years ago, when agricultural demands resulted in destruction of large areas of natural vegetation. Currently, therefore, *Piper neesianum* is usually found at the edge of disturbed secondary forests, at 20–400(–700) m alt., where it is one of the more common understory shrubs. In more remote areas of the Yucatán Peninsula, such as portions of the Petén region of Guatemala, one should still be able to find this species in its undisturbed native habitat.

Phenology. Flowering February to June, but most prominently in April and May; specimens with mature fruits collected from June to November.

Representative specimens. **Mexico.** Veracruz: Papantla, *Liebmann 18* (G, K, US); Lomas al sur del Poblado 11, ca. 30 km E del campamento La Laguna, Minantitlán, *Wendt et al. 2633* (ENCB, MEXU, NY). Chiapas: 20 mi N of Ocozocoautla, near km 31 marker, toward Apitpac, *Croat 40640* (MO); camino a Jato del Tigre, cerca Laguna Galón, *Miranda 6245* (MEXU); near El Ocote, 30 km NW of Ocozocoautla, *Miranda 6252* (MEXU, US). Tabasco: 100 m del limite con México sobre carretera 15-E, *Novelo et al. 178* (MEXU). Campeche: along Hwy. 186 between Escárcega and Xpujil at km 87 marker, *Bornstein & Chase 69* (MICH); Campo Experimental Forestal Tropical "El Tormento," km 5 on road between Escárcega & Candelaria, *Chavelas ES-932* (MEXU), *ES-1041* (MEXU), *ES-1553* (MEXU), *ES-1631* (MEXU); zona arqueológica de Becan, Loma central, *Cowan 2997* (ENCB, MEXU); Tecolutla, *Liebmann 17* (G, GH); Reforma, *Lundell 834* (F, ILL, MICH, MO, US); Pixoyal, *Ross 128* (GH, MEXU, US); 14 km S of Xpujil, *Shepherd 68* (ENCB, MICH). Yucatán: Chichén Itzá, *Lundell 7406* (F, GH, MICH (2 sheets), NY, TEX, US). Quintana Roo: along Bacalar shoreline pkwy., 1.1 km S of school, *Bornstein & Rutledge 27* (MICH); 1.9 km S of Bacalar–Cenote Azul turnoff along Hwy. 307, *Bornstein & Rutledge 30* (MICH); 0.3 km SE of km 20 marker along Hwy. 196, *Bornstein & Rutledge 33* (MICH); along Hwy. 186 between Escárcega and Chetumal, 1.9 km E of km 225 marker, *Bornstein & Rutledge 38* (MICH); Lake Chichankanab, *Gaumer 23678* (F, GH, MO, NY, US); 26 km S of Tulum, *Téllez & Cabrera 2606* (MEXU); 8 km NE of Felipe Carillo Puerto, sobre camino a Vigio Chico, *Téllez & Cabrera 2838* (MEXU). **Belize.** Belize: Gracie Rock, 1.5 mi S of mi 22 on Western Hwy., *Dwyer 10940* (K, MO, NA, WIS). Cayo: 9.5 mi S of Georgeville on road to Augustine, *Croat 23440* (ENCB, F, GH, MEXU, MO, TEX); Chalillo Crossing, *Lundell 6510* (F, GH, MICH, NY, TEX, US). **Guatemala.** Petén: Uaxactún, *Bartlett 12326* (ILL, MICH, NY, UC, US); 10 km E of Remate, *Contreras 916* (F, G, MEXU, TEX, US); 22 km W of Remate, *Contreras 1033* (MICH, TEX (2 sheets), US); Tikal Natl. Park, *Contreras 1246* (G, MICH, TEX, US); Lake Macanche, *Contreras 5518* (F, MO, NY, US); Lake Petén Itzá, Santa Elena, *Contreras 5763* (F, GH, TEX); Macanche, *Contreras 5840* (F, GH, TEX, US); km 32 bordering Melchor de Mencos road, *Contreras 5863* (GH, TEX); N shore of Lake Yaxhá, *Croat 24680* (BR, MO); Carmelita, *Egler 42-234* (F, TEX); El Paso, *Lundell 1457* (GH, MICH, NY, US); La Libertad, *Lundell 3500* (F, ILL, MICH, US); Ixlu, *Lundell 3828* (ILL, MICH, TEX); 35 km E of Santa Elena, *Molina 15482* (F, NY); Santa Elena, km 6 on road to San Andres, *Ortíz 1978* (F, MO, NY, US); 2 km NE of Uaxactún, *Ortíz 2609* (F, MICH, US); bordering Lake Macanche, 35 km from Flores, *Ortíz 2696* (F, MICH, US); Cerro

Ceibal, between mouth of Río Santa Monica & Río San Martin, *Steyermark 46061* (F, MICH (2 sheets), NY, US). ALTA VERAPAZ: Cerro Chinaja between Finca Yalpemech and Chinaja, *Steyermark 45581* (F, MICH). IZABAL: Cienaga, on Petén–Guatemala road, *Contreras 10851* (MEXU, MO, TEX, US).

Piper neesianum is commonly confused with its sympatric congener, *P. yucatanense*. Both species have leaves distinctly longer than broad, but *P. neesianum* has a more dense, shrubby habit; firm, shiny, nonrugulose (vs. membranous, dull, and rugulose or bullate) leaves; smaller, narrower floral bracts; and conspicuously ribbed (vs. smooth) fruits (especially when dry). A third species with lance-ovate leaves, *P. muelleri*, has rarely also been mistaken for *P. neesianum*. However, it can be easily distinguished by its rather heavy indument of eglandular hairs along the veins on the leaf undersurface, its pubescent floral bracts and rachis, its long staminal filaments, and its uniquely shaped gynoecium.

11. **Piper novogalicianum** Bornstein, sp. nov. FIGURE 15.

Frutex 1.5–5 m altus, ramunculis puberulis ad dense pubescentibus; prophyllum usque ad 1 cm longum, puberulum vel dense pubescens; folia laminis ovatis vel late ovatis vel suborbiculatis, 4.9–13.2 × 4.1–11.5(–13.5) cm, breviacuminatis vel acuminatis, basi rotundatis vel cordatis, supra puberulis vel pubescentibus, subter puberulis vel pubescentibus vel tomentosis; inflorescentia 6.2–14.3(–16) cm longa, rhachidi sparsim ad dense pubescenti; bracteae usque ad 0.75 mm longae, spathulatae vel spathulicupulatae, sparsim puberulae vel pubescentes vel dense pubescentes; pedicelli 0.5–1.5(–2) mm longi; stamina hypogyna vel interdum ut videtur basi ovarii adnata; ovarium ellipsoideum vel subglobosum; stylus depresso-ovoideus vel breviconicus vel brevicolumnaris, 0.5–0.75 mm longus; fructus immaturus transverse-ellipsoideus, puberulus.

TYPE. Mexico, Jalisco, 5.1 km W of Hwy. 80 along Hwy. 200 toward Puerto Vallarta, 300 m alt., 20 June 1983, *Bornstein 99* (holotype, MICH; isotypes, CHAP, GH, INIF, MEXU, NY).

Small to medium-sized shrub, often treelike, 1.5–5 m tall; youngest twigs puberulent to densely pubescent, glabrescent, the hairs predominantly eglandular; older stems gray-brown to ash-gray, with swollen nodes and round, warty lenticels, maximum diameter to 6 cm. Prophylls to 1 cm long, base truncate, apex acute, abaxially puberulent to densely pubescent with eglandular hairs. Leaves with petiole 0.4–2.7 cm long, narrow to moderately broad, pubescent to densely long-pubescent with eglandular hairs; blade ovate to broadly ovate to suborbiculate, 4.9–13.2 × 4.1–11.5(–13.5) cm, truncate to rounded to cordate at base, gradually short-acuminate to acuminate at apex, 5- to 7- (to 9-)nerved, puberulent to pubescent above with both hair types in ± equal abundance, puberulent to pubescent to tomentose beneath with eglandular hairs predominant along and ± restricted to major veins. Inflorescences 6.2–14.3(–16) cm long, yellowish white to white; peduncle puberulent to pubescent with eglandular hairs, remaining rachis sparsely pubescent to pubescent with eglan-

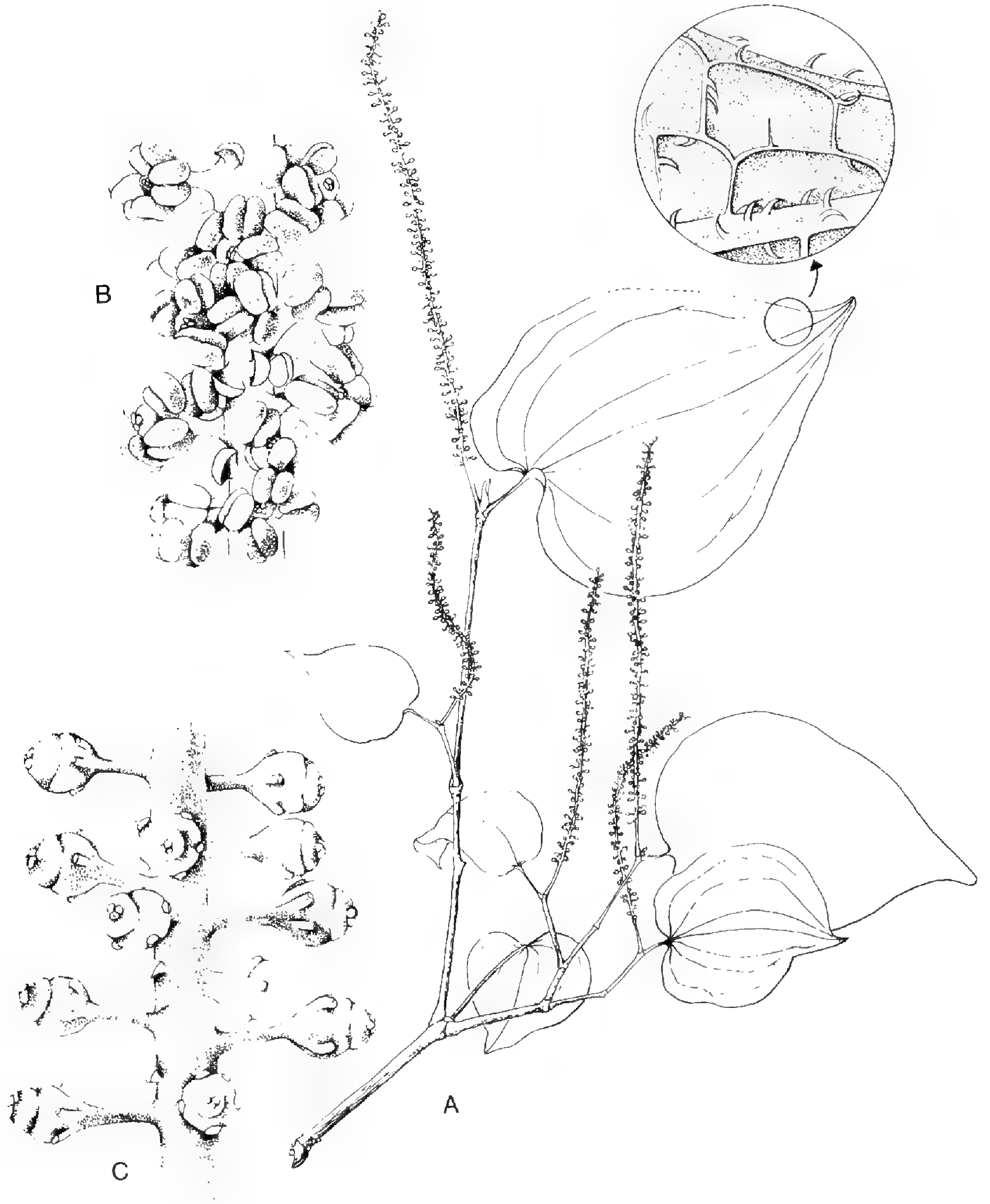


FIGURE 15. *Piper novogalicianum*: A, flowering branch, × 0.42, with detailed inset of lower leaf surface to show indument; B, portion of inflorescence, × 6.3; C, portion of infructescence, × 6.3.

dular hairs; bracts sessile to subsessile, spatulate to spatulate-cupulate, to 0.75 mm long, abaxially sparsely puberulent to densely pubescent with eglandular hairs. Flowers with pedicel (0.5–)1–1.5(–2) mm long, usually puberulent with glandular and/or eglandular hairs; stamens 4 to 6 (or 7), hypogynous or occasionally appearing as if adnate to base of ovary, filaments and anthers ± equal in length (to 0.5 mm), anthers dehiscing slightly to conspicuously upward from lateral; ovary ellipsoid to subglobose, puberulent with glandular hairs, the style depressed-ovoid to short-conical or short-columnar, 0.5–0.75 mm long, ca. ½ to equal length of ovary when in flower, the stigma 3- to 5-lobed. Fruits (when partially mature) transversely ellipsoid, ca. 1 × 1.5 mm, puberulent, style persistent.

DISTRIBUTION. Southwestern Jalisco and neighboring Colima; disjunct in state of Mexico (see MAP 2).

HABITAT. Steep hillsides in subdeciduous forests, from near sea level to 1350 m alt.; apparently also in second-growth woodlots, especially inland and at higher elevations.

PHENOLOGY. Flowering May to mid-July or into August. Fruits appearing as early as mid-June, but most commonly July to September.

SPECIMENS EXAMINED. **Mexico.** JALISCO: 1 km NE of Cihuatlán along small stream parallel to Río Cihuatlán, *Bornstein & Hensold 5* (MICH); 2 km S of La Manzanilla on road to Tamarindo beach, *Bornstein & Hensold 8* (MICH); along Hwy. 80 between Autlán and Melaque, 4 km N of side road to Casimir Castillo, *Bornstein 76* (MICH); ca. 11 km S of Autlán on Hwy. 80 to Barra de Navidad, *Bornstein 96* (MICH); Santa Cruz, *Delgado 348 & Hernández 2599* (ENCB, MEXU); ca. 22 mi SSW of Autlán, *Wilbur 1589* (MICH); 0.5 mi N of La Resolana, *Wilbur 1591* (MICH); 2 mi W of Autlán, *Wilbur 1675* (MICH). COLIMA: 2.5 km S of coastal Hwy. 200, W of Santiago along gravelly dirt road to Vida del Mar, *Bornstein & Hensold 2* (MICH); 5 mi W of Santiago, then 2.5 mi on road to Peña Blanca, *McVaugh 15691* (MICH). MEXICO: Tejupilco in district of Temascaltepec, *Hinton 4287* (ILL, K, MICH, NA, US).

In my dissertation (Bornstein, 1985) I recognized the high-elevation collections (*Bornstein 96, Hinton 4287, Wilbur 1675*) as a distinct species, *Piper tejupicoanum* Trel. ex Bornstein, with the Hinton collection at MICH designated as the holotype. At that time I also noted my concern about the recognition of this taxon, since the characters that serve as the basis for the distinction (i.e., leaf size and pubescence, rachis and bract pubescence, and pedicel length) are usually rather variable. After reconsidering this situation, I have decided to recognize a single variable species, *P. novogalicianum,* while noting that the populations at high elevations apparently represent one extreme in which the leaves are smaller and the plant parts more pubescent. This matter will only be settled with additional collecting (especially of flowers and fruits from the same plant), as well as field studies of populations at various elevations.

This species, as presently circumscribed, is distinguished from *Piper brevipedicellatum* on the basis of having longer and narrower pedicels.

12. **Piper rosei** C. DC. Annuaire Conserv. Jard. Bot. Genève **21:** 316. 1920. TYPE: Mexico, Sinaloa, Colomas, 13–20 July 1897, *Rose 3234* (lectotype, here chosen, US 302199!). FIGURE 16.

Piper rosei C. DC. ex Trel. Amer. J. Bot. **8:** 215. 1921. TYPE: Mexico, Sinaloa, Colomas, 13–20 July 1897, *Rose 3234* (holotype, US!).

Piper diguetianum Trel. Amer. J. Bot. **8:** 215. 1921. TYPE: Mexico, Jalisco, *Diguet s.n.* (holotype, US!).

Medium-sized treelike shrub, 2–5 m tall; youngest twigs glabrous to puberulent with short eglandular hairs; older branches soon glabrous, with brown,

FIGURE 16. *Piper rosei*: A, flowering and fruiting branch, × 0.42; B, portion of inflorescence, × 6.3; C, portion of infructescence, × 6.3.

elliptic, warty lenticels, maximum diameter to 7.5 cm. Prophylls to 10 mm long, base truncate, apex acute, glabrous to puberulent with short eglandular hairs. Leaves with petiole 0.7–1.9(–3.1) cm long, narrow, glabrous to puberulent with glandular and eglandular hairs; blade ovate to most commonly broadly ovate to suborbiculate, (5.3–)6.7–13(–15.6) × 4.2–12.1 cm, rounded to shallowly cordate at base, short- to long-acuminate at apex, 5- (to 7-)nerved, glabrous to puberulent, the hairs largely restricted to petiole-blade junction, glandular and short eglandular. Inflorescences (5–)6.3–15.5 cm long, greenish yellow when young, white to cream colored in full flower; peduncle glabrous to sparsely pubescent, remaining rachis sparsely to densely pubescent with eglandular hairs;

bracts sessile to subsessile, spatulate to cupulate, 0.25–0.75 mm long, sparsely pubescent to pubescent (often on both surfaces, but especially abaxially and marginally) with eglandular hairs. Flowers with pedicel 0.5–1.5(–1.75) mm long, usually glabrous to puberulent, but occasionally sparsely pubescent near base with both glandular and eglandular hairs; stamens (3 or) 4 or 5 (or 6), hypogynous but often appearing adnate to base of ovary, filaments and anthers to 0.5 mm long, anthers dehiscing laterally or conspicuously upward from lateral; ovary ovoid-ellipsoid to widely depressed-ovoid to subglobose, puberulent with glandular hairs, the style depressed-ovoid to short-conical to short-columnar, from ¼ to equal length of ovary when in flower, the stigma 3- to 5-lobed. Fruits subglobose to globose, 1–2 × 1–2 mm, puberulent, style becoming obscure with fruit maturation.

DISTRIBUTION. Southern Sinaloa south through southwestern Jalisco and northern Colima (see MAP 4). Apparently absent from Nayarit (probably a reflection of limited collecting throughout Nueva Galicia).

HABITAT. Prefers steep hillsides or slopes in relatively open, disturbed, semi-deciduous or deciduous forests. At low elevations found with other pipers in the coastal palm forests dominated by *Orbignya cohune*. At high elevations occurring in oak forests, above coffee plantations, and in forests dominated by *Bursera* spp. From near sea level to 1400 m, but mostly below 1000 m alt.

PHENOLOGY. Flowering late May to early July. Young fruits appear by mid-June; mature fruits collected in September and October. A second period of flowering may also occur at this time (end of rainy season).

REPRESENTATIVE SPECIMENS. **Mexico.** SINALOA: Colomas, *Rose 1657* (GH, K, US); Copalita, *Moran 13310* (UC). JALISCO: ca. 2 km S of La Manzanilla on road to Tamarindo beach, *Bornstein & Hensold 6* (MICH); ca. 15 km S of Autlán on Hwy. 80 toward Barra de Navidad, *Bornstein 97* (MICH); 5.1 km W of Hwy. 80 along Hwy. 200 toward Puerto Vallarta, *Bornstein 100* (MICH); 4 mi NE of Talpa, *Chase 83127* (MICH); 5 mi S of Talpa on road to Tomatlán, *Chase 83129* (MICH); 16 km N of Mascota on road between Mascota and San Sebastián, *Lott et al. 1349* (MICH); ca. 5.5 mi N of Tecalitlán, *McVaugh 15436* (MICH); ca. 16.9 mi NW of Hwy. 80–200 junction (near Melaque) along Hwy. 200, *Stevens & Fairhurst 1868* (ENCB, TEX); 8 mi S of Autlán toward La Resolana, *Wilbur 2190* (MICH). COLIMA: 1.3 mi W of San Antonio, *Chase 83113* (MICH).

TAXONOMIC NOTES. *Piper rosei* C. DC. and *P. rosei* C. DC. ex Trel. are independent descriptions based on the same type material; i.e., they are nomenclatural synonyms. De Candolle examined the Rose collections at US in the late 1890's, apparently supplying a name for the collections but not publishing it until over 20 years later. Trelease saw these same Rose collections while preparing his first publication on the Piperaceae and adopted the herbarium epithet suggested by De Candolle. De Candolle's treatment of the Mexican Piperaceae was published several months prior to Trelease's treatment of the North American pipers of sect. *Ottonia*, and therefore Trelease's name is an illegitimate later homonym.

The characters cited by Trelease to distinguish *Piper diguetianum* and *P. rosei* are not reliable. The racemes in the former are shorter because they are obviously broken. The pedicel length difference (1.5 vs. 1 mm, respectively) is a result of the level of floral maturation: the flowers of the Rose collections are considerably younger, and therefore the pedicel has not fully elongated. The third distinction, stamen number (5 vs. 3 or 4), has been shown to be a poor character on which to base species differences. Again examining the Rose material, I have seen numerous flowers with five stamens in addition to those with three or four.

In my original investigation of this species (Bornstein, 1985), I separated the low-elevation collections (*Stevens & Fairhurst 1868*; *Bornstein & Hensold 6, 7, & 9*) as a distinct taxon, *Piper palmicola* Bornstein, with the Stevens & Fairhurst collection at TEX designated as the holotype. This species was recognized as distinct on the basis of its less-pubescent floral rachis and bracts, its short-acuminate to acuminate leaf apex, and its shorter (0.5–1 vs. 1–1.5 mm) pedicels. After further consideration, I have decided that these features either are essentially continuous (pedicel length) or are too variable (pubescence and leaf shape) to warrant the recognition of *P. palmicola,* which remains an unpublished name, and I have consequently interpreted *P. rosei* in a rather broad sense. The low-elevation collections form a group that tends to obscure the boundary between *P. brachypus* and *P. rosei,* strongly suggesting that these two species are closely related.

13. **Piper stipulaceum** Opiz *in* Presl, Reliq. Haenk. **1**(3): 160. 1828. TYPE: Mexico, locality unknown, *Haenke s.n.* (lectotype, here chosen, PR!; isolectotypes, B (destroyed?), PR!). FIGURE 17.

Enckea stipulacea (Opiz) Kunth, Linnaea **13**: 600. 1838. *Ottonia stipulacea* (Opiz) Presl, Epimel. Bot. **231.** 1851. *Arctottonia stipulacea* (Opiz) Trel. Proc. Amer. Philos. Soc. **75**: 716. 1935.

Piper aguilanum C. DC. Annuaire Conserv. Jard. Bot. Genève **21**: 318. 1920. TYPE: Mexico, Guerrero, Santa Rosa près d'Aguila, 650 m alt., 16 July 1898, *Langlassé 248* (holotype, G!; isotypes, GH! K!, US!).

Piper albicaule Trel. Amer. J. Bot. **8**: 216. *pl. 8, fig. 2.* 1921. TYPE: Mexico, Guerrero, Santa Rosa près d'Aguila, 650 m alt., 16 July 1898, *Langlassé 248* (holotype, US!; isotypes, G!, GH!, K!).

Medium-sized treelike shrub, sparsely branched from base, 2–4 m tall; youngest twigs pubescent to densely pubescent, glabrescent, ash-gray and with conspicuous warty brown lenticels, to ca. 5 cm in diameter. Prophylls 6–10(–15) mm long, base truncate, apex acute, abaxially pubescent to densely pubescent to occasionally tomentose with eglandular hairs. Leaves with petiole 0.6–3.5 cm long, stout, pubescent to densely soft-pubescent with eglandular hairs; blade ovate to broadly ovate-suborbiculate, (4.5–)6.3–13.7(–14.6) × (2.4–)4.8–12.6 (–14) cm, rounded to truncate to mostly shallowly cordate at base, short-acuminate to acuminate at apex, (5- to) 7- (to 9-)nerved, puberulent to pubescent above, puberulent to densely pubescent beneath especially along major veins (both hair types present, with glandular ones more prevalent in areolar regions and eglandular ones ± restricted to veins). Inflorescences (5.8–)7–12.9 cm long, yellow-green when young, whitish in full flower; peduncle stout,

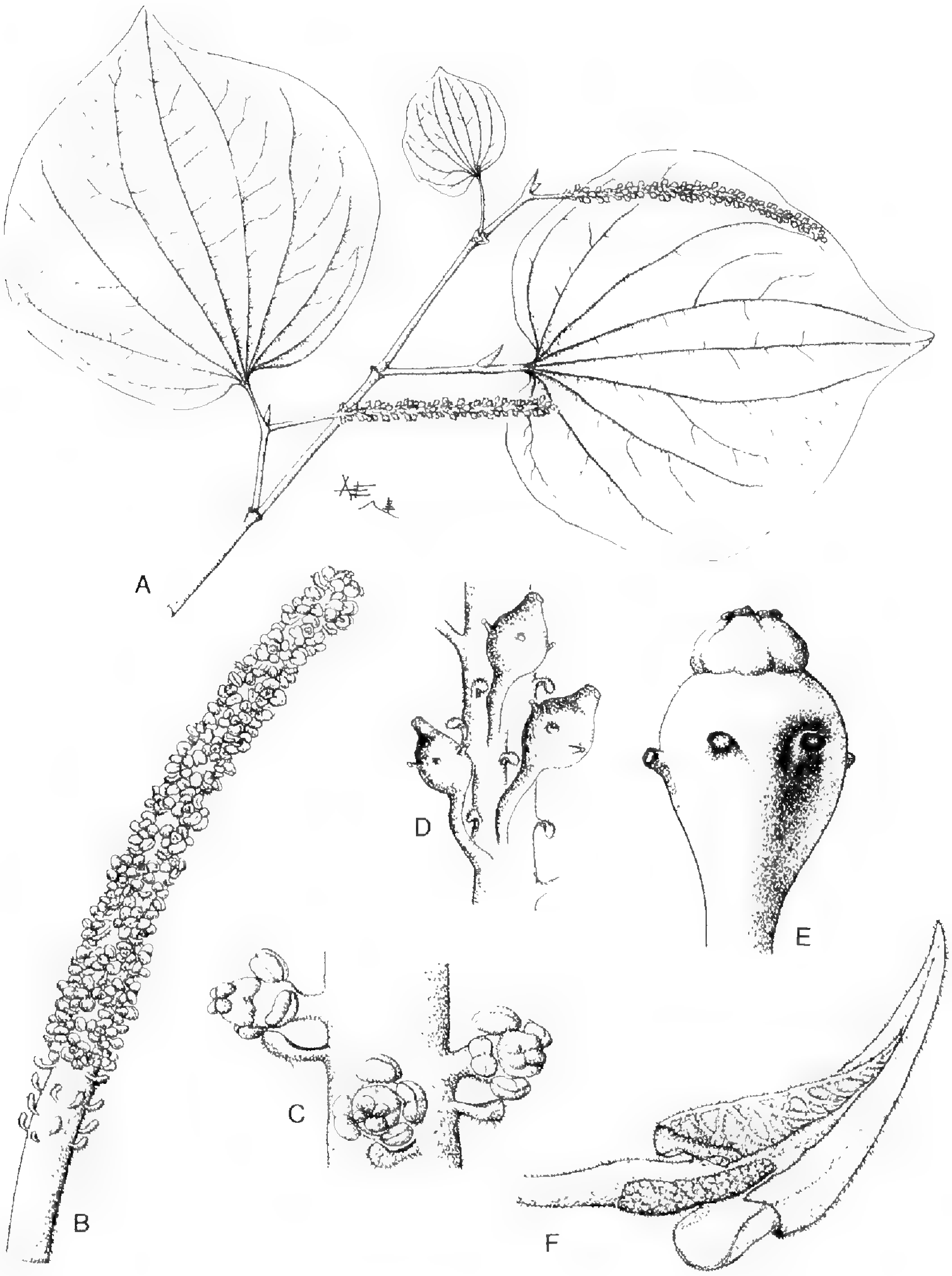


FIGURE 17. *Piper stipulaceum*: A, fruiting branch, × 0.43; B, inflorescence, × 8.6; C, flowers and associated bracts, × 8.6; D, portion of young infructescence, × 8.6; E, mature fruit, × 12.9; F, prophyll with emergent young leaf and inflorescence, × 8.6.

puberulent to pubescent at base with glandular and eglandular hairs, gradually transitional to glabrous to puberulent to sparsely pubescent rachis; bracts occasionally sessile, but usually with narrow stalklike basal portion that broadens gradually to abruptly into narrow to broadly spatulate to spatulate-cupulate apical region, 0.5–0.75(–1.25) mm long, abaxially puberulent to pubescent. Flowers with pedicel 0.5–2 mm long, ca. 0.5 mm wide, glabrous to puberulent with glandular hairs; stamens 4 or 5 (or 6), adnate to ovary from near base to middle, the filaments to ca. 0.5 mm long, the anthers depressed-ovoid, usually longer than filaments, dehiscing laterally or occasionally slightly divergent upward; ovary ovoid to subglobose, puberulent with glandular hairs, the style depressed-ovoid to conical, to 0.5 mm long, from ⅓ to nearly equal length of ovary when in flower, the stigma 3- or 4- (or 5-)lobed. Fruits ovoid to globose to slightly obloid, usually ca. 2 × 2 mm, drying brown to black, with glandular hairs, the style usually persistent to some degree, but not more than ⅓ length of ovary.

DISTRIBUTION. Southwestern Jalisco south to northwestern Guerrero, near Zihuatanejo, in narrow band from Pacific Ocean to foothills of Sierra Madre (see MAP 4).

HABITAT. Variable: at low elevations near coast, a relatively frequent understory shrub in palm forests dominated by *Orbignya cohune*; at higher elevations farther inland, found along edges of ravines above intermittent mountain streams in subdeciduous forests usually dominated by *Brosimum alicastrum, Ficus* spp., or *Bursera* spp. From near sea level to 650 m alt.

PHENOLOGY. Flowering May to July, rarely later. Young fruits appearing late May or early June; mature fruits collected from August to September, but probably persisting on plants into dry season.

SPECIMENS EXAMINED. **Mexico.** JALISCO: 5.1 km W of Hwy. 80 along Hwy. 200 toward Puerto Vallarta, N side of road, *Bornstein 79* (MICH); 7.9 km WNW of Hwy. 80 along Hwy. 200 toward Puerto Vallarta, S side of road, *Bornstein & Weber-Bornstein 83* (MICH); ca. 12 km NE of Nacastillo on road to San Miguel Purificación and Purificación, *Iltis & Nee 1531a* (NY); 1–4 km E of Casimir Castillo, ca. 20 km SSW of Autlán, "Arroyo de Tacubaya," at base of "Cerro la Petaca," *Iltis et al. 296* (NY); ca. 2 km N of division line of UNAM, road to Nacastillo, *Magallanes 754* (TEX). COLIMA: 7.8 km N on Hwy. 98 toward Minatitlán, E side of road, *Bornstein 86* (MICH); 0.5 km S of Comatlán on Hwy. 98 toward Minatitlán, E side of road, *Bornstein 98* (MICH); Playa de Santiago, on road to Manzanillo airport, *McVaugh 15594* (MICH). MICHOACÁN: 2 mi N of San Juan de Lima (on road to Coahuayana), *Hansen, Hansen, & Nee 1442* (MEXU, MICH, US, WIS); La Placita (Río de Aquila), *Turner 2035* (MICH); 1 mi E of La Placita, *Turner 2071* (MICH). GUERRERO: Vallecitos, Montes de Oca, *Hinton 11372* (F, K, MEXU, MO, NY, US); 2 mi E of Vallecitos de Zaragoza (between kms 52 & 53) on Hwy. 200 toward Ciudad Altamirano, *Murray & Johnson 1433* (MICH).

TAXONOMIC NOTE. As in the *Piper michelianum–Piper mas* and *Piper rosei* situations, both Casimir de Candolle and William Trelease published new species, *Piper aguilanum* and *Piper albicaule,* respectively, on the basis of the same type material. These taxa are thus nomenclatural synonyms.

Piper stipulaceum is most often confused with *Piper abalienatum* because in both the stamens are adnate to the ovary (only *P. mcvaughii* also shares this character, and it is easily distinguished by its puberulent vegetative parts, very-short-pedicellate flowers, and smaller leaves). The characters and character states that I use to distinguish these two species are summarized in the TABLE. When the opposite extremes of these characters are expressed, which is frequently the case, these species are quite different and readily separable. There are, however, a few specimens that approach the established limits of the range of the character states, often appearing to bridge the gap that separates the species. Usually all or most of these characters are affected simultaneously in a given specimen, possibly suggesting that introgressive hybridization might be the cause rather than abnormal extremes of variation. Although I have not observed these species growing together, their geographic ranges do overlap in portions of Jalisco, Colima, and Michoacán. In addition, habitat preferences of the species are similar, although *P. stipulaceum* does seem to be more restricted to cool, moist sites. Therefore, the potential for hybridization exists, as do the newly disturbed, unstable habitats that hybrids may need to become established. However, detecting and documenting introgressive hybridization would require more extensive collection of specimens in the areas of geographic overlap. In the meantime, I have placed those "intermediate" specimens in one or the other species on the basis of overall similarity using the criteria available.

A somewhat different problem occurs in trying to distinguish *Piper stipulaceum* and *P. novogalicianum*. As presently circumscribed, the taxa differ significantly only in the position of the stamens relative to the ovary (adnate and hypogynous, respectively). As I have mentioned previously for several taxa, *P. novogalicianum* among them, there is a strong tendency for the stamens to appear to be adnate to the base of the ovary. This feature is most apparent in the fruiting condition, where the ovary has expanded, thereby partially incorporating the upper portion of the pedicel (the receptacle). This, in turn, causes the stamens seemingly to "shift" to the adnate position. Since the remaining features of these two species are quite similar, this apparent change can lead to identification problems, especially with pressed specimens. To enable distinction between the taxa, flowering material should be obtained, preferably in pickled form. Fortunately, most of the specimens that I have examined have had some flowers, so that when they are restored to their original state with a detergent solution, it is possible to assign them to the appropriate species.

14. **Piper yucatanense** C. DC. Linnaea **37:** 334. 1872. TYPE: Mexico, Yucatán, July 1840, *Linden s.n.* (holotype, G!). FIGURE 18.

Piper thiemeanum Trel. Amer. J. Bot. **8:** 214. *pl. 5, fig. 2.* 1921. *Ottonia thiemeanum* (Trel.) Yuncker, Ann. Missouri Bot. Gard. **37:** 71. 1950. TYPE: Honduras, Cortés, San Pedro Sula, June 1887, *Thieme 5455* (holotype, US!; isotypes, GH!, K!, UC!, US (3 sheets)!).

Piper tatei Trel. Amer. J. Bot. **8:** 215. 1921. TYPE: Nicaragua, 1867–8, *Tate 367* (holotype, K!).

Piper chichankanabanum Trel. J. Wash. Acad. Sci. **19:** 330. 1929. TYPE: Mexico, Quintana Roo, Lake Chichankanab, April 1917, *Gaumer 23699* (holotype, F!).

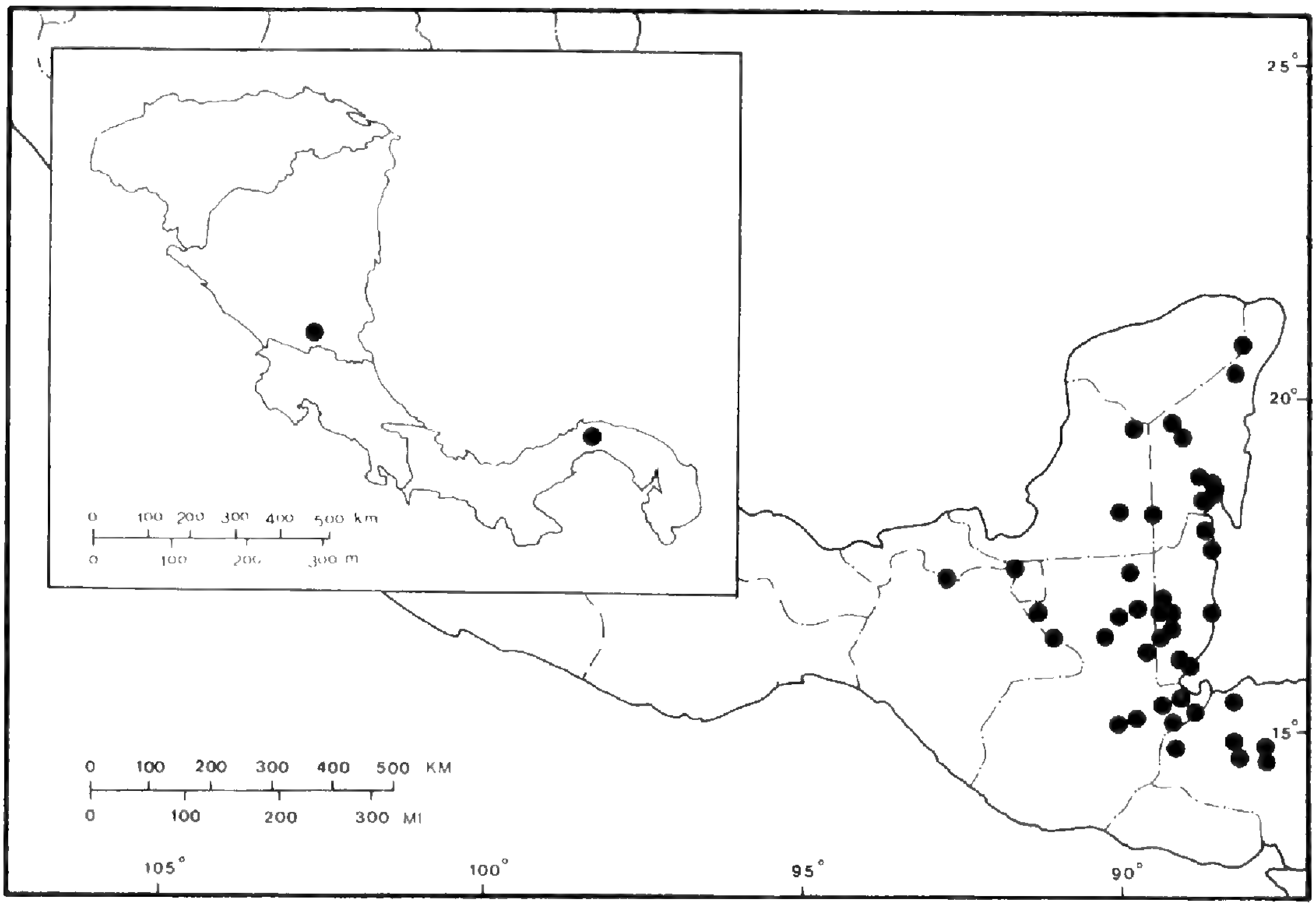
Arctottonia pittieri Trel. Proc. Amer. Philos. Soc. **73:** 328. 1934. TYPE: Panama, Canal Zone, Alhajuela, 11–14 May 1911, *Pittier 3458* (lectotype, here chosen, F!; isolectotypes, F!, US!).

Arctottonia tuxpenyana Trel. ex Lundell, Publ. Carnegie Inst. Wash. **436:** 311. 1934, *nomen nudum*. *Arctottonia tuxpenyana* Trel. ex Standley, Field Mus. Nat. Hist., Bot. Ser. **12:** 406. 1936. *Piper tuxpenyanum* (Trel. ex Standley) Lundell, Publ. Car-

FIGURE 18. *Piper yucatanense*: A, flowering branch, × 0.4; B, inflorescence, × 8; C, flower with bracts, × 10; D, immature (unfertilized?) and mature fruits with bract, × 10; E, prophyll with emergent young leaf and inflorescence (detached and displaced from normal position), × 8.

negie Inst. Wash. **478:** 208. 1937. TYPE: Mexico, Campeche, Tuxpeña, 7 Feb. 1932, *Lundell 1300* (holotype, MICH!; isotypes, F!, ILL!, NY!).

Slender, loosely branched shrub 0.5–3 m tall, appearing glabrous throughout. Prophylls to 10 mm long, base truncate, apex narrowly acute, with very sparse glandular hairs. Leaves with petiole 1–10 mm long, slender, with sparse glandular hairs at least when young; blade lanceolate-ovate to oblong-ovate to ovate-elliptic, 6.5–15 × 2.2–5.5 cm, acute to more commonly rounded (rarely shallowly cordate), slightly unequal and occasionally minutely auriculate at base, gradually acuminate to very long-acuminate, occasionally cuspidate at apex, 5- to 7-nerved (3 most central protracted to apex), membranous, drying thin and generally rugulose (rarely bullate), appearing glabrous but with glandular hairs when young. Inflorescences 2–5.5(–6.3) cm long, white at maturity, fragrant; peduncle slender, rachis appearing glabrous but with glandular hairs; bracts broadly spatulate-cupulate to strongly cupulate (occasionally appearing



Map 5. Distribution of *Piper yucatanense*; inset of Central America shows isolated collecting localities in Nicaragua and Panama.

petiolate), 0.25–1.5(–2) mm long, nearly glabrous. Flowers with pedicels divaricate, 1–4 mm long, very sparsely puberulent with glandular hairs; stamens 4 to 8, hypogynous, the filaments less than 0.25 mm long, the anthers subglobose, dehiscing laterally; ovary obloid to ovoid-ellipsoid, puberulent with glandular hairs, the style from ⅓ to nearly equaling length of ovary, becoming largely obliterated in fruit, the stigma lobes (2 or) 3 or 4 (or 5), persistent in fruit. Fruits ovoid to ovoid-ellipsoid, to 3 × 2 mm at maturity, with numerous glandular hairs.

Distribution. Most prevalent in Yucatán Peninsula, where sympatric with *Piper neesianum*; ranging naturally into western Honduras. One collection known from Nicaragua, one from Panama (see Map 5).

Habitat. Originally most often in "ramonales"; currently in second-growth forests with *Piper neesianum*. From near sea level to 1000 m alt.

Phenology. Flowering February to late June or early July, most commonly late April to early June. Mature fruits from August until early in next flowering period.

Representative specimens. **Mexico.** Chiapas: Yaxchilán, *Breedlove 42858* (MEXU, MO). Tabasco: 2 km [?] de Teapa, *Cowan 3161* (ENCB, MEXU); San Isidro near Balancán, *Matuda 3382* (F, GH, MEXU, MICH, NA, NY). Campeche: 3.5 km S of Xpujil, *Bornstein & Chase 68* (MICH); ruinas de Chicana, Hopelchén, *Chan & Ucán 994* (MEXU); 2 km S of Xpujil, *Shepherd 25* (F). Yucatán: Xcan, *Miranda 8248* (MEXU, US). Quintana Roo: 1.6 km S of Santa Cruz Chico along Hwy. 307, *Bornstein & Rutledge 23* (MICH); 0.3 km SE of km 20 marker along Hwy. 196, *Bornstein & Rutledge 34* (MICH); along Hwy. 186 toward

Chetumal, 1 km E of intersection with Hwy. 307, *Bornstein & Rutledge 37* (MICH); 1.9 km S of Bacalar–Cenote Azul turnoff along Hwy. 307, *Bornstein & Chase 71* (MICH); 8 km S of Xactun, Felipe Carillo Puerto, *Pérez 418* (MICH); 25 km N of Cobá, *Téllez & Cabrera 2534* (MEXU). **Belize.** ORANGE WALK: Honey Camp, *Lundell 312* (F, GH, ILL, MO, NY). BELIZE: mi 24–25 on Northern Hwy., *Dwyer & Liesner 12037* (GH, MO); Maskall, *Gentle 1246* (GH, ILL, MICH, NY). CAYO: 9.5 mi S of Georgeville on road to Augustine, *Croat 23337* (F, MO); vic. of Cuevas, S of Millionario, *Croat 23629* (MO); 4 mi S of Grano de Oro on road to La Flor, *Dwyer 10906A* (F, MO, NY); Cuevas, *Dwyer 11572* (MEXU, MO); Vaca, *Gentle 2511* (GH, MICH, TEX); 6 mi S of Grano de Oro, La Flor camp, *Lundell 6289* (F, GH, MEXU (3 sheets), MICH, NY, TEX, US); Cohune Ridge, *Lundell 6499* (GH, MEXU, MICH, NY, TEX); Chiquibal Forest Reserve, *Proctor 30064* (TEX). STANN CREEK: Silk Grass Creek Reserve, *Gentle 3102* (MICH); between Silk Grass and Railway, *Sampson 12* (K (2 sheets)). TOLEDO: Columbia Forest Reserve (1–2 mi N of entrance), *Croat 24174* (MO); Punta Gorda–Seven Hills road, *Gentle 5040* (F, TEX); near San Antonio, *Gentle 7530* (GH, TEX); between Orange Point and Moho R., *Gentle 7679* (F, G, TEX, UC, US); trail from Columbia Forest Station to Esperanza, *Gentry 8171* (F, MO); Forest Home, *Schipp 506* (F). DISTRICT UNKNOWN: Prospecto–Maskall road, *Gentle 895* (GH, ILL, MICH, MO, NY). **Guatemala.** PETÉN: La Libertad, *Aguilar 251* (ILL, MICH, MO, NY); Dolores, *Contreras 2557* (NY, TEX); Lacandón, *Contreras 3412* (TEX); 1 km S of Lacandón, *Contreras 3519* (TEX); 6 km SSW of Lacandón, *Contreras 3538* (F, G (2 sheets), MICH, TEX); Macanche, *Contreras 5807* (GH, TEX); Tikal Natl. Park, *Gentry 8327* (F, GH, MO); El Paso, *Lundell 1487* (F, GH, MICH, MO, NY, US); Santa Elena, at km 38 near road to Remate, *Ortíz 2048* (F, MO, NY, US). ALTA VERAPAZ: finca Argentina above Papalja, 15 mi W of Teleman on road from Tucuru to El Estor, *Croat 41539* (MO); Cacao, Trece Aguas, *Lewton 333* (F). IZABAL: 6 km from La Ruidoza, *Contreras 10796* (MEXU, MO, TEX); Cienaga, on Petén–Guatemala road, *Contreras 10853* (MEXU, MO, TEX); ENE of finca El Zapotillo, E of El Estor, Lake Izabal, *G. C. Jones & Facey 3434* (F, MEXU, MICH, NY, TEX, US); vic. of Quiriguá, *Standley 23952* (GH, ILL, MO, NY). **Honduras.** COPÁN: between Santa Rita and Copán ruins, *Molina 30605* (F (2 sheets), MO). SANTA BARBARA: W side of Lake Yojoa, *Williams & Molina 11423* (F, GH, MO, US); near village of Las Vegas, *Yong et al. 85* (MO). CORTÉS: valley W of San Pedro Sula, *Bangham 345* (F, GH); canyon of Río Piedras, 3 km from San Pedro Sula, *Molina 3432* (F, US). COMAYAGUA: near La Libertad, *Molina 7009* (F (2 sheets), TEX); valley of Jamalteca, *Molina 7185* (F (2 sheets), TEX); Jardines, *Barkley & Hernández 40847* (GH). **Nicaragua.** ZELAYA: mountains and rain forests between Toro Bayo and Esquipulas, *Shank & Molina 4637* (F).

Piper yucatanense is, at first glance, vegetatively similar to *P. muelleri*, but it is easily distinguished by its glabrous appearance. However, several collections (*Burch 6094, Contreras 10796, Gentry 7830, Molina 30605, Standley 24675, Williams & Molina 11423,* and *Yong et al. 85*), primarily from the Guatemala-Honduras border, do have considerable pubescence on the prophylls, petioles, leaf blades, rachises, and bracts, reminiscent of *P. muelleri.* Fortunately, these two species can be distinguished on the basis of filament length and fruit shape, and they are geographically separated as well.

Piper yucatanense has also often been confused with its sympatric neighbor *P. neesianum.* It is distinguished from that species by its smaller, less dense habit, its membranous, rugulose (vs. coriaceous, nonrugulose) leaves, and its longer, broadly spatulate bracts. In addition, it occurs in more open areas of the forest and is not a dominant member of the understory.

Yuncker (1950), when making the new combination *Ottonia thiemeana* (Trel.) Yuncker, cited *Pittier 3458* as the type collection. This is clearly incorrect because the type must be that of the basionym, *Piper thiemeanum* (*Thieme 5455*).

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APPENDIX. **Index to collectors.***

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*The designations in parentheses refer to the corresponding taxa in the text.

THE DIOSCOREACEAE IN THE SOUTHEASTERN UNITED STATES[1]

IHSAN A. AL-SHEHBAZ AND BERNICE G. SCHUBERT[2]

DIOSCOREACEAE R. Brown, Prodr. **1**: 294. 1810, "Dioscoreae," nom. cons.

(YAM FAMILY)

Twining [rarely erect] herbs [lianas or subshrubs] with rhizomes or fleshy [rarely woody or corky] tubers, the tubers derived from the hypocotyl, the internode above it, or both; plants with raphides in mucilaginous idioblasts, frequently rich in steroidal sapogenins, and usually accumulating chelidonic acid and lactone alkaloids. Stems smooth, winged [or spiny]; vascular bundles closed, arranged in 2 [or 1] ring(s), the vessels restricted to the roots, stems, and petioles, with scalariform perforation plates; sieve-tube plastids with cuneate, proteinaceous inclusions. Leaves alternate, rarely opposite or whorled, long petiolate, simple [rarely palmately compound, with 3–7 leaflets], usually cordate, entire, undivided [or palmately lobed], often with embedded mucilaginous pits or nectaries, the tips usually with a distinct pore; venation palmate, with 3–13 converging main veins and anastomosing lateral veinlets; stomata anomocytic, rarely different; trichomes unicellular, eglandular, simple [sometimes peglike, furcate (T-shaped), or stellate], often confined to the abaxial surface and along the veins, rarely occurring on the petiole or stem. Inflores-

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[1] Prepared for the Generic Flora of the Southeastern United States, a long-term project made possible by grants from the National Science Foundation and currently supported by BSR-8415769 (C. E. Wood, Jr., principal investigator), under which this research was done, and BSR-8415637 (N. G. Miller, principal investigator). This account, the 124th in the series, follows the format established in the first paper (Jour. Arnold Arb. **39**: 296–346. 1958) and continued to the present. The area covered by the Generic Flora includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with information about extraregional members of a family or genus in brackets. The references that we have not verified are marked with asterisks.

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FIGURE 1, b and k, were drawn by the late Dorothy H. Marsh (DHM), e and m–o by Ihsan Al-Shehbaz (IAS), and the remainder by Karen Stoutsenberger (KS) under earlier grants. Carroll Wood and Kenneth R. Robertson prepared the material and supervised the illustrations. Preserved material, as well as herbarium specimens in the Arnold Arboretum and the Gray Herbarium, was used as the basis for the drawings.

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cences axillary racemes, spikes, panicles, or cymes, many flowered, usually bracteate. Flowers trimerous, actinomorphic [very rarely zygomorphic], imperfect (the plant dioecious [rarely monoecious]) [or perfect], subtended by 1 small [to large] bract and 1 [rarely 2] bracteoles. Tepals 6, in 2 whorls, distinct [or connate], the perianth rotate [tubular to campanulate]. Stamens (absent in the carpellate flowers but often represented by staminodia) 6, in 2 whorls [the inner 3 sometimes staminodial or obsolete]; filaments distinct [connate at base, or fused into a tube]; anthers 2-locular and the lobes contiguous or separated, tetrasporangiate, dehiscing by longitudinal slits, introrse [or extrorse]; microsporogenesis simultaneous; pollen grains binucleate, 2- to 4- [rarely 1-]sulcate [or 4- or 5-foraminate]. Gynoecium (rudimentary in the staminate flowers) 3-carpellate; ovary inferior, 3-locular, the placentation axile, septal nectaries usually present; styles 3, connate at base [or distinct]; ovules 2 [to many] in each locule, anatropous, bitegmic, crassinucellate, endosperm development nuclear, the megagametophyte (embryo sac) of the Polygonum type. Fruits triangular, 3-winged capsules [1-seeded samaras, or berries]. Seeds flattened [or globose], winged [or wingless]; embryos small, well differentiated, with a subterminal plumule and a broad, flat, nearly lateral cotyledon embedded in the hard, copious endosperm that contains lipids and aleurone, as well as hemicellulose deposited in its thick cell walls. Base chromosome numbers 9, 10, 12. (Including Androsynaceae Salisb., Cladophyllaceae Dulac, Stenomeridaceae J. G. Agardh, Tamaceae Gray.) TYPE GENUS: *Dioscorea* L.

A family of seven genera and approximately 900 species of tropical, subtropical, or rarely warm-temperate plants. *Avetra* Perr. (monotypic) is endemic to Madagascar, while *Borderea* Miégeville (two species; Heywood) is restricted to the Pyrenees. See, however, Miège (1986; reference under *Dioscorea*) for assignment of *D. Gillettii* Milne-Redhead (Kenya, Ethiopia) to *Dioscorea* sect. BORDEREA (Miégeville) Bentham. *Epipetrum* Phil. (three species; Reiche) is confined to Chile, *Rajania* L. (25 species) is native to the West Indies, *Stenomeris* Planchon (two species) is indigenous to Malaysia (Borneo, Malay Peninsula, Philippines, Sumatra), and *Tamus* L. (five species) is widespread in the Mediterranean area (southwestern Asia; southern, central, and western Europe; northwestern Africa) and Macaronesia. *Dioscorea*, the largest genus of the family, has approximately 850 species distributed on all continents except Antarctica.

The limits of the Dioscoreaceae are controversial, and Knuth (1930) and Burkill (1960) recognized ten and six genera, respectively. Both authors and Cronquist have retained *Trichopus* Gaertner (monotypic; Sri Lanka, southern India, Malaysia) in the family, while Ayensu (1966, 1972), Hutchinson (1973), Dahlgren (1980, 1983), and Dahlgren, Clifford, & Yeo placed it in a monotypic family, the Trichopodaceae Hutchinson, assigned to the Dioscoreales, a view with which we agree. *Trichopus* differs from genera of the Dioscoreaceae in having an erect (nontwining) herbaceous stem with one or a few flowers borne opposite the leaf, glandular hairs, successive microsporogenesis, and long-appendiculate anthers. It also differs in nodal anatomy and chromosome number (see below). The monotypic *Petermannia* F. Mueller (New South Wales and Queensland, Australia), which was retained in the Dioscoreaceae by Knuth

(1924, 1930), is now believed to represent a unigeneric family, the Petermanniaceae Hutchinson, somewhat related to the Dioscoreaceae (Conran; Dahlgren, Clifford, & Yeo; Tomlinson & Ayensu). However, Hutchinson (1973) assigned this family to the Alstroemeriales, while Cronquist placed *Petermannia* in the Smilacaceae Vent. We prefer to associate the Petermanniaceae with the Dioscoreales for reasons discussed by Conran.

Burkill (1960) reduced both *Borderea* and *Epipetrum* to sections of *Dioscorea.* The presence in *Borderea* of wingless seeds, nontwining stems, unbranched leaf veins, and a base chromosome number of 12 supports its recognition as a distinct genus. Furthermore, in *Epipetrum* the lack of wings around the seeds, the presence of well-developed stylar rudiments in the staminate flowers, and the spiral twisting of pedicels of the carpellate flowers are sufficient grounds for its maintenance at the generic rank.

On the basis of their perfect flowers, prominent staminal appendages, and thin, nonfleshy rhizomes, both *Avetra* and *Stenomeris* were considered to be anomalous in the Dioscoreaceae. *Avetra* was placed in the Trichopodaceae by Hutchinson (1973), but the climbing habit, three-winged fruits, and nodal anatomy (Ayensu, 1972) strongly support its retention in the Dioscoreaceae, as was initially recognized by Perrier de la Bâthie. *Stenomeris* also deviates from the rest of the Dioscoreaceae in having linear fruits with numerous seeds. It was placed in the Stenomeridaceae by many authors, but the overwhelming anatomical evidence favors its placement in the Dioscoreaceae. Dahlgren, Clifford, & Yeo assigned *Avetra* and *Stenomeris* to subfam. Stenomeridoideae and suggested that they should perhaps be treated in two unigeneric subfamilies or even in an independent family. Knuth's (1924, 1930) division of the Dioscoreaceae into the tribes Dioscoreae and Stenomerideae Planchon may be useful only after the exclusion of *Petermannia* and *Trichopus* from the latter tribe. *Avetra* may represent a monotypic tribe. However, reorganizing the subfamilial classification of the Dioscoreaceae is beyond the scope of this flora.

The remaining genera of the Dioscoreaceae are easily distinguished by their fruits. *Rajania* has one-seeded samaras, *Tamus* has berries, and *Dioscorea* has three-winged, few-seeded capsules like those of *Borderea* and *Epipetrum. Higinbothamia* Uline, a monotypic genus described from the Yucatán, was said to differ from *Dioscorea* in having four instead of two seeds per locule. It is now recognized as a section of *Dioscorea* with two species, one of which is endemic to Belize (see Schubert (1966) under references for *Dioscorea*).

The evolutionary relationships among the genera of the Dioscoreaceae have not been fully resolved. Because of their perfect flowers and long-appendiculate stamens, *Avetra* and *Stenomeris* are probably basal (Burkill, 1960). The remaining genera of the family have imperfect flowers (the plants dioecious), and with the exception of *Dioscorea* they all have a restricted distribution. According to B. W. Smith (see under *Dioscorea*), these small genera have arisen from *Dioscorea.* However, this view implies that *Dioscorea* is paraphyletic. The development of one-winged fruits in *D. cyphocarpa* Robinson ex Knuth and *D. tacanensis* Lundell may suggest a closer relationship between *Rajania* and *Dioscorea.* It is possible, however, that samaroid fruits evolved independently in the two genera.

The ordinal disposition and familial relationships of the Dioscoreaceae are controversial. A few authors (e.g., El-Gazzar & Hamza) advocated that the family be placed in the dicotyledons near the Aristolochiaceae Juss. because of its twining stems, petiolate, exstipulate leaves, trimerous, epigynous flowers, anatropous ovules, loculicidal capsules, endospermous seeds, and binucleate pollen. Furthermore, the presence in both families of PIIC-type sieve-tube plastids, which is universal in the monocotyledons, may be considered as evidence supporting this view. However, because of the presence of other plastid types in the family, Dahlgren & Rasmussen believe that the occurrence of these plastids in only two genera of the Aristolochiaceae is by convergence. Similarities between the Dioscoreales and the Magnoliales were summarized by Dahlgren & Clifford, who suggested (p. 342) that the extant forms of these orders do not represent "missing links or relicts of the common ancestors of the monocotyledons."

Lawton & Lawton, who studied the seedlings of five species of *Dioscorea,* suggested that the first seedling leaf is homologous to a modified second cotyledon, whereas the first cotyledon remains in the seed as an absorbing structure. However, P. M. Smith (reference under *Dioscorea*) did not find any structure comparable to a second cotyledon in the Dioscoreaceae. The slightly lateral position of the cotyledon in the family is considered to be ancestral among the monocotyledons, which otherwise have terminal cotyledons (Dahlgren, Clifford, & Yeo).

The close relationship between the Dioscoreaceae and the Smilacaceae was pointed out as early as 1810 by Brown. Most recent authors (e.g., Cronquist; Dahlgren, Clifford, & Yeo; Takhtajan) accept such a relationship. They and Thorne also associate the Dioscoreaceae closely with the Stemonaceae Engler (see Rogers), the Taccaceae Dumort., and the Trichopodaceae. However, these authors have variously placed the Dioscoreaceae under the Dioscoreales, the Liliales, or the Smilacales. The Dioscoreales (*sensu* Dahlgren, Clifford, & Yeo) are somewhat homogeneous and are apparently monophyletic. On the other hand, raising the Trilliaceae Lindley, the Taccaceae, and the Smilacaceae-Petermanniaceae to three orders, as suggested by J. W. Walker (pers. comm.), may be more appropriate. Evidently, the placement of the Dioscoreaceae with 14 other families in the order Liliales (Cronquist) needs further study.

The Dioscoreales have been considered to be the most central order in the monocotyledons (Dahlgren, Clifford, & Yeo). However, since various families of the Dioscoreales have several specialized features, particularly tetramery, epigyny, complex nodal anatomy, and fleshy fruits, a critical evaluation of the order is needed.

According to Coursey (1967; see under *Dioscorea*), the Dioscoreaceae likely evolved before the end of the Cretaceous, and *Dioscorea* was probably widespread before the separation of America from Africa. Pax listed *Majanthemophyllum petiolatum* O. Weber from the Miocene of Germany and *Dioscorites resurgens* Saporta from the Tertiary of southern France. Daghlian suggested that fossils described as *Dioscorites* Saporta from the Upper Cretaceous (Maastrichtian), as well as from many other Tertiary sediments, are disputable as to familial and generic identity. Pollen of *Rajania* described from the Miocene of Veracruz (Graham), if indeed dioscoreaceous, may well belong to *Dioscorea.* The identity of the North American fossil *D. cretacea* Lesq. is questionable.

Pollen of the Dioscoreaceae is heterogeneous. *Tamus* has reticulate, 2-colpate pollen (Clarke & Jones). In *Dioscorea* pollen is monocolpate in the presumably primitive sect. STENOPHORA Uline and 2-colpate in four other sections (Su; see under *Dioscorea*). Monosulcate, multiaperturate pollen has been found in *D. polygonoides* Humb. & Bonpl. (Zavada). *Avetra* deviates strongly from the rest of the Dioscoreaceae in having spinulose, 4- or 5-foraminate pollen.

Cytology of the Dioscoreaceae has not been surveyed adequately, and chromosome numbers are known for only about nine percent of the entire family. *Petermannia* ($x = 5$) and *Trichopus* ($x = 7$), which are now placed in monotypic families, are evidently different not only in base number but also in chromosome size (Ramachandran, 1962, 1968). Diploid counts of $2n = 24$ in *Borderea* support its separation from *Dioscorea,* a genus uniformly based on either nine or ten. The closely related *Rajania* is apparently a polyploid based on nine, but only *R. cordata* L. ($2n = 36$) has been studied cytologically. Polyploidy based on $x = 12$ probably played an important role in the evolution of *Tamus,* as is evidenced by its occurrence in the tetraploid *T. communis* L. ($2n = 48$) and the octoploid *T. edulis* Lowe ($2n = 96$).

Goldblatt (1980) suggested that the base chromosome number for the Dioscoreaceae may be seven and that such a number is found in the relict *Trichopus,* as well as in the families Stemonaceae and Taccaceae. As indicated above, however, *Trichopus* does not belong to the Dioscoreaceae, and it is more appropriate to assume that the base number for the family is ten. No chromosome counts are known for *Avetra* or *Stenomeris.*

The Dioscoreaceae are characterized by three anatomical peculiarities that are unusual among the monocotyledons. First, xylem and phloem glomeruli are present at the nodes. These represent an interlacing mass of prosenchymatous xylem that encloses one to many phloem glomeruli, each with interlacing sieve tubes and sieve plates of various sizes (see Behnke (1965) for further details). Karnick (1970; see under *Dioscorea*) believed that this "nodal plexus" is the site of various chemical activities, including the biosynthesis of diverse constituents. Second, vascular bundles of the stem are often arranged in two circles. Those of the outer circle have a V-shaped group of metaxylem vessels and tracheids, with two phloem units terminating the flanges and a third one at the converging ends of the V. Bundles of the inner circle have an elliptic arrangement of metaxylem vessels and tracheids, with one or two large phloem units on the inner side of the innermost pair of the larger metaxylem vessels and at least one at the outer end (Ayensu, 1972). Third, the sieve tubes are rather large and have highly oblique, compound sieve plates and numerous sieve areas. Because of their size, sieve elements could easily be mistaken for vessels.

The presence of these three anatomical features in *Avetra* and *Stenomeris* supports their placement with *Dioscorea, Rajania,* and *Tamus* in the Dioscoreaceae, instead of in two other families (Ayensu, 1972). Furthermore, *Tri-*

chopus and *Petermannia* have nodal and vascular-bundle anatomy quite different from that of the Dioscoreaceae and are therefore appropriately assigned to monotypic families (Ayensu, 1966, 1972; Tomlinson & Ayensu).

Vessels of the Dioscoreaceae have scalariform perforations; these are present in the roots, aerial stems, and petioles but absent in leaf blades, bulbils, rhizomes, and tubers. Although most fibers of the Dioscoreaceae have tapered ends, a large proportion have square ones (Ayensu, 1972).

Stomata of the Dioscoreaceae are anomocytic and are not associated with morphologically differentiated subsidiary cells. Furthermore, the contiguous epidermal cells have no distinctive arrangement (Ayensu, 1972; Stebbins & Khush). However, Patel and others (e.g., Ekundayo; Ling *et al.*; Purnima & Srivastava; G. L. Shah & Gopal; references under *Dioscorea*) have indicated that other types of stomata may also be found. The stomata are distributed primarily on the abaxial leaf surface, but in a few species (e.g., *D. bulbifera* L.) they are present on both surfaces.

Dispersal in the Dioscoreaceae is primarily by wind. In *Rajania* and *Dioscorea,* which produce samaras and variously winged seeds, respectively, short-distance dispersal is usually accomplished by seeds or fruits gliding or whirling from carpellate plants that can climb to heights of more than 30 feet. The red berries of *Tamus* are dispersed in the Mediterranean region by birds (Burkill, 1937), whereas in species of *Epipetrum* the capsules become buried in the vicinity of the mother plant.

Numerous species of *Dioscorea* are important medicinal or food plants. They are discussed in some detail under the generic account. The remaining genera of the Dioscoreaceae have little or no economic value.

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Dioscorea Linnaeus, Sp. Pl. **2:** 1032. 1753; Gen. Pl. ed. 5. 456. 1754.

Twining [rarely erect] herbs [or lianas]; glabrous or with unicellular, eglandular, simple [or variously branched] trichomes. Underground organs rhizomes, woody corms, or usually fleshy, single or clustered, edible [or poisonous], smooth [or spiny] tubers with thin [or thick to corky] skin. Stems almost always produced annually from underground structures, smooth, winged [or armed], terete or angled, dextrorse or sinistrorse. Leaves alternate, opposite, or whorled, petiolate, simple [or palmately compound, with 3–7 leaflets], cordate to nearly deltoid, undivided [or palmately lobed]; main veins 3–13, converging, the lateral ones reticulate, usually horizontal; petioles usually with a pulvinus at both ends, sometimes with a bulbil at the axil. Inflorescences axillary, many-flowered, bracteate racemes, panicles, spikes, or cymes. Flowers imperfect (plants dioecious or—abnormally—monoecious), actinomorphic, with rotate [funnelform or campanulate] perianth; tepals 6, in 2 similar [or sharply differentiated] whorls, distinct or variously connate; staminate flowers usually grouped in cymes borne on racemes, often with stylar rudiments, the stamens usually 6, in 2 whorls, all fertile [or the inner 3 either staminodial or absent], the filaments free [or connate], very short [or as long as the tepals]; carpellate flowers usually in spikes or spikelike racemes, epigynous, with 6 [3 or 0] staminodia; styles 3, branched. Fruits dehiscent, 3-winged, leathery or membranaceous capsules. Seeds flattened [or not], reticulate or smooth, broadly [to narrowly] winged all around [or only at 1 end, rarely wingless], 2 [or 4] per locule. Base chromosome numbers 9, 10. (Including *Androsyne* Salisb.; *Botryosicyos* Hochst.; *Elephantodon* Salisb.; *Hamatris* Salisb.; *Helmia* Knuth; *Higinbothamia* Uline; *Hyperocarpa* (Uline) Barroso, Guimarães, & Sucre; *Merione* Salisb.; *Nanarepenta* Matuda; *Polynome* Salisb.; *Rhizemys* Raf.; *Sismondaea* Delponte; *Strophis* Salisb.; *Testudinaria* Salisb.; *Ubium* Cothenius.) LECTOTYPE:[3] *D. bulbifera* L.; see Green in Hitchcock & Green. (Name commemorating the Greek Pedanios Dioscorides (fl. ca. A.D. 40–80), naturalist, physician, and officer in the army of Nero. His *De Materia Medica,* which was published in five volumes during the period A.D. 50–70 (Riddle), was the leading text on pharmacology for 16 centuries and contained medicinal properties of more than 1000 drugs derived primarily from plants.)—YAM.

A genus of approximately 850 species, of which the majority grow in the humid tropical and subtropical areas of the world, and only several occur in the warmer parts of the temperate zones. Small's estimation of 160 species for *Dioscorea* is well below the mark. As was suggested by B. W. Smith, nearly 50 percent of the species of *Dioscorea* are found in South America. There are approximately 130 species in Brazil, 120 in Central America and Mexico, 160 in Africa, and 250 in Asia (authors' compilation). The genus is poorly represented in Europe and adjacent Asia (three species), Australia (four), and the United States and Canada (three). Three of the six species growing in the southeastern United States are naturalized weeds of Asiatic origin.

The sectional classification of *Dioscorea* is controversial. About 75 sections, including 60 in Knuth (1924), have been recognized by various authors. Knuth

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[3] The lectotypification of *Dioscorea* has not been fully resolved. Britton & Brown, who were the first to lectotypify the genus, chose *D. sativa* from the eight species described by Linnaeus (Sp. Pl. **2:** 1032, 1033. 1753). Prain & Burkill (1919) clearly demonstrated that Linnaeus, in his citations under *D. sativa,* included elements now believed to belong to five species of *Dioscorea,* as well as one each of *Cardiopteris* Wall. ex Blume (Cardiopteridaceae Blume) and *Tinospora* Miers (Menispermaceae Juss.). Hooker's suggestion (p. 291) that "the plant figured in *Hortus Cliffortianus* must be accepted as [*D.*] *sativa* Linn." was followed by Prain & Burkill (1919), who also argued that the name *D. sativa* must be abandoned because the figure in *Hortus Cliffortianus* represents a plant with leaves from *D. villosa* L. and fruits from another species. The single specimen (*1184.4*) in the Linnaean herbarium, which was annotated by Linnaeus as *D. sativa,* was collected by Kalm from eastern North America and is generally agreed (Prain & Burkill, 1919) to belong to *D. villosa.* As indicated by Jackson's letter to Bartlett (see Bartlett, p. 8), "I do not find any specimen named by Linné "*villosa*" in his herbarium, but as *sativa* is an East Indian species, and the specimen is of Kalm's collection, it is patent that there is a blunder." If *D. sativa* is lectotypified on Kalm's specimen above, we would be forced to replace the well-known North American *D. villosa* by *D. sativa.* This, however, would be a serious mistake because Linnaeus had indicated in his original description of *D. sativa* that the plant grows in the "Indiis" (East Indies; see Bartlett) and implied that it is a cultivated plant. *Dioscorea villosa* is neither cultivated nor edible. Evidently *D. sativa* was based on materials inadequate and highly controversial with respect to citations, diagnosis, illustrations, and specimens. No matter how the species is typified, there would still be several unresolved problems. On the basis of these facts, *D. sativa* could be maintained as the lectotype of the genus only if it is satisfactorily typified. It is doubtful, however, that this will ever be accomplished. In fact, the report of the Standing Committee on Stabilization of Species Names (Taxon **24:** 171–177. 1975) listed *D. sativa* as a nomen ambiguum to be rejected under Article 69 of the ICBN. Therefore, we are accepting *D. bulbifera* L. as the lectotype of the genus, as was proposed by Green (in Hitchcock & Green).

has often been criticized for his narrow sectional concept, particularly with respect to the New World taxa. Burkill (1960) assigned the Old World species to 23 sections (including *Borderea*) and placed particular emphasis in his keys on aspects of the underground parts. On the other hand, Knuth (1924, 1930, family references) divided *Dioscorea* into four subgenera based on the position of the seed wing, relying heavily on characters of the staminate flowers and fruits in his sectional divisions of subgenera. Some of the sectional realignment proposed by Ayensu (1972) on the basis of anatomy should be taken into consideration. In our opinion, the number of New World sections accepted by Knuth (1924) should be reduced. However, it is beyond the scope of this flora to do that.

Burkill (1960) and Prain & Burkill (1939) suggested that *Dioscorea* evolved during the Cretaceous in what are now the temperate areas of the Far East, where the presumably primitive sect. STENOPHORA Uline is primarily distributed, and that the genus later migrated to the tropics. Burkill (1960) believed that the formation of the Atlantic rift was responsible for the separation of the range of *Dioscorea* into two portions, each of which evolved independently because no sections or species are now common to the New and Old worlds. Section STENOPHORA is considered primitive on the basis of having primarily diploid taxa, monocolpate pollen, and rhizomatous underground organs (Burkill, 1960; Pei *et al.*).

The assignment of the eastern North American species of *Dioscorea* to sect. STENOPHORA by Burkill (1960), Coursey (1967), and Prain & Burkill (1936) is unacceptable because seeds of these species are broadly winged all around, while those of sect. STENOPHORA are winged above (distally). We follow Uline (1897) and Knuth (1924) in placing these species in sect. MACROPODA Uline but disagree with the latter author on the sectional limits. Uline admitted only three species in this section: *D. villosa* and two unnamed ones that were said to grow in the Caucasus and the Himalayas. Therefore, *D. villosa* has to be considered as the sectional type. Coursey (1967) has suggested that the eastern North American taxa evolved from ancestors that migrated from eastern Asia across the Bering Strait land bridge. However, there is no evidence at present that supports this speculation.

Section MACROPODA Uline (stems sinistrorse; staminate flowers grouped in verticillate to subcapitate cymes borne on racemes; fertile stamens 6, inserted at base of perianth, the filaments short; capsules large, obovate) is represented in the United States and Canada by three species that also grow in the Southeast.

Dioscorea quaternata J. F. Gmelin (*D. villosa* L. subsp. *quarternata* (J. F. Gmelin) Knuth, *D. paniculata* Michx., *D. villosa* subsp. *paniculata* (Michx.) Knuth, *D. paniculata* var. *glabrifolia* Bartlett, *D. villosa* subsp. *paniculata* var. *glabrifolia* (Bartlett) Knuth, *D. villosa* var. *glabrifolia* (Bartlett) Blake, *D. villosa* f. *glabrifolia* (Bartlett) Fern., *D. glauca* Muhl., *D. villosa* subsp. *glauca* (Muhl.) Knuth, *D. quaternata* var. *glauca* (Muhl.) Fern., *D. villosa* var. *glabra* C. G. Lloyd, *D. Lloydiana* Krause), $2n = 36, 54, 60$, is the most variable and widely distributed of the North American species. It is distributed primarily east of the 95th meridian and between 27 and 45° north latitude. It does not grow in New England and is very rare in New Jersey, New York, Wisconsin, Minnesota, Iowa, Kansas, Oklahoma, and Texas, but is quite common in the remaining states that fall within its geographic range. It is sporadic in southern Ontario, Canada. *Dioscorea quaternata* grows in moist, rich or rocky woods and thickets, on limestone or talus slopes, in creek bottoms, and along roadsides, railroad tracks, and borders of swamps, ponds, and marshes.

Dioscorea villosa L. (*D. hirticaulis* Bartlett, *D. villosa* subsp. *hirticaulis* (Bartlett) Knuth, *D. villosa* var. *hirticaulis* (Bartlett) Ahles) is distributed from southwestern Massachusetts (Bristol County), Rhode Island (Washington County), and western Connecticut (Fairfield, Hartford, Middlesex, New Haven, and New London counties) southward along the Coastal Plain of all states to northern Florida. We have not seen any material from Delaware, and the records from New York and New Jersey are based on old collections. Furthermore, *D. villosa* is disjunct and probably introduced to Kentucky; it is first recorded here (*Beckett 651*, GH; Clark County). The species is common in Virginia and the Carolinas, where it grows in bogs, peaty depressions, and swamps. Linnaeus (Sp. Pl. **2**: 1033. 1753) stated that it occurs in Florida, but this has not previously been confirmed. We are recording *D. villosa* from Alachua (*Arnold s.n.*, 1931; FLAS), Jackson (*Godfrey 76493*; FSU), and Leon (*Lazor 922*; FSU) counties, Florida.

Dioscorea villosa is easily recognized by its narrowly winged, polygonal (8- to 14-angled) stems (FIGURE 1m), alternate lower leaves, and densely grouped glomerules on short (usually 2–4 cm) staminate inflorescences. The closely related *D. quaternata* has terete, wingless stems, whorled lower leaves (three to nine per node), and lax, longer inflorescences. Field notes on the phyllotaxy of lower nodes are useful for separating the two species. *Dioscorea quaternata* is the earliest published binomial for the North American dioscoreas with whorled lower leaves.

The identities of *Dioscorea hirticaulis, D. quaternata,* and *D. villosa* have been confused. A few authors (e.g., Ahles, 1968; Gleason; MacRoberts; E. B. Smith) suggested that the first and/or second be reduced to synonymy of the last. As shown above, however, *D. quaternata* and *D. villosa* are very distinct and should therefore be maintained at the specific rank.

Dioscorea villosa was typified by Blake on *Clayton 94* (BM) from Virginia. Charles E. Jarvis (pers. comm.) has indicated that there are two Clayton sheets in the British Museum (photos, A!), one bearing staminate material and the other a carpellate plant. The staminate material, annotated as *Clayton 94* and with a handwritten note by Gronovius that male and female flowers are borne on separate plants, is the type. It has narrowly winged, 8- to 14-angled, very sparsely pubescent stems and alternate lower leaves. Previously these features have been attributed to *D. hirticaulis*. Therefore, what has been called *D. hirticaulis* by all North American authors is in fact *D. villosa*. Accordingly, the range of *D. villosa* becomes restricted to only the coastal states above, and all records from the other states should belong to *D. quaternata*. Evidently, Deam's record of *D. villosa* (as *D. hirticaulis*) from six counties in Indiana belongs to *D. quaternata*.

Both *Dioscorea villosa* and *D. quaternata* are highly variable in stem and leaf pubescence. Forms with densely pubescent to completely glabrous leaves that are either glaucous or nonglaucous occur in populations of both species.

Bartlett's recognition of four species in this complex was based primarily on differences in the branching of rhizomes and in pubescence, color (green vs. glaucous), and number of leaves per node. These alleged distinctions are far from being realistic. In fact, characters of rhizome branching, thickness, and surface configuration can be modified by soil texture, habitat, and environment. Furthermore, petiole length, leaf pubescence and glaucescence, and fruit length show continuous variations of no taxonomic value.

Dioscorea floridana Bartlett (*D. villosa* subsp. *floridana* (Bartlett) Knuth, *D. villosa* var. *floridana* (Bartlett) Ahles) is the most distinctive of the North American species. It is readily distinguished by its two or three staminate inflorescences in the axils of upper leaves, longer (ca. 0.4 mm), inwardly curved filaments, connate anther lobes (see FIGURE 1n, o), and oblong tepals. Both *D. quaternata* and *D. villosa* have single staminate inflorescences in the axils of upper leaves, shorter (ca. 0.2 mm), straight filaments, separated, didymous anther lobes (see FIGURE 1e), and ovate tepals. Differences in the anthers of these species were first observed by Bartlett (see p. 18), but they have been overlooked by subsequent workers.

Dioscorea floridana grows in moist thickets and swamps, as well as in moist to dry woods and hammocks in South Carolina (Berkeley, Charleston, Dorchester, Orangeburg, and Williamsburg counties), Georgia (Baker, Chatham, Clarke, Dougherty, Jenkins, Lowndes, Sumter, and Tattnall counties), and Florida (Alachua, Calhoun, Columbia, Duval, Hernando, Hillsborough, Jackson, Levy, and Santa Rosa counties). It has been mapped from Bamberg and Beaufort counties, South Carolina (Ahles, 1968), but we have not seen any material from either.

No chromosome counts are available for either *Dioscorea floridana* or *D. villosa*. The few counts for *D. quaternata* are inconsistent, and more studies are needed before any meaningful conclusions can be reached.

Dioscorea bulbifera L. (*Helmia bulbifera* (L.) Kunth; see Coursey (1967) for ten additional synonyms), aerial or potato yam, $2n = 36?, 40, 54?, 60, 70, 80, 100$, is the only edible yam believed to be native to both Asia and Africa (Prain & Burkill, 1936). Introduced to the New World during the slave trade, it is a widespread weed in Florida, where it grows in disturbed woods and thickets (Wunderlin), but is uncommon in Mississippi. Edible and poisonous forms are known, but the Florida populations produce bulbils that remain inedible and nauseating even after repeated washing and boiling (Ward). Prain & Burkill (1934) recognized ten varieties primarily on the basis of the shape and taste of both bubils and tubers. It is doubtful, however, that these entities are significant taxonomically. Tubers of *D. bulbifera*, if produced, are very small, bitter, and usually hard. The bulbils, on the other hand, may weigh up to 2 kg. The species is easily distinguished from the other introduced dioscoreas that grow in the Southeastern States by its sinistrorse, terete, wingless stems; large, alternate, broadly cordate, acuminate leaves with rounded lobes; large, smooth, subspherical bulbils; and auriculate petiolar bases.

The sectional disposition of *Dioscorea bulbifera* is problematic. If the species is accepted as the lectotype of the genus, as is done here, it should be assigned to sect. DIOSCOREA. Accordingly, sect. OPSOPHYTON Uline, to which *D. bulbifera* is assigned by nearly all students of the Dioscoreaceae, should be reduced to

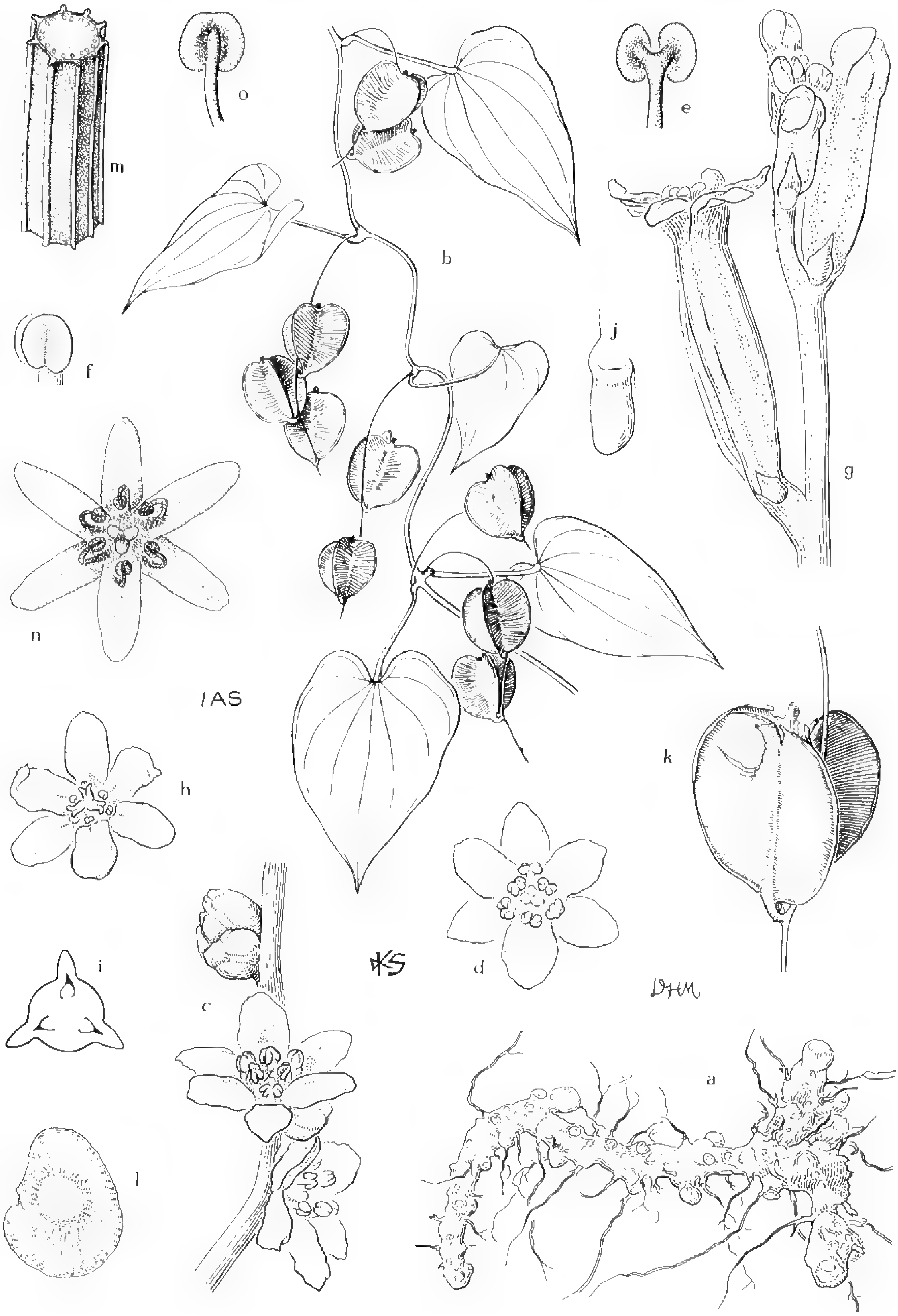

FIGURE 1. *Dioscorea*. a–l, *D. quaternata:* a, rhizome, × ½—note scars left by annual aerial stems; b, portion of mature plant with fruits, × ½; c, flowers and buds from staminate plant, × 6; d, staminate flower from above, × 6; e, abaxial view of anther, × 40; f, lateral view of anther, × 40; g, tip of carpellate inflorescence with buds and 1

a synonym of sect. DIOSCOREA. Knuth (1924) recognized 26 species and three subsections in sect. OPSOPHYTON and placed *D. bulbifera* in subsect. *Euopsophyton,* which also included three other species believed to be of hybrid origin. Prain & Burkill (1936), on the other hand, defined the section to include only *D. bulbifera* and its putative hybrids with three members of sect. ENANTIOPHYLLUM Uline.

The two remaining species of *Dioscorea* that are naturalized in the Southeastern States are *D. alata* L., white yam, greater yam, $2n$ = 20, 30, 40, 50, 60, 70, 80, and *D. oppositifolia* L. (*D. batatas* Dcne.; *D. opposita* Thunb., see Taxon **24**: 173. 1975), Chinese yam, cinnamon vine, $2n$ = 138, 140, 142, 144. They belong to sect. ENANTIOPHYLLUM Uline (tubers nonpoisonous, stems dextrorse, leaves alternate or opposite, filaments as long as the anthers, seeds winged all around). This section, the largest in *Dioscorea,* includes about 120 species restricted to Africa and Asia, none of which is common to both continents (Prain & Burkill, 1939).

Dioscorea alata, a native of southeastern Asia not known to grow in the wild state (Coursey, 1967), is the most widely cultivated edible species in the genus. It has escaped from cultivation in several counties in Florida (Ward; Wunderlin) but is not naturalized in the other Southeastern States. *Dioscorea alata* is highly variable, and many cultivars with different ploidy levels are grown. It resembles *D. bulbifera* in the production of bulbils and in having auriculate petiolar bases but differs in having dextrorse, quadrangular, broadly winged stems.

Dioscorea oppositifolia, which is naturalized in North and South Carolina, Georgia, Tennessee, Alabama, and Arkansas, is native to China and is widely cultivated in eastern Asia for its edible tubers. It is grown in the United States primarily as an ornamental (Bailey *et al.*) and has escaped from cultivation in many parts of the country. It is a weed of thickets, alluvial woods, waste places, flood plains, roadsides, limestone outcrops, slopes, and fence rows. According to Purseglove, *D. oppositifolia* (as *D. opposita*) was cultivated experimentally in Europe during the mid-nineteenth century as a substitute for potatoes (*Solanum tuberosum* L.) that were threatened by blight. *Dioscorea oppositifolia* is most likely a 14-ploid based on ten, and the aneuploid counts above are probably approximations of $2n$ = 140. It is readily distinguished from the other bulbil-producing species by its terete, dextrorse, wingless stems, nonauriculate petiolar bases, and somewhat hastate, usually opposite leaves.

Hooker's statement (p. 288) that "the species of *Dioscorea* are in a state of indescribable confusion" may be justified because of the inadequacy of material for many tropical species. It is often difficult, if not impossible, to identify specimens that lack well-developed staminate flowers or mature fruits. Because of dioecism, there are many cases in which the carpellate and staminate plants of a given species were described as two species assigned to different sections.

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opened flower, × 6; h, carpellate flower from above, showing 3 styles and 6 staminodia, × 6; i, cross section of ovary of carpellate flower, × 10; j, ovule, × 25; k, mature capsule, × 1; l, winged seed, × 2. m, *D. villosa,* stem, × 6. n, o, *D. floridana:* n, staminate flower from above, × 10—note stylar rudiments and 6 inwardly curved filaments; o, abaxial view of anther, × 40.

A case in point is *D. hondurensis* Knuth: carpellate material was described in sect. TRIANGULARES Knuth, while staminate material of the same species was described as *D. tabascana* Matuda in sect. MACROGYNODIUM Uline. According to Schubert (1966), *D. hondurensis* probably belongs to the South American sect. SARCANTHA Uline.

The reproductive biology of *Dioscorea* has been poorly studied. Although all species are dioecious, monoecism is known in at least 17 species (Burkill, 1960; Hawley). It is not known, however, if the carpellate flowers of monoecious plants are fertile. The flowers of *Dioscorea* are generally small, and their diameter in the great majority of species is 2–4 mm. The smallest flowers (ca. 1 mm wide) are found in the Madagascan *D. nako* Perr. (Burkill, 1960), while the largest (tepals more than 3 cm long) belong to the Mexican *D. insignis* Morton & Schubert (see Schubert & Morton).

Because of their reduced size and dull colors (usually dirty white, creamy, greenish, or brownish), the flowers of *Dioscorea* were believed to be wind pollinated. However, this is highly unlikely because the pollen is glutinous. Furthermore, Coursey (1967) suggested that the flowers are sweetly scented and are likely to be pollinated by night-flying insects. Sadik & Okereke observed thrips of the genus *Larothrips* carrying pollen from the staminate to the carpellate flowers of *D. rotundata* Poiret. The flowers of *D. composita* Hemsley and *D. floribunda* Martens & Gal. are said to be inefficiently wind pollinated in Puerto Rico (Martin, Cabanillas, & Ortiz).

Chromosome numbers have been reported for about 90 species (ca. 9.5 percent) of *Dioscorea*. Apparently all of the Old World species are either diploids or polyploids based on ten, while most of the New World ones are polyploids based on nine (Martin & Ortiz, 1963a). However, only about three and 17 percent, respectively, of the New and Old World species have been surveyed, and more counts are needed to confirm these cytological observations.

Aneuploidy has been well documented in *Dioscorea alata, D. bulbifera, D. cayenensis* Lam., *D. dumetorum* (Kunth) Pax, and *D. oppositifolia*. All of these species are among the principal food yams, and it is not unusual to encounter variations in chromosome numbers of crop plants that have been propagated vegetatively for hundreds or perhaps thousands of generations. A continuous ploidy series (2–8x) is known in *D. alata* (Bolkhovskikh *et al.*), and higher ploidy counts (10–14x) based on ten are known in at least 12 species. The lowest chromosome number ($2n = 20$) in the genus characterizes most species of sect. STENOPHORA, the most primitive group in *Dioscorea* (Chin *et al.*; Pei *et al.*), while the highest ($2n = 140$) has been reported for *D. cayenensis, D. oppositifolia,* and *D. pentaphylla* L. Onwueme's conclusion (p. 3) that "the highest chromosome numbers and the smallest chromosome sizes occur in the more tropical *Dioscorea* spp., while the smallest numbers and largest sizes occur in the more temperate species" needs further study. It is evident, however, that polyploidy has played a major role in the evolution of *Dioscorea* (Ramachandran, 1962).

Except for a few aberrant cases, species of *Dioscorea* are always dioecious, and within a given population staminate plants usually outnumber the carpellate ones by three to five times. The mechanism of sex determination in *Dioscorea* is controversial. Nakajima, Ramachandran (1962), and B. W. Smith have all suggested that the staminate plant is heterogametic and that the "male-determining" genes are borne on the Y chromosome. On the other hand, Bhat & Bindroo concluded that in *D. deltoidea* Wall. staminate plants have homomorphic chromosomes and carpellate ones have heteromorphic. Furthermore, Jensen could not find any evidence of sex chromosomes in *D. quaternata,* and Martin & Ortiz (1963a) and V. R. Rao & Murty reached similar conclusions for four Central American species. The presence of an extra chromosome in *D. alata* and *D. brachybotrya* Poeppig (as *D. reticulata* C. Gay) was considered to be responsible for "male" expression in an XO sex-determining mechanism (B. W. Smith).

Because of their high numbers and small sizes, the chromosomes of *Dioscorea* are very difficult to distinguish morphologically. As suggested by Martin (1966), however, the cytological evidence supports the staminate plant as heterogametic, and therefore an XO sex-determining mechanism is highly unlikely. It is possible that the staminate plants are produced by different mechanisms. Sex ratios of progeny from a carpellate parent vary according to the staminate plant, and such ratios are constant among the progeny of a staminate parent. On the basis of these facts, Martin (1966) concluded that in tetraploid taxa the staminate plants have XXYY or XXXY genotypes.

Natural interspecific hybridization is very rare in *Dioscorea.* The origin of one such hybrid (*D. composita* × *D. floribunda*) has been supported by chemical, cytological, and morphological data (Martin & Cabanillas, 1963). Artificial crosses among some of the New World species (*D. composita, D. floribunda, D. Friedrichsthalii* Knuth, and *D. spiculiflora* Hemsley) are successful in all possible combinations (Martin & Cabanillas, 1966; V. R. Rao *et al.*; V. R. Rao & Murty). The reduction of hybrid fertility is caused by some meiotic abnormalities (univalent and multivalent formations), high percentage of abnormal pollen, low crossability of hybrids, and poor seed set. Crosses between the Old and New World species, as well as between *D. alata* and *D. deltoidea,* have been unsuccessful (V. R. Rao *et al.*).

Alkaloid production in the tubers is apparently restricted to some of the Old World species of *Dioscorea* that belong to sects. LASIOPHYTON Uline, PARAMECOCARPA Prain & Burkill, and TESTUDINARIA (Salisb.) Prain & Burkill. The principal compounds are dioscorine and its stereo isomer dihydrodioscorine. These highly toxic alkaloids cause general paralysis of the central nervous system. The African *D. Dregeana* (Kunth) Durand & Schinz and *D. dumetorum* and the Asiatic *D. hispida* Dennst., which are rich in alkaloids, are used locally to poison animals (see below). No attempts have been made to determine the chemotaxonomic significance of these compounds in the genus.

A few Asiatic species accumulate in their tubers relatively high concentrations of tannins that are economically important. *Dioscorea cirrhosa* Lour. (= *D. rhipogonoides* Oliver) contains between six and 13 percent tannins per dry weight and is widely used in Taiwan and Indochina for tanning leather and for fishing cordage and nets (Burkill, 1966).

More than 20 steroidal sapogenins have been isolated from some 70 species of *Dioscorea.* Diosgenin is found in all the saponin-containing species. Its content in the tropical dioscoreas is generally much higher than in those of other regions (Takeda). The distribution of sapogenins in *Dioscorea* supports certain sectional groupings and is therefore of some chemotaxonomic value (Akahori, 1965a; Kadkade *et al.*; Takeda). For example, sect. ENANTIOPHYLLUM, which contains the most important food crops of the genus, lacks the steroidal sapogenins. These compounds are also lacking in a few sections that produce bulbils and have sinistrorse stems. On the other hand, sections with alternate leaves, sinistrorse stems, and no bulbils are often rich in sapogenins. Takeda concluded that the chemical data tend to support Prain & Burkill's (1936, 1939) sectional classification of the eastern Asiatic *Dioscorea.* However, the chemistry of the genus is far from being adequately studied, and the great majority of the New World sections have not been surveyed.

Using polyacrylamide-gel electrophoresis of tuber proteins, Ikediobi & Igboanusi have found significant differences in the locations and intensities of certain bands in five species. They were also able to distinguish among nine cultivars of *Dioscorea rotundata.* Several authors (e.g., Rašper & Coursey) observed that differences in the viscosity, size, and shape of the tuber starch grains are useful in separating several edible species of *Dioscorea.* Only a few species, however, have been surveyed for tuber proteins and starch grains.

Ayensu (1972, 1973) observed that stems of the Old World species have two distinct phloem units below the innermost pair of metaxylem vessels, whereas those of the New World species have only one. This anatomical differentiation between the two groups of *Dioscorea,* however, requires further study to assess its phylogenetic value.

On the basis of stem anatomy, Ayensu (1972) concluded that the anatomical data are very useful taxonomically at the intersectional level but have little value within sections. He proposed several alterations to the sectional classification of Knuth (1924), including the reduction of many sections to synonymy and the elevation of a few subsections to sectional rank. In general, stem anatomy supports the sectional subdivision of the genus as accepted by Prain & Burkill (1936, 1939) and Matuda (1953b) but not by Knuth (1924).

Extrafloral nectaries of certain species (e.g., *Dioscorea rotundata*) are embedded in the leaf blade and open on the lower leaf surface. Each gland consists of small cells with dense cytoplasmic contents and is surrounded by a layer of cells with apparently little or no cytoplasm. The secretions of these nectaries contain fructose, glucose, and sucrose, as well as ninhydrin and traces of galactose (Grout & Williams). Leaf glands of the West African *D. macroura* Harms form enlarged pockets within the mesophyll and are connected to the upper leaf surface by slits or ducts. The pockets are lined with multicellular glandular "trichomes" that secrete mucopolysaccharide, on which nitrogen-fixing bacteria grow (Orr). As shown by Behnke, however, these bacteria are parasitic, and in response to their presence the plant produces an abundance of simple trichomes that fill the pockets and cause the bacteria to disintegrate.

In the African *Dioscorea praehensilis* Bentham and the Asiatic *D. esculenta* (Lour.) Burkill and *D. piscatorum* Prain & Burkill, roots produced on the tuber surface are modified into thorns or spines. Such modified roots apparently evolved independently several times within the genus.

Tubers of *Dioscorea* originate primarily from the seedling hypocotyl following the initiation of a cambial zone around the vascular tissue. The intensive activity of the cambium produces the storage parenchyma. These tubers differ from stem tubers of other genera in lacking both scale leaves, buds, or eyes that identify nodal positions and a terminal bud that marks the growing point of the tuber. Furthermore, most tubers of *Dioscorea* exhibit positive geotropism.

The corky outer portion of the tuber is derived from successive cork cambia each originating beneath another. The ground tissue, which is derived from the vascular cambium, forms the bulk of the tuber and consists of thick-walled parenchyma densely packed with starch grains. The vascular bundles are collateral and have xylem comprising tracheids and parenchyma but no vessels.

Some species of *Dioscorea* develop enormous tubers: up to 365 kg in *D. elephantipes* (L'Hér.) Engler (Purseglove) and up to 110 kg and 3.5 m long in *D. alata* (Haynes & Coursey).

Species of *Dioscorea* can be propagated by tubers, bulbils, vine cuttings, tissue cultures, or seeds. A leaf cutting with the complete pulvinus dipped in "hormone powder" is capable of producing new plants (Blunden, Hardman, & Trease). Bulbil production, which is reduced by the increase of day length (Allard), promotes dispersal, particularly in habitats that are subjected to floods or rain washes. Because of their occurrence in many species of unrelated sections, bulbils probably evolved independently a few times within *Dioscorea*. Murty & Purnima, who studied 11 species, suggested that bulbils develop as composite structures from the diffused growth of accessory buds that arise on the abaxial side of the axillary bud. Ayensu (1972) and Burkill (1960) define the bulbil as a modified branch of the aerial stem. They stated that it resembles the tuber anatomically.

Little is known about the ecology of *Dioscorea*. Although the majority of species are tropical, many rhizomatous taxa grow in temperate areas. In general, most species require more than 1 m of annual rainfall and temperatures higher than 25°C (Purseglove). The effect of photoperiodism has not been studied adequately. According to Purseglove, long days apparently favor the development of aerial parts, whereas short days promote the growth of tubers.

Food crops of the genus *Dioscorea*, which are known as yams in most parts of the world but are often confused with the sweet potatoes (*Ipomoea Batatas* (L.) Lam., Convolvulaceae) in the United States, provide the staple foodstuff for millions of people in many subtropical and tropical countries, particularly in West Africa (Coursey, 1967). The dietary position of yams in the tropics, however, has declined substantially due to socioeconomic reasons, introduction of better crops, and higher costs and greater labor needed for the cultivation and preparation of yams for food. The so-called "yam zone," which extends from the Cameroun Mountains west into central Ivory Coast, is the area where most of the world's yams are grown. In fact, Nigeria alone produces nearly half of the world's crop (Ayensu & Coursey; Coursey, 1967). Yams are eaten baked, boiled, fried, mashed, pounded, or roasted. They are also used to prepare chips, flakes, and flour.

Although about 50 species of *Dioscorea* are collected from the wild or cultivated as food crops, only ten are considered to be of major importance. These are associated with three independent centers of domestication. In southern China and southeastern Asia *D. alata, D. bulbifera, D. esculenta, D. japonica* Thunb., *D. oppositifolia,* and *D. pentaphylla* were first domesticated, while in the Caribbean region *D. trifida* L. and in the West African forest belt *D. cayenensis, D. dumetorum,* and *D. rotundata* were first brought into cultivation. It has been suggested that the domestication of *Dioscorea* probably took place ca. 10,000 B.P. in Asia and ca. 11,000 B.P. in Africa (Coursey, 1976a).

The West African *Dioscorea cayenensis* and *D. rotundata* were described from plants cultivated in Jamaica and French Guiana, respectively. Both species were introduced to the New World during the slave trade (Ayensu & Coursey). There is some controversy whether *D. rotundata,* the most important African yam that is not known to grow in the wild, is a distinct species or a subspecies of the earlier-published *D. cayenensis.* It has been suggested that *D. rotundata* probably evolved from hybridization between *D. cayenensis* and *D. praehensilis,* although the second parent may have been either *D. abyssinica* Hochst. or *D. togoensis* Knuth (Akoroda & Chheda; Coursey, 1976a).

The medicinal value of various species of *Dioscorea* has increased dramatically following Marker's (see Tyler *et al.*) pioneering research on the conversion of diosgenin to precursors of steroidal drugs. These drugs include the sex hormones androgen, estrogen, and progestogen, as well as oral contraceptives and anti-inflammatory compounds such as the systemic corticosteroids and topical hormones. Diosgenin is commercially extracted mainly from the tubers of the Mexican *D. composita, D. floribunda,* and *D. spiculiflora,* the South African *D. sylvatica* Eklon, and the Himalayan *D. deltoidea* and *D. Prazeri* Prain & Burkill. Sapogenin content in the tubers of the Mexican species above can be as high as 10–15 percent of the dry weight. Although the use of *Dioscorea* tubers in traditional medicine is likely based on superstition and magic rather than on actual physiological effects, some of the sapogenins and other steroidal components may have certain medicinal properties. In fact, preparations from the tubers of various species have been prescribed to cure colic, dysentery, ulcers, syphilis, sore throat, swellings, pulmonary complaints, diarrhea, hemorrhoids, boils, tumors, corns, diabetes, cuts, superficial lesions, and hysteria (Hartwell; Karnick, 1969; Perry; Sastri; Watt & Breyer-Brandwijk).

Tubers of numerous species of *Dioscorea* are highly toxic. The poisonous substances are alkaloids, sapogenins, or tannins. Because of their hemolytic properties, sapogenins are highly toxic if introduced into the bloodstream. Therefore, the tubers have been widely used as a source of poison for fishing, hunting, or criminal purposes. Fish poisons are obtained from *D. deltoidea* in India, *D. hispida* in Java, *D. piscatorum* in Malaya, *D. Poilanei* Prain & Burkill in Vietnam, *D. Prazeri* in Sikkim, *D. sansibarensis* Pax in tropical East Africa, *D. tokoro* Makino in China, *D. composita* in Mexico, and *D. bulbifera, D. Dregeana,* and *D. rupicola* Kunth in various parts of Africa. The placement of grated tubers into a stream can stupefy fish at a considerable distance. Arrow or dart poisons are prepared in Malaysia and Sikkim by mixing the juice of *Antiaria toxicaria* Lesch (Moraceae Link) with that of the tubers of *D. hispida,* and in Africa by using the tuber extracts of *D. dumetorum* or *D. sansibarensis* with extracts of *Strophanthus* DC. (Apocynaceae Juss.). These poisons are employed to kill tigers and monkeys. In India tigers are hunted by placing pounded tubers of *D. hispida* in carcasses (Karnick, 1969).

Because of their high saponin content, tubers of various species, particularly *Dioscorea deltoidea* and *D. Prazeri,* are used in Burma, southwestern China (Yunnan), and northern India as soap for washing hair, silk, or wool. Decoctions of the tubers are also used in these countries to kill lice in human hair and clothing. In Malaysia tubers of *D. piscatorum* are used in the preparation of an insecticidal powder and are employed to destroy rice parasites (Coursey, 1967), while in Tanzania the tubers of *D. dumetorum* are used as a remedy for schistosomiasis (Watt & Breyer-Brandwijk). A paste prepared from the bulbils of *D. bulbifera* is said to cure scorpion stings and snake bites (Karnick, 1969). Bulbils of the last species are also used as a fish bait in Kashmir (Sastri).

Other minor uses of *Dioscorea* include extracting starch from *D. alata,* distilling alcohol from certain species (Sastri), brewing beer from *D. dumetorum* (Corkill; Irvine), substituting *D. polygonoides* Humb. & Bonpl. (as *D. lutea* G. F. W. Meyer) for coffee (Uphof), tanning leather and making fishing nets (see above), dyeing clothes and cotton threads with tubers of *C. cirrhosa* (Karnick, 1969; Uphof), coloring ice cream with phenolic pigments extracted from *D. alata* (Ingram & Greenwood-Barton), feeding livestock (Bailey *et al.*), and utilizing stems as cordage (Burkill, 1966). A drink prepared by the Meskwakis from the rhizomes of *D. villosa* is said to relieve the pain of childbirth (Lewis & Elvin-Lewis). The juice of a certain *Dioscorea* is used in Tanganyika for tattooing (Watt & Breyer-Brandwijk).

Several species of *Dioscorea* are grown as outdoor twining ornamentals, and forms of *D. alata* and *D. oppositifolia* with variegated foliage or colored younger parts are highly desirable (Hawley). *Dioscorea elephantipes,* elephant's foot, is occasionally grown in Europe and North America as an indoor plant for its large, curious, above-ground tubers with corky bark.

Yams have played a central role in the social and religious life of people in the tropics, particularly in West Africa. Cultural, social, magic, and religious practices associated with almost every aspect of yam planting, harvest, and storage are especially evident in Nigeria and neighboring countries (Ayensu & Coursey; Coursey, 1967, 1972; Purseglove). The cultivation of *Dioscorea pentaphylla* has been intimately associated with priesthood and has therefore been considered sacred in various parts of Malaysia and Indonesia (Coursey, 1967). The poisonous properties of many species form the basis of several magical beliefs in West Africa. Many of the highly toxic species (e.g., *D. dumetorum* and *D. hispida*) are used during famine for food. The tubers are peeled, sliced, boiled, pounded, and placed in running water for a few days to remove the toxins before they are consumed (Irvine; Karnick, 1969). Different tribes, however, follow different procedures to detoxify the tubers.

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THE GENERA OF COMMELINACEAE IN THE SOUTHEASTERN UNITED STATES[1]

GORDON C. TUCKER[2]

COMMELINACEAE R. Brown, Prodr. 268. 1810, "Commelineae," nom. cons.

(SPIDERWORT FAMILY)

Perennial or annual, mucilaginous herbs [twiners]. Roots fibrous or thickened. Stems soft. Leaves several, cauline or basal; sheaths closed; blades flat to V-shaped, the margins often with short prickles; vernation involute or supervolute. Inflorescences 1 to several, variously thyrsiform or cymose, terminal or axillary, sometimes subtended by spathes. Pedicels slender. Flowers perfect [imperfect], actinomorphic or zygomorphic, unscented [strongly or weakly scented]. Sepals 3, narrowly oblong to ovate, free. Petals 3, oblong to broadly ovate, sometimes clawed, free or connate. Stamens [1 or] 2–4 or 6; staminodia, if present, 2–4; filaments glabrous or hairy; anthers narrowly oblong, dorsifixed, tetrasporangiate, introrse [extrorse or poricidal]; pollen ovoid, monosulcate [trisulcate], binucleate [trinucleate]. Ovary syncarpous, [2- or] 3-locular; ovules

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Irene Brady prepared the illustration of *Callisia* under Carroll Wood's direction from material that R. J. Eaton collected in Citrus County, Florida, and that Wood cultivated at the Arnold Arboretum. Dorothy H. Marsh prepared the illustration of *Commelina* under R. B. Channell's direction from material Mrs. Marsh collected in Cambridge, Massachusetts, and Wood collected in Ayer, Massachusetts.

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1–3 per locule, orthotropous. Fruit a loculicidal capsule [berry or nutlet]. Seeds small, circular to oblong, flattened laterally [winged], often reticulately pitted [arillate]; endosperm abundant; embryo small, broadly capitate, beneath a disclike callosity on seed coat. TYPE GENUS: *Commelina* L.

A medium-sized family of 40–50 genera and 500–600 species. The largest genus is *Commelina,* with about 230 species. The family is pantropic and warm temperate, with centers of diversity in Mesoamerica, tropical Africa, and southern India. There is general agreement that the family most closely related to the Commelinaceae is the Mayacaceae (see Thieret, Tomlinson). No consensus exists, however, concerning suprageneric classification in the family: although two tribes have commonly been recognized, their circumscriptions have varied. The system of Faden (1985) is followed here. The Tradescantieae C. B. Clarke are characterized by stomata with four subsidiary cells (except two in *Callisia* sect. CUTHBERTIA (Small) Hunt); inflorescences consisting of basally fused pairs of cincinni or thyrses of cincinni subtended by large to small leaflike or modified spathes; generally actinomorphic and most often self-incompatible flowers; a gynoecium of three locules, each with two ovules; and six stamens, all fertile. This chiefly New World tribe is represented in the United States by three genera, all with species present in the Southeast: *Tradescantia* L. (including *Zebrina* Schnizl., *Setcreasea* K. Schum. & Sydow, and *Rhoeo* Walp.), *Callisia* Loefl. (including *Cuthbertia* Small and *Tradescantella* Small), and *Gibasis* Raf.

Representatives of tribe Commelineae have stomata with six subsidiary cells (Tomlinson, 1969). Flowers are often zygomorphic and are generally self-compatible. There are usually only three stamens and three (four) or no staminodia. The Commelineae are most diverse in the Old World tropics. Two genera, *Commelina* and *Murdannia* Royle, are represented in the United States, both in the Southeast.

Clarke (1881) recognized three tribes: the Pollieae C. B. Clarke (fruits indehiscent), the Tradescantieae (stamens 5 or 6, staminodia lacking; fruits capsular), and the Commelineae (stamens 2 or 3, staminodia lacking or 1–4; fruits capsular). Brückner (1930) followed Clarke but treated the last two tribes as subfamilies (with the Pollieae included in the Tradescantioideae Brückner). Pichon, in an apparent frenzy of taxonomic splitting, recognized ten tribes and accorded familial status to the Australian genus *Cartonema* R. Br. Brenan (1966) recognized 15 groups to which he assigned no rank, although several of them correspond to tribes recognized by Pichon. Brenan's insightful (but informal) classification pointed out morphological similarities among groups of genera; these have later been confirmed by anatomical or cytological studies. Hutchinson recognized no suprageneric ranks in the family, noting that relationships of genera were poorly understood and largely defined by "Linnean" characteristics such as stamen number. Woodson emphasized the importance of inflorescence characters for classification. He noted that some genera placed by Brückner (1930) in the supposedly "zygomorphic" subfam. Commelinoideae actually had actinomorphic flowers. Faden (1985) recognized two subfamilies, the Cartonematoideae[3] and the Commelinoideae, the latter with two tribes, the Tradescantieae and the Commelineae, a classification followed here. Recent diverse studies (discussed below) have provided eclectic information on the distribution of characters in the family. So far, these data have not been brought together and used for a synthetic classification based on evolutionary relationships.

In the present account, broad generic concepts are followed. This seems prudent both in view of the difficulty in defining genera and because of the diverse circumscriptions given to many of them (e.g., *Callisia* and *Tradescantia*). The generic classification of the Tradescantieae following Hunt is accepted here. Thus, *Tradescantia* is defined by its conspicuous, paired spathes and its fused cincinni. It is amply distinguished from *Tripogandra* Raf., which has zygomorphic flowers and dimorphic pollen (Handlos, 1975; Mattson). The various satellite genera near *Tradescantia,* such as *Rhoeo* and *Zebrina,* are treated as sections, as this seems a better indication that they differ less from sect. TRADESCANTIA than does *Tripogandra. Callisia* includes *Phyodina* Raf. and *Cuthbertia.* The genus as so circumscribed is defined by its reduced bracts and solitary cymes. *Gibasis* presents comparatively little problem in circumscription. It has paired (but unfused) cymes, with bracteoles and flowers arranged distichously on a conspicuous axis. The American species included in *Aneilema* R. Br. by recent authors (e.g., Fernald; Radford *et al.*) are placed here under *Murdannia* (*q.v.*).

Various workers agree that *Cartonema* is the most anomalous genus in the family, differing from all other Commelinaceae in its spiciform raceme, its lack of glandular microhairs and of raphides, and its poorly developed embryo and embryostega. Tomlinson (1969) has brought to light some additional anatomical differences (lack of transverse leaf veins and stem collenchyma, presence of radiate chlorenchyma in leaves) that support the unique status of *Cartonema.*

Triceratella Brenan, a genus endemic to southern Africa, has similarities both to *Cartonema* and to other genera of the family. Like *Cartonema, Triceratella* lacks glandular microhairs. However, it has raphide canals in the leaves, although the canals are adjacent to the veins, while in the remainder of the family they are not. Tomlinson (1969) suggested (but did not validly publish) subfamilial status for *Triceratella.*

Vessels are present in the vascular tissue of roots, stems, and leaves in all genera of the family that have been investigated except *Cartonema,* where they are present only in the roots (Tomlinson, 1969). The vessels have simple perforation plates. Sieve-tube plastids are of the "monocotyledonous type," in which there are several to many cuneate proteinaceous crystalloids. Although silica bodies are generally absent in the Commelinaceae, specialized epidermal cells containing silica are known from *Callisia* (including *Hadrodemas* Moore), *Coleotrype* C. B. Clarke, *Forrestia* A. Rich., *Gibasis,* and *Tripogandra.* Stomatal types have been surveyed by Tomlinson (1969). Both hexacytic and tetracytic stomata are known. (In the Mayacaceae they are paracytic.)

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[3] **Cartonematoideae** (Pichon) R. Faden ex G. Tucker, stat. nov., based on Cartonemataceae Pichon, Not. Syst. Paris **12:** 219. 1946.

The family has received much attention from cytologists; the chromosomes are generally large and the meiotic material easy to work with. Chromosome numbers have been published for all but six genera, and numbers for one third of the species are in the literature. The family shows a wide range of variation in base number and other features of the karyotype. Base numbers vary from four to 20, including nearly every value between. The chromosomes of most karyotypes are generally alike in size. Species of the genus *Stanfieldiella* Brenan are a notable exception: their chromosomes are small, but there is typically one in the complement that is twice as long as the others. The species of *Stanfieldiella* have the smallest chromosomes (2–3 μm), and *Tradescantia virginiana* L. and its allies the largest (about 12–14 μm). Most genera have asymmetric karyotypes—i.e., most of the chromosomes have an acrocentric or telocentric kinetochore.

In this family a genus is usually characterized by a single base chromosome number and a particular karyotype. The lowest base chromosome number recorded (4, 5) is for species of *Gibasis* and the highest (20) for *Palisota* Reichenb. Each of the tribes (groups used by Brenan) shows considerable chromosomal diversity, which in some cases argues against their naturalness.

Polyploidy has been detected in several genera. Usually the taxa are tetraploids, although higher levels have been reported. Polyploidy is also known within species. Chromosomal change is a common feature of speciation in the family. Closely related species often differ in chromosome number or in karyotype.

The family is characterized by the presence of various flavonols and glucoflavones, often in quantity. Syringic acid and cyanidin are common. Sulfated phenolic acids have been detected in species of *Coleotrype, Commelina, Gibasis, Tradescantia,* and *Tripogandra.* Quercetin 3-glycoside is also widespread in the family but is most common in the genera of the Commelineae (Del Pero de Martínez). Steroidal saponins are known only from *Cyanotis* D. Don. Some 30 species have been examined for cyanogenesis, which is apparently rare (reported from *Commelina* and *Tinantia* Scheidw.). In *T. erecta* Schlecht. the cyanogenic glucoside is taxiphyllin (Tjon Sie Fat). The report of cyanogenesis in *Commelina benghalensis* L. by Juliano is considered doubtful (Tjon Sie Fat). Calcium-oxalate raphides in raphide canals are common; they are generally found in the members of the Commelinaceae but are absent in the Cartonematoideae and the Mayacaceae. Commelinin, a magnesium-containing metallo-anthocyanin, gives the blue color to the petals of *Commelina* species (Goto *et al.*; Hayashi).

Zantovska Stirton & Harborne investigated anthocyanins in 28 species representing seven genera (as recognized herein following Hunt, 1975; 1980; 1986a, b, d). All species were found to contain acylated glucosides, a rare class of anthocyanins not reported from any other monocotyledonous family. In *Cyanotis, Dichorisandra* Mikan, *Gibasis, Tradescantia* (including representatives of the segregate genera *Campelia* L. C. Rich., *Rhoeo,* and *Zebrina*), and *Tripogandra,* the most abundant anthocyanin was cyanidin 3,7,3′-triglucoside. In *Commelina* (seven species tested), however, the most abundant was *p*-coumaroyl-delphinidin 3,5-glucoside (commelinin). Thus there are two different anthocyanins responsible for blue petal color in the family. It would be enlightening to learn whether other genera purportedly related to *Commelina* (e.g., *Murdannia, Aneilema*) also contain commelinin. It would also be interesting to identify the compounds responsible for the yellow petal color of such species as *C. africana* L.

Cleistogamous flowers are produced by certain species of *Commelina, Murdannia* (both Commelineae), and *Tinantia* (Tradescantieae).

There are six fertile stamens per flower in more than half the genera of the family (including the Cartonematoideae). Numerous genera have only three stamens, these alternating with or opposing in an adaxial-abaxial situation two to four staminodia. There is a single functional stamen in some species of *Callisia, Murdannia,* and *Pseudoparis* H. Perr. The filaments are hairy in many genera such as *Cartonema, Cyanotis, Tinantia,* and *Tradescantia* (including sect. RHOEO), and the filaments are fused in *Cochliostema* Lem. Anthers are tetrasporangiate (vs. bisporangiate in the Mayacaceae) and generally introrse. A few taxa are characterized by extrorse dehiscence, but *Dichorisandra* and *Porandra* Mikan (and members of the Mayacaceae) have poricidal anthers. The anther walls have girdle-type thickenings, and the tapetum is plasmodial. The pollen grains are always binucleate (seven genera studied by Owens) except in *Floscopa* Lour., where they are reported to be trinucleate (Davis). Poole & Hunt surveyed pollen morphology with scanning electron microscopy. All grains are monosulcate, except those of one species of *Tinantia,* which are trisulcate. Pollen dimensions are variable within and among genera. Four main types of ornamentation are encountered in the Tradescantieae and five in the Commelineae. The tectum tends to be insulate in species with actinomorphic flowers and spinulate, verrucate, or tuberculate in those with zygomorphic ones; in some species of *Callisia* and of *Gibasis* it is finely reticulate. All species of *Tradescantia* (including *Rhoeo* and *Zebrina*), the remaining species of *Gibasis,* and *Callisia* sects. HADRODEMAS (Moore) Hunt and CUTHBERTIA are characterized by the "*Tradescantia*-type" tectum (i.e., insulate, the insulae forming a cerebroid pattern). Species of *Commelina* and *Aneilema* have a perforate tectum bearing spinules; those of *Murdannia* have tubercles.

Species of *Tripogandra* are characterized by dimorphic pollen (Handlos) produced by two kinds of stamens: monosulcate, spheroidal, and fertile by the three anthers on short filaments; anasulcate, oblong, and infertile by the three on long filaments (Mattson). Both kinds of pollen have a granular-verrucate tectum interspersed with micropores (Poole & Hunt).

Placentation is axile in the Commelinaceae (vs. parietal in the Mayacaceae). The ovules of most genera are orthotropous, although they are hemianatropous in some and anatropous in *Cartonema* (orthotropous in the Mayacaceae). A parietal cell is generally present in the family but is known to be lacking in *Commelina* and *Cyanotis.* Megagametophyte development is of the Polygonum type in most genera but of the Allium type in *Tradescantia.* The ovary is syncarpous, and the style is three-branched. *Aneilema, Callisia, Commelina,* and *Tradescantia* have dry stigmas, while *Cyanotis, Gibasis, Thyrsanthemum* Pichon, and *Weldenia* Schultes f. have wet ones (Heslop-Harrison & Shivanna).

Endosperm formation is nuclear (several genera reported). Embryogeny conforms to the Asterad type. Endosperm is abundant and starchy. The mature embryo is capitate, broad, and achlorophyllous.

Fruits are capsules in most genera, except in *Athyrocarpus* Schlecht., *Pollia* Thunb. (both nutlets), and *Palisota* Reichenb. (berries). A few genera (*Amischotolype* Hassk., *Dichorisandra, Porandra*) have arillate seeds.

Pollination biology is little known, considering the size of the family. Faden (1983) studied isolating mechanisms in *Aneilema*. At a site in lowland Kenya where five species were growing in a small area, no hybrids were found. Some species pairs were separated by time of flower opening (morning vs. early afternoon), others by soil preference (well-drained sandy soils vs. waterlogged ones). Bees of several genera visited the flowers. The size of the flowers determined the bee that could gather pollen, thereby enforcing pollinator constancy. In certain species the lateral stamens were covered by the vernate petals, while in others the lateral and medial stamens were exposed simultaneously. Faden hypothesized that species in which the lateral stamens are covered longer would have a greater likelihood of outcrossing, since bees could gather less pollen from a flower with one or two anthers exposed than from one with three and would thus visit more flowers in a collecting trip.

Numerous species from several genera are worthy horticultural subjects. Several species of *Tradescantia* are cultivated in gardens in the United States and southern Canada. Trailing species of *Commelina* are used as ground covers. The most commonly cultivated taxa are *T. virginiana* and its hybrids with *T. subaspera* Ker or *T. ohiensis* Raf. ("*T.* ×*Andersoniana,*" nom. inval.; see Hunt, 1984), all easily grown in well-drained garden soils. *Tradescantia Zebrina* Bosse (*Zebrina pendula* Schnizl.), wandering Jew (a name also applied to *T. fluminensis* Vell. and *T. albiflora* Kunth), is commonly grown as an indoor hanging-basket plant. The common cultivar is 'Purpusii'. All the above species are readily propagated by division or from seed. Some species of the African genus *Palisota* are occasionally grown indoors.

Murdannia nudiflora (L.) Brenan and several species of *Commelina* are serious weeds in numerous warm-temperate and tropical countries worldwide. *Commelina* species, especially *C. benghalensis,* are persistent and not easily controlled by herbicides (Wilson).

The tuberous roots of certain western African species of *Aneilema* contain abundant starch and are eaten (Augier), while those of *Commelina coelestis* Willd. (Sturtevant), *C. graminifolia* HBK., and *C. tuberosa* L. have been a source of food in Mexico. The young stems and leaves of *C. communis* L. (Sturtevant; Gibbons & Tucker), *C. diffusa* Burman f., and (according to Tanaka), *C. benghalensis* are edible as a cooked vegetable. The tender young shoots of *Tradescantia occidentalis* were eaten uncooked by Indians of the Great Plains (Yanovsky); the leaves and new shoots of *T. virginiana* L. can be similarly used (Fernald & Kinsey).

The fresh or dried leaves of *Tradescantia Zanonia* (L.) Sw. (Hegnauer) and *Commelina communis* (Preston) have been employed as a treatment to stop the flow of blood from surface wounds. A Mexican species (perhaps *C. virginica*) has similar effects and has also been reported to cure cancer of the stomach

(Herrera). *Commelina virginica* and *T. elongata* G. F. W. Meyer have been employed as diuretics in Latin America. The medically active principle in these species has apparently never been isolated.

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KEY TO THE GENERA OF COMMELINACEAE IN THE SOUTHEASTERN UNITED STATES

General characters: *fibrous-rooted or tuberous perennials (annuals) of open or disturbed places in full sun or light shade; stems and leaves soft, exuding mucilage when bruised; leaves basal or cauline, the sheaths closed, the blades linear, lanceolate, or broadly ellipsoid; inflorescences terminal or axillary and terminal, variously thyrsiform or cymose; flowers trimerous, perfect, actinomorphic or zygomorphic, sepals somewhat persistent, petals deliquescent, staminodia sometimes present; fruits more or less dehiscent 2- or 3-locular capsules; seeds oblong, ellipsoid, or triangular, often operculate, the seed coat pitted or roughened.*

A. Fertile stamens 6; filaments hairy (rarely glabrous).
  B. Inflorescences subtended by conspicuous, paired, leaflike spathes; anther connectives trapezoidal or triangular. .... 1. *Tradescantia.*
  B. Inflorescences subtended by inconspicuous, paired or solitary, scarious or scalelike bract(s); anther connectives rectangular.
    C. Inflorescences dense, branches inconspicuous or absent; cymes solitary, without conspicuous axis. .... 2. *Callisia.*
    C. Inflorescences open, branches conspicuous; cymes paired, with evident axis bearing 2-ranked orbiculate bracteoles. .... 3. *Gibasis.*
A. Fertile stamens 3, staminodia 3; filaments glabrous.
  D. Spathes inconspicuous, scalelike; petals equal; stamens alternating with staminodia. .... 4. *Murdannia.*
  D. Spathes conspicuous, leaflike; petals unequal; stamens below staminodia. .... 5. *Commelina.*

SUPPLEMENTAL KEY EMPHASIZING VEGETATIVE FEATURES ESPECIALLY FOR USE WITH DRIED SPECIMENS[4]

A. Spathes paired, terminating stem. .... 1. *Tradescantia.*
A. Spathes single, terminal or axillary.
  B. Inflorescences unbranched, closely enclosed by spathe.
    C. Spathes composed of sheath only. .... 2. *Callisia.*
    C. Spathes with oblong to orbiculate blades, sheathless or nearly so. .... 5. *Commelina.*
  B. Inflorescences branched (or if unbranched, the individual flowers pedicellate, not closely enclosed by spathe).
    D. Leaves asymmetric basally. .... 3. *Gibasis.*
    D. Leaves symmetrical.
      E. Stems creeping. .... 2. *Callisia.*
      E. Stems ascendent or erect.
        F. Leaves linear; stamens 6, staminodia lacking. .... 2. *Callisia.*
        F. Leaves lanceolate; stamens 3, staminodia 3. .... 4. *Murdannia.*

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[4] Provided because floral characters distinguishing genera are not well preserved in dried specimens.

Tribe TRADESCANTIEAE Meisner ex C. B. Clarke in DC. Monogr. Phanerog. **3:** 120. 1881.

1. **Tradescantia** Linnaeus, Sp. Pl. **1:** 288. 1753; Gen. Pl. ed. 5. 139. 1754.

Perennial herbs. Roots fibrous, fleshy, sometimes tuberous. Stems branched or simple, erect to ascendent [creeping], sometimes much shorter than the leaf blades. Leaves several, both cauline and basal [basal only]; sheaths closed; blades broadly lanceolate to linear, sometimes slightly constricted just above sheath, apex acute to broadly rounded, membranaceous or succulent, narrowly to broadly canaliculate to flat, glabrous or pubescent [villous]. Inflorescences 1 to several, terminal [and/or axillary], cymose, forming tight umbels, subtended by 2 opposed, linear to broadly lanceolate, oblong, or suborbiculate spathes (sometimes the uppermost internode so short that the uppermost leaf appears to be a third spathe). Pedicels slender, erect or spreading, reflexed after anthesis, sometimes colored like petals. Flowers several, perfect, actinomorphic [slightly zygomorphic]. Sepals 3, equal [the uppermost larger], oblong, broadly rounded to acute. Petals 3, ovate [obovate], not clawed [clawed], distinct or sympetalous (fused along edges to each other) [or fused to edges of filaments]. Stamens 6, identical, all fertile; filaments densely hirsute, trichomes moniliform; anthers ellipsoid, the connective broad, trapezoidal to triangular, the anther sacs reniform, dehiscent longitudinally. Ovary ovoid to obovoid, glabrous or pubescent, 3-locular; ovules (1 or) 2 or 3 per locule, orthotropous. Fruit a capsule, more or less dehiscent [fleshy]. Seeds oblong to ovoid, laterally compressed, funicular scar linear, ½ to nearly equal the length of the seed. Base chromosome number 6. (Including *Cymbispatha* Pichon, *Setcreasea* K. Schum. & Sydow, *Rhoeo* Walpers, *Zebrina* Schnizl.; excluding *Cuthbertia* Small, *Tradescantella* Small.) TYPE SPECIES: *T. virginiana* L., the only species included by Linnaeus. (Named for John Tradescant, Jr., 1608–1662, British naturalist and gardener.)—SPIDERWORT.

A genus of about 60 species of the tropical and warm-temperate regions of the New World. Seventeen species occur in the Southeast, 13 of them native. This circumscription follows Hunt (1975a, 1980, 1986b), who recognized 12 sections, five of which are represented in our area. *Cuthbertia* is included in *Callisia* following Hunt.

The largest section, TRADESCANTIA, was divided by Hunt (1980) into four series. All the southeastern species of this section are in ser. TRADESCANTIA (ser. *Virginianae* Hunt, nom. superfl.), the members of which are perennials with short rhizomes, linear (leaflike) inflorescence spathes, and glandular-pubescent or glabrous pedicels and calyces.

All 17 species of ser. TRADESCANTIA are native to the United States, and 13 of these occur in the Southeast. The remainder are present in the Great Plains and the Southwest. The taxonomy of this series is rather well known, thanks to monographs by Anderson & Woodson and MacRoberts and the cytotaxonomic studies by Anderson & Sax and Anderson (1954). All are diploids or tetraploids with a similar karyotype (six or 12 large metacentric chromosomes), and all are self-incompatible (Anderson & Sax; Anderson & Woodson; Owens). An account of the southeastern species of ser. TRADESCANTIA follows, then discussion of the three remaining series of sect. TRADESCANTIA.

Tradescantia subaspera Ker-Gawl. (*T. pilosa* Lehm.) is the tallest (30–100 cm) species of the series. The stems are conspicuously flexuose, and the broad leaf blades are lanceolate (not linear as in the other species of the series) and constricted to a subpetiolate base. It ranges from West Virginia to northern Illinois south to northwestern Florida, southern Alabama (Lelong), and southern Louisiana. The eastern populations have been distinguished as var. *montana* (Shuttlew. ex Small & Vail) Anderson & Woodson on the basis of their narrower leaves and sessile cymes. MacRoberts questioned the significance of the varieties because populations from Louisiana were intermediate between var. *montana* and the typical variety.

Tradescantia gigantea Rose ($2n = 12$; stems 30–60 cm tall; spathes saccate, velutinous; petals broadly obovate) is endemic to sandy soils of central and eastern Texas and three parishes of western Louisiana (MacRoberts).

Tradescantia virginiana L., the type species ("perhaps the most characteristic feature . . . is its turgid or inflated, delicately foliaceous, eglandular pubescent calyx"—Anderson & Woodson, 1935, p. 65), has long been cultivated both in the United States and in temperate regions worldwide. Its original range in North America can only be surmised. It is now known from southwestern Connecticut, southern Michigan, and western Wisconsin south to north-central North Carolina, northwestern Georgia, central Tennessee, and southeastern Missouri. Reports from the Gulf Coastal Plain are apparently based on misidentifications of *T. hirsuticaulis* (MacRoberts). Many cultivated plants identified as *T. virginiana* (especially outside North America) are actually "*T.* ×*Andersoniana*," the hybrids of *T. virginiana* and *T. ohiensis.*

Tradescantia Ernestiana Anderson & Woodson (basal and juvenile leaves linear, narrower than mature leaves and spathes; leaf blade broader than sheath, lacking basal constriction; roots long, slender, not fleshy), an Ozarkian endemic, occurs in southwestern Missouri, western Arkansas, and eastern Oklahoma. It is intermediate between *T. virginiana* and the Texas endemic *T. edwardsiana* Anderson & Woodson.

Tradescantia ohiensis Raf. (*T. canaliculata* Raf., *T. reflexa* Raf.) (roots slender, plants glaucous, upper leaves as long as the lower, the blades narrower than sheath, sepals glabrous) is a wide-ranging species found from Massachusetts, Michigan, Minnesota, and Nebraska south to southern Florida and southern Texas.

Tradescantia paludosa Anderson & Woodson (roots slender, fleshy; upper leaves shorter than lower; base of leaf blade not constricted; foliage not glaucous) is closely related to *T. ohiensis.* Its range is much more restricted (southern Alabama, southeastern Arkansas, eastern Louisiana, and perhaps also Mississippi). MacRoberts treated this as *T. ohiensis* var. *paludosa* (Anderson & Woodson) MacRoberts.

Tradescantia hirsutiflora Bush (stems spreading-pubescent; leaves broad, stiff; roots glabrous, not thickened; sepals glandular-pubescent or not), the most poorly understood species of ser. TRADESCANTIA (Anderson & Woodson), is closely related to *T. virginiana.* It occurs from Georgia and western Florida to eastern Oklahoma and central Texas.

Tradescantia longipes Anderson & Woodson ($2n = 24$; stems 2–10 cm tall, leaves and spathes pilose, hairs eglandular), was described from southern Missouri and has recently been reported from northern Arkansas (Montgomery County; see Timme & Faden). It is limited to acidic soils in pine-oak forests. A close relative, *T. Tharpii* Anderson & Woodson, occurs only on calcareous soils derived from limestone or chert, in southwestern Missouri.

Tradescantia Reverchonii Bush, a close relative of *T. hirsutiflora,* can be distinguished by its densely tomentose roots. Such hairy roots are unique in the genus. The species is rare (southern Arkansas, Louisiana (Natchitoches and Caddo parishes), and westward to central Texas).

Tradescantia ozarkana Anderson & Woodson (leaf blades abruptly constricted just above the sheath, veinlets obvious in dried specimens, capsules 6–8 mm long) is perhaps not distinct from *T. edwardsiana* of central Texas. It is a rare species of western Arkansas, southwestern Missouri, and eastern Oklahoma.

Tradescantia occidentalis (Britton) Smyth (*T. virginiana* var. *occidentalis* Britton) is a species mainly of the Great Plains (Minnesota, Arkansas, and Louisiana west to southeastern Montana, southern Utah, and southern Arizona). The plants are glabrous, with the spathes leaflike, the sepals having some glandular hairs, and the hilum about half as long as the seed. *Tradescantia occidentalis* var. *melanthera* MacRoberts is distinguished only by its brown anther connectives (other North American species have yellow ones). Its more restricted range includes southern Arkansas, eastern Oklahoma, western Louisiana, and eastern Texas (MacRoberts).

Tradescantia roseolens Small is close to *T. occidentalis,* from which it differs in its longer hilum (nearly as long as the seed) and its allopatric distribution (western South Carolina and northern Georgia to southern Florida). The species grows in sandy soil in open woods. Its fresh flowers smell like tea roses (Anderson & Woodson).

Tradescantia hirsuticaulis Small (sepals petaloid, pinkish to purplish) has a peculiar distribution: Georgia, Alabama, Arkansas, and eastern Oklahoma. MacRoberts considered it a dubious species.

The three remaining series of sect. TRADESCANTIA comprise species of Mexico and the southwestern United States. Series SILLAMONTANAE Hunt (plants perennial, shortly rhizomatous, nontuberiferous, lanate) is restricted to northeastern Mexico and consists of two species, *T. sillamontana* Matuda (*T. pexata* H. E. Moore), $2n = 24$, and *T. Rozynskii* Matuda, $2n = 12, 24$, both of which are self-incompatible (Owens).

Series TUBEROSAE Hunt comprises about ten species of tuberous perennials of southern Arizona, southern New Mexico, and Mexico. All are self-incompatible. There are diploid, tetraploid, and hexaploid species (base number 6).

Members of series ORCHIDOPHYLLAE Hunt are subacaulescent tuberiferous perennials with glandular pedicels and calyces. There are two species, *Tradescantia orchidophylla* Hemsley and *T. Mirandae* Matuda, both $2n = 24$ and both of western Mexico. *Tradescantia Mirandae* is known to be self-incompatible.

The five remaining sections of *Tradescantia* are widely distributed in the warm regions of the New World, although none is represented by indigenous species in the Southeast.

The single species of sect. SEPAROTHECA (Waterfall) Hunt, *Tradescantia pygmaea* Hunt ($2n = 12$), is a tuberiferous perennial of the mountains of northwestern Mexico (Waterfall; Hunt, 1975a). Its anthers have broad connectives, and the edges of the filaments are adnate to the edges of the petals, forming a tube at least 1 mm long. The plants are self-incompatible.

Section MANDONIA Hunt (*Mandonia* Hasskarl, non Wedd.) comprises about ten species of tuberiferous perennials of Mexico, Guatemala, Bolivia, Brazil, and northern Argentina. There are both self-compatible and self-incompatible species. *Tradescantia crassifolia* Cav. ($2n = 12, 24$; self-incompatible) is an important weed in Mexico (Holm *et al.*).

In sect. PARASETCREASEA Hunt the petals and filaments of the three antesepalous stamens are fused along their edges to form a short tube (Hunt, 1980). There is but one species, *T. Andrieuxii*, $2n = 12, 24$, which is native to Mexico from Oaxaca to Chihuahua. Both self-compatible and self-incompatible plants have been reported (Owens).

Plants of sect. SETCREASEA (K. Schum. & Sydow) Hunt (*Setcreasea* K. Schum. & Sydow) are rhizomatous. The petals are fused basally to different heights in the five species, which occur in the southwestern United States and Mexico: *Tradescantia brevifolia* (Torrey) Rose, $2n = 24$, *T. Buckleyi* (Rose) I. M. Johnston, $2n = 24$, *T. hirta* Hunt, $2n = 24$, *T. leiandra* Torrey, $2n = 12$, and *T. pallida* (Rose) Hunt (*Setcreasea pallida* Rose), $2n = 12, 18, 24$. All are self-incompatible. *Tradescantia pallida* has recently been reported as an adventive in Pinellas County, Florida (Wunderlin *et al.*).

Section CYMBISPATHA (Pichon) Hunt (*Cymbispatha* Pichon) differs from sect. TRADESCANTIA in its base chromosome number ($x = 7$ vs. 6) and in having various acrocentric karyotypes derived by Robertsonian fusions. The uppermost sepal is larger than the others. This section is intermediate between sects. ZEBRINA (discussed below) and TRADESCANTIA (Hunt, 1980). It includes about seven species that occur from the mountains of western Mexico south to Brazil and Bolivia. There are both self-compatible and self-incompatible species, and *T. commelinoides* Schultes f., $2n = 14, 22, 23, 30$, includes both self-compatible and self-incompatible plants.

Section ZEBRINA (Schnizl.) Hunt (*Zebrina* Schnizl.) comprises two species of southern Mexico and northern Central America, *Tradescantia Schippii* Hunt and *T. Zebrina* Bosse (*Z. pendula* Schnizl.), $2n = 22, 23, 24, 41, 47$. The corolla is sympetalous to various degrees, and the hilum is punctiform. The karyotype is variable, a mixture of meta-, subtelo-, and telocentric chromosomes. The plants are self-compatible. *Zebrina* has sometimes been accorded generic status, but sympetaly varies in degree within the two species and has arisen elsewhere in the genus (e.g., sect. SETCREASEA). *Tradescantia Zebrina* is reported as a rare escape from cultivation in central Florida (Wunderlin).

Section RHOEO (Hance) Hunt (*Rhoeo* Hance) includes only *Tradescantia discolor* L'Hér. (*T. spathacea* Sw., *Rhoeo spathacea* (Sw.) Hance), boat-lily, Moses-in-the-bulrushes, three-men-in-a-boat, $2n = 12$, which is native to the Yucatan peninsula and Belize and naturalized in southern Florida. The plants are succulent and bromeliadlike in habit. The spathes are broadly ovate, not linear as in sect. TRADESCANTIA, and there is only one ovule per locule. The karyotype, similar to that of the species of sect. TRADESCANTIA (Hunt, 1986b), consists of small, meta- to submetacentric chromosomes. Many translocations have occurred because the chromatids form rings or chains meiotic at metaphase (Lin & Paddock). Some plants are self-compatible, while others are not. The boat lily is widely cultivated in tropical regions and in greenhouses.

Three of the remaining four sections are monotypic. Section CAMPELIA (L. C. Rich.) Hunt (*Campelia* L. C. Rich.) has one species, *Tradescantia Zanonia* (L.) Sw., $2n = 16$. Its fleshy capsules and sepals are an adaptation to dispersal by birds. The axillary inflorescences perforate the subtending sheaths (Faden, 1985). The karyotype comprises 2 meta-, 2 submeta-, and 12 acrocentric chromosomes. The plants are self-incompatible.

In the one species of sect. COHOLOMIA Hunt, *Tradescantia guatemalensis* C. B. Clarke ex J. D. Smith, coholom, $2n = 42$, the spathes subtending the inflorescence are connate basally, forming a short tube that encloses the buds. The species is endemic to southern Mexico and northern Central America. The plants are self-incompatible.

Section CORINNA Hunt also includes a single species, *Tradescantia soconuscana* Matuda (*Campelia Standleyi* Steyerm.), $2n = 26$, of southern Mexico and Guatemala. Its karyotype consists of small chromosomes, of which six are metacentric, 16 acrocentric, and four telocentric.

Plants of sect. AUSTROTRADESCANTIA Hunt are procumbent and leafy stemmed; the spathes are conspicuously broader than the stem leaves. The chromosomes are very small for the genus, the diploid number ranging from 40 to 110. The four to six species are found in southeastern Brazil, Uruguay, Paraguay, and northern Argentina. *Tradescantia fluminensis* Vell., $2n = 40$, 67 (Owens), a native of southeastern Brazil, is adventive in southwestern Georgia, central and western Florida, southern Alabama, Louisiana, and California. In New Zealand, where it is also naturalized, it forms dense, matlike stands in lowland forests. These populations exclude most tree seedlings and inhibit the reproduction of the native woody plants. Apparently all reproduction of *T. fluminensis* in New Zealand is vegetative. A node with as little as 1 cm of stem attached is able to sprout and form a new plant. Thus, trampling stands of *T. fluminensis* fragments the plants and enhances their reproduction (Kelly & Skipworth).

Tradescantia virginiana, T. ohiensis, and *T. paludosa,* or hybrids between them, are regularly used to monitor radiation and other environmental contaminants. Clones heterozygous for flower color are exposed to the prospective hazard. Radiation or chemical mutagens cause somatic mutations, resulting in production of pink (recessive) rather than blue (dominant) flowers. When a cell of a stamen hair is affected, the change can be readily spotted under low-power magnification. When exposed to X rays, gamma rays, or neutron radiation, the number of pink cells per flower increases linearly with the intensity of radiation. Chemical mutagens have a similar effect. Ichikawa (1984) surveyed 16 clones of *Tradescantia* (pure species, hybrids, diploids, triploids, and tetraploids). The sensitivity to radiation damage was 50–60 times greater in the most than in the least sensitive clone. The differences in sensitivity of the taxa showed no apparent taxonomic correlation but were believed to result from differences in the genetic repair system.

The *Tradescantia* micronucleus-test (Ma, 1981) makes use of the highly synchronous prophase and tetrad stages in microsporogenesis in clones of *T. paludosa.* Radiation or chemical mutagens can break chromatids, and acentric fragments are formed. At the tetrad stage these fragments form micronuclei that are easily spotted and tallied from aceto-carmine squashes. The frequency of micronuclei is indicative of the level of radiation or the mutagenicity of the chemical in question. This highly sensitive test is often used to monitor the purity of drinking-water supplies (Ma *et al.*).

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2. **Callisia** Loefling, Iter Hisp. 305. 1758.

Perennial [annual] herbs. Rhizomes present or lacking. Stems erect or decumbent and rooting at the nodes. Leaves several to many, cauline, spiraled or distichous; sheaths shorter than blades, the apex ciliate; blades oblong-lanceolate to linear. Inflorescences axillary or terminal, cymose; spathe solitary, with or without leaflike blade; bracteoles smaller than leaves, generally scarious. Pedicels elongate or very short, glandular-pubescent and/or villous. Sepals 3, equal, broadly elliptic to lanceolate, the apex rounded or acute, free or connate for the basal ⅓, the outer surface with many short glandular hairs. Petals (2 or) 3, orbiculate to narrowly oblong, free, subequal, glabrous. Stamens [1, 3, or] 6, all fertile; filaments slender, glabrous or hairy; anthers broadly ovate, the connective rectangular, about as wide as the anther locule. Ovaries oblong-ellipsoid, 3-locular, each locule with 2 ovules; style shorter than to 2–3 times longer than ovary; stigma club shaped, rough (sometimes shortly plumose). Fruit a capsule, [2- or] 3-locular, each locule containing [1 or] 2 seed(s). Seeds ovoid, dorsiventrally flattened, the surface rugose. Base chromosome numbers 6, 7, 8. (Including *Aploleia* Raf., *Cuthbertia* Small, *Leptorhoeo* Hemsley, *Phyodina* Raf., *Tradescantella* Small.) TYPES SPECIES: *C. repens* L. (Name from Greek *kallos,* pretty.)—BASKET-PLANT.

A genus of about 20 species of the tropical and subtropical regions of the New World. The circumscription of the genus adopted here follows that of Hunt. Four of the six sections are represented in the United States, with three of these in our area. Like its close relatives *Tradescantia* and *Tripogandra, Callisia* has fused pairs of cymes. It differs from *Tradescantia* in having single (vs. paired) inflorescence spathes and glabrous (vs. hairy) filaments; from *Tripogandra,* in lacking dimorphic pollen (Mattson) and in having actinomorphic (vs. zygomorphic) flowers. Ecologically, species of *Callisia* generally grow in drier situations than those of either *Tradescantia* or *Tripogandra.*

Section CUTHBERTIA (Small) Hunt (*Cuthbertia* Small) consists of three species, all endemic to the Coastal Plain and Piedmont from Virginia to Florida. They are erect plants with linear leaves and both lateral and terminal inflorescences subtended by inconspicuous spathes. The base chromosome number is 6, and the karyotype comprises 2 metacentric and 4 subtelocentric chromosomes. Although these species have been included in *Tradescantia* by some workers, they differ from that genus in morphology, anatomy (Tomlinson, 1969), cytology (Giles, 1942, 1943), and chemistry (Matthews). The removal of *Cuthbertia* from *Tradescantia* has gained general acceptance. Rohweder included the species in *Phyodina,* which in his classification comprised sects. CUTHBERTIA and LEPTOCALLISIA. The three species have all been treated as varieties of *Cuthbertia rosea* (= *Callisia rosea*) by some workers (e.g., Fernald).[5]

Callisia rosea (Vent.) Hunt (*Tradescantia rosea* Vent.; *Cuthbertia rosea* (Vent.) Small) (stems approximate, leaf blades as broad as or broader than sheaths), the most wide ranging of the three species, occurs from central North Carolina to southeastern Georgia and northeastern Florida.

Callisia graminea (Small) G. Tucker (stems densely caespitose, roots glabrous, inflorescence equaling or surpassed by leaf blades, spathes somewhat foliaceous) occurs on the Coastal Plain from southeastern Virginia to southern Florida. (It has also been reported from southeastern Oklahoma (Cleveland and Oklahoma counties) by Stemen & Myers, but I have seen no specimens to confirm this.) There are diploid, tetraploid, and hexaploid populations (Giles, 1942, 1943). The diploids are endemic to the sandhills region along the western edge of the Coastal Plain in southern North Carolina, while the tetraploids occupy habitats on the Coastal Plain from southeastern Virginia to southern Florida. Hexaploids are rare and have only been found from sites in South Carolina and Florida. The tetraploids averaged 25 percent larger in vegetative and floral parts than diploids. Lakela described a white-flowered form from central Florida, *C. graminea* f. *leucantha* (Lakela) G. Tucker. It produces vegetative plantlets from the axils of the upper leaves, but there are no other reports of vivipary in the genus.

Callisia ornata (Small) G. Tucker (stems approximate, roots woolly, inflorescence surpassing leaf blades, spathes scarious) is endemic to palm or pine scrub in central Florida.

Section LEPTOCALLISIA Bentham & Hooker (*Aploleia* Raf., *Leiandra* Raf., *Phyodina* Raf. in part, *Leptorhoeo* Hemsley, *Tradescantella* Small) includes six species of Florida, Texas, Mexico, and Central America. The base chromosome number is 7, and the stigmas are subcapitellate to penicilliform. One species, *Callisia cordifolia* (Sw.) Anderson & Woodson (*Tradescantia floridana* S. Watson, *Tradescantella floridana* (S. Watson) Small), grows in central and southern Florida. It is a procumbent plant that forms small mats on shaded rock or moss. The inflorescence is terminal, and the flowers pedicellate. The Neotropical *C. multiflora* (Martens & Gal.) Standley (*Aploleia multiflora* (Martens &

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[5] Three new combinations are needed for the inclusion of *Cuthbertia* in *Callisia*:

Callisia graminea (Small) G. Tucker, based on *Cuthbertia graminea* Small, Fl. Southeast. U. S. 237, 1328. 1903.

Callisia graminea f. **leucantha** (Lakela) G. Tucker, based on *Cuthbertia graminea* f. *leucantha* Lakela, Sida 5: 28. 1972.

Callisia ornata (Small) G. Tucker, based on *Cuthbertia ornata* Small, Man. Southeast. Fl. 259. 1933.

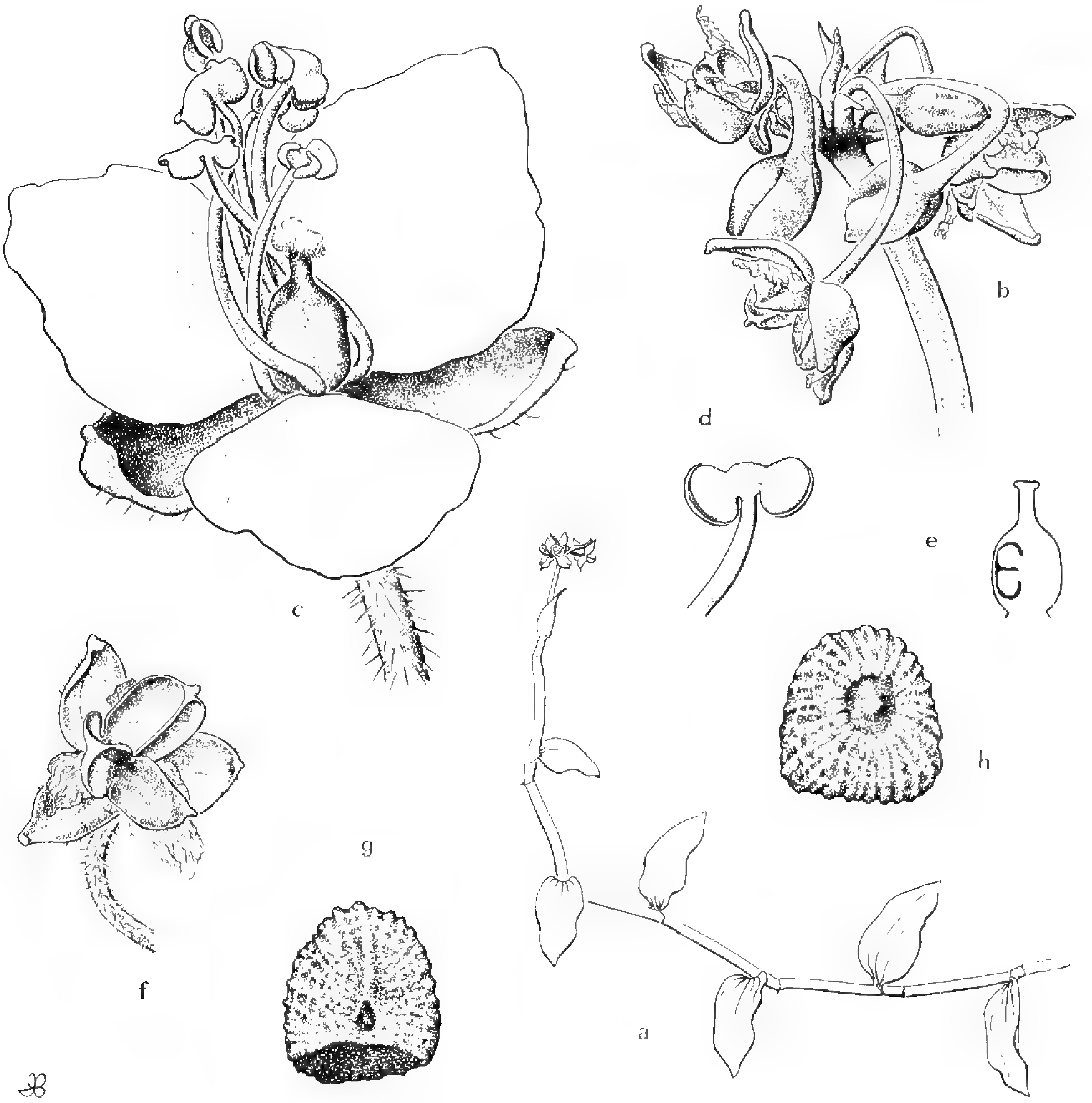

FIGURE 1. *Callisia* sect. LEPTOCALLISIA. a–h, *C. cordifolia*: a, stem with inflorescence, × 1; b, inflorescence with buds and 3 opened capsules, × 6; c, flower, × 15; d, stamen, × 25; e, diagrammatic longitudinal section of gynoecium showing 2 orthotropous ovules in 1 locule, × 12; f, open loculicidal capsule with marcescent petals and persistent sepals, × 8; g, seed, hilum below center, × 25; h, seed from opposite side, operculum at center, × 50.

Gal.) H. E. Moore), $2n = 28$, is self-incompatible, while *Callisia cordifolia* is unknown in this regard. The flowers of *C. multiflora* are unscented.

Section BRACHYPHYLLA Hunt (*Phyodina* Raf., in part) includes two species of Texas and northern Mexico. The plants are procumbent perennials with short, succulent leaves, subsessile terminal inflorescences, six stamens per flower, barbed filaments, and capitate stigmas. *Callisia navicularis* (Ortg.) Hunt (*P. navicularis* (Ortg.) Rohw.), $2n = 32$, and *C. micrantha* (Torrey) Hunt (*Tradescantia micrantha* Torrey, *P. micrantha* (Torrey) Hunt), $2n = 24$, are both self-incompatible (Owens).

Section HADRODEMAS (Moore) Hunt contains only *Callisia Warszawicziana* (Kunth & Bouché) Hunt, $2n = 16$, of Guatemala, a self-incompatible species.

The plants are thick-stemmed perennials with broadly lanceolate leaves, and their purple sepals are persistent (see Moore, 1962, for illustration).

Section LAUIA Hunt contains just *Callisia Laui* (Hunt) Hunt (*Phyodina Laui* Hunt), $2n = 12$, which is known only from southeastern Oaxaca, Mexico. The plants are tuberous, the inflorescences terminal and pedunculate, and the flowers pedicellate. The species is self-incompatible.

Section CALLISIA (*Hapalanthus* Jacq., nom. superfl., *Spironema* Lindley non Raf., *Rectanthera* Degener) comprises some ten Neotropical species with the base chromosome number six. The small, often bladeless petals and the bushy, exserted stigmas may be an adaptation to wind pollination, but this has not been demonstrated. One species, *Callisia repens* L. (including *C. insignis* C. B. Clarke), basket-plant, $2n = 24$, occurs in the Florida panhandle (Franklin County) and in peninsular Florida from Pinellas and Broward counties, and southward through the West Indies and Mexico to Brazil and Peru. It is similar in habit to *C. cordifolia* but has both axillary and terminal inflorescences of subsessile flowers partly enclosed in a bladeless sheath. The flowers of *C. repens* are unscented. *Callisia repens* is self-compatible, while the three other species of this section for which information is available—*C. Gentlei* Matuda (*C. elegans* E. J. Alexander ex H. E. Moore; *C. Macdougallii* Miranda) of northern Central America, *C. fragrans* (Lindley) Woodson of southeastern Mexico, and *C. soconuscensis* Matuda of Guerrero, Mexico, all $2n = 12$ (Owens)—are all self-incompatible.

Several species of *Callisia* are cultivated as creeping ground covers in frost-free areas. *Callisia fragrans* and similar procumbent species are sometimes grown indoors as hanging-basket plants.

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3. **Gibasis** Rafinesque, Fl. Telluriensis **2:** 16. 1837.

Sprawling, weak-stemmed [erect] perennials [annuals]. Roots fibrous [tuberiferous]. Stems much branched, rooting at the nodes. Leaves several; sheaths ciliate apically; blades oblong-lanceolate to broadly or narrowly ovate. Inflorescences several, terminal or axillary and terminal, cymose, 2[–8] per stipe; cincinnal axis short, thick; cincinnal bracts distichous, broadly rounded, suborbiculate; pedicels short. Flowers perfect, actinomorphic. Sepals 3, oblong-ovate, more or less keeled. Petals 3, oblong [orbiculate]. Stamens 3; filaments bearded, the hairs moniliform; anthers orbiculate, dehiscing laterally; connective rectangular, broader than long. Ovary 3-locular, ovules 2 per locule; style glabrous; stigma subtly 3-lobed, capitellate. Fruit a capsule. Seeds ovoid [oblong-ovoid], the hilum elongate-punctiform [linear]. Base chromosome number 6. TYPE SPECIES: *Tradescantia pulchella* HBK. (= *G. pulchella* (HBK.) Raf.), the only species included by Rafinesque. (Name from Latin *gibba,* gibbous, and *basis,* base, referring to the "gibbous base," presumably of the asymmetric leaves.)—BRIDAL-VEIL.

A genus of 11 species of Mexico and, to a lesser extent, the Caribbean region and tropical South America. *Gibasis* is characterized by features of the inflorescence, which is made up of paired cymes borne on stipes. The paired cymes are not fused, as in the closely related *Tradescantia.* The cyme axis in *Gibasis* bears two rows of broad scalelike bracteoles, each subtending a single flower.

In his revision of the genus, Hunt (1986a) recognized two sections. Section GIBASIS has tuberiferous roots, oblong-lanceolate to broadly ovate leaves, and pink flowers. The plants are self-incompatible. The chromosomes are large, and the base numbers are 4, 5, or 6. Sulfated phenolic acids are absent (Del Pero de Martínez). There are eight species, mostly restricted to the uplands of Mexico: *G. chihuahuensis* (Standley) Rohw.; *G. consobrina* Hunt, $2n = 20$; *G. Karwinskyana* (Schultes f.) Rohw., $2n = 10, 20, 30$; *G. linearis* (Bentham) Rohw., $2n = 10, 12, 20, 22$; *G. Matudae* Hunt, $2n = 10$; *G. pulchella,* $2n = 10, 15$; *G. triflora* (Martens & Gal.) Hunt, $2n = 10$; and *G. venustula* (Kunth) Hunt, $2n = 12$. Cyme axes in *G. pulchella* are reflexed 180° and fused to the upper stipe, so the first flowers to open seem to be those most distal in the inflorescence.

Plants of sect. HETEROBASIS Hunt have nontuberiferous roots, linear to ovate-lanceolate leaves, and white, self-compatible flowers. The chromosomes are small, and the base number is 8 (Owens, 1977). Sulfated phenolic acids are present. There are three species. *Gibasis oaxacana* Hunt, $2n = 12$, is endemic to Oaxaca, Mexico. *Gibasis pellucida,* $2n = 10, 16$, with leaves and stems glabrescent, and filaments hairy throughout, is widespread in the lowlands of southern Mexico (dubiously reported from Cuba and the Dominican Republic); it has been collected as a weed in southern Florida (Dade County, *Hansen & Sauleda 10732,* USF, and Sarasota County, *Waldo s.n.,* 4 May 1971, NYS). *Gibasis geniculata,* $2n = 48, 52$, with leaves and stems villous and filaments hairy basally, is the only wide-ranging species, occurring from Haiti and southern Mexico south to northern Argentina. It has been reported from central Florida as an escape (Wunderlin), but I have seen no specimens. Hunt (1986a) did not mention the genus as being represented in the United States.

Leaf anatomy of *Gibasis geniculata, G. Matudae,* and *G. Schiedeana* (Kunth) Hunt (= *G. pellucida*) has been investigated by Stant. She found three kinds of hairs: short, 2-celled, hook or prickle hairs; glandular, 3-celled ones; and long, 4- to 6-celled trichomes. All three types were present in various amounts in the three species, but differences were apparently not taxonomically useful.

Gibasis pellucida, Tahitian bridal veil, is widely cultivated in the United States and Mexico. It has often been confused with *G. geniculata* (Hunt, 1986a).

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Tribe COMMELINEAE

4. **Murdannia** Royle, Illus. Bot. Himalayan Mtns. 403. 1840, nom. cons.

Perennial or annual herbs. Roots fibrous [sometimes uniformly thickened throughout]. Stems smooth. Leaves several, cauline [basal only, or both basal and cauline]; sheaths closed; petioles lacking; blades [broadly] narrowly lanceolate, the base rounded [cordate], the margins and apex with papillae or prickles. Inflorescences axillary and terminal [terminal only], thyrsiform, open. Pedicels erect to ascending. Flowers 1 to many, perfect, actinomorphic. Sepals 3, equal. Petals 3, equal, oblong, not clawed. Stamens 2 or 3, antesepalous; filaments glabrous or bearded; staminodia [lacking, 1, 2, or] 3, antepetalous; sterile anthers 3-lobed. Ovary trilocular, glabrous or glandular-pubescent; ovules uni- or biseriate, 2 (or 3) per locule; stigma capitate. Fruit a capsule. Seeds broadly oblong, hilum punctate to linear. Base chromosome number 10. TYPE SPECIES: *Commelina scapiflora* Roxb. (*M. scapiflora* (Roxb.) Royle = *M. edulis* (Stokes) Faden). (Named for Murdan Aly, plant collector and keeper of the herbarium at Saharanpur, India, in the mid-nineteenth century.)

A genus of 40–45 species of tropical and warm-temperate regions of the Old and New worlds. The genus is most diverse in southern Asia, where some 30 species occur (Faden, 1975). There are seven species in the New World, four of them South American endemics.

Murdannia has long been confused with *Aneilema* R. Br., but Faden (1975) pointed out that the confusion seems to have been from the publication of numerous species of *Murdannia* under *Aneilema* rather than from close relationship. The two genera are distinguished on the basis of androecial structure, but since floral features are poorly preserved in pressed specimens, this character has often been overlooked. In *Murdannia* the stamens alternate with the staminodia, while in *Aneilema* they are clustered below the staminodia (see Faden, 1975, for illustration). The closest relative of *Murdannia* is the monotypic African genus *Anthericopsis* Engler.

The alternating arrangement of stamens and staminodia that characterizes *Murdannia* is also found in *Palisota* Reichenb. (in this genus the stamens are antepetalous and the staminodia antesepalous, the reverse of the situation in *Murdannia*), *Pseudoparis* (antepetalous staminodia, but petiolate leaves), and *Anthericopsis* (3-locular dehiscent capsules as in *Murdannia,* but sessile subopposite inflorescences, larger chromosomes, and base chromosome number 7).

Murdannia nudiflora (L.) Brückner is widespread in Latin America and extends northward to Florida and southeastern Georgia; it is also known from Louisiana (reported from coastal North and South Carolina by Radford and colleagues; no specimens seen). The plants are caespitose and do not root at the nodes. The longest pedicels about equal the capsule, which is usually 1.25 times longer than wide. When the fruit is mature, the sepals are hyaline. The seeds are 1.2–1.5 mm long. *Murdannia spirata* (L.) Brenan, an Asian species, is adventive in southern Florida (specimens seen from Charlotte, Glades, Lee, Hendry, and Collier counties). Although this species and *M. nudiflora* are similar, *M. spirata* has persistent bracteoles on the inflorescence branches and the longest pedicels two to three times longer than the capsules. It was first reported in the New World from Collier County, Florida, in 1968 (Lakela).

Murdannia Keisak (Hassk.) Hand.-Mazz. (*Aneilema Keisak* Hassk.), $2n = 32, 40$, is naturalized in the area from eastern Maryland to Florida westward to Louisiana, and it has recently been reported from central and eastern Tennessee and southeastern Kentucky. The plants are single stemmed and often root at the lower nodes, the pedicels are several times longer than the capsules, the sepals are green and develop sessile reddish glands in fruit, and the seeds are about 3 mm long. The karyotype of *Murdannia Keisak* comprises five metacentric, 12 submetacentric, and three subtelocentric pairs of chromosomes (Fujishima). Fernald thought this species to be native to eastern North America, but Shinners pointed out that its rapid spread since the 1930's indicated the weedy behavior of an adventive.

In western Australia *Murdannia nudiflora* produces cleistogamous flowers during rainy weather and chasmogamous ones when it is sunny (Keighery). Chasmogamous flowers are self pollinated, with the anthers dehiscing directly onto the receptive stigmas. No pollinators were observed visiting the open flowers. *Murdannia nudiflora* is self-compatible (Owens), as is *M. simplex* (Vahl) Brenan.

Murdannia Keisak is a significant weed in Japan. Although it has spread rapidly in the Southeast in the last 50 years, it does not appear to have become a weed here.

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5. **Commelina** Linnaeus, Sp. Pl. **1:** 40. 1753; Gen. Pl. ed. 5. 25. 1754.

Annual or perennial herbs. Rhizomes lacking; roots fibrous. Stems simple or slightly branched [acaulescent], glabrous. Leaves several, cauline; sheaths closed; blades broadly to narrowly lanceolate, flat or nearly so. Inflorescences axillary [scapose], each subtended by an orbiculate to oblong, acuminate to acute, strongly conduplicate spathe, its margins free or fused basally. Flowers several, perfect, zygomorphic. Sepals 3, ovate, equal. Petals 3, unequal, clawed, the upper 2 broadly ovate to suborbiculate, the lower 1 oblong. Stamens 3, dimorphic; staminodia 3. Ovary 2- or 3-locular; ovules 1 or 2 per locule. Fruit a capsule. Seeds rectangular to oblong. Base chromosome numbers 11, 14, 15. LECTOTYPE SPECIES: *C. communis* L. (Britton & Brown, Illus. Fl. No. U. S. & Canada. ed. 2. **1:** 457. 1913). (Named for Caspar Commelijn [also spelled Commelin], 1667/1668–1731, and Jan Commelijn, 1629–1692, Dutch botanists.[6] — DAYFLOWER.

Commelina, with some 250 species, is the largest genus in the family. The center of diversity for the genus is southern Asia, but there are also numerous representatives in tropical Africa and a lesser number in the Neotropics. There are five native species in the United States (four in the Southeast) and four introduced ones, all of which occur in the Southeast.

Commelina virginica L. ($2n$ = 30, 60; perennial; leaves broadly lanceolate; inflorescences terminal, 1 to several together; spathes oblong, the margins fused for the basal ⅓–½), occurs from Maryland, southern West Virginia, Kentucky, Illinois, and Missouri south to southern Florida and southern Texas; it is also found in the Neotropics. The apex of the leaf sheath bears reddish, uniseriate, multicellular trichomes 2–5 mm long, a feature that distinguishes this species from other native species of the genus in North America.

Commelina erecta L. ($2n$ = 60; perennial; inflorescences single, terminal and axillary; spathes orbiculate, the basal ⅓ of the margins fused), occurs from New Jersey to northern Illinois, southern Wisconsin, and Nebraska south to Florida, Texas, and Arizona. *Commelina erecta* is cytologically diverse in West Africa (Morton, 1967).

Commelina dianthifolia Delile (leaves linear; spathes long-attenuate, the margins free) occurs from western Texas, eastern Colorado, and Arizona south to El Salvador. Its long-attenuate spathes distinguish it from other New World species. The southern Asian *C. appendiculata* C. B. Clarke, which also has long-attenuate spathes, appears to be closely related.

Commelina gigas Small (perennial; weak stemmed, clambering; spathes oblong, the margins free) is endemic to the Lake Okeechobee area in Florida (Wunderlin). The plants have a few white trichomes 1–2 mm long at the apex of the leaf sheaths.

Commelina communis L. ($2n$ = 48, 90; annual; leaves 15–40 mm wide; spathes oblong (orbiculate when spread out and pressed flat), acute, the margins free) occurs spontaneously in an area from southwestern Maine, southern New Hampshire, southwestern Quebec (vicinity of Montreal), southwestern Ontario, central Michigan, southern Minnesota, and Nebraska south to Georgia, northern Mississippi, and northeastern Texas. Pennell believed it to be native

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[6] "*Commelina* has flowers with three petals, two of which are showy, while the third is not conspicuous: from the two botanists called Commelin: for the third died before accomplishing anything in botany." Linnaeus, Crit. Bot. (transl. A. Hort), 62, 63. 1737. The third Commelin was Caspar, Jr., 1700–1734, son of Caspar Commelin. "Actually *Commelina* was coined by Plumier, who was probably not aware of the existence of Caspar, Jr." (Wijnands, pp. 10, 11).

to eastern North America, while Brashier thought it was introduced from Asia. It is occasionally cultivated in the eastern United States (Bailey *et al.*). There are two varieties: var. *communis* (petals light blue, anthers entirely yellow) occupies the entire range of the species in North America; var. *ludens* (Miq.) C. B. Clarke (*C. communis* subsp. *ludens* (Miq.) Penn.; petals intense violet, anther connective with purplish brown eye spot) occurs from New England to Kentucky southward to Virginia. Both varieties are also present in eastern Asia. The smut *Ustilago commelinae* (Komarov) Zundel (*Tilletia commelinae* Komarov) infects var. *ludens,* but not var. *communis,* even when the two varieties are found growing together.[7] *Ustilago commelinae* is also known to parasitize *C. communis* (variety unknown) in China, Japan, and the eastern Soviet Union. The restriction of the smut to one of the two varieties of *C. communis* in eastern North America suggests a biochemical difference between the varieties, emphasizing their taxonomic significance.

Commelina diffusa Burman f. (*C. caroliniana* Walter) ($2n = 28, 30, 56, 60, 72$; annual; leaves 9–15 mm wide; spathes oblong when flattened, acuminate, the margins free) is a pantropic and warm-temperate species found in North America from Maryland, southern Ohio, northern Illinois, and eastern Kansas south to southern Florida and southern Texas. It has prostrate stems and erect flowering shoots. Japanese populations are $2n = 72$ (Fujishima, 1984). The west African *C. diffusa* var. *aquatica* (Morton) Morton, $2n = 28$, grows in shallow water in seasonally inundated grasslands.

Commelina nigritiana Bentham var. *gambiae* (C. B. Clarke) Brenan is native to West Africa and a recent adventive in central Florida (Manatee Co., *Wunderlin 5721,* USF; Polk Co., *Wunderlin & Beckner 9096,* USF). Its flowers are peach colored; the spathe is fused for the basal half along the margin and bears long white trichomes on the abaxial surface.

Commelina benghalensis L., $2n = 22, 28, 44, 56$, is an important weed in the croplands of tropical Africa and Asia. A recent adventive in the Southeast, it was first noted in southeastern Georgia in 1966 (Duncan) and has since been reported from central and western Florida. It has broadly ellipsoid, distinctly petiolate leaves with reddish trichomes at the apex of the sheath. The spathe margins are fused for the basal third of their length. The plants bear both chasmogamous and cleistogamous flowers. Seeds from the former weigh about one seventh as much as those from the latter (see Wilson for illustrations of both kinds of seeds).

Dormant seeds that are able to germinate far below ground, easy vegetative reproduction from fragments, and resistance to weeding are features accounting for the spread and abundance this species. Mechanical cultivation breaks up the plants. Fragments of stems can root in wet weather, reestablishing the population; they are able to sprout even if buried beneath 2 cm of soil. Seeds are dormant when freshly shed. After disruption of the seed coat by scarification or pricking, 40–70 percent of treated seeds germinate in 20 days (Budd *et al.*). The larger seeds from cleistogamous flowers are able to germinate if covered

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[7] Data on smut parasites kindly provided by Clark T. Rogerson (New York Botanical Garden), based on unpublished observations by him and the late Stanley J. Smith (New York State Museum).

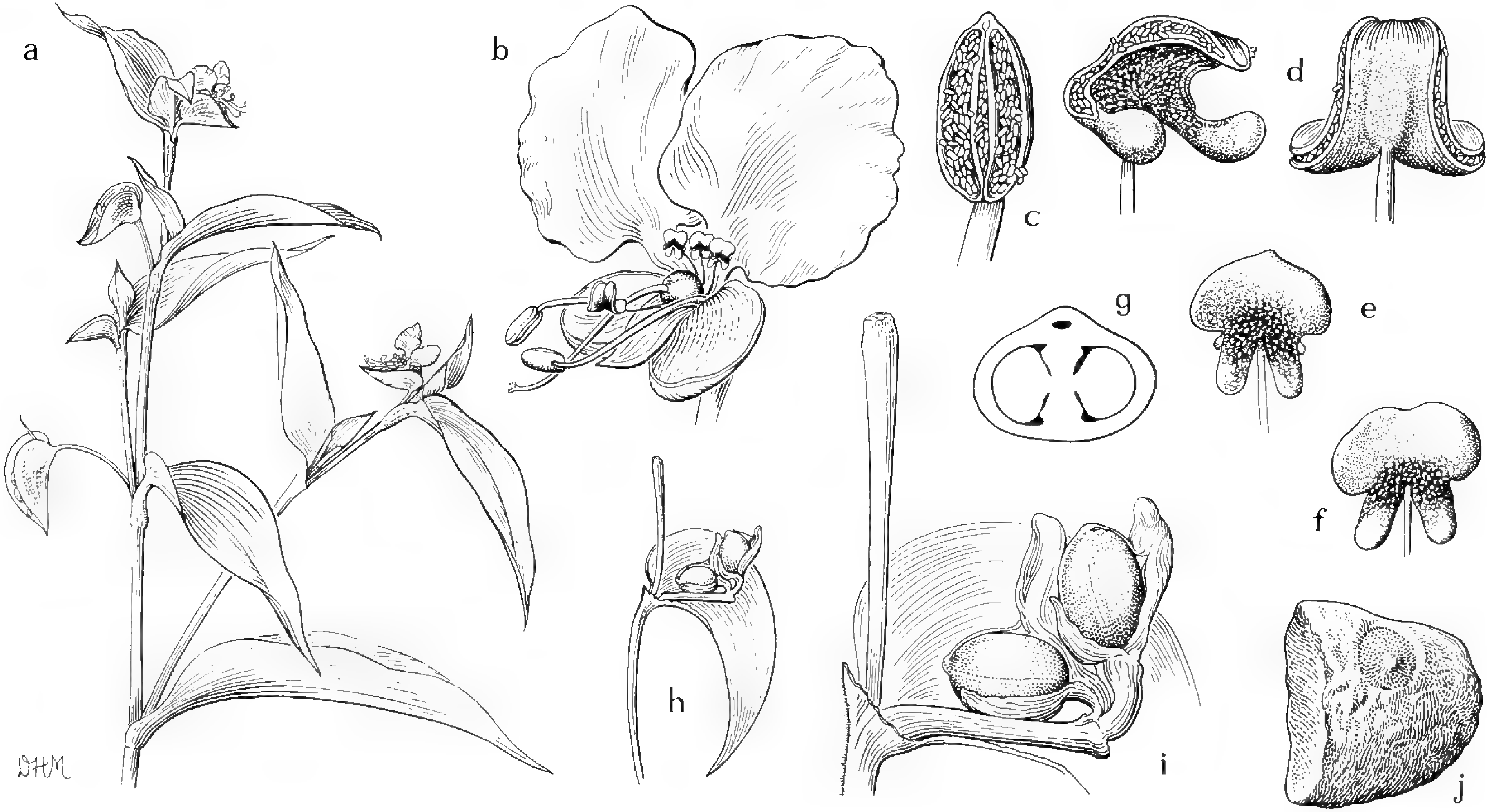

FIGURE 2. *Commelina communis* var. *communis*: a, stem with flowers and fruits, × ½; b, flower, showing 2 sepals, 2 conspicuous petals, reduced petal (below), 3 fertile stamens, and 3 staminodia, × 3; c, 1 of the 2 isomorphic fertile stamens, × 10; d, 2 views of anisomorphic fertile stamen, × 10; e, staminodium with rudimentary anthers, × 10; f, staminodium, completely sterile, × 10; g, diagrammatic transverse cross section of ovary at anthesis, showing 3 locules (2 fertile, each with 1 ovule; 1 sterile), × 15; h, infructescence with 2 capsules, 1 side of folded spathe removed, × 1; i, detail of same, × 3; j, seed, showing operculum, × 20.

by less than 14 cm of soil; the smaller seeds from open flowers, only if covered by less than 7 cm. In a natural population, 88 percent of the seedlings came from large seeds.

Another introduced species in the Southeast is *Commelina Forskalaei* Vahl, known only from southern Florida (Dade County, *D. S. Correll & Popenoe 51166,* USF, and *H. B. Correll, Popenoe, & Sanders 54190,* USF). It is distinguished from other species in our area by its undulate leaf margins. The spathes are orbiculate, and the margins are fused for the basal third. Like *C. benghalensis,* it also produces cleistogamous flowers on short subterranean shoots. In West Africa, where it is native, some plants have both perfect and staminate flowers (Morton, 1967).

Morton (1967) has provided much information on the biosystematics of the genus in West Africa. *Commelina ascendens* Morton, $2n = 28$, is a scrambling herb with the leaves and stems covered with uncinate hairs. The main stems are procumbent, and the erect branches bear inflorescences. *Commelina zambesiaca* C. B. Clarke, $2n =$ ca. 56, has leaf blades that are asymmetric at the base. *Commelina africana* L., $2n = 28$ (30), has yellow flowers. As a generalization, the polyploid West African taxa of *Commelina* occur at higher elevations and in moister habitats than the diploids.

Barnes, in an excellent account of floral biology of the southern Indian species, documented a diversity of phenological types in the genus. The opening and pollination of flowers in a cyme affect the flower type and maturation of remaining flower buds. In general, if early flowers of a cyme are pollinated and set seed, the remaining flower buds develop stamens only. If the buds or earlier flowers are removed, the later buds may develop ovaries and stamens. There is a developmental interdependence among the flowers of an inflorescence that probably is mediated by as-yet-undetermined plant growth substances.

Barnes also described anthesis and self-pollination. After the flower has been open for a few hours, the filaments coil, bringing the anthers into contact with the stigma and effecting self-pollination, as in *Commelina clavata* C. B. Clarke and *C. attenuata* Koenig, $2n = 48$. In *C. hirsuta* C. B. Clarke, the filaments coil, but not enough to bring the anthers into contact with the stigmas. Neither style nor filaments coil in *C. indehiscens* E. Barnes, and no selfing occurs. Selfing occurs before coiling in *C. tricolor* E. Barnes, where the anthers are very close to the stigma at anthesis. In *C. Kurzii* C. B. Clarke and *C. undulata* R. Br., both the style and the filaments coil two to three times, bringing about effective selfing. In *C. Forskalaei* the filament of the median stamen bends slightly, while the style coils strongly, bringing it into contact with the stigma and effecting self-pollination.

Owens tested 13 species of *Commelina* (including *C. benghalensis, C. diffusa,* and *C. erecta* from the Southeast) and found that all were self-compatible.

Faden has investigated the floral biology of *Commelina erecta* in eastern Texas. As in the Indian species, both perfect and staminate flowers are produced in the same cyme. Perfect flowers are produced first, and if seed set occurs, later flowers are staminate. Little selfing occurs.

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THE GENERA OF ERIOCAULACEAE IN THE SOUTHEASTERN UNITED STATES[1]

ROBERT KRAL[2]

ERIOCAULACEAE Desvaux, Ann. Sci. Nat. XIII. **39:** 45. 1828, "Eriocauloneae," nom. cons.

(PIPEWORT FAMILY)

Annual or perennial, monoecious (less often dioecious), diminutive or robust, stemless or caulescent, usually rosulate, scapose aquatic or wetland herbs, mostly of acidic waters and substrates. Rootstock a rhizome or caudiciform, the roots fibrous, spongy, or spongy-septate (diaphrammed), with simple or paired root hairs. Stems short or elongate (in the latter often spreading-ascending), repent or prostrate, the axis sympodial or monopodial, sometimes branching. Leaves mostly polystichous, usually in rosettes, sometimes in looser spirals in the elongate-stemmed species, in rosettes spaced along an elongate slender axis, or in involucral rosettes in compound-scaped species, mostly graminiform, linear-lingulate, parallel nerved, the bases usually broad, open, clasping, the stomata paracytic. Scape(s) simple or compound, originating from or toward rosette center, 1 to many, each arising axillary to a rosette leaf, enclosed at base by a tubular, distally open, spathelike sheath, the scape axis terete, usually twisted, mostly few-to-many-costate, terminating in a single,

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The illustration of *Syngonanthus* was drawn for the Generic Flora in 1975 from dissections made by Kenneth R. Robertson. The liquid-preserved specimens used were collected by R. E. Umber in Hillsborough County, Florida; herbarium material by Kral and Kral (*6777*; GH) in Hernando County, Florida. Living plants brought by George K. Rogers from Columbus County, North Carolina, were used to check various details.

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chaffy, involucrate, sometimes proliferative, buttonlike head, the involucral bracts usually spirally imbricate in few to many gradate series, the receptacle smooth or variously hairy or chaffy. Flowers (florets) imperfect, regular (actinomorphic) or irregular (zygomorphic). Sepals 2 or 3, distinct or variously fused, usually diverging from a stipelike base (part of an androphore or gynophore). Petals lacking, 2, or 3, evident as lobes diverging from a stipelike base (androphore or gynophore) or merely a part of a lobeless column. Stamens 2–4(–6), when 2 or 3 alternating with sepals, often unequal; filaments epipetalous or appearing to arise from the apex of an androphore when petal lobes are reduced; anthers introrse or versatile, 2- or 4-sporangiate, 1- or 2-locular, dehiscing longitudinally; pollen monosulcate, trinucleate. Staminodia present in some 2- or 3-merous flowers, then glandlike or peglike and sometimes fimbriate or variously cleft, rarely with a stipitate blade. Gynoecium syncarpous, 2- or 3-carpellate; style terminal, 2- or 3-branched, the branches simple or rebranched apically, in some species the stylar apex producing appendages alternate with style branches; ovary superior, raised on a gynophore, 3-locular, the ovules 1 in each locule, ventral-apical, pendulous, orthotropous, 2-integumented. Fruit a thin-walled, loculicidal capsule; seeds small, variously ribbed or sculptured, the embryo small, apical, the endosperm copious, mealy-starchy, with compound starch grains. TYPE GENUS: *Eriocaulon* L.

A large, mainly pantropic family of about 13 genera and at least 1200 species, with a distinct majority in the Neotropics and in the genera *Paepalanthus* Mart. (about 500 species), *Eriocaulon* L. (about 400), and *Syngonanthus* Ruhland (about 200). Under the assumption that reduction in ovule number and uniformly imperfect flowers constitute evolutionary advancements, a present and popular view is to place the family as derived from the Commelinales, but distinct from that order (cf. Cronquist; Hutchinson; Takhtajan, 1980; Thorne, 1983).

In the New World only five genera—namely (in order of number of species) *Eriocaulon, Paepalanthus, Lachnocaulon* Kunth, *Syngonanthus,* and *Tonina* Aublet—are known to occur north of South America; just three of these are found in the United States, with only *Eriocaulon* being represented outside the Southeast. Of the three, *Eriocaulon* is the sole representative of the subfamily Eriocauloideae, while *Lachnocaulon* and *Syngonanthus* are treated under the other subfamily, Paepalanthoideae Ruhland.

The family is mainly distinguished by its combination of rosulate and sheathed-scapose habit; vessels with simple or scalariform perforations in all organs; leaves with polystichous arrangement and open, clasping bases (true wetland or aquatic species often with lacunar tissue evident); vascular bundles of stem closed and bicyclic; cuneate proteinaceous inclusions in sieve-tube plastids; root hairs on most roots; monoecious [or dioecious] habit; flowers and involucral bracts and bractlets chaffy, the flowers crowded in tight spirals in involucrate heads; perianth 2- or 3-merous, 1- or 2-cyclic, regular or irregular, usually valvate in bud and often with mealy pubescence, the petals distinct or variously connate, at base incorporated into an androphore or a gynophore; androecium of 2 or 4, or 3 or 6 stamens, often in the trimerous flowers with

3 staminodia or glands at tube apex; gynoecium variously raised on the gynophore, 2- or 3-carpellate, the ovary 2- or 3-locular, each locule with a single ventral-apical, pendulous ovule; style branches 2 or 3, sometimes rebranching at stigma level [in many species producing appendages from the apex of the stylar column]; and fruit capsular, thin walled, loculicidal, the seeds small, with copious mealy endosperm and a tiny lateral-apical embryo.

Trichomes in most species are many and varied on all or nearly all organs. These may constitute at once the most neglected and the most useful taxonomic characters.

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Key to the Genera of Eriocaulaceae in the Southeastern United States

A. Lacunar tissue evident at leaf bases; larger roots thickened, septate, appearing articulated and unbranched; perianth parts in 2's [3's in the Asian adventive *Eriocaulon cinereum*], each petal adaxially glandular; stamens (3 or) 4(–6), the anthers 2-locular, staminal column apically with 2 or 3 glands at center; carpels 2, style branches unappendaged, 2 [carpels 3, style branches 3 in many western, tropical American, or Asian species]. .... 1. *Eriocaulon.*

A. Lacunar tissue not evident at leaf bases; larger roots either fibrous and evidently branched or thickened and fleshy (and then appearing neither septate nor branched); perianth parts in 3's, the petals if present eglandular; stamens 2 or 3, the anthers 1- or 2-locular, apex of staminal column usually with 3 appendaged or unappendaged glands; carpels (2 or) 3.

B. Roots dark, slender, fibrous, evidently branched; scapes smooth or hairy, the hairs neither swollen nor glandular apically; expanded inflorescence globose or short-cylindrical, the outermost involucral bracts reflexed and obscured by the rest of the inflorescence; trichomes of perianth tips clavate; staminal filaments fused to rim of an androphore, the anthers unilocular; style branched with bifid stigmas. .... 2. *Lachnocaulon.*

B. Roots pale, thickened, spongy, appearing unbranched; scapes hairy, at least some of the hairs swollen at base, often glandular distally; expanded inflorescence hemispheric, outer bracts not obscured by the rest of the inflorescence; trichomes of perianth tapering, acute, not clavate; staminal filaments separating from corolla toward apex of tube, the anthers bilocular; style branches undivided. .... 3. *Syngonanthus.*

Subfamily ERIOCAULOIDEAE [Ruhland]

1. **Eriocaulon** Linnaeus, Sp. Pl. **1**: 87. 1753; Gen. Pl. ed. 5. 38. 1754.

Rosulate, scapose, often tufted herbs, the roots evidently cross partitioned, the stems short or elongate, sometimes sparingly branched. Leaves linear-lingulate, often attenuate, gradually or abruptly flaring toward a clasping base, there often noticeably lacunar and pale, greener and less distinctly lacunar distally, the chlorenchymatous part of leaves increasing with extent and duration of emergence. Inflorescences scapose, the usually fluted scape encased at base by a tubular, fluted, distally open, often bifid or trifid sheath and terminating in a single hemispheric to globose or short-cylindrical, involucrate head, all parts chaffy and imbricate in several to very many tight spirals. Involucral bracts in gradate spirals, hardly (if at all) longer than flowers, usually broad, green, gray-green, or paler, at least the margins translucent; receptacle trichomiferous, chaffy, or smooth. Sepals 2, scarious, usually equal, fused to a stipelike base, pale or colored, often translucent, navicular, frequently covered toward tips with farinose or translucent, multicellular trichomes. Petals mostly 2, fused at least toward bases, equal or unequal, similar to sepals but generally narrower, shorter, separated from them by a pronounced tubular stalk (partly petal and, in staminate flowers, partly stamen) and distinguishable from them by a dark gland on adaxial distal surface of each; outer and sometimes inner surfaces or margins frequently with multicellular, translucent or opaque trichomes; distal end of staminate perianth tube concave, sometimes with 2 or 3 dark glands at its center like those on corolla lobes. (Sepals and petals 3 [in the Californian *E. microcephalum* and] in the Asian adventive *E. cinereum.*) Stamens 3 or 4 to 6, 2 or 3 opposite the petals, the anthers introrse, dorsifixed and usually versatile, bilocular, tetrasporangiate, well exserted from the inflorescence at anthesis. Carpels 2, the ovary on a gynophore, 2-locular, the style

2-branched (carpels 3, locules 3 in *E. microcephalum, E. cinereum*). Pericarp thin, often velumlike, the style persisting. Seeds ovoid, ellipsoid, or broadly fusiform, variously lined, ridged, or papillate. LECTOTYPE SPECIES: *E. decangulare* L.; see Britton & Brown, Illus. Fl. No. U. S. & Canada, ed. 2. **1**: 454. 1913. (Name from Greek *erion,* wool, and *caulos,* stalk, from the wool at the base of the scape in the original species, *fide* Arthur Stanley Pease in Fernald (1950).)—PIPEWORT, BUTTON-RODS, HAT-PINS (Small).

About 400 species, mostly pantropic, with a few representatives extending to temperate or boreal-transitional climates in both Asia and eastern North America, and only one (*Eriocaulon aquaticum* (Hill) Druce) in northern Europe (the Hebrides, Scotland).

Of the ten species reported for the United States and Canada, one (*Eriocaulon cinereum* R. Br.) is Asian, now sporadically established in rice-growing parts of California and Louisiana; another (*E. microcephalum* HBK.) is disjunct from the montane Neotropics and has been collected only once from southern California; and two (*E. aquaticum* and *E. Parkeri* B. L. Robinson) are principally of Pleistocene-glaciated latitudes in the eastern or central United States and Canada, each with extensions southward along the Appalachians or the coast into the southeastern United States. The remainder either center in the Coastal Plain of the Southeast with a few extensions into contiguous areas or are endemic to it; of these, only *E. decangulare* extends to (or is extended from) the Neotropics; not surprisingly, this is perhaps the most ecologically ample of our species.

Of the three southeastern genera in the Eriocaulaceae, *Eriocaulon* has the largest number of truly wetland or aquatic species and the most anatomical characters associated with an aquatic habit.

As to soil or soil-water reactions, all species except *Eriocaulon Parkeri,* usually in tidally influenced, circumneutral or even brackish sites, and *E. Ravenelii* Chapman, which favors wetlands transitional to brackish marsh, are found in acidic wet sites, such as pine flatwoods, low savannas, acid pond shores and shallows, sphagnous seeps and bogs, and seeps or pools on or around arenaceous rock. Of these, *E. decangulare* appears to be the most drought tolerant and is commonest in the drier transitions to wetlands.

Harold N. Moldenke, the world authority on the family, treated 43 species for the *North American Flora* (1937); a clear majority are comparatively narrow endemics, some still unknown beyond the type or a few collections. Since trichome characters and the relative dimensions of accrescent parts tend to vary considerably within well-known species, it is quite possible that a biosystematic overview will be more conservative.

Of the three genera that occur in the Southeast, only *Eriocaulon* has nectariferous glands. Insect visitors are rare. It could be assumed that, for our species, the most common agent of pollination is wind.

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Subfamily PAEPALANTHOIDEAE Ruhland

2. **Lachnocaulon** Kunth, Enum. Pl. **3:** 497. 1841.

Annual or perennial, rosulate, scapose, often tufted herbs, the roots branched, slender, fibrous, with paired root hairs; perennation by lateral offshoots or short ascending rhizomes. Rosette leaves linear, acute or attenuate, in very flat spirals toward the apex of a short or elongate, sparingly branched stem, the bases clasping, crowded, none of the leaf evidently lacunar, often hairy with slender, multicellular, translucent hairs; old leaf bases persisting as scales on stems. Inflorescences with scape base in a tubular, costate, apically open sheath, this hairy like leaves; scapes usually several, from axils of central rosette leaves, slender, twisted, variously costate, often with trichomes, terminating in a small (1 cm broad or narrower), white, gray, gray-brown, or brown, globose to ovoid or short-cylindric, involucrate head, each comprising an outer involucre of few to many spirally imbricate series of bracts and an inner bracteate, spirally imbricate mass of bracteate, chaffy, imperfect flowers, both staminate and carpellate. Receptacle of head covered by pale or yellowish, multicellular, filiform trichomes and by the floral bracts (1 or 2 per flower), these mostly about the size of involucral bracts, often navicular or strongly convex and with a few translucent or opaque, usually clavate, multicellular trichomes at the tip. Sepals 3, nearly distinct, similar to receptacular bracts, smooth or sparingly clavate-hairy. Petals lacking or reduced to hairs or small scales. Stamens 2 or 3, elevated on a tubular androphore at least as long; filaments linear; anthers oblong-linear, bisporangiate, unilocular, yellowish or pale, dorsifixed, introrse or versatile, exserted from heads at anthesis; staminodia (2? or) 3, lance-ovoid or peglike, often with fimbriate appendages. Gynoecium on a short, usually comose gynophore, 3-carpellate, the ovary 3-locular, 3-ovulate (2-merous in *L. digynum*); styles (2- or) 3-branched, the stylar column appendaged at apex, with appendages similar to those of staminate flowers. Fruit and seeds like those of *Eriocaulon*. TYPE SPECIES: *L. Michauxii* Kunth (*Eriocaulon villosum* Michx.) = *L. anceps* (Walter) Morong. (Name from Greek, *lachnos*, wool, and *chaulos*, stem, in reference to the long, soft, upwardly pointed hairs on the scapes of the type species.)—HAIRY PIPEWORT, BOG BUTTONS.

Seven species confined to the southeastern United States and Cuba. This small genus evidently centers in the Coastal Plain of the Southeastern States, with two species (*Lachnocaulon cubense* Ruhl. and *L. Ekmannii* Ruhl.) endemic to Cuba.

Our *Lachnocaulon* and *Syngonanthus* species inhabit ecologically drier sites than most species of *Eriocaulon* within the Coastal Plain, the physiographic province in which all the species occur. The optimum habitat is an acid, sandy, or sandy-peat-loam soil, usually one with a gley horizon and therefore saturated much of the year, but definitely one in which water does not stand except during the wettest periods. Soil and soil-water reaction are distinctly acid. *Sphagnum* is the most commonly associated bryophyte. All species appear to be best adapted to moist ecotones around acid wet areas, with the most diminutive species, *L. digynum* Koern., tolerating the wettest—and *L. anceps* and *L. Beyrichianum* Sporl. extending into the least moist—sites. Root systems within the genus are shallow, fine, and diffuse; the roots are eseptate and with paired, elongate and delicate hairs, providing a good adaptation to drier situations.

Both staminate and carpellate flowers develop peglike, often cleft or fringed appendages apically, in the former case on the androphore and alternating with the filament bases and in the latter alternating with the style branches. In the carpellate flowers, petals are reduced to three clumps of trichomes arising from

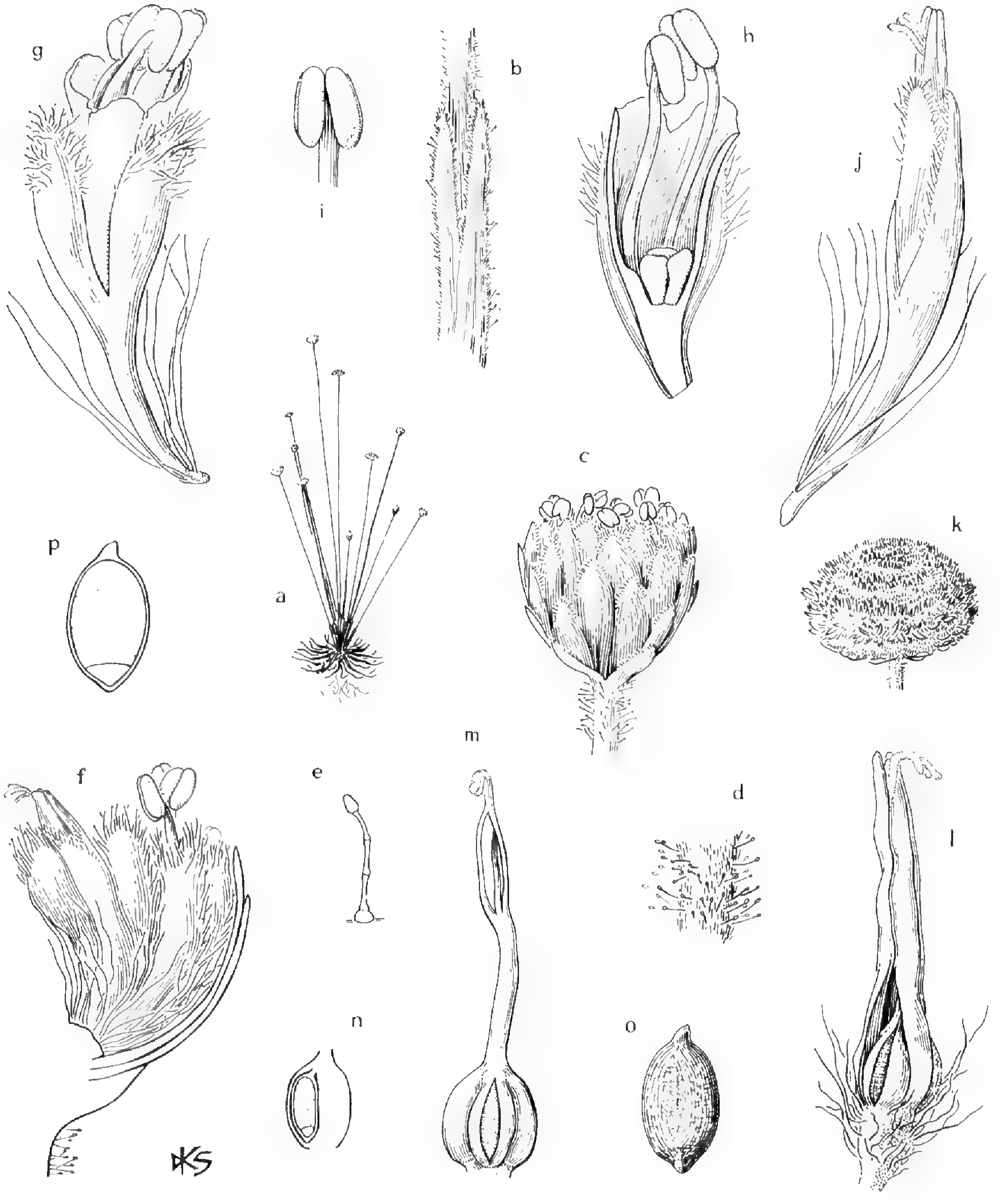

FIGURE 1. *Syngonanthus*. a–p, *S. flavidulus*: a, flowering plant, leaves decumbent from the basal rosette, showing sheaths at bases of peduncles, × ½; b, sheath enclosing base of peduncle, × 12; c, flowering head at beginning of anthesis, bracts of head and anthers of staminate flowers visible, × 12; d, detail of peduncle just below head, showing indumentum of divergent glandular trichomes and adpressed, simple ones, × 24; e, uniseriate, septate, glandular trichome, × 100; f, portion of head in vertical section, anthers of staminate flower and styles and petals of carpellate flower projecting above bracts, 2 bracts in section at extreme right, × 24; g, staminate flower, the calyx lobes connate below, pubescent above, the petals united, vertically folded around the filaments, the anthers exserted, × 40; h, upper portion of staminate flower in vertical section, showing rudimentary, 3-lobed gynoecium, × 40; i, adaxial surface of anther, × 50; j, carpellate flower, free petals (see "l") projecting beyond pubescent calyx lobes, tips of 3 stigmas protruding between petals, × 40; k, head in fruit, carpellate flowers in concentric bands, × 6; l, fruit partly enclosed by persistent petals (calyx lobes removed), showing seed through opening in 1 locule of capsule, × 50; m, fruit, perianth removed, styles

the gynophore above the sepals. Stamens provide yet another distinguishing feature, the anthers being bisporangiate but one-locular at anthesis.

REFERENCES:

Under family references see KRAL and MOLDENKE (1937); under references for *Eriocaulon,* see KRAL and MOLDENKE (1956).

3. **Syngonanthus** Ruhland in Urban, Symbol. Antill. **1:** 487. 1900.

Low [to moderately tall, slender to coarse, solitary to] densely caespitose, [annual or] perennial, monoecious [or dioecious], rosulate herbs, the stems short [to very elongate], the primary roots mostly thickened-porous, pale, eseptate, the branch roots much more slender, angular, with paired root hairs. Stems short [to elongate, sometimes branched]. Leaves mostly slenderly linear, smooth or variously hairy, often recurved, mostly firm and not evidently lacunar. Scape(s) solitary or many, from axils of inner rosette leaves, each enclosed at base by a tubular, open-ended, costate sheath, slender, terete and smooth or variously costate and hairy, erect or declinate, simple and arising directly from a basal rosette [or 1 or more times compound, each secondary or subsequent whorl subtended by an involucre or "rosette" of bracteal leaves comparable to but progressively smaller than those of the basal rosette, or scapes proliferative and substoloniferous, glabrous to sparsely or copiously pubescent, usually pilose and with sharp- or gland-tipped hairs often mixed with shorter, glandular ones]. Heads globose, urceolate, turbinate, or hemispheric, with many involucral bracts, these pale, papery-chaffy, imbricate in several tight, flat spirals, often gradate, shorter or longer than florets. Receptacle of heads pilose to subglabrate, the hairs elongate, sharp tipped, mostly silvery. Flowers trimerous and nearly regular. Sepals mostly chaffy and pale, distinct to near base, there comprising the outer part of the column (androphore, gynophore), smooth or with long hairs comparable to those of receptacle. Petals subequal; in the staminate flowers much more connate, the androphore a pronounced stipe, at the apex flaring into a cuplike, funnelform or clavate, concave-apexed corolla, the rim of which is often 3-toothed; in the carpellate with 3 blades departing from the gynophore and connate or connivent above at the level of the ovary or higher. Stamens 3, the filaments adnate to corolla at apex of androphore, alternating with 3 central glands at its concave center and opposite the lobes of its flaring rim (corolla limb), exserting the anthers beyond them; anthers 2- to 4-sporangiate, bilocular, the locules basally divergent. Ovary trilobed, tricarpellate, the gynophore shorter than the androphore of staminate flowers, the style elongate [or short, clavate], at apex with 3 elongate-linear, papillose stigmatic branches [their bases alternating with stipitate-bladed or

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connate below and above but free in middle, seed visible through slit in capsule, × 50; n, fruit in diagrammatic vertical section, seed pendulous from apical, axile placenta, endosperm evenly stippled, embryo unshaded, × 50; o, seed, funiculus above, micropyle below, × 100; p, same in vertical section, endosperm evenly stippled, seed coat and embryo unshaded, × 100.

simple peglike, bearded appendages, or these lacking.] Capsule and seeds as in *Eriocaulon*. LECTOTYPE SPECIES: *Eriocaulon umbellatum* Lamarck (= *Syngonanthus umbellatus* (Lam.) Ruhland). (Name from Greek *syngonos*, joined together, and *anthos*, flower, from the connate petals of the carpellate flowers.)

About 200 species in Africa, the West Indies, and Central and South America, the earlier-described ones placed in various sections of *Paepalanthus*, subsequently transferred to *Syngonanthus* by Ruhland (1900). The center for these is the planalto of Brazil. In the Neotropics the genus becomes progressively less well represented northward. In North America north of Mexico, there is only *S. flavidulus* (Michx.) Ruhland (*Paepalanthus flavidulus* Kunth), shoebuttons, bantam buttons, a caespitose plant with rhizomes slender, ascending; rosette leaves narrowly linear, acute, strongly recurved, often with a scattering of pustular-based, uniseriate, multicellular hairs; scapes numerous, pilose-glandular, wiry, erect or ascending, to 30 cm long; heads pale whitish yellow, chaffy, hemispheric, ca. 5–10 mm broad; receptacles densely translucent-pilose; androphores and gynophores hairy at the base; staminate corollas broadly funnelform, with 3 broadly triangular lobes; and carpellate corollas with 3 narrow lobes connivent over the ovary, with the slender stylar apex unappendaged.

Syngonanthus flavidulus is one of the commoner associates of most *Lachnocaulon* species, usually in sandy-peaty bog ecotones, flat, exposed sandy washes and seeps, and savannas and flatwoods in the lower Coastal Plain from eastern North Carolina, south through Florida, and west in the Gulf Coastal Plain to northwestern Florida and contiguous Alabama.

While this species agrees with many of the tropical ones in the character of its androphore (which appears as a long, pedicellike stipe) and in its cuplike or funnellike corolla with a triglandular center, it differs from most in having staminate flowers with densely pubescent sepal tips, carpellate flowers with a hairier gynophore and petals connate only at the base, and an unappendaged stylar apex. Interpretation of the evolution of species in this now very large genus is best left to those tropical botanists who work within its centers of diversity, particularly Brazil.

Many of the tropical species of *Syngonanthus* and *Paepalanthus* are both large and showy; the ones with larger and papery heads produce effects much like the "everlastings" (e.g., *Helichrysum* Gaertner, *Anaphalis* DC.) and are commercially exploited for dried plant decorations.

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RECENT PLANT COLLECTIONS FROM DOMINICA

C. WHITEFOORD[1]

Recent collections from the Commonwealth of Dominica, Lesser Antilles, are reviewed, and attention is drawn to first records of 40 phanerogams and six ferns. Second collections are also listed where they are considered noteworthy.

Dominica is a volcanic island about 28 miles long and 15 miles wide. It is the third largest of the Lesser Antilles and has the highest rainfall. Its mountainous terrain has so far protected its magnificent forests from the intensive agricultural development that has cleared the other, less-rugged islands of the group. An account of the ecology and botanical exploration of the island can be found in Hodge (1954).

Between 1888 and 1889 Ramage collected plants in Dominica, and the British Museum (Natural History) has 485 of his excellent specimens. The Museum's Dominican holdings were later increased by duplicates from Hodge, collected between 1937 and 1940, and from Howard, collected in 1950. Other botanists, notably the Bredin-Archbold-Smithsonian collectors of the 1960's and 1970's, have subsequently visited the island, but few of their duplicates have reached the British Museum. Since Ramage and Hodge made their collections, there have been major changes in Dominica. The hurricanes of 1979 and 1980 devastated both the natural vegetation and the agricultural industry, and much of the resulting financial aid went toward building roads, making more of the island accessible for farming and logging. Large areas of rainforest known to Ramage are now under cultivation, and the pressure to plant more and more bananas is ever increasing.

I have visited Dominica on four occasions: 28 August–19 October 1983 (collection numbers *3400–4126*), 17 September–7 November 1984 (*4130–4706*), 11 January–16 February 1986 (*5130–5528*), and 18 March–12 April 1987 (*5550–5859*). About 1600 numbers were collected, the first set being deposited at the British Museum (Natural History) (BM), with incomplete sets at the Roseau Botanic Garden, the Smithsonian Institution (US), the Arnold Arboretum (A), and the Missouri Botanical Garden (MO). The following notes draw attention to those collections that are first records for the island, or are otherwise of interest. The families are listed systematically in the BM and Kew herbarium order, which is modified from Bentham & Hooker (1862–1883).

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SPERMATOPHYTA

NYMPHAEACEAE

Nymphaea rubra Roxb. (First record; cultivated)

5509, growing in the pool at Canefield, where it had presumably been planted for ornament. Since there is a photograph of this striking plant on the tourist brochure, it is strange that it has not been previously recorded.

MELIACEAE

Trichilia septentrionalis C. DC. (Second record)

4329, growing in forest at the edge of the ravine at Syndicate; sterile. Fruiting material (*5351*) was later collected from the same tree. It was first collected by Ramage at Laudat in 1888. This species occurs in mainland Central America from Costa Rica to Panama, and in northern South America.

OLACACEAE

Schoepfia schreberi Gmelin (Second record)

5207, with very young fruit, growing in dry scrub vegetation near Dublanc, and *5252*, in similar scrub on the Cabrits. The previous record of this plant was based on an Imray specimen collected sometime between 1832 and 1875. Widespread in the West Indies, it occurs in both Guadeloupe and Martinique (Fournet, 1978).

CELASTRACEAE

Celastrus racemosus (Reisseck) Loes. (First record)

3869, in fruit, growing in montane thicket at Freshwater Lake. It is distributed throughout Central America. *Celastrus grenadensis* Urban, from Grenada, is considered a synonym.

RHAMNACEAE

Gouania lupuloides (L.) Urban (Second record)

4666, scrambling over thickets at Petite Coulibrie. Fruiting material (*5202*) was later collected near Dublanc. Although common in the West Indies, this plant had not been recorded from Dominica since Imray's collection (Nicolson, unpubl. ms.), sometime after 1837.

SAPINDACEAE

Allophylus racemosus Sw. (First record)

4440, growing in dry woodland between Fond Hunte and Fondchère. It occurs generally in Central America and the West Indies but apparently has not been collected in Dominica before.

LEGUMINOSAE

Acacia tortuosa (L.) Willd. (First record)

5686, in fruit, growing beside the road near St. Joseph. It occurs in Florida, the West Indies, and South America.

Anadenanthera peregrina (L.) Speg. var. **peregrina**
(First record; cultivated or naturalized)

5833, in full flower, and *5834,* with older flowers and a few pods. Both were growing near the bottom of the road to Springfield Estate. Native to northern Brazil, Guyana, Colombia, and Venezuela and probably naturalized in some of the West Indies, it is often planted for ornament.

Calopogonium mucunoides Desv. (Second record; naturalized)

5399, trailing among grasses beside the road near La Plaine. It was collected in Dominica once before, by Fairchild in 1932. It is native to South America and has become naturalized in the West Indies.

Cassia javanica L. (First record; cultivated)

5856, growing in Roseau Botanic Garden; sterile. It is native to Indonesia but is cultivated in the West Indies for its large, attractive, pink and white flowers.

Indigofera hartwegii Rydb. (First record)

5550, growing beside the path to Scotts Head. It is a Mexican species and new to the West Indies.

Inga vera Willd. subsp. **vera** (First record)

5634, bearing very young pods, growing at the edge of a banana field near Syndicate. Although it is native from Mexico to northern South America and the Greater Antilles, it is new to the Lesser Antilles.

Mimosa arenosa (Willd.) Poiret var. **arenosa** (First record; naturalized)

5360, in flower, growing beside the road near Coulibistri. A specimen bearing pods (*5822*) was later collected from the waste ground below the road near Mahaut. Native to Venezuela and naturalized in Mexico, it has been collected recently in Martinique and Puerto Rico (Nicolson, pers. comm.).

Mucuna pruriens (L.) DC. f. **cochinchinensis** (Lour.) Backer (Second record)

5562, growing in dry roadside scrub near Dublanc. Stehlé collected it on Guadeloupe and reported it as introduced from Dominica (Nicolson, unpubl. ms.), but this may be the first collection from this island.

Piscidia carthagenensis Jacq. (First record)

5710, in flower, growing high up on a cliff near Coulibistri. Fournet (1978) described it as endemic to Guadeloupe.

Rhynchosia phaseoloides (Sw.) DC. (Second record)

5704, growing at Milton. Widely distributed throughout the Caribbean and South America, it was first collected in Dominica by Imray.

HALORAGACEAE

Myriophyllum aquaticum (Vell.) Verdc. (First record)

3745, a pondweed from Canefield (sterile), and *5512* (fertile). This is a South American species naturalized in North America, Southeast Asia, and Australia. It is the first record of the family for the Lesser Antilles.

LYTHRACEAE

Cuphea hyssopifolia Kunth (Second record; cultivated)

5457, growing at Baiac. It is native to Central America. This plant was attributed to Dominica by Grisebach (1860), based on an Imray specimen that may have been misidentified (Nicolson, unpubl. ms.).

Lagerstroemia speciosa (L.) Pers. (First record; cultivated?)

5828, in fruit, growing beside the road near Hillcrest Estate, east of Portsmouth. Occurring from India to south China and from Indonesia to northern Australia, it is often planted for ornament in the tropics.

BEGONIACEAE

Begonia heracleifolia Schldl. & Cham. (First record; cultivated)

5459, growing at Baiac. It is native to southern Mexico, Guatemala, and Belize.

RUBIACEAE

Hedyotis callitrichoides (Griseb.) W. Lewis (Second record)

5374, growing out of concrete steps, at La Plaine. This is a West Indian species and occurs on Guadeloupe, but it has not yet been recorded from Martinique. Ernst made the first collection in Dominica, about 1964.

Hedyotis commutata Schultes (First record)

4589, growing at the edge of a cultivated field beside the road between Trafalgar and Trafalgar Falls. Originally from tropical Africa and Madagascar, it has become naturalized in the West Indies.

Vangueria madagascariensis Gmelin (Second record; cultivated)

3747, bearing a few flowers and young fruits, growing beside the road above Canefield. It is also cultivated at Baiac. The previous record was based on a tentatively identified specimen collected by Ernst (Nicolson, unpubl. ms.). This plant is grown for its fruits, which are sold in the market and are known locally as "tamarins des Indes."

COMPOSITAE

Chromolaena integrifolia (Bertero ex Sprengel) King & Robinson (First record)

5816, growing on rough ground below the path east of Capucin. It is known from Guadeloupe and Montserrat but not from Martinique.

Pectis elongata Kunth var. **floribunda** Kiel (First record)

4039, growing thickly in a large patch beside the path between the swamp and the sea, East Cabrit. It is no longer to be found there because of the new road to Fort Shirley, but a few more plants were seen on the roadside between Petite Baie and the Picard Estate. It is native to Central America and the West Indies. In Jamaica the popular name for this plant is "verbena grass" (Adams, 1972).

ERICACEAE

Gaultheria domingensis Urban (First record)

4212, with flowers and fruits, growing in boggy soil in the Valley of Desolation, and *5482,* from the same locality. First described from Hispaniola, it has also been recorded from Guadeloupe and Martinique (Fournet, 1978).

MYRSINACEAE

Ardisia crenata Sims (First record; cultivated)

5464, planted at Baiac. It is native to Japan and northern India.

ASCLEPIADACEAE

Cynanchum parviflorum Sw. (Second record)

5298, hanging from a roadside thicket near Portsmouth. This specimen has exceptionally large, pale yellow flowers. It is the first collection from Dominica since Imray's (Nicolson, unpubl. ms.), although the species is generally common in the West Indies.

CONVOLVULACEAE

Ipomoea obscura (L.) Ker Gawler (First record)

5505, twining among roadside vegetation near Massacre. It is an Asiatic species but has been recorded from Marie Galante and Guadeloupe (Fournet, 1978).

SOLANACEAE

Solanum triste Jacq. (First record)

3769, growing near the Belvédère Estate, Délices. Native to coastal Venezuela and Trinidad, it is fairly common on Martinique but is not yet recorded from Guadeloupe.

SCROPHULARIACEAE

Stemodia verticillata (Miller) Hassler (Second record)

5573, growing on a path at Syndicate. It was previously collected by Hodge in 1938 (Nicolson, unpubl. ms.). Widespread in the Neotropics, it is often found as a weed of cultivation.

GESNERIACEAE

Chrysothemis pulchella (Don ex Sims) Decne. (First record; cultivated?)

3638, growing at the edge of a banana field at Syndicate, but perhaps planted for ornament. Native to Panama and Trinidad, it is sometimes cultivated.

Gloxinia perennis (L.) Druce (First record; cultivated)

5458, growing at Baiac. It occurs naturally from Colombia to Peru and is well known in cultivation.

ACANTHACEAE

Asystasia gangetica (L.) T. Anderson (First record; cultivated)

4218, with mauve flowers, and *4219,* with greenish yellow ones, both growing near the house at Baiac. This is an Indian plant, sometimes cultivated, and is naturalized on the Malay Peninsula and in tropical Africa.

Justicia betonica L. (First record; cultivated)

4225, growing at Baiac. It is native to India.

LABIATAE

Plectranthus verticillatus (L. f.) Druce (First record; cultivated)

4222, flowering, trailing over a tree stump at Baiac. It is South African in origin.

AMARANTHACEAE

Celosia argentea L. (First record)

4080, growing in swampy ground near the sea, East Cabrit. This is a common tropical plant and has been collected in both Guadeloupe and Martinique.

EUPHORBIACEAE

Breynia disticha J. R. & G. Forster (First record; naturalized)

5192, growing at the edge of scrub woodland near the beach at Douglas Bay. Originally from the Pacific islands, it is often found naturalized in the tropics and is commonly known as "snow-bush."

Sebastiania hexaptera Urban (First record)

3649, growing in hurricane-damaged forest beside the Picard gorge, Morne Diablotin. Fruiting specimens, *4333* and *5356,* were later collected at the same locality. It is reported as rare on Guadeloupe and Martinique (Howard, 1974).

ORCHIDACEAE

Elleanthus dussii Cogn. (First record)

3862, in fruit, growing beside the road from Laudat to Freshwater Lake. It is endemic to the Lesser Antilles and has been recorded from Guadeloupe and Martinique (Howard, 1974).

Pleurothallis wilsonii Lindley (First record)

5676, in fruit, growing in Milton on the trunk of *Syzygium jambos* (L.) Alston. It is distributed throughout the Greater Antilles and has been recorded from Guadeloupe.

Spiranthes adnata (Sw.) Bentham (First record)

5638, growing at the edge of the Picard gorge. It is widely distributed in Central America and the West Indies and has been collected in several of the Lesser Antilles.

HELICONIACEAE

Heliconia psittacorum L. f. (First record; naturalized)

3762, growing in Délices on a slope below a path. It is native to Central and South America, commonly cultivated in the West Indies, and often found as an escape.

DIOSCOREACEAE

Dioscorea bulbifera L. (First record; naturalized)

3903, fruiting, found in the forest above Fond Pie, and *3941,* a sterile specimen bearing aerial tubers. This is an Old World species, but it is widely cultivated as a food plant, often escaping and becoming naturalized.

AMARYLLIDACEAE

Zephyranthes rosea Lindley (First record; naturalized)

4670, growing in a deserted garden near Morne Rouge. It is Central American and occurs generally in the West Indies.

HYDROCHARITACEAE

Hydrilla verticillata (L. f.) Royle (First record)

5508, growing in the pool at Canefield. This plant is distributed throughout the warmer parts of the Old World and has now become a nuisance in Florida.

CYPERACEAE

Cyperus iria L. (First record)

3744, growing in waterlogged pasture at Canefield. It occurs in most tropical parts of the Old World, Australia, and North America. In the West Indies it has been recorded only from Cuba.

Eleocharis cellulosa Torrey (First record)

5283, growing in the Cabrit swamp. It is widespread in Central America but new to the Lesser Antilles.

Fimbristylis littoralis Gaudich. (First record)

4474, growing beside the track from Syndicate to Trou Cochon, and *5271,* from the Cabrit swamp. This is an Old World sedge that has been recorded from St. Lucia and Grenada.

Kyllinga nemoralis (J. R. & G. Forster) Dandy ex Hutch. (First record)

3726, growing near the sea at Pointe Mulâtre. It was also found at Fort Shirley and on waste ground near the bridge at Goodwill. Originally from the Pacific islands, it has been recorded from Jamaica and Trinidad.

Scleria distans Poiret (First record)

4526, growing beside the road above Salisbury. It is known in Jamaica, Cuba, and the Dominican Republic but is new to the Lesser Antilles.

GRAMINEAE

Pennisetum purpureum Schum. (First record)

5365, growing on a bank at La Plaine. It is native to tropical Africa but has become naturalized in the West Indies and tropical America, where it has been introduced as a forage crop.

PTERIDOPHYTA

POLYPODIACEAE[2]

Acrostichum aureum L. (First record)

4054, growing in large clumps in the Cabrit swamp. It is found generally in the tropics, including the other Lesser Antillean islands.

Elaphoglossum smithii (Baker) Christ (First record)

4552 and *4554*, epiphytic on buttresses on Morne Diablotin. This is endemic to the Lesser Antilles and has been recorded from St. Vincent and Grenada.

Polypodium aureum L. var. **areolatum** (Humb. & Bonpl. ex Willd.) Baker (First record)

3609, epiphytic on citrus, Syndicate. It occurs in the Greater Antilles, continental tropical America, the Galapagos Islands, and Guadeloupe.

Polypodium plumula Humb. & Bonpl. ex Willd. (First record)

3842, on a fallen slab of bark at Baiac. It is distributed in Florida, the Greater Antilles, continental tropical America, and the Lesser Antilles (Saba, Guadeloupe, and Martinique).

Pteris grandifolia L. (First record)

3937, on a buttress, in forest near Syndicate. It occurs in the Greater Antilles, the Lesser Antilles (Guadeloupe, Grenada), Trinidad, and continental tropical America from Mexico to Peru.

Thelypteris reptans (J. F. Gmelin) Morton var. **tenera** (Fée) Proctor (First record)

4073, growing on a wall, Fort Shirley. It may occur in Puerto Rico and has been recorded from St. Kitts, Nevis, and Guadeloupe in the Lesser Antilles.

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[2] The following ferns were not recorded from Dominica in Howard's *Flora of the Lesser Antilles* (Vol. 2, 1977) and so are listed as first records.

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THE BIOSYSTEMATICS AND EVOLUTION OF THE POLYALTHIA HYPOLEUCA COMPLEX (ANNONACEAE) OF MALESIA, I. SYSTEMATIC TREATMENT

STEVEN H. ROGSTAD[1]

A component of tropical lowland rain-forest flora diversity is the presence of series of sympatric, closely related species. The three major hypotheses forwarded to explain the coexistence of such species are discussed, and an argument is presented that small, monophyletic groups are the most appropriate objects of investigation when examining them. To that end, a classification of the *Polyalthia hypoleuca* complex (Annonaceae) is provided to form the foundation for a set of forthcoming articles exploring which of the three hypotheses best applies to the complex. After presentation of evidence that the complex is monophyletic, the results of uni-, bi-, and multivariate statistical analyses of character data taken from herbarium specimens are reviewed and shown to support the delimitation of six species in the complex, with members distributed sympatrically in various combinations throughout Malesia. One new species, *P. ovalifolia,* is described. The hypothesis of coexistence that best applies to the complex is briefly noted, with supporting details to be given in subsequent articles.

> *If the traveller notices a particular species and wishes to find more like it, he may often turn his eyes in vain in every direction. Trees of varied forms, dimensions, and colours are around him, but he rarely sees any one of them repeated. Time after time he goes toward a tree which looks like the one he seeks, but a closer examination proves it to be distinct.*
>
> Alfred Russel Wallace (1878, p. 65)

> *As the species of the same genus have usually, though by no means invariably, much similarity in habits and constitution, and always in structure, the struggle*

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> *will generally be more severe between them, if they come into competition with each other, than between species of distinct genera. . . . One species of charlock has been known to supplant another species, and so in other cases. We can dimly see why the competition should be most severe between allied forms, which fill nearly the same place in the economy of nature. . . .*
>
> Charles Darwin (1859, p. 76)

INTRODUCTION

Although the prodigious organismic diversity of tropical lowland rain forests (TLRFs) is increasingly being catalogued, the biological principles generating and maintaining it remain enigmatic. This study has been conducted as part of an attempt to illuminate one aspect of the biology of tropical lowland communities that contributes to such diversity: the occurrence of series of morphologically very similar yet consistently distinct entities, or species, in apparent sympatry. In this Introduction, I first review the relevant observations and explanatory theories of previous researchers who have contemplated such series of species. Then I summarize them as a set of competing hypotheses. Finally, I outline the research methods I have used to test these hypotheses with one such series of entities. As will be demonstrated, a clear understanding of the systematics of these species complexes is extremely important to the examination of the competing hypotheses forwarded to explain their existence. I therefore include a systematic treatment of a complex of Malesian TLRF trees, the species of the *Polyalthia hypoleuca* complex (Annonaceae), that will serve as the foundation for a series of forthcoming articles investigating the outlined hypotheses with regard to this species constellation. Each of these articles will be related to and will reflect upon the data and conclusions presented in all of the others. For example, the results to be reported in subsequent papers on the distributional ecology (Rogstad, in prep. a) and floral biology (Rogstad, in prep. b) of the species included in the complex both are based on and support the systematic conclusions reached primarily on morphological grounds here.

THE PROBLEM OF SERIES OF CLOSELY RELATED, SYMPATRIC SPECIES

One often-noted component of the high species diversity of TLRFs is the presence of series of morphologically very similar, sympatric entities (e.g., see Klopfer & MacArthur, 1961; Fedorov, 1966; Ashton, 1969; Richards, 1969; Van Steenis, 1969; Hubbell, 1979; Leigh, 1982; Whitmore, 1984). These entities are usually recognized at the species level, and because of their morphological similarity, they are presumed to be closely related species. I will give a more precise definition of these species complexes below.

That these series pose a problem for community theory can be traced back at least to the work of Lotka, Volterra, and Gause (Hardin, 1960; Armstrong & McGehee, 1980). Gause demonstrated experimentally that the predictions of the Lotka-Volterra equations were fulfilled in competition experiments between two closely related *Paramecium* species. This principle is usually referred to as Gause's Principle of Competitive Exclusion: two or more species that occupy the same niche cannot coexist in the same habitat.

While theoreticians (e.g., Hubbell, 1979; Huston, 1979; Armstrong & McGehee, 1980; Pickett, 1980; Agren & Fagerstrom, 1983) have argued that this principle probably is not valid for nonequilibrium environments, a large body of empirical evidence (see, for example, MacArthur, 1957; Hutchinson, 1959; Mayr, 1963, 1970; Schoener, 1974, 1983; Harper, 1977; Jones, 1978; Werner, 1979; Aarssen, 1983, 1985; Armbruster, 1985; Pulliam, 1985), based primarily on geographic distributions or niche shifts of closely related species, suggests that it generally holds, at least in temperate environments. The many studies on character displacement (e.g., Grant, 1972) are also germane, because they indicate that even species without broad overlap in many niche characteristics may compete intensively with regard to the overlapping areas.

For temperate trees, the prevailing belief has been summed up by Fedorov (1966, p. 1): "... taxonomically close ... species of plants, do not as a rule occupy the same area, but are most usually geographically isolated from one another ... the isolation of closely allied species may be not only geographical, but ecological as well, as when such species are found in different habitats within one area." According to V. Grant (1963), this principle becomes more evident as the size of the organisms under consideration increases, due to more intense competition for scarce resources among larger organisms. He cited several temperate examples of this concept, noting that while some herbs may have series of sympatric, closely related species, this condition is rare for trees. Two often-noted, seeming exceptions (members of the genera *Quercus* and *Pinus*) show, upon detailed examination, clear geographic or ecological separation of closely related species (also see Stebbins, 1950; Reich & Hinckley, 1980). There may be a few groups of temperate trees that do not conform to Gause's Exclusion Principle, but these should generally be regarded as the anomalies that highlight the rule.

In contrast, forests of the humid tropics often appear to deviate significantly from Gause's principle. For example, in Ashton's (1977, 1984) surveys of five two-hectare (ha) plots in TLRF at Pasoh Forest Reserve (central peninsular Malaysia), 484 species were identified (DBH > 10 cm); approximately 40 percent of the 191 genera had three or more congeners, and 15 percent of the genera had six or more congeners. Some genera had many species, with *Eugenia* topping the list at 28. Viewed in another manner, if (as Ashton extrapolates) 700 species can be found on 50 ha at Pasoh, more than 300 (43%) will be growing sympatrically with at least five congeners. Interestingly, Pasoh is by no means the most species rich of the forests that have been surveyed in Malesia (Ashton, 1984), so even more striking examples probably exist. Sympatric ensembles of closely related species also exist in the richest TLRFs of South America, such as the Yanomamo region of Amazonian Peru, and in Africa, where *Cola* (Sterculiaceae) and *Diospyros* (Ebenaceae) are examples of genera exhibiting this pattern (A. Gentry, pers. comm.). Thus, while the intensity of this phenomenon may vary from region to region, it appears to be a general feature of TLRF communities.

As noted above, the occurrence of sympatric, closely related species is not cause to discard the Competitive Exclusion Principle if such species are found to have diverged in at least one niche characteristic. However, it will be seen below that some authors have argued, on both theoretical and empirical grounds, that series of closely related species may coexist in forests of the humid tropics without such niche divergence. Are there fundamental differences in temperate and tropical forests in the forces guiding evolution and community organization?

DEFINITIONS

Greater precision can be given to the above concepts, and to the development of a means to investigate them, by defining a few of the terms more rigorously. The term "sympatry" has a long and varied history of usage (e.g., see Mayr, 1970). Here I use it to mean the concurrent, regular occurrence of different taxa within potential gene exchange distance of one another. This rather broad definition has been chosen over more restrictive ones that may overlap with niche definitions (e.g., ecological or temporal sympatry).

The concept of the niche has also been extensively debated (e.g., see discussion in Aarssen (1983)). I use Whittaker's (1967, p. 210) definition: "the position of the species in the community, its particular way of relating to other species, environment and space within the community, and seasonal and diurnal time." A niche difference between two tree species exists if they interact with other species differently (e.g., pollinators or herbivores), if they differ in some aspect of the environments and space they occupy (e.g., understory vs. canopy; differences in substrate requirements), or if their seasonal or daily rhythms of activity differ temporally (e.g., flowers functional at different times of the year or day).

It is also not always clear what is meant by the various authors cited above when they use concepts such as "morphologically very similar," "closely related," "taxonomically allied," or "congeneric." All of these expressions refer to groups of species whose members are assumed to have a close phylogenetic relationship. However, they are relative, depending upon context, and they can be (and have been) applied to different types of groups. Several discussions of the types of groups that can be constructed exist in the literature (e.g., see Wiley, 1981), but for present purposes I will follow Eldredge and Cracraft (1980) in reducing the possibilities to two main classes, monophyletic and nonmonophyletic groups. As will be seen below, these groups differ as to their precision in delimiting assemblages of species with immediate phylogenetic proximity. After a brief explanation of the differences in the construction of these two types of groups, the importance of the type chosen to examine the phenomenon of series of "closely related" sympatric species will be outlined. I will establish that monophyletic groups are preferred over nonmonophyletic ones in investigating this phenomenon.

A comparison of these two types of groups is presented in FIGURE 1. In this discussion, it is assumed that the phylogenetic relationships among the taxa (designated by letters) as drawn reflect the "true" history of the groups.

Monophyletic groups, as defined by Hennig (1966), comprise all and only

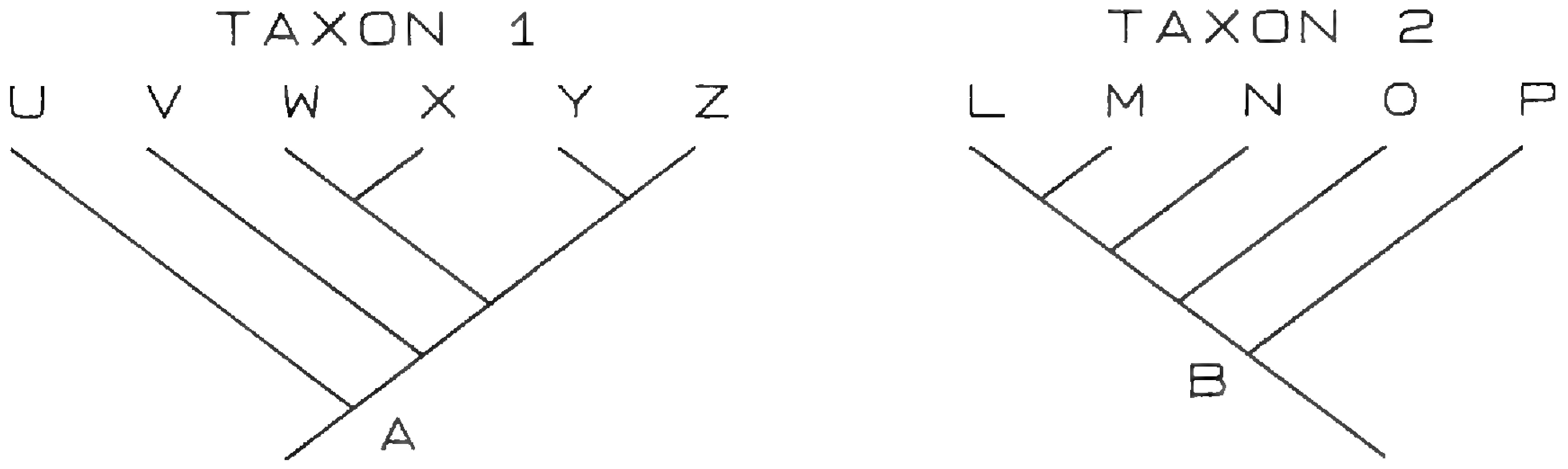

FIGURE 1. Monophyletic and nonmonophyletic groups (see text for explanation).

those taxa descended from a common ancestor (the "strict" monophyletic groups of Stevens (1986)). Examples include such terminal groups as W and X (note that these are sister taxa); W, X, Y, and Z; or all of taxon 1, in which case node A may be considered as the common ancestor. Monophyletic groups are usually recognized by the presence of a unique character or suite of characters (synapomorphies) that is shared among all the members of the group and that presumably arose only once in the ancestral lineage before its diversification. Nonmonophyletic groups do not include all and only the species descended from a single ancestor but rather exclude at least one of the terminal taxa. For example, nonmonophyletic groups would include, for taxon 1, ones made up of only V, W, and Y, or of V, W, X, and Z (often referred to as "paraphyletic" groups). They can also be constructed of taxa with even more distant phylogenetic relationships such as only taxa V, Y, and M (they are then frequently termed "polyphyletic"). While monophyletic assemblages are by definition composed of taxa with the most immediate phylogenetic relationships (the *most* closely related contemporary species), nonmonophyletic groups exclude some of these taxa.

THE NEED FOR MONOPHYLETIC GROUPS

Of these two types of groups, small monophyletic ones will always be most informative in examining whether or not series of "closely related" species live in sympatry in TLRFs. Although series of apparently sympatric, congeneric species have been identified at several tropical forest sites (e.g., see Ashton, 1977; Wheelwright, 1985), a phylogenetic perspective of these genera is required to demonstrate that any particular congeners occurring at one site can be considered to be members of a small monophyletic group. For example, the genus under investigation here, *Polyalthia* Blume, comprises up to 150 species, nine of which have been found at Pasoh Forest Reserve, Peninsular Malaysia (P. S. Ashton, pers. comm.). If, upon analysis of the systematics of the entire genus, no two of these nine species can be placed together in a small monophyletic group, and all nine are best described as phylogenetically distant from one another within the genus, then making a case that a series of "closely related," sympatric species of *Polyalthia* occurs at Pasoh becomes more difficult. In studying this interesting ecological phenomenon, then, a clear understanding of the systematics and biogeography of the group is crucial.

If, as is widely believed (e.g., see Mayr, 1970) allopatric speciation is more prevalent than other modes of speciation, it might be expected that sister species, especially recently derived ones, will rarely occur in sympatry. The term "monophyly" has nothing to do with age, of course, yet when most or only some of the members of a small monophyletic group are found sympatrically, their coexistence is still of interest as they are perhaps the most closely related entities of the group that can be found growing together in nature.

For several reasons, either small monophyletic groups or those including only all the species of a small monophyletic group that occur in sympatry locally are also preferred over nonmonophyletic groups when investigating the origin and maintenance of series of "closely related" sympatric species with regard to competitive exclusion. First, if nonmonophyletic groups are chosen to examine "closely related" species in sympatry, it is possible to miss one or more interactions between sympatric species of closer phylogenetic relationship than those studied. As an example, consider a forest where all of the congeneric species of taxon 1 in FIGURE 1 are known to occur in sympatry. If an investigator chooses to study only species V and X and finds that they have differentiated niches, the implications of this finding would have to be revised if, later, no niche differences could be detected among species V, W, Y, and Z. Alternatively, an investigator might find an extensive and seemingly random pattern of overlap with regard to some niche gradient measured for all of the species of FIGURE 1 but may discover well-differentiated patterns when comparing only the members within taxon 1 or taxon 2.

Another approach to understanding why small monophyletic groups are preferred in addressing the problem of series of closely related, sympatric species derives from a consideration of how phylogenetic distance may be related to niche distance. It is thought often to be the case that, *ceteris paribus*, the closer the degree of phylogenetic relationship, the greater the degree of morphological similarity. It follows that monophyletic groups are often (although not always) those with the greatest degree of morphological similarity among member taxa. If structure is related to function, then members of monophyletic groups should have the most similar niches. It is also often argued (e.g., see Grant, 1963; Wheelwright, 1985; Glazier, 1987) that since most closely related species have the same ecological and physiological heritage via their common ancestral lineage, such species will usually have relatively similar niches (for a contrasting view, see the discussion of the adaptive speciation model, below). This principle has been invoked, at least implicitly, in many of the experimental studies purporting to investigate competitive exclusion, beginning with Gause's experiments with two *Paramecium* species. Studying the niche characteristics of the members of monophyletic groups ensures that the most closely related entities at a site are under consideration and therefore provides the most rigorous test of whether or not sympatric closely related species show niche differentiation.

Finally, if one is interested not only in present patterns (for example, patterns of niche differences of contemporary species) but also in evolutionary processes, monophyletic groups are again the more informative type. To use another illustration from FIGURE 1, if sympatric species U and Z are found to have only slight niche differences, this might be interpreted as indicating a minimal degree of niche divergence from the state of their common ancestor at node A. However, if niche characteristics of V, W, X, and Y are subsequently found to diverge greatly in a similar fashion from U, then it is most parsimonious to interpret the slight differences between U and Z as convergence.

In conclusion, monophyletic groups are the preferred groups for interpreting the biological significance of series of sympatric, closely related species. Such groups are composed of the most phylogenetically recent products of speciation, and thus their members are always the most closely related species that can be investigated when considering any lineage. Only the study of monophyletic groups gives a minimal estimate of the total extent of niche divergence of a lineage radiating from a common ancestor and may yield information about this divergence in relation to speciation and the total pattern of the geographic distribution of the descendant species. As speciation is the wellspring of diversity, an understanding of sympatry-allopatry patterns in relation to niche divergence within small monophyletic groups will be informative as to the origin and maintenance of TLRF diversity.

Unfortunately, most, if not all, of the studies purporting to investigate sympatric, closely related species were carried out at a time when such considerations concerning monophyletic groups were not appreciated. For example, several studies have examined flowering phenology and have arrived at a range of conclusions for different groups. However, what appear to be either random or highly organized patterns of flowering may require reinterpretation in relation to new information concerning the monophyly, phylogeny, and biogeography of the taxa involved (or a more inclusive set of taxa), if monophyletic groups have not been used in such studies. With this caveat in mind, it is important to note that, as will be shown in the systematic treatment below, congeneric groups are by no means necessarily monophyletic ones.

PREVIOUS OBSERVATIONS AND HYPOTHESES

Hypothesis I. Polymorphic Entities

One explanation of monophyletic series of sympatric species in TLRFs is that the phenomenon has been largely misinterpreted: many or all of the members of such series are more appropriately combined into single polymorphic species (e.g., see Levin, 1979). To establish, on morphological grounds, that this is the case for any group of entities, at least one of three fundamental patterns of morphological variation must be demonstrated for the group. The first consists of a few or many characters that are extremely variable on a local scale. The second has been termed "kaleidoscopic" character distributions (Cullen, 1968). In this case, the possible character states for a number of characters exhibit several or all of the possible permutations among taxa. While Cullen used this term to indicate patterns of characters among species, it is also applicable at other levels. The third pattern, clinal variation (e.g., see Mayr, 1970), can lead to problems of classification when two taxa from distant sites are recognized as distinct until morphologically intermediate specimens are found. However, even if local species can be thus "explained away," local differentiation may be biologically significant despite a broader geographic pattern of kaleidoscopic or clinal variation within a taxon. Hence, Leenhouts's (1967) reduction of approximately 255 species of *Allophylus* (Sapindaceae) to one, Jacobs's (1962) similar reduction of species in *Pometia* (Sapindaceae), and descriptions of variable taxa such as *Diospyros* (Ebenaceae) species by White (1962), *Ficus deltoidea* Jack (Moraceae) by Corner (1970), *Drimys piperita* Hooker f. (Winteraceae) by Vink (1970), *Licania* (Chrysobalanaceae) species by Prance (1972), *Calophyllum blancoi* Planchon & Triana and *C. canum* Hooker f. (Guttiferae) by Stevens (1980), *Calamus* (Palmae) species by Dransfield (1981), and *Chisocheton* (Meliaceae) species by Mabberley (1979), among others (see list in Leenhouts, 1967), are difficult to interpret. Some may indeed be examples of taxa in which a high degree of polymorphism leads to problems of definition of morphological species.

In this context species delimitations based upon morphological criteria may require revision as new data from allied studies (e.g., chemosystematics, reproductive biology, or ecology) accumulate, since such new information may not support the decisions based upon morphological patterns alone (Raven, 1976; Levin, 1979; Stevens, 1980). Collections for the great majority of tropical taxa are sparse, and as areas become more thoroughly studied, any one of the above possibilities might alter taxonomic decisions about groups previously recognized as species rich.

It is important to note here that hybridization and hence hybrid swarms are thought to be rare in TLRFs (Ashton, 1969, 1984; Burger, 1980). On the other hand, if it is determined that facultative apomixis occurs to a significant degree in TLRF communities (Kaur *et al.*, 1977; Jong, 1980; Kaur, 1980), then polymorphic apomictic assemblages are to be expected (V. Grant, 1971). A high degree of polymorphism may also be expected for species in which inbreeding is the rule. On theoretical grounds the latter has been proposed as the case for trees of the humid tropics (Corner, 1954; Baker, 1959; Fedorov, 1966; Van Steenis, 1969; but see Chapter 4 in Rogstad, 1986).

Hypothesis II. Groups of Discrete, Closely Related Species Do Occur in Sympatry

Various investigators (references below) have accepted that a number of these complexes comprise discrete, sympatric species, and two further hypotheses have been forwarded to explain their existence.

HYPOTHESIS IIA. SPECIES HAVE OVERLAPPING NICHES. It has been suggested that members of such series may have similar or identical niche characteristics; sympatry here contradicts the competitive exclusion principle, or at least the observations on temperate forest communities noted above. This line of thought has developed from empirical observations, as well as from theoretical considerations of evolutionary and community-organizing forces occurring in TLRF communities. Fedorov (1966, 1976), Poore (1968), Richards (1969), Van Steenis (1969, 1976, 1981), Baker (1970), Wong and Whitmore (1970), Hubbell (1979), Ashton (1979, 1984), Gan *et al.* (1981), Tanner (1982), Yap (1982), and Wheelwright (1985) have all discussed examples where no evidence could be found of niche divergence or niche specialization among sympatric groups of TLRF tree species (also see Klopfer & MacArthur (1961) and Terborgh (1985a) for interesting studies of TLRF birds).

It has been proposed that in many cases where series of very similar species are sympatric in TLRFs, the distinguishing morphological characters are not associated with differences in niche parameters, implying that these series arise not by differential adaptation but rather by selection-neutral processes. Noting that correlates of the high species diversity of these forests are a low density of individuals and, therefore, a small effective population size for most species, Fedorov (1966) suggested that these conditions favor speciation by random drift. His proposal stems, in part, from the work of Wright (1931), who presented a population genetics model in which random fixation of changes in gene frequencies (drift) is likely in organisms with small effective population sizes. If gene flow among small populations is consistently low, speciation by random drift results (King & Jukes, 1969; Maynard Smith, 1970; Stern & Roche, 1974; Bernstein *et al.*, 1985; Slatkin, 1985).

Hubbell (1979) and Ng (1983) have demonstrated that a large percentage of the species found locally in TLRFs exhibit extremely low population numbers and patchy distributions. For example, Ng examined Poore's (1968) data and determined that of the 377 species identified on 23 ha of peninsular Malaysian TLRF, 307 (81%) had ten or fewer mature individuals and 143 (38%) were represented by only one (see Lovejoy (1975) and Terborgh (1985a) for parallel results with TLRF bird species). Such low population densities and patchy distributions of species increase the chances for disruption of gene flow by population isolation, leading to heightened localized inbreeding, and therefore also increase the chances for random drift. For an even more radical yet supportive view, see Barton and Charlesworth (1984).

In this connection, several authors have indicated that since tropical forests are less seasonal than temperate ones, the environmental cues triggering intraspecifically synchronized flowering in temperate forests are largely absent. Flowering within local populations of some species of TLRFs may thus be asynchronous (Holttum, 1953; Koriba, 1958; Fedorov, 1966; Wong, 1983). The occurrence of noncoordinated flowering within species with small population sizes would act to inhibit gene exchange even further and would promote random drift.

The few investigations documenting levels of gene flow for TLRF tree populations (Whiffin, 1978; Chan, 1980; Gan *et al.*, 1981) give evidence that gene exchange is very local and occurs at low levels. In addition, Lovejoy (1975) and Terborgh (1985a) have shown that a large proportion of the birds found in TLRFs have low population densities and very low vagility. Similar patterns have been found for TLRF canopy insect species (Elton, 1975). Gene dispersal in TLRF tree populations will be commensurate with the density and the degree of vagility of their pollen and seed vectors.

Lewis's (1966) suggestion that small populations with a high degree of inbreeding are more susceptible to novel chromosome rearrangements that potentially lead to speciation is worthy of consideration with respect to TLRF tree population structure (also see Bush, 1981). It is important to note that speciation via such changes no longer necessarily requires the troublesome bottleneck of Goldschmidt's (1940) hopeful monsters but rather may occur through genetic phenomena in small populations (Dover & Flavell, 1982; Rose & Doolittle, 1983; Fitch & Atchley, 1985; Wallace, 1985; Krieber & Rose, 1986).

Several authors (e.g., Fischer, 1960; Baker, 1970; Stebbins, 1974; Van Steenis, 1978) have argued that tropical environments are more stable than temperate biomes with respect to the degree and predictability of the fluctuations of physical parameters and are therefore more neutral in selection of variation by physical extremes. In other words, TLRFs are benign environments where a greater degree of marginal or nonselected variation persists. Many of the characters distinguishing among similar species are apparently not adaptive (e.g., see Ashton, 1979) but have arisen through genetic discontinuities originating in stochastic processes (drift) and are functionally of little consequence (Van Steenis, 1969, 1976, 1978). A contrasting view of the effects of relaxed abiotic selection in TLRFs is presented below.

Another theoretical approach that predicts little chance for niche differentiation within complexes of similar species (or among anything but very general guilds of species, for that matter) derives from community-level considerations. If TLRF communities are nonequilibrium communities (Connell, 1978; Hubbell, 1979; Acevedo, 1980, 1981; Chesson & Warner, 1981; Abugov, 1982; Wright & Hubbell, 1983) the composition of any local biota may be more a product of historical chance events than of the relative competitive interactions of the species involved. The taxonomic assemblage at any locale is constantly and randomly changing, a phenomenon that Hubbell (1979) has termed "community drift." Several authors (e.g., Aubréville, 1938, 1971; Grubb, 1977; Strong, 1977; Ewel, 1980; Lang & Knight, 1983; Brokaw, 1985; Lieberman *et al.,* 1985) have noted the importance to all TLRF tree species of regeneration at tree-fall sites. If successful reproduction is largely dependent on having progeny in the appropriate stage of development present in unpredictable forest gaps, then forest structure has a proportionately large stochastic component (Connell, 1978; Burger, 1980; Buckley, 1983; Connell *et al.,* 1984; Comins & Noble, 1985). Since most TLRF species have extremely low population densities, if the community-drift hypothesis holds most TLRF species will be randomly associated through time. Competitive interactions between or among species, as well as resource availability, will be completely unpredictable, and therefore persistent directional selection will be rare. Such stochastic competition and distribution of resources may lead to selection for generalists (Went, 1973; Hubbell, 1979; Burger, 1980; Buckley, 1983; Ashton, 1984) and thus act upon a significant portion of TLRF species by generalizing their niches rather than driving niche divergence.

The consequences of nondirectional selection can also be explored in more formal terms. Kimura and Weiss (1964) and Kimura and Ohta (1971) have shown that in diploid populations, mutations become fixed predominantly by random drift when the quantity $4N_es$ (N_e represents the effective population size, and s denotes the coefficient of selection) is sufficiently smaller than 1 (for example, Hartl and colleagues (1985) suggest when $4N_es < 0.1$). In tropical humid forests the unpredictability of both one's competitors and the matrix of available resources over long periods of time may give vastly varying and often conflicting values of s for most alleles, thus reducing the value of s to close to 0 (selection nondirectional). As s approaches 0, $4N_es$ becomes $\ll 0.1$, and this is exacerbated by the small population sizes found in TLRF trees. Lande (1976) has presented a model that suggests phenotypic evolution may be subject to drift even in large effective populations where selection is weak. A few empirical studies (Malecot, 1959; Selander, 1970; Carson *et al.,* 1982) have shown that when directional selection is weak or nonexistent, character variability may increase or drift.

The link between the theories of community drift and the random drift of species in TLRF communities (and the implications of this link for niche divergence of sister species descendent from a TLRF tree ancestor) is perhaps best established by considering the most widely accepted model of speciation, an allopatric one. Under this model, two lineages from a common ancestor first become geographically isolated. Due to the low population sizes common to TLRF trees, random sampling of the once-common genetic pool and accumulation of different mutations in the two isolated lineages lead to genetic divergence of the daughter populations. Gottlieb (1984, 1985) has pointed out that many of the morphological differences distinguishing species are under simple genetic control involving a low number of alleles, a situation facilitating rapid fixation of morphological differences by random drift. Since competitors and resource distribution are unpredictable, no directional selection takes place. Divergence is due to genetic sampling errors only, and morphological differences need not have any pronounced functional significance (Van Steenis, 1978, 1981; King, 1984; Davis & Gilmartin, 1985), especially if selection for generalists prevails. If the two sister lineages subsequently achieve sympatry, it is highly unlikely, due to the extremely low population numbers and densities of species in TLRF tree communities, that the two lineages will ever compete over resources in any predictable manner; therefore, the forces driving competitive exclusion and niche divergence (or character displacement) envisioned as active in temperate communities will be extremely weak in TLRF communities. Daughter populations that have diverged morphologically and genetically (to a degree that they have become genetically incompatible) may coexist indefinitely in TLRF communities without having diverged with regard to realized niche characteristics. Community drift and random drift thus may interact to generate series of closely related, sympatric species with broad niche overlap in these biomes.

HYPOTHESIS IIB. SPECIES HAVE DIVERGENT NICHES. An alternative hypothesis has also been forwarded to describe the sympatric occurrence of series of closely related entities (e.g., species), granted that it can be demonstrated that distinct entities exist. A number of authors have argued that similar species coexist in TLRFs by occupying narrowly defined, distinct niches, thereby not engaging in competition along at least one niche gradient. Wallace (1878, p. 66) noted that, "In the equatorial zone, there is no struggle against climate." The forces of natural selection arise from biological interactions rather than physical constraints, leading ". . . to the filling up of every place in nature with some specially adapted forms." Dobzhansky (1950) and Williams (1964) have reemphasized that biological competition is the most important factor in natural selection in the tropics (as opposed to physical environmental factors in temperate forests), and that this has led to more specialization for narrow niches and, in turn, a greater diversity of species.

Dobzhansky (1950) also pointed out that TLRFs have a greater variety of niches than other terrestrial forest habitats due to their greater structural complexity, a notion that has been further reinforced by Corner (1954), Ricklefs (1977), and Terborgh (1985b). If this is true, the higher structural heterogeneity of TLRF communities would increase the possibilities for the coexistence of similar, closely related species, each with a distinct niche, thereby permitting greater species packing.

Ashton (1969) has proposed that such series of species may be the result of adaptive speciation (see Ringo *et al.*, 1985, for a summary of the model). Each species in such a series may actually have subtly different niche characteristics with respect to at least one resource gradient. Such niche differentiation may take place with allopatric speciation or occur through divergent selection driven by competition between sister species once they come into sympatry again.

Studies of TLRF organisms reporting empirical evidence of similar, closely related species each having at least one unique niche characteristic and growing sympatrically include those by Snow (1965), Diamond (1973), Burger (1974, 1980, 1981), Vandermeer and colleagues (1974), Stiles (1975), Gentry (1976, 1982), Chan and Appanah (1980), Janzen (1980), Haber and Frankie (1982), Fleming (1985; although significant overlap was found for all parameters examined), Martin (1985), and Moulton (1985).

Burger (1974, 1981), Stevens (1980), and Ashton (1984) have argued that in many cases, sister species grow allopatrically in the tropics. Such patterns, however, need careful scrutiny, as they may reflect more about how taxonomists recognize taxa than about anything of biological significance (Stevens, 1980) and may therefore falsely support Gause's conclusions.

A METHOD OF EXAMINING THE COMPETING CONCEPTS

Most of the theorizing and supporting evidence reviewed in the paragraphs above are based on preliminary, descriptive, or anecdotal information. The monophyly of the groups discussed has not been established, and quantitative studies of character-state variation within and among putative entities to estabish their delimitation are lacking. Further, attempts to demonstrate the sympatry of distinct entities of advocated monophyletic groups, and then to distinguish whether the entities of such a complex are in fact ecologically equivalent or rather have differentiated with respect to one or more niche characteristics, have been neglected.

Obviously, a clear understanding of the taxonomy of the members of any group intended for such investigations is crucial. Attempting to compare niche characteristics of sympatric entities whose definitions as species are not well understood will most likely be misleading. The following systematic treatment of the *Polyalthia hypoleuca* complex is the foundation for a series of articles in which I will address all of the concerns noted in the previous paragraph, thereby enabling a choice of which of the above three hypotheses is most applicable with regard to this group of taxonomically allied Malesian tree species.

To examine whether or not the niches of the species in this complex were segregated in any way, I employed methods commonly used to define niche characteristics for temperate plants, recognizing from the outset that this approach might yield only negative evidence. That is, the failure of these methods to detect niche differentiation would not eliminate the possibility that niche differentiation does exist between entities for one or more uninvestigated features. Nevertheless, the finding that two morphologically similar species have similar or identical niche characteristics as defined by techniques that have successfully detected niche differentiation in temperate plants is theoretically interesting and prepares the ground for alternative or more detailed future investigations. However, as will be seen in the subsequent associated articles, such negative evidence was not a problem in this case. In fact, information concerning the niche characteristics of the species of this complex serves to support my systematic conclusions and must thus be consulted if one is interested in understanding the sum of the evidence speaking to the systematic decisions, based primarily on morphometric analyses, presented here.

Only one group was examined in this research. A number of them will have to be investigated with regard to these hypotheses before we can do much more than speculate about the causal forces generating the patterns. Information on these issues is central to understanding the origin and maintenance of TLRF diversity. A forest structured predominantly under hypothesis I is a very different community than one composed of groups conforming strictly to hypothesis IIB. Of course, a range of possible combinations between these two extremes is probable locally (will generalizations be possible at more synoptic levels?), and a more accurate description of the distribution curve for the realized possibilities will yield deeper insight into evolutionary processes in TLRF biomes, as well as have implications for forest utilization and management practices.

SYSTEMATICS OF THE POLYALTHIA HYPOLEUCA SPECIES COMPLEX

After examining several groups of potential candidates for this investigation, I chose the *Polyalthia hypoleuca* complex. I was able to determine several characters suggesting that it was a monophyletic group, and in preliminary field work I found that some of the species do grow in sympatry in statistically tractable sample sizes.

The specific goals of this systematic treatment are to demonstrate that this complex of species is indeed monophyletic, to apply various morphometric techniques to support the conclusion that discrete entities (morphological species) exist within this monophyletic group, and to present a formal classification for the group.

THE GENUS POLYALTHIA AND THE PLACEMENT OF THE P. HYPOLEUCA COMPLEX

Polyalthia comprises approximately 100 to 150 species and is therefore one of the larger genera of the Annonaceae. Members of the genus are generally restricted to tropical latitudes and lower altitudes. They are distributed in humid regions of Africa and Madagascar, and from India and Sri Lanka through Southeast Asia and Malesia to Fiji and the associated islands. Sinclair (1955), the last author to revise a significant portion of the genus, placed it in tribe Unoneae, which he defined primarily on the basis of a single character: petals that are valvate in the flower buds. This agrees with the placement of the genus by other systematists, including Bentham and Hooker (1862), Fries (1959; he further subdivided the tribe into informal groups, *Polyalthia* being placed in the *Polyalthia* group), and Hutchinson (1964; *Polyalthia* is placed in Group A of subtribe Xylopineae). In contrast, Walker (1971) included *Polyalthia* in his tribe Uvarieae, based upon considerations of pollen morphology.

However, all of these classification schemes need further investigation. For example, as is shown in FIGURE 2, within the *Polyalthia hypoleuca* complex, which as I shall demonstrate below is clearly monophyletic, some members (e.g., *P. discolor* Diels) have petals that are distally (but not basally) imbricate in the floral buds, while at least one (*P. glauca* (Hassk.) Mueller) apparently has only valvate petals. Imbricate bud petals have been noted for other species in *Polyalthia* and in other genera usually placed in the Unoneae (Okada & Ueda, 1984; pers. obs.), suggesting that the distribution and the taxonomic importance of this character are in need of review. Further examinations of petal aestivation should include observations on degree of petal overlap, and whether the petals overlap distally, basally (including insertion), or both.

Indication that previous treatments are in need of further scrutiny also derives from Walker's (1971) observations that two species of *Polyalthia* differ in pollen characters from the other congeners examined. These characters, as well as several other nonpollen characters (discussed below), unite these two species with four not examined by Walker, and the mutual possession of these characters constitutes the evidence for the monophyly of the *P. hypoleuca* complex (the pollen data will be treated in detail in Rogstad & Le Thomas, in prep.). The pollen morphology of these species is different from that of the other *Polyalthia* species examined to date, with the few important exceptions discussed below.

It is difficult to reconcile the pollen characters of the *Polyalthia hypoleuca* complex with those of Walker's Uvarieae, to which other members of *Polyalthia* conform (see also Le Thomas, 1988). The distally imbricate floral bud petals and the distinguishing pollen type within the complex render its placement both within the genus and within the subfamilial classification proposals noted above problematic. Thus, the clearly monophyletic *P. hypoleuca* complex may be the sister group to some taxon in another tribe, or it may be derived from within *Polyalthia*. Until the phylogenetic relationships of the complex are more clearly understood, assigning new generic or sectional status to this constellation of species may create future nomenclatural problems. Thus, for

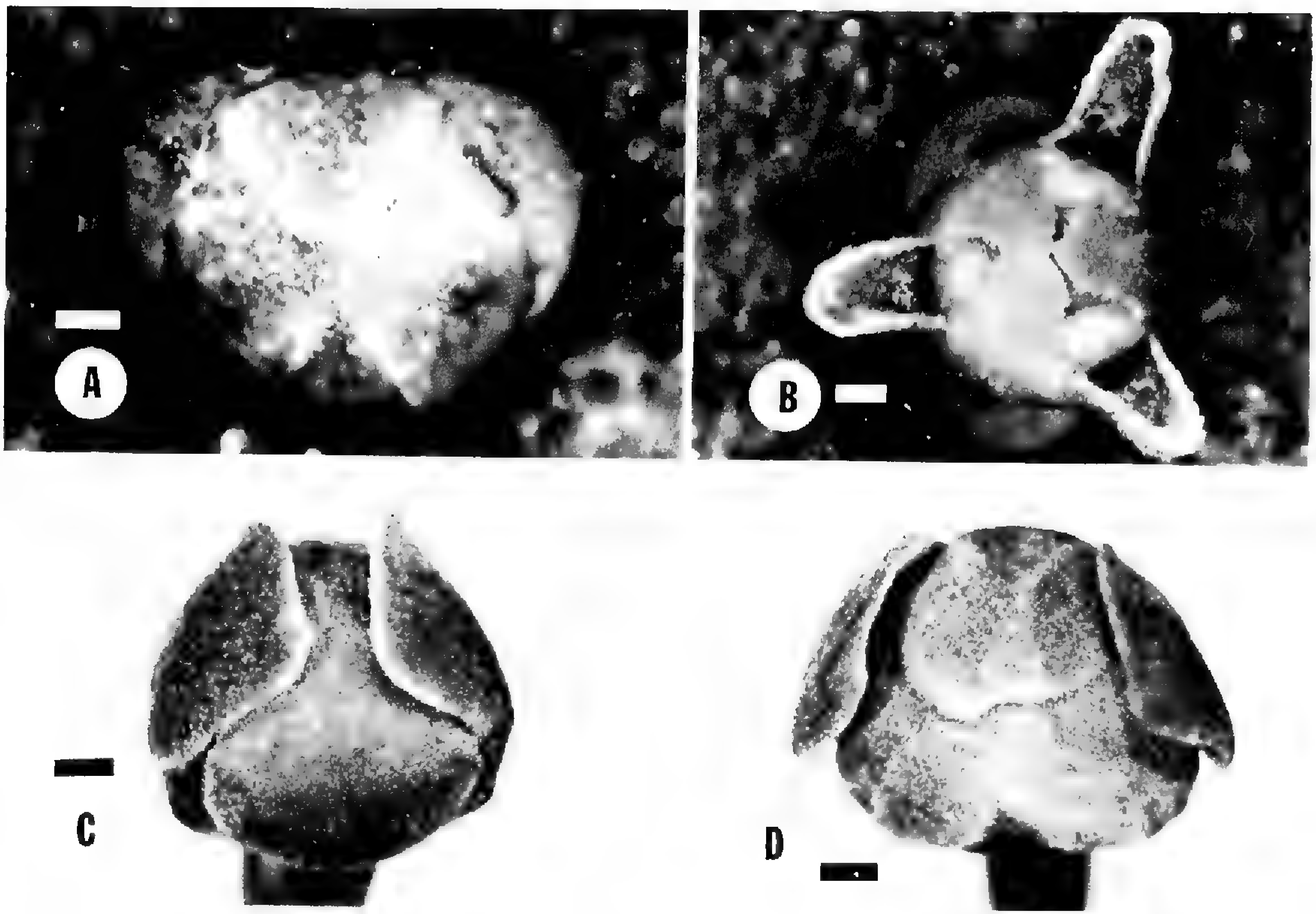

FIGURE 2. Petal aestivation in buds from *Polyalthia hypoleuca* complex. A, B, *P. glauca* (*Rogstad 939*): A, outer petals not substantially overlapping; B, inner petals not substantially overlapping (outer ones pulled back). C, D, *P. discolor* (*Rogstad 814*): C, outer petals slightly overlapping; D, inner petals significantly overlapping (lower outer one removed). Scale bars = 1 mm.

the purposes of this investigation, the most prudent approach is to maintain the group within *Polyalthia* until the needed reclassification is attempted. The implications of the above taxonomic problems when using congeneric species to investigate the problem of closely related, sympatric species are explored below.

Sinclair (1955, and references therein) followed most previous researchers in dividing the genus into two sections, *Eu-Polyalthia* Blume (or, by later convention, *Polyalthia*), defined as those species with two or more ovules per carpel, and *Monoon* Miq., comprising those with only one. Sinclair further suggested that distinct species groups existed within each section but did not explicitly propose character suites by which they could be distinguished. Examining these groups as candidates for a monophyletic group with sympatric species, I determined from herbarium and field work that one complex of species, the *P. hypoleuca* complex, was especially suitable in that a unique suite of characters is shared by all the members of the group and various members were found growing sympatrically at different field sites. My final concept of this complex, although related to Sinclair's Group 1 of sect. *Monoon* (1955; he included only *P. sumatrana* (Miq.) Kurz, *P. hypoleuca* Hooker f. & Thomson, *P. glauca, P. longifolia* (Sonn.) Thwaites, and *P. parkinsonii* Hutch.), is quite different from his as to both the limits of the group and the circumscriptions

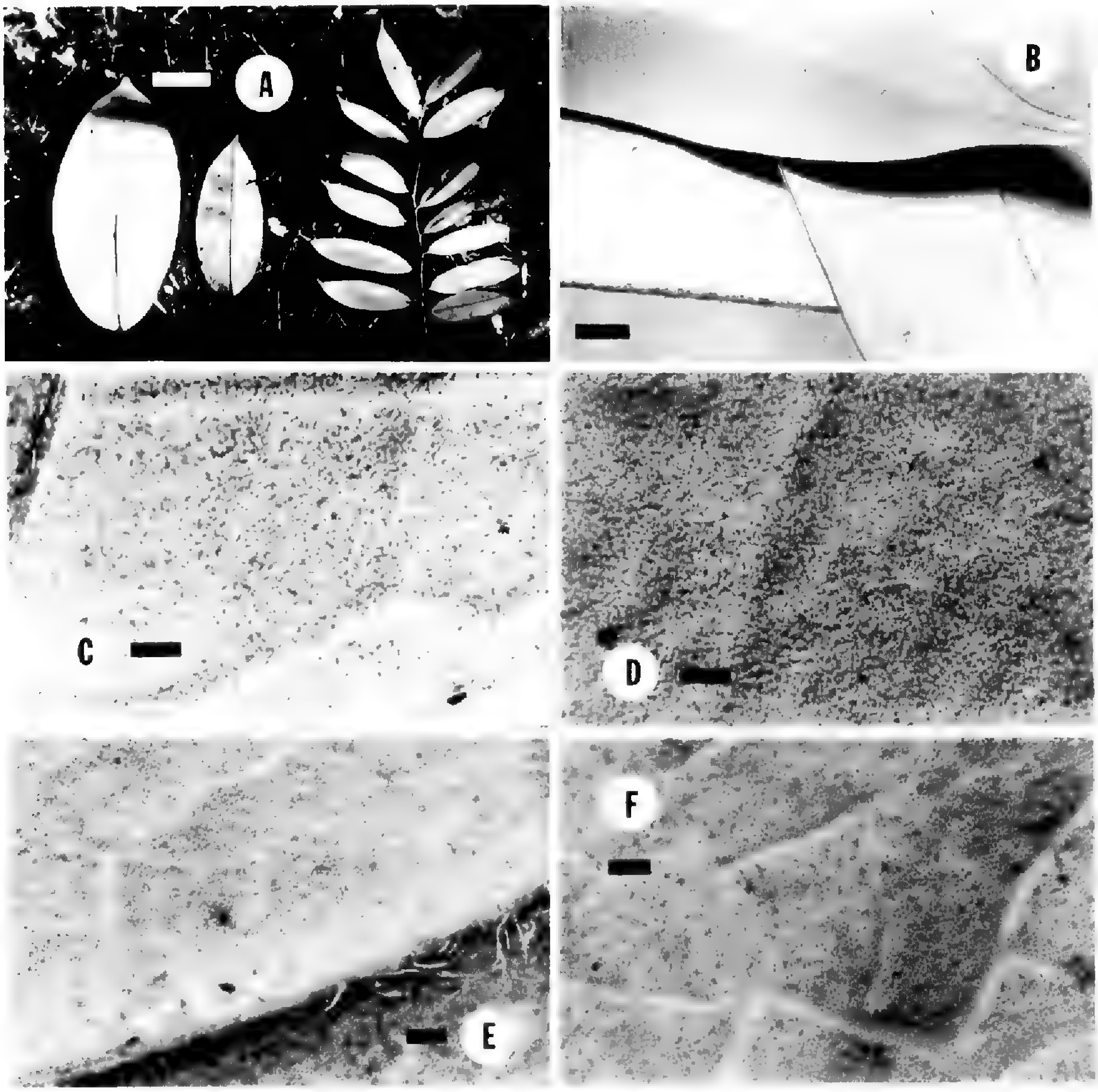

FIGURE 3. Leaves. A–D, species of *Polyalthia hypoleuca* complex (note weak secondary venation and uniformly white abaxial surfaces): A, *P. ovalifolia* (left; *Rogstad 843*) and *P. hypoleuca* (right; *Rogstad s.n.*, 19 Dec. 1983), scale bar = 5 cm; B, 3 species sympatric at Pasoh Forest Reserve, peninsular Malaysia (*P. hypoleuca* above, *P. sumatrana* lower right, *P. glauca* lower left), scale bar = 0.5 cm; C, *P. glauca* (*FRI 27582*), uniformly distributed papillae, scale bar = 0.5 mm; D, *P. multinervis* (*Rogstad 813*), uniformly distributed papillae, scale bar = 0.5 mm. E, F, abaxial surfaces representative of *Polyalthia* species not in *P. hypoleuca* complex (note absence of dense, uniformly distributed papillae): E, *P. cauliflora* (*Nur 18585*); F, *P. insignis* (Hooker f.) Airy-Shaw (*SAN A 4325*); scale bars = 0.5 mm.

of the species within it. Nevertheless, Sinclair was probably segregating his Group 1 by implicitly recognizing some of the characters by which I explicitly delimit the *P. hypoleuca* complex here.

THE LIMITS OF THE POLYALTHIA HYPOLEUCA COMPLEX

I include in the *Polyalthia hypoleuca* complex only those species with all of the following seven characters: densely and uniformly distributed papillae cov-

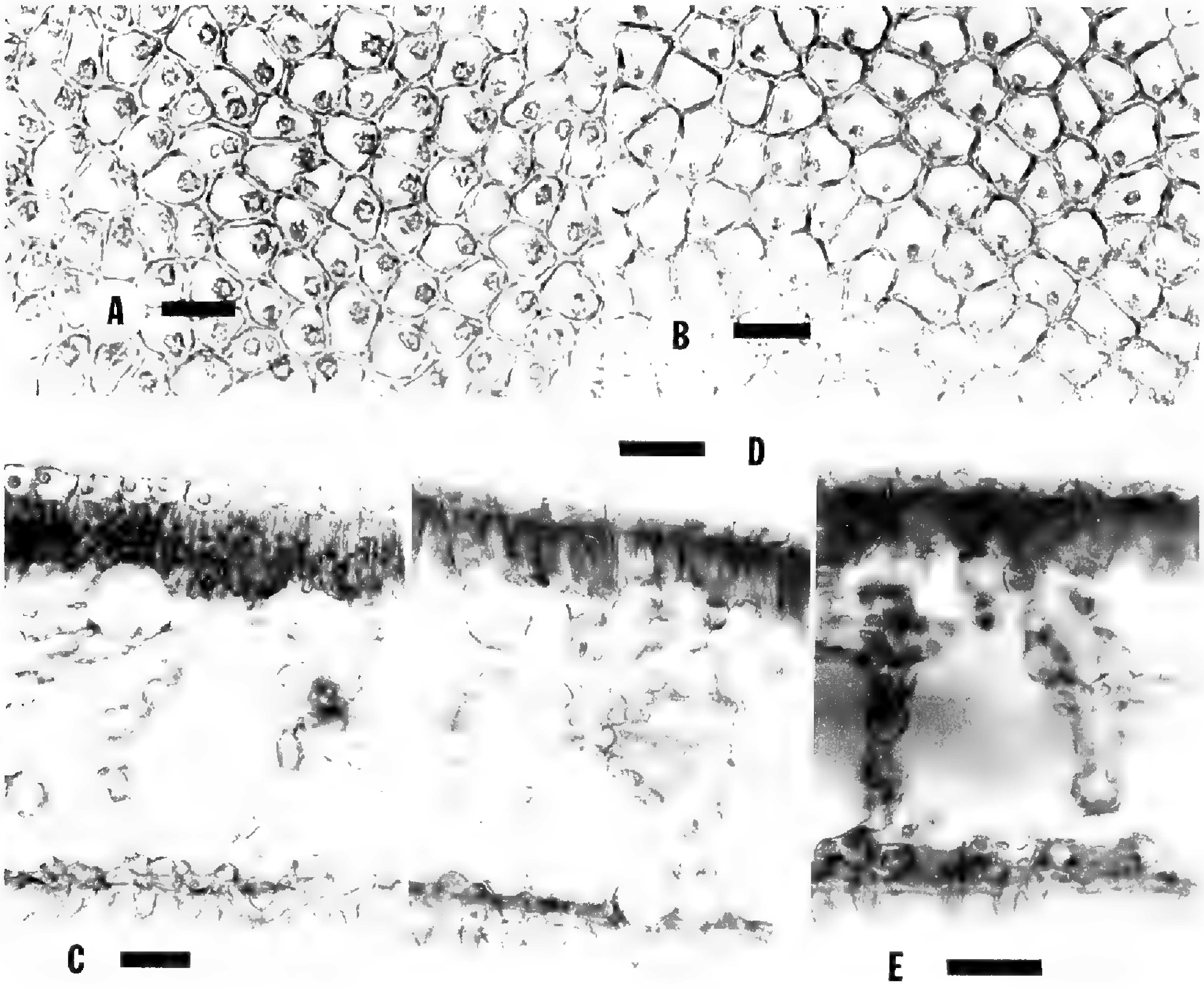

FIGURE 4. Features of leaf anatomy shared by all members of *Polyalthia hypoleuca* complex. A, B, epidermal peels showing thickened anticlinal walls: A, *P. sumatrana* (*Rogstad 508*); B, *P. discolor* (*Rogstad 814*). C–E, cross sections showing abaxial papillae: C, *P. glauca* (*Rogstad 939*); D, *P. sumatrana* (*Rogstad 508*); E, *P. multinervis* (*Rogstad 813*). Scale bars = 30 μm.

ering the abaxial surface of leaves; extremely thin secondary veins differing little in diameter from the tertiary ones; secondary veins usually not forming a strong or relatively straight intramarginal vein, and relatively more numerous and closer together than in most taxa of the family; fundamentally white bark; monosulcate, "boat-shaped" pollen; pollen-wall architecture including a psilate, moderately perforated tectum, regular columellae, and a bipartite, foliated basal layer (Rogstad & Le Thomas, in prep.); and spiniform endosperm ruminations.

The most easily recognized of these characters is the densely and uniformly distributed papillae on the abaxial surface of the leaves (FIGURES 3, 4C–E). These papillae, which are lacking in all other species of *Polyalthia* (see, for example, FIGURE 5), cannot be seen readily with a 10× hand lens, and so the use of a dissecting microscope (at least 25×) is recommended. It is probably the dense distribution of these papillae that colors the lower leaf surfaces of all species in this group white (often mixed with pale green, brown, gray, or gold). While several genera of this family (e.g., the *Dasymaschalon* Dalla Torre &

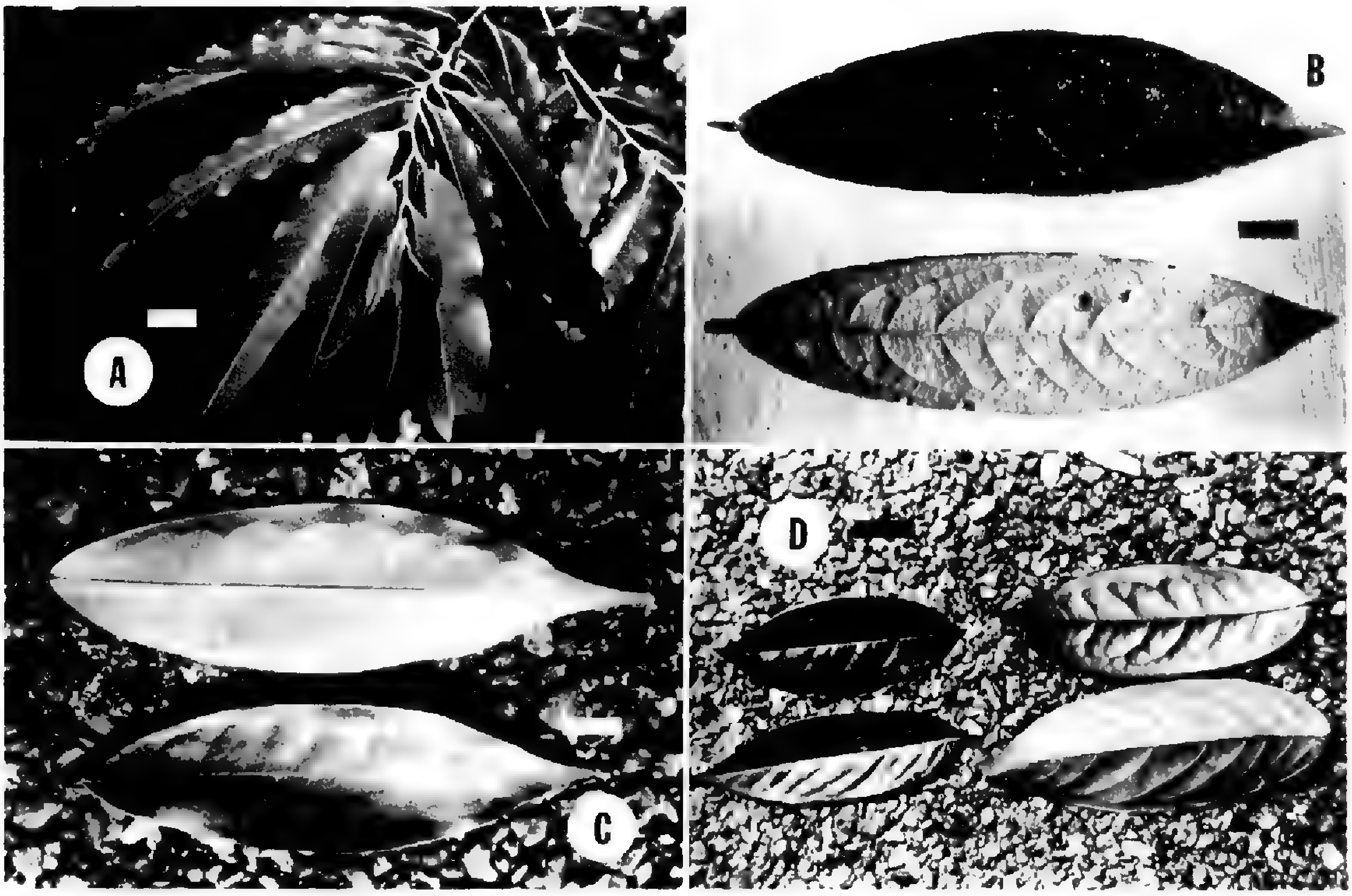

FIGURE 5. Leaves from *Polyalthia* species not in *P. hypoleuca* complex (note strong secondary venation): A, *P. longifolia* (*Rogstad 960*), scale bar = 2 cm; B, *P. cinnamomea* (*Rogstad 936*), scale bar = 2 cm; C, *P. cauliflora* (*Rogstad 951*), scale bar = 1 cm; D, *P. rumphii* (above; *Rogstad 922*) and *P. jenkinsii* (below; *Rogstad 956*), scale bar = 3 cm.

Harms–*Desmos* Lour. complex; some species of *Friesodielsia* Steenis, *Popowia* Endl., and *Xylopia* L.) have at least a few species with white abaxial leaf surfaces, most lack papillae, so this color must be caused in the latter genera by some other feature of the abaxial surface, for example, the nature of the waxy cuticle.

As far as I am aware, with the possible exceptions discussed here and below, leaf papillae of similar distributional uniformity, density, and structure are not found regularly in any other taxa of the Annonaceae. Roth (1981; pers. comm.) has indicated that within the family, the papillae most similar to those of the *Polyalthia hypoleuca* complex are found in *Onychopetalum* R. E. Fries, *Bocageopsis* R. E. Fries, *Richella* A. Gray, *Rollinia* St. Hil., *Ruizodendron* R. E. Fries, and *Woodiella* Merr. I have examined the holdings of these taxa (see APPENDIXES 1, 2) at A, GH, MO, and US, and in none have I seen leaf papillae identical in form or distribution to those found in the *P. hypoleuca* complex. Further, all of these taxa are quite different in floral and fruit morphology from members of the complex; only *Woodiella* is also an Old World genus. In a survey of 38 Neotropical genera, Van Setten and Koek-Noorman (1986) reported papillae for at least some species in *Bocageopsis, Ephedranthus* S. Moore, *Onychopetalum, Ruizodendron, Annona* L., and *Rollinia*. However, a comparison of their description of the papillae and their *figs. 4* and *9* with FIGURE 4 here demonstrates differences in papilla structure and distribution between members of the *P. hypoleuca* complex and all of the genera they listed. Still, further investigations of the distribution and taxonomic importance of abaxial leaf papillae in the genera noted by Roth, as well as by Van Setten and Koek-Noorman, are needed. While none of the members of these genera has all seven of the characters defining the *P. hypoleuca* complex, and all share with their congeners numerous characters not found in the complex, some of these species are worthy of consideration in the search for possible outgroups to the complex.

Of all the characters setting the *Polyalthia hypoleuca* complex apart, those relating to leaf venation are the most difficult to describe because occasionally only subtle differences exist between members of the complex and other species. Rarely, no differences are readily apparent. Thus, these characters are best examined in direct comparisons between specimens. First, the secondary veins are very fine and differ little in diameter from the tertiary ones, while in most Annonaceae they are much broader. In the *P. hypoleuca* complex, veins of both degrees are only very slightly raised above the leaf surface and are often difficult to see. Second, the secondary veins do not usually form a strong or relatively straight intramarginal vein, and they are relatively more numerous and closer together than in most taxa of the family. The vein characters of the *P. hypoleuca* complex can be compared with those of other representative species of the genus in FIGURES 3 and 5.

The bark of species of the *Polyalthia hypoleuca* complex is a rare type in the family in that it is fundamentally white (FIGURE 6), although especially on the young twigs and branches it may be tinted with shades of yellow or red in some species. I have been unable to find identical bark coloration in any other species of the genus, or even within the family (e.g., see Sinclair (1955); pers. obs.), with the following exceptions. White bark has been noted for *Pseudoxandra cuspidata* Maas (although brown bark also occurs in this species) and in *Oxandra leucodermis* (Spruce) Warm., apparently the only two known Neotropical species with this characteristic (Maas *et al.,* 1986).

Another character uniting the species of the *Polyalthia hypoleuca* complex was first noted by Walker (1971). In his survey of annonaceous pollen types, he placed *Polyalthia* in his tribe Uvarieae, which consists of those taxa with solitary, inaperturate, radiosymmetric pollen. He noted, however, that of the 22 species examined, *P. glauca* and *P. hypoleuca* stood apart in having sulcate, "boat-shaped" pollen. All of the taxa in the *P. hypoleuca* complex have pollen that is indistinguishable from that of these two species (Rogstad & Le Thomas, in prep.). I have also examined the pollen of four other Malesian species of *Polyalthia* (i.e., *P. lateriflora* (Blume) King, *P. obliqua* Hooker f. & Thomson, *P. sclerophylla* Hooker f. & Thomson, *P. socia* Craib; *Rogstad 931, 935, 930,* and *958,* respectively) not treated by Walker; none of these species has pollen of the type found in the *P. hypoleuca* complex (see also Le Thomas, 1988). Walker (1971) found that sulcate, boat-shaped pollen was extremely rare in the Old World, occurring only in the genus *Enantia* Oliver of Africa and the two species of *Polyalthia* noted above. Walker did find such pollen in ten Neotropical genera, and these along with *Enantia* constitute his tribe Malmeae. Le Thomas (1981) has also found this pollen shape in a few other African genera and, more importantly here, in at least seven species of *Polyalthia* from

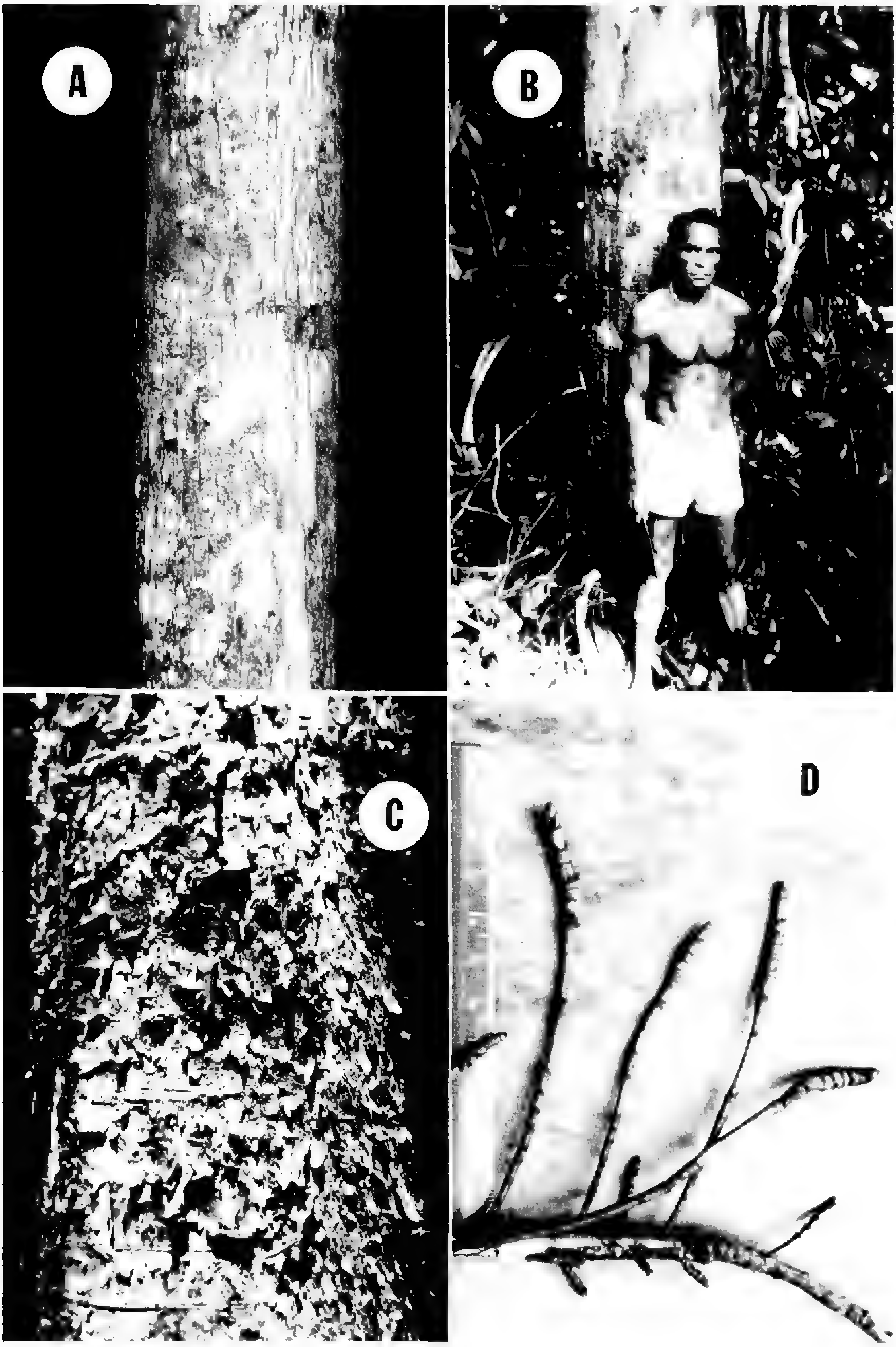

FIGURE 6. A–C, bole characters in *Polyalthia hypoleuca* complex: A, *P. hypoleuca* (79 cm girth at breast height), fissured bark lacking hoop marks; B, *P. discolor* (123 cm girth at breast height), smooth bark with horizontal hoop marks; C, *P. glauca* (104 cm

Africa and Madagascar. It should be noted that Gottsberger and Silberbauer-Gottsberger (1984) have cautioned that the apparent pollen shape of some Annonaceae may be an artifact of preparation.

Another feature that indicates a close genealogical relationship among the species here included in the *Polyalthia hypoleuca* complex is the architecture of the pollen wall (Rogstad & Le Thomas, in prep.). The five species of the complex for which pollen-wall examinations have been possible have a psilate, moderately perforated tectum, with regular columellae and a bipartite, foliated basal layer. While pollen appropriate for TEM observation of this feature has not yet become available for the sixth member of the complex (*P. ovalifolia* S. H. Rogstad), observations by compound microscope indicate that it agrees in external tectal construction with that from other members here incuded in the complex. This type of pollen architecture appears to be rare in the family; *Enantia chlorantha* Oliver (Le Thomas, 1981) and *Ephedranthus amazonicus* R. E. Fries (Waha, 1985), both placed by Walker in his tribe Malmeae, are the only examples thus far known from outside of the genus. The majority of the numerous other Annonaceae examined have a different surface architecture (Walker, 1971; Le Thomas, 1981; Waha, 1985; pers. obs.). Within *Polyalthia*, Le Thomas (1981) has described a pollen-wall architecture very similar to that of the species of the *P. hypoleuca* complex for *P. capuronii* Cav. & Keraudren, *P. emarginata* Diels, *P. heteropetala* Diels, and *P. oligosperma* (Danguy) Diels, all from Madagascar.

A final character that unites the members of the *Polyalthia hypoleuca* complex concerns the nature of the endosperm ruminations. All Annonaceae have endosperm that is divided by "ruminations as transverse folds of the tegmen or, also, of the testa or middle integument" (Corner, 1976, p. 68). In cross section the seeds have ruminations that can be a) very regular and platelike with a central "cross" of endosperm (Corner, 1949, *fig. 12A*; FIGURE 7C); b) irregular as though the regular plates just mentioned are broken into pieces of various sizes and distributions (Corner, 1949, *fig. 14D, E*; FIGURE 7D); or c) numerous, very fine, and needlelike (spiniform; FIGURE 8A, B). The endosperm ruminations of most of the annonaceous species that have been described in the literature are type a or b (e.g., Corner, 1949, 1976; Periasamy & Swamy, 1961; Rao, 1975, 1979, 1982), while those of all of the species here included in the *P. hypoleuca* complex are spiniform. Outside of the genus *Polyalthia*, spiniform ruminations have been found in *Bocageopsis*, *Cremastosperma* R. E. Fries (not all species), *Enantia*, *Onychopetalum* R. E. Fries, *Oxandra* A. Rich. (not all species), *Piptostigma* Oliver, *Polyceratocarpus* Engler & Diels, *Popowia* Endl., *Pseudoxandra* R. E. Fries, *Pseuduvaria* Miq., *Richella* A. Gray, and *Unonopsis* R. E. Fries (see APPENDIX 1).

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girth at breast height), mature tree, flaking white bark with red bole beneath (note hoop marks). D, *P. glauca*, distal portion of emergent pneumatophore (note annular scars indicating rhythmic extension growth).

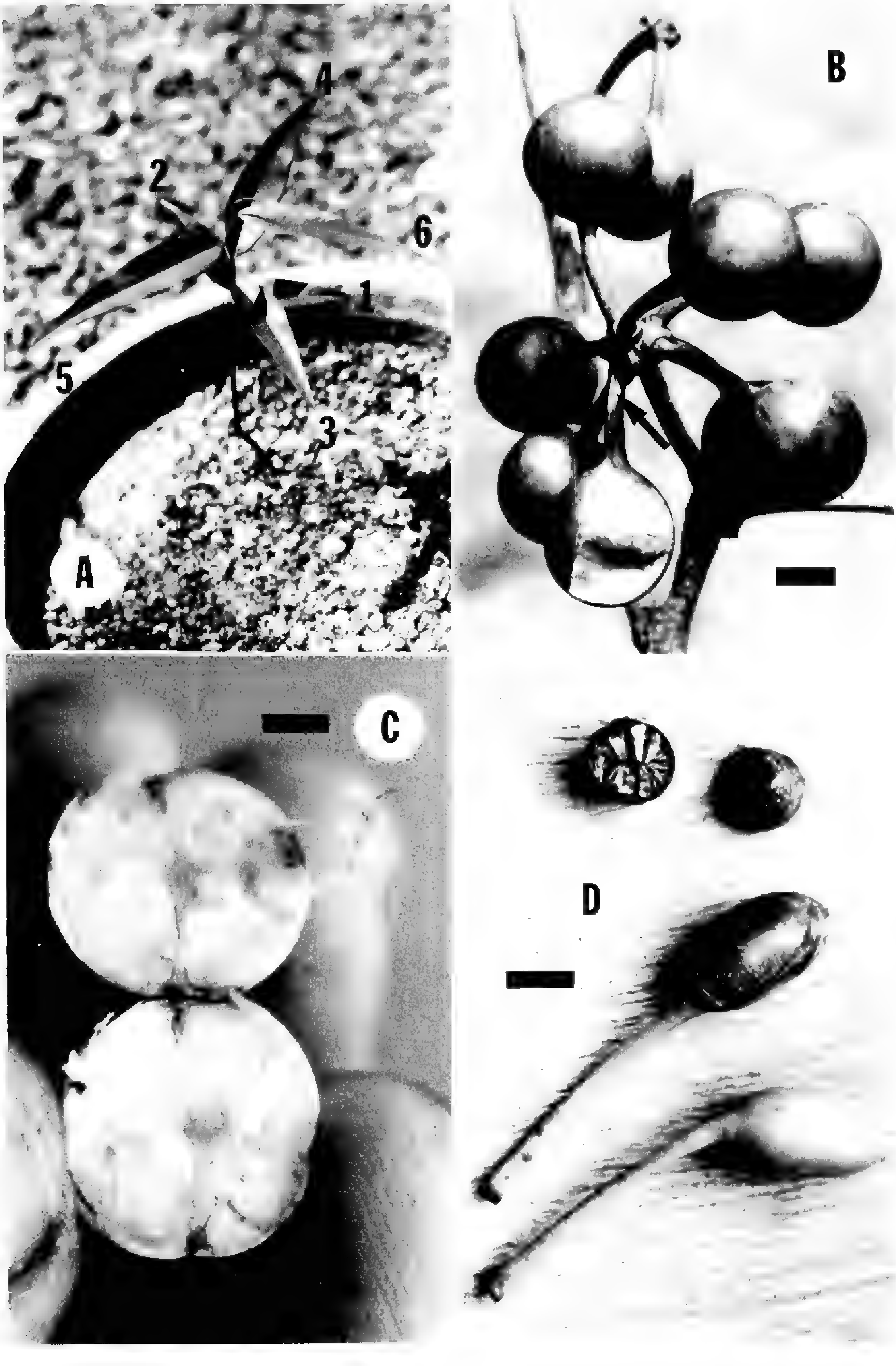


FIGURE 7. Seedling, fruits, and seeds: A, *Polyalthia hypoleuca* seedling, mature leaves numbered in order of development; B, *P. discolor* (*Rogstad 814*), mature fruits, micropylar region of seed exposed indicating ventral orientation of seed (arrow indicates

FIGURE 8. Seeds of *Polyalthia hypoleuca* complex: A, *P. multinervis* (*Rogstad 813*), ellipsoid, with spiniform endosperm ruminations, pronounced aril scar (arrow), and circumferential ridge; B, *P. sumatrana* (*Rogstad 508*), sections at various levels, showing spiniform endosperm ruminations throughout; C, *P. discolor* (*Rogstad 814*), regular, lozenge shaped, circumferentially grooved, lacking pronounced aril scar at micropylar region (arrow); D, *P. glauca* (left; *Rogstad 939*), *P. hypoleuca* (center; *Rogstad 912*), *P. sumatrana* (right; *Rogstad 508*).

I have also examined species from over 24 additional genera of Annonaceae (including 34 species of *Polyalthia*, and all genera now known to share at least one other character from the suite defining the *Polyalthia hypoleuca* complex) for this character (see APPENDIX 1). Seeds with exclusively needlelike ruminations were lacking in these other genera but were found in *P. oliveri* Engler & Diels, *P. stuhlmannii* (Engler) Verdc., *P. suaveolens* Engler & Diels, *P. suberosa* (Roxb.) Thwaites, *P. capuronii*, and *P. oligosperma*. Of these species, only the latter two have as many as three of the seven characters I use to delimit the complex, a finding discussed further below. Although wider surveys of this seed character are needed, the above evidence indicates that the spiniform endosperm ruminations found in all of the species of the *P. hypoleuca* complex can be included in the suite of characters distinguishing this group.

"stigmatic crest" remnant on stipe), scale bar = 1 cm; C, *P. longifolia* (*Rogstad 960*), cross section of mature seed, scale bar = 3 mm; D, *P. jenkinsii* (*Rogstad 956*), near-mature carpels and seed, scale bar = 5 mm.

Another character deserves mention as a potential member of the suite defining the *Polyalthia hypoleuca* complex. A survey of the leaf anatomy of several species of the genus has revealed that all species of the complex have an adaxial epidermis in which all or most cells have straight, thickened anticlinal walls (FIGURE 4A, B). In this survey 34 other species from the genus were examined for this character (see APPENDIX 2); it was lacking in all but two of them. These results contrast with the findings of Van Setten and Koek-Noorman (1986), who found similar-looking adaxial epidermis in several taxa, which they did not list. These authors suggested that the anticlinal walls appear thickened due to "thickened cuticular ledges following the anticlinal . . ." walls (p. 22; see *figs. 6, 7*). With the species of the *P. hypoleuca* complex, it is not clear whether thickened ledges or thickened anticlinal walls give rise to this effect (see FIGURE 4C). While this character is not common in *Polyalthia,* its distribution in the rest of the family is unclear, so it cannot yet be included in the list of characters defining the complex. Interestingly, the only other two species of *Polyalthia* found to have an adaxial epidermis similar to that seen in all members of the *P. hypoleuca* complex are from Africa, and one of these, *P. oligosperma* (Dangy) Diels, is a leading potential candidate as an outgroup species for the complex.

In summary, a unique suite of seven characters is shared by all and only the members I am placing in the *Polyalthia hypoleuca* complex. Although these characters are uncommmonly found in other taxa of the family, each usually occurs in relative isolation from the other characters. A detailed analysis of the distribution of these characters outside of the *P. hypoleuca* complex has been conducted (Rogstad & Le Thomas, in prep.), and only an outline of the resulting conclusions regarding the monophyly and taxonomic position of the complex is given here. Within *Polyalthia,* only *P. capuronii* and *P. oligosperma* (both from Madagascar) have as many as three of the seven characters, making them the best congeneric choices as possible sister lineages to the *P. hypoleuca* complex. Outside of the genus, it is interesting that the seven characters find their densest distribution in a group of eleven genera designated by Walker (1971) as tribe Malmeae. Of these, one African and four Neotropical genera have species possibly possessing three of the seven characters, while only the Neotropical genera *Oxandra* and *Pseudoxandra* have species perhaps possessing as many as five, making these latter species the most likely choices as sister taxa to the complex. Note that all of the species having more than two of the seven characters are from Africa/Madagascar or the Neotropics, giving strength to the notion that at the least, the members of the *P. hypoleuca* complex are the only Asian-Oceanic members of a larger monophyletic group with other members occurring in other areas. Further, all of the taxa noted above as having at least one of the seven characters share with their congeners characters not found in the *P. hypoleuca* complex (Rogstad & Le Thomas, in prep.). The latter finding, together with the fact that the character suite discussed above is found only in all members of the *P. hypoleuca* complex, leads to the conclusion that, by parsimony, the *P. hypoleuca* complex either is a monophyletic group (Rogstad & Le Thomas, in prep.) or is composed of all the Malesian members of a larger, small monophyletic group with complementary members in Africa or the Neotropics.

TAXA EXCLUDED FROM THE POLYALTHIA HYPOLEUCA COMPLEX

One group of species, treated by Sinclair (1955) as members of the genus *Melodorum* Lour., is problematic because they bear abaxial leaf papillae most similar to those of the *Polyalthia hypoleuca* complex. In his survey of leaf papillae, Roth (1981; pers. comm.) did not see a close similarity between the papillae in *Melodorum* and those of the *P. hypoleuca* complex. The placement of *Melodorum* is contested (e.g., see Okada & Ueda, 1984), and various authors have described some of the relevant taxa as species in *Polyalthia* (including *P. aberrans* Maingay ex Hooker f. & Thomson, *P. aberrans* Pierre ex Finet & Gagnep., *P. affinis* Teysm. & Binnend., *P. diospyrifolia* Pierre ex Finet & Gagnep., and *P. siamensis* Boerl.).

While this is not the place to discuss in detail the proper placement of *Melodorum,* in my opinion these species differ from the genus *Polyalthia* because they are climbing shrubs, the sepals are connate, the petals are thick and coriaceous, with the inner ones distinctly smaller than the outer and not spreading as in *Polyalthia* (see Sinclair, 1955), and the chromosome number ($2n = 16$) has not yet been found in *Polyalthia* (Okada & Ueda, 1984; Rogstad, unpubl. data). Further, although the papillae of some of the specimens of *Melodorum* are similar to those found in the *P. hypoleuca* complex (sheets that are clearly *Melodorum* according to the characters listed below are occasionally annotated as *P. glauca*), they are less dense and are only sometimes present. Additionally, the species of *Melodorum* (as denoted by Sinclair, 1955, for example) differ from all the species I assign to the *P. hypoleuca* complex in having very distinct leaf venation with an intramarginal vein well removed from the leaf margin, deeply grooved stigmas, globose pollen (Walker, 1971), and platelike endosperm ruminations. In light of these considerations, I conclude that little justification exists for including the taxa of Sinclair's *Melodorum* in *Polyalthia* or the *P. hypoleuca* complex, and that any similarity between their abaxial leaf papillae is of dubious value in trying to establish a close phylogenetic relationship between them.

Polyalthia longifolia must also be considered for inclusion in the complex. Although Sinclair (1955) placed this species in his Group 1, several lines of evidence argue against it. As noted above, Sinclair did not explain criteria for group inclusion, so I cannot address his reasons for the placement of *P. longifolia.* However, the species has not one of the seven character states listed above that I am using to define the *P. hypoleuca* complex (e.g., see FIGURES 5A and 7C, and Rao (1979)). Further, the staminate and carpellate portions of the torus in *P. longifolia* are pubescent, a character altogether lacking in any of the members of the *P. hypoleuca* complex. I would include *P. longifolia* in Sinclair's Group 6 because it has a pubescent torus, midribs deeply grooved longitudinally on the abaxial surface of dried leaves, platelike endosperm ruminations with a "cross" of endosperm clearly visible, the outer seed-coat surface marked with parallel fine striations running perpendicular to the circumferential ring of the seed, and the first above-ground growth of the germinating shoot deriving from extension of the first internode above the cotyledons rather than from the hypocotyl (the latter being the case for all members of the *P. hypoleuca* complex).

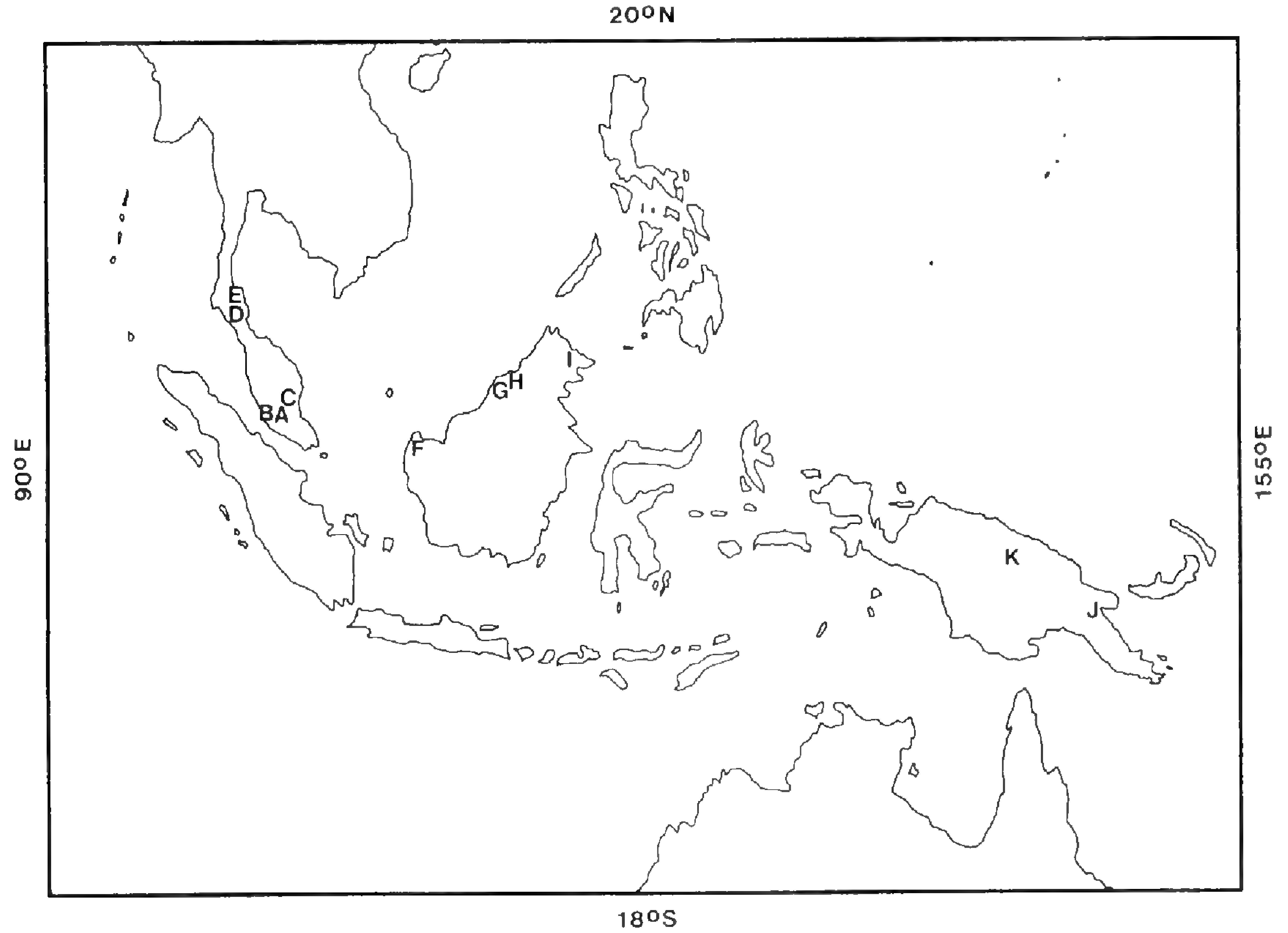
Species that other authors recognize but that I have reduced to synonymy under other species within the *Polyalthia hypoleuca* complex are discussed below.

SPECIES CONCEPT

While it is not my purpose here to discuss the nature of species, it is important that I provide the working definition I have employed to define the species of the *Polyalthia hypoleuca* complex. My species decisions have been made primarily on a morphological basis: are there clear discontinuities by which species can be delimited? I have searched for such discontinuities by recording data on numerous characters from both herbarium and living specimens and then analyzing these data in several different ways, as outlined in the methods section below. Clear discontinuities were found in character-state distributions, and these form the basis for my species concepts. For two cases where these discontinuities are relatively slight, and in fact for all of the species discussed, the decisions reached here will be supported in later articles detailing the comparative autecologies of these species. Thus, my species are defined not only on morphological considerations, but also on an assessment of whether or not they are likely to be isolated genetically or ecologically in nature. The reader interested in weighing the sum of all the evidence bearing on the taxonomic decisions presented here may wish to consult the subsequent articles. Ultimately, the species concept I have used in this treatment is perhaps most fully in accord with the "evolutionary" species concept of Simpson (1961, p. 153): "a lineage (an ancestral-descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies." This is not to say that the evolutionary species concept is the preferred one for all plant species, but after considering all of the information bearing on species in the *P. hypoleuca* complex, I believe it to be the most applicable here.

METHODS

Morphometric analyses were used to search for evidence of morphological species. Character observations and measurements were taken both from herbarium specimens at A, BK, BKF, BO, F, GH, K, KEP, KLU, L, LAE, MO, P, PNG, SAN, SAR, SING, U, US, and Yezin (Burma) and from living specimens collected in several Malesian locations (see MAP 1). All of the herbarium specimens used in these analyses, as well as representative voucher specimens of species for which field measurements are analyzed (*Rogstad* numbers deposited at A), are noted in the specimen citations. An attempt has been made to include specimens covering the full range of character variability for each species. The known geographic range determined from herbarium specimens for each species of the *Polyalthia hypoleuca* complex is depicted in maps accompanying the species



MAP 1. Sites visited. Peninsular Malaysia: Pasoh Forest Reserve (A), Telok Forest Reserve (B), Tasek Bera Reserve (C). Thailand: Khao Chong Forest Reserve (D), Khao Tha Phet Forest Reserve (E). Sarawak: Bako National Park (F), Lambir and Niah national parks (G), Baram River Site (H). Sabah: Sandakan (I). Papua New Guinea: Aluki Village (J), April River (K).

descriptions; specimens from the entire known range of each species have been included in the morphometric analyses. Coverage of character variability and geographic distribution is thus most comprehensive for the better-collected species.

Measurements of herbarium specimens were recorded from all sheets bearing several intact flowers and/or any fruits and were made with a ruler or with a dissecting microscope fitted with an ocular micrometer when appropriate. The most mature flower or fruit present with all the relevant characters intact was measured. Flowers were denoted as mature or immature based on characteristics determined from field observations. For most of the species, petals of immature flowers are open and radiating, while those of mature ones are erect and closely parallel to the longitudinal axis of the flower (Rogstad, in prep. b). In *Polyalthia glauca* and probably *P. ovalifolia,* the outer petals are erect until they turn yellow-orange at maturity, then the distal portion bends outward to 30° or more. Petals were also designated as being mature if label data indicated that they were other than greenish. Fruits were deemed mature if they were at least as large as the smallest fruit of a species for which label data indicated fruit color as deep red to black; fruits of all these species achieve maximum size while still green, turning black when mature a number of weeks later (pers. obs.). Specimens with only one or a few flowers were generally not measured for all characters unless the specimen was judged as crucial to the study (e.g., at the edge of a species range or bearing an unusual character). To avoid unusual phenotypic effects on measurement of leaf characters, an average-size leaf was subjectively chosen from each specimen. Pertinent herbarium label data were recorded for the specimens. The categories of data collected for each herbarium specimen and used variously in the morphometric analyses reported below are listed in APPENDIX 3. A copy of the full data set stored on double-sided, double-density, 5.25-inch diskettes utilizing MS/PC-DOS format has been deposited with Rogstad (1986) in the Botany Libraries of Harvard University. A copy can be obtained free on request, provided the user agrees to share the results of any analyses of these data with the author and sends a self-addressed, stamped envelope containing an appropriate diskette.

In the case of living specimens, tree heights were measured with a Suunto PM5/360PC Clinometer following the directions provided. The girth of trees at breast height (GBH) was measured at 1.5 m by tape measure and converted to diameter at breast height (DBH).

These data were analyzed by several different methods utilizing the SYSTAT (Wilkinson, 1984; in conjunction with an IBM PC-AT), SAS Version 5 (SAS Institute, Inc., Cary, North Carolina), and BMDP (Health Science Computing Facility, University of California, Los Angeles, California) statistical packages. The last two packages were used as available at the Washington University Computing Facilities, St. Louis.

While the univariate and bivariate analyses presented in the results section below are widely used and self-explanatory, my choice of multivariate techniques requires justification. As stated above, the species concept I develop with regard to the *Polyalthia hypoleuca* complex is based on morphological analyses. I begin, therefore, by searching for discontinuities in morphological characters, attempting to apply the widely held tenet that good taxa are best defined not on one character, but on a suite of them.

Patterns of variation within and among characters are often very complex. Sokal (1985) argued that many taxa are polythetic, that is, are groups that can be defined by a suite of characters, with some or all of the members lacking one or another character. The literature is replete with disputes over the proper classification of organisms, and these are testimony both to the complex nature of character variation among organisms and to the fact that each investigator carries personal biases into subjective decisions about the importance of conflicting characters. Sokal and Rohlf (1980) have demonstrated that different taxonomists achieve different subjective classifications based on the same set of taxa, but the differences are greatly reduced when investigators employ standardized morphometric analyses of explicitly coded character states (Sokal & Rohlf, 1970). The task for the taxonomist, then, is to search for nonsubjective signals of morphological discontinuity (at best based on several covarying characters) that rise above the noise of characters exhibiting more or less random variation.

A review of literature descriptions, and of the sorting and annotation of herbarium specimens by previous researchers of taxa I have included in the *Polyalthia hypoleuca* complex, indicated that this assemblage was in need of revision due to complex character distributions that did not always result in congruent or stable taxonomic entities. I have used multivariate analyses as an aid in defining the taxa in this group based upon characters and techniques that are repeatable and explicit.

Several multivariate statistical techniques have been designed to search for patterns in complex character-state data sets. A review of plant taxonomists' use of these techniques (Duncan & Baum, 1981) indicates that cluster analysis has been the most widely employed. However, since the first step in my analysis is an attempt to demonstrate whether or not any groups (clusters) exist based upon character variation, and since cluster techniques always give clusters even if a random data set is used, searching for the possible existence of clusters with a method that always yields them seemed questionable. Here I used a two-step approach that does not necessarily sort specimens into groups, but rather summarizes the degree to which character states covary among specimens and then, if groups are detected, permits a statistical test of group membership for each specimen.

The first step was to examine the data matrix by principal-components analysis, or PCA (SYSTAT; Wilkinson, 1984). Reviews of PCA theory, methodological assumptions, and constraints can be found in most texts treating multivariate methods (e.g., Nie *et al.,* 1975; Neff & Marcus, 1980; and their references), and the following discussion is simplified for brevity. With PCA as utilized here, the raw data matrix—in this case measurements of a set of characters taken from herbarium specimens—is analyzed to derive its corresponding correlation matrix (a covariance matrix can also be used, but since this approach is strongly influenced by characters of larger size, only correlation matrices have been employed here). From this matrix, principal components (axes) are extracted that are descriptors, in serial fashion from greatest to least, of variance among character states across the specimen set. The first principal component is the axis with the maximum variance. The second component axis is derived in the direction of greatest variance orthogonal to the first one, and thus successive axes are computed until all the variance in the data set is accounted for. Each principal component is a mathematical equation (eigenvector) that includes a term for each character weighted by a coefficient commensurate to that character's contribution to the total variance of that component. Each specimen can be assigned a numerical value along each component (the character coefficient times the character value for each character of that specimen summed over all of its characters) that summarizes the degree to which its characters covary with the other specimens in characters that heavily influence each component.

Specimens more similar to one another in the ways their characters covary are thus placed in closer proximity along the principal components than are those that differ. If strong patterns of character covariance exist, these will be detected in the first three or four components, where the greatest degree of variance is accounted for, the later components accounting for very little of the total variance. If patterns of character distributions are more or less random, then the first components will not explain much more variance than later ones. If all specimens are plotted for their scores on three components, specimens with similar patterns of character correlation are placed in groups in the principal-components space defined by the three components. Use of PCA enables one to search for groups defined by suites of (covarying) characters and, once the principal components are calculated, to identify the characters that contribute most to the differentiation of groups along any particular axis. As indicated above, groups defined by suites of characters are preferred over groups defined by only one.

Two further steps often taken in PCA analyses should be mentioned. First, once all of the data have been analyzed, characters with no high loadings on any component can be removed from the data matrix and the analysis recalculated. This eliminates characters that vary randomly with respect to strongly covarying characters and therefore contribute only "noise" to the analyses. Groups or loadings on remaining characters may thus be given clearer definition. While I have conducted this type of exploration with the data sets used here, removal of low-weighted characters did not significantly improve the results (and is a somewhat subjective decision in any case), so only results including all of the continuous characters are reported here. Second, once a set of principal components has been determined for a data set, the corresponding component axes can be rotated to search for more meaningful components by simplifying the component structure (Nie *et al.*, 1975). Although rotation may thus improve the interpretability of the component loadings, it did not in the examples discussed below, so only unrotated solutions are presented.

Note that PCA does not always give clear groups; decisions of group membership may be difficult and sometimes ultimately rest upon the discretion of the practitioner. As far as I am aware no method has yet been devised for PCA that permits a statistical test of the strength of groups or of group membership by individual cases.

When visual inspection of the PCA analyses of the *Polyalthia hypoleuca* complex data set resulted in hypotheses of groups of specimens, I utilized discriminant analysis (again, see standard texts on multivariate statistical techniques: e.g., Nie *et al.* (1975), Neff & Marcus (1980), and their references) to test the statistical strength of the membership of each specimen in the hypothesized group. The same data matrix as used above in the PCA can be analyzed by discriminant analysis techniques, although in the latter case each specimen must be designated, before the analysis is undertaken, as belonging to one of the hypothesized groups.

The specific technique used here is a jackknifed discriminant analysis, in which the first step is to remove one specimen from the data set. Next, a set of linear discriminant functions (axes) is derived, each maximizing, in decreasing order, the separation of the groups. In other words, the first function maximizes the separation of the groups, the second function is orthogonal to the first and is the next best function at maximizing group separation, and so on, until the maximum number of functions has been derived. If the members of the *a priori* groups are much more similar to one another than they are to members of other groups, their placement on a discriminant function axis should cluster them in relative proximity on that axis away from other groups or specimens. As with PCA above, once the discriminant functions are calculated, the characters that contribute most to the differentiation of groups along any particular axis can be identified.

If a set of variables is found in the first three or four discriminant functions that provides satisfactory discrimination for the *a priori*-defined groups, then the excluded specimen can be statistically "classified" as to the group in which it belongs. This specimen is then returned to the total data set, and the next specimen in the data table is excluded and the above procedure repeated. In this way, each specimen can in turn be removed from the data set and then classified as to group membership in relation to the remainder of the specimens. If groups are well defined, all specimens should be correctly placed with high statistical confidence as belonging to the group to which it was assigned *a priori*. If no clear groups are present, many individuals will be assigned to groups other than those in which they were first placed as a result of the PCA analyses.

It is important to keep in mind that the species assignations indicated in all of the results below have been ultimately decided *a posteriori* with respect not only to the totality of the morphometric evidence presented here, but also with regard to ecological characteristics to be detailed in related articles (Rogstad, in prep. a, b).

A valuable feature of both PCA and discriminant analysis is that the percentage of the total variance or dispersion in the data set explained by each extracted principal component or discriminant function, respectively, is calculated. In a totally random data set, little underlying structure of correlation of variation of variables would be expected, so a particular principal component or discriminant function will not explain much more of this variance or dispersion than the one immediately following. However, if there is structure in the data, then at least the first principal components or discriminant functions derived should explain a disproportionately large portion of the variance or dispersion. In all of the results reported below, the latter possibility will be seen to be the case.

Another useful type of information obtainable from both PCA and discriminant analysis derives from the calculation of the component loadings and the coefficients for the canonical variables, respectively. These are informative as to which of the characters are most important with regard to the variance or dispersion explained by each principal component or discriminant function. Characters with larger loadings or coefficients on a principal component or discriminant function have patterns of correlated variation with regard to that component or function and can likely be used in suites of correlated characters that best define discontinuous groups (species).

Discriminant analysis and PCA are subject to certain constraints and restrictions. For example, both methods assume multivariate normality for the data. While PCA is thought to be robust against all but extreme deviations from normality (e.g., see Sneath & Sokal, 1973), discriminant analysis also includes the further assumption of equal variance-covariance matrices within groups (Neff & Marcus, 1980). However, use of discriminant analysis is not invalidated even when both assumptions are violated to some degree if errors of classification are small (Neff & Marcus, 1980), which is the case for all the results presented below. Only characters that are continuous or meristic over broad ranges are included in the data matrices analyzed by PCA and discriminant analysis here. Those that are clearly not normally distributed (e.g., information, such as color, that is designated by arbitrary coding; presence-absence data) are not included in the PCA and discriminant-analysis results described below, although, as will be seen, such data can be used informatively in conjunction with these analyses. Each analysis also includes only specimens with no missing values for any character employed. Additionally, both the principal components and the discriminant functions of the respective methods are based on linear models, and for present purposes this approach has been accepted. Finally, the species treated here have not been equally well collected, and therefore the sample sizes are not equal. While this is not a major problem for PCA, it can affect discriminant analysis. Thus, in the results reported here, all discriminant analyses were performed with the BMDP option PRIOR adjusted to reflect the sample size of each species.

Obviously, the ideal statistical requirements of these methods are only at best approached, rather than met entirely, in the analyses discussed here. This will probably always be the case for systematists' data sets due to the problems inherent in collecting biological information. Does this indicate that these tests should not be utilized? I maintain that they should be used as exploratory and descriptive tools. The results detailed below are not presented as incontrovertible systematic truth, but rather as aids that influenced my taxonomic decisions. Further, the characters, methods, and decisions are explicit and repeatable, and other workers can follow the development of concepts, modify the analyses, or contribute additional information in a prescribed manner. At the very least, the presentation of systematic analyses by these methods is heuristic in rapidly conveying to the reader not only the extremes of variation important in defining groups (the usual information provided in systematic treatments), but also the degree to which variation exists within each group. For example, after PCA of the character matrix, data for any desired character are separately available for statistical analysis within selected groups. Graphic depictions of the distribution of individuals according to their scores on various components provide rapid understanding of their dispersion, due to the covariance of the characters heavily weighted on those components.

RESULTS

Since over 50 characters from 172 flowering specimens and 16 characters from 230 fruiting specimens were recorded, it would be inefficient to reproduce all of the possible permutations of uni-, bi-, tri-, and multivariate character analyses here. Instead, only a few representative examples will be presented.

In the graphic presentation of these results, the species designations have been made after consideration of all of the data and analyses presented here and in subsequent related articles (Rogstad, in prep. a, b). In an evaluation of only two or three characters, a few specimens of a species may exhibit character states of another species for any (or rarely all) of them, but they otherwise

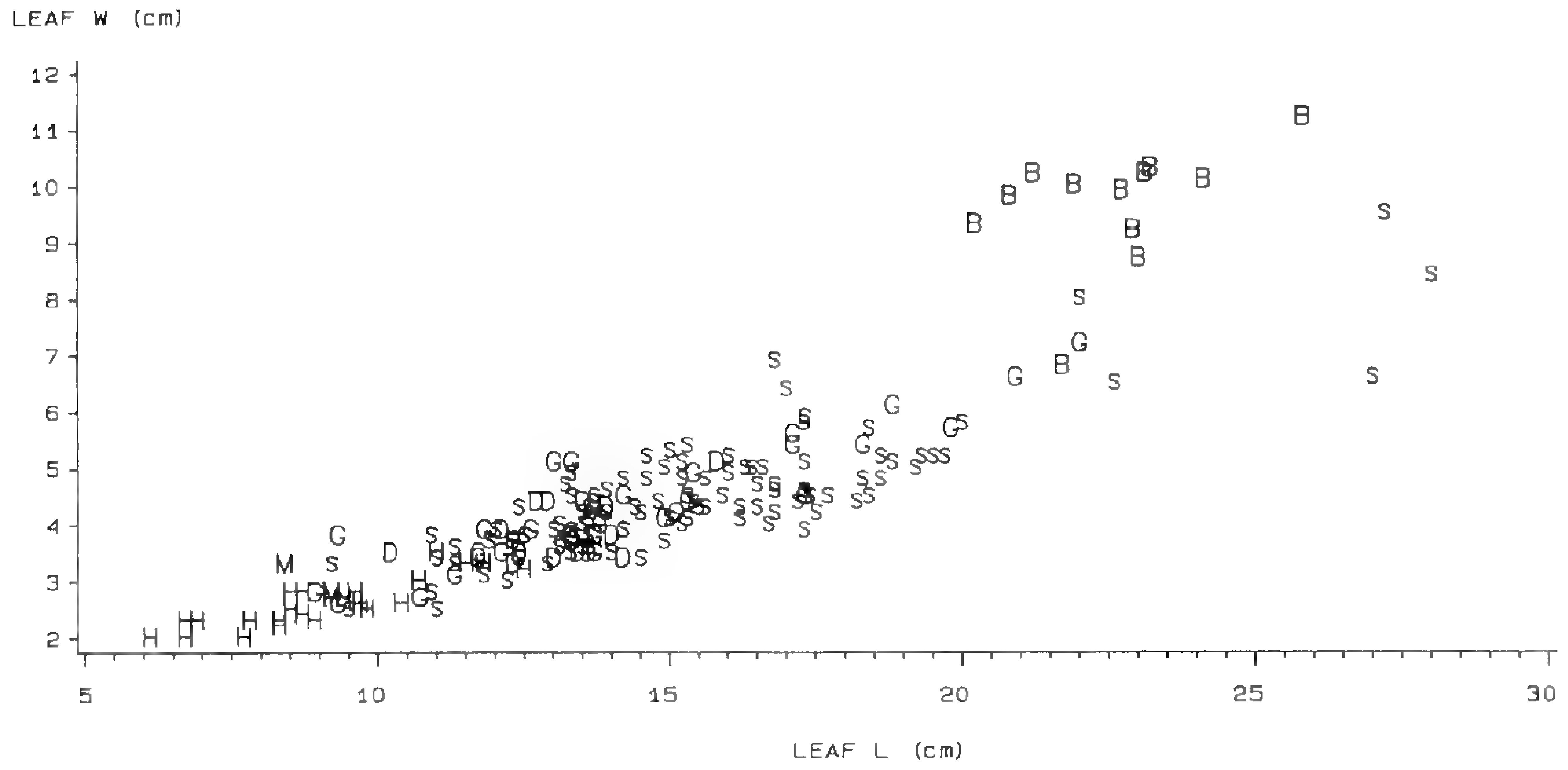


FIGURE 9. Leaf length vs. width for specimens of *P. hypoleuca* complex: B = *P. ovalifolia,* D = *P. discolor,* G = *P. glauca,* H = *P. hypoleuca,* M = *P. multinervis,* S = *P. sumatrana.*

conform with the species to which I have assigned them. It will be seen from a comparison of the following bivariate and multivariate analyses that a systematist giving more weight to certain characters than others (as judged from bivariate comparisons) may arrive at different conclusions than those reached by multivariate analyses.

Sinclair (1955) noted that although leaves of *Polyalthia sumatrana* and *P. glauca* are nearly indistinguishable, those of *P. hypoleuca* are smaller and have closer veins. However, as is shown in FIGURE 3B, there is some overlap of specimens assigned to both *P. sumatrana* and *P. glauca* with *P. hypoleuca* with respect to leaf size. This is not to say that there are not tendencies in leaf sizes of these species, but this overlap negates leaf size as a simple character by which these species can be delimited absolutely. In fact, if one examines each data point in FIGURE 9, disregarding the species designations that have been made based on the sum of the vegetative, floral, fruit, and ecological data, it is difficult to define distinct groups, except perhaps one comprising specimens of *P. ovalifolia* and another composed of three outlying specimens of *P. sumatrana.* This overlap has no doubt contributed to problems of classification and identification.

Sinclair (1955, p. 322) further indicated that *Polyalthia glauca* can be distinguished from *P. sumatrana* by its mature fruit "with thinner [carpel] stalks and pedicels." FIGURES 10 and 11 demonstrate that, again, while there are central tendencies in these species, the amount of overlap renders these characters of little use in discriminating clearly between the two species. In FIGURES 10 and 11 it can be seen that the length and width of carpel stalks and pedicels from mature fruits are not very useful in discriminating any of the species except perhaps the group comprising *P. hypoleuca* and *P. multinervis* Diels specimens. Even these are not clearly bounded from the *P. glauca* and *P. sumatrana* specimens.

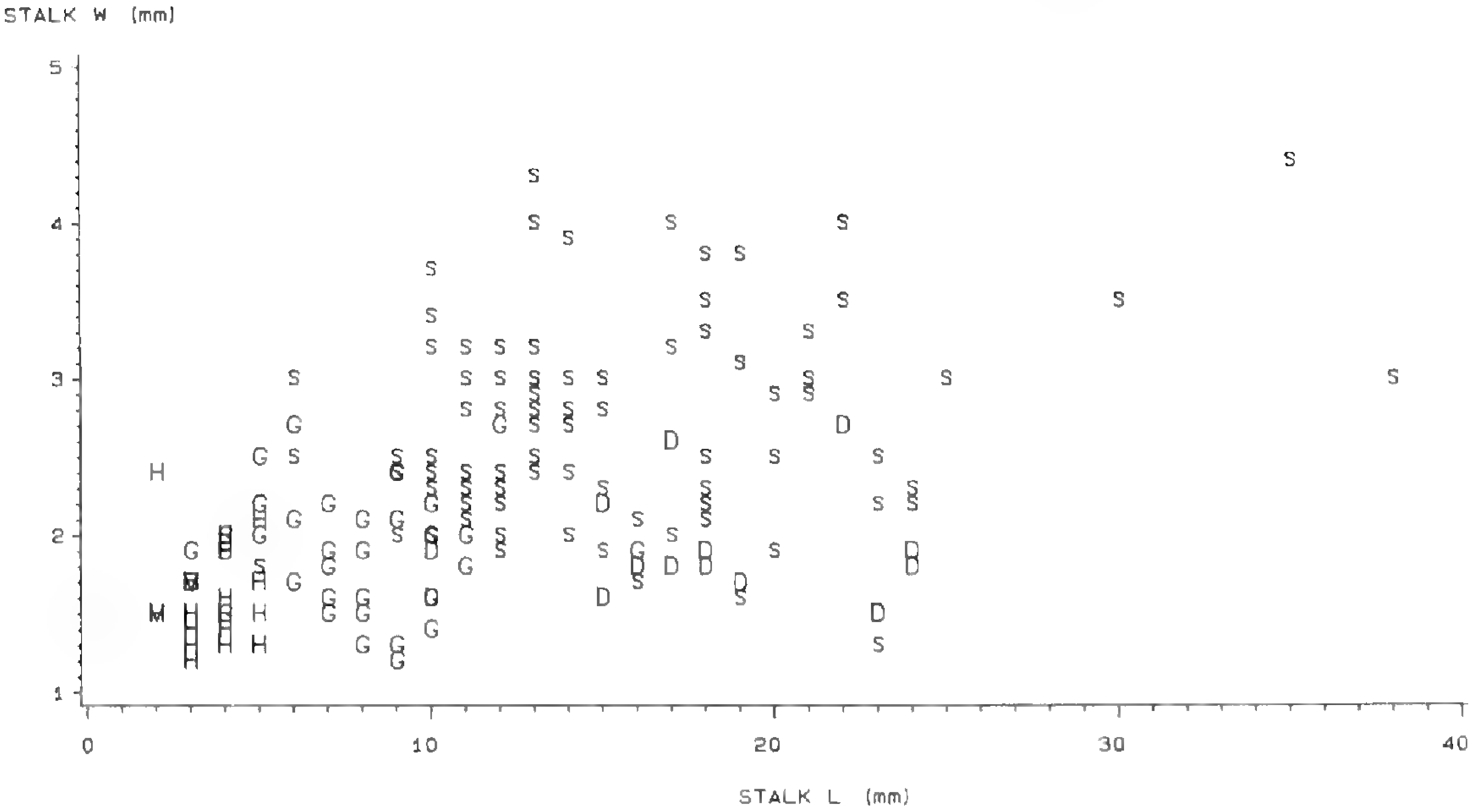


FIGURE 10. Stalk length vs. width for mature carpels of *P. hypoleuca* complex: B = *P. ovalifolia,* D = *P. discolor,* G = *P. glauca,* H = *P. hypoleuca,* M = *P. multinervis,* S = *P. sumatrana.*

An examination of floral characters used by Sinclair (1955) also suggests why herbarium workers have had problems identifying specimens in this group. For example, Sinclair described the petals of *Polyalthia glauca* as 16–20 mm long, and thus larger than those of *P. hypoleuca* (8–12 mm long). FIGURE 12 depicts the relationship of petal length to widest petal width for all the mature

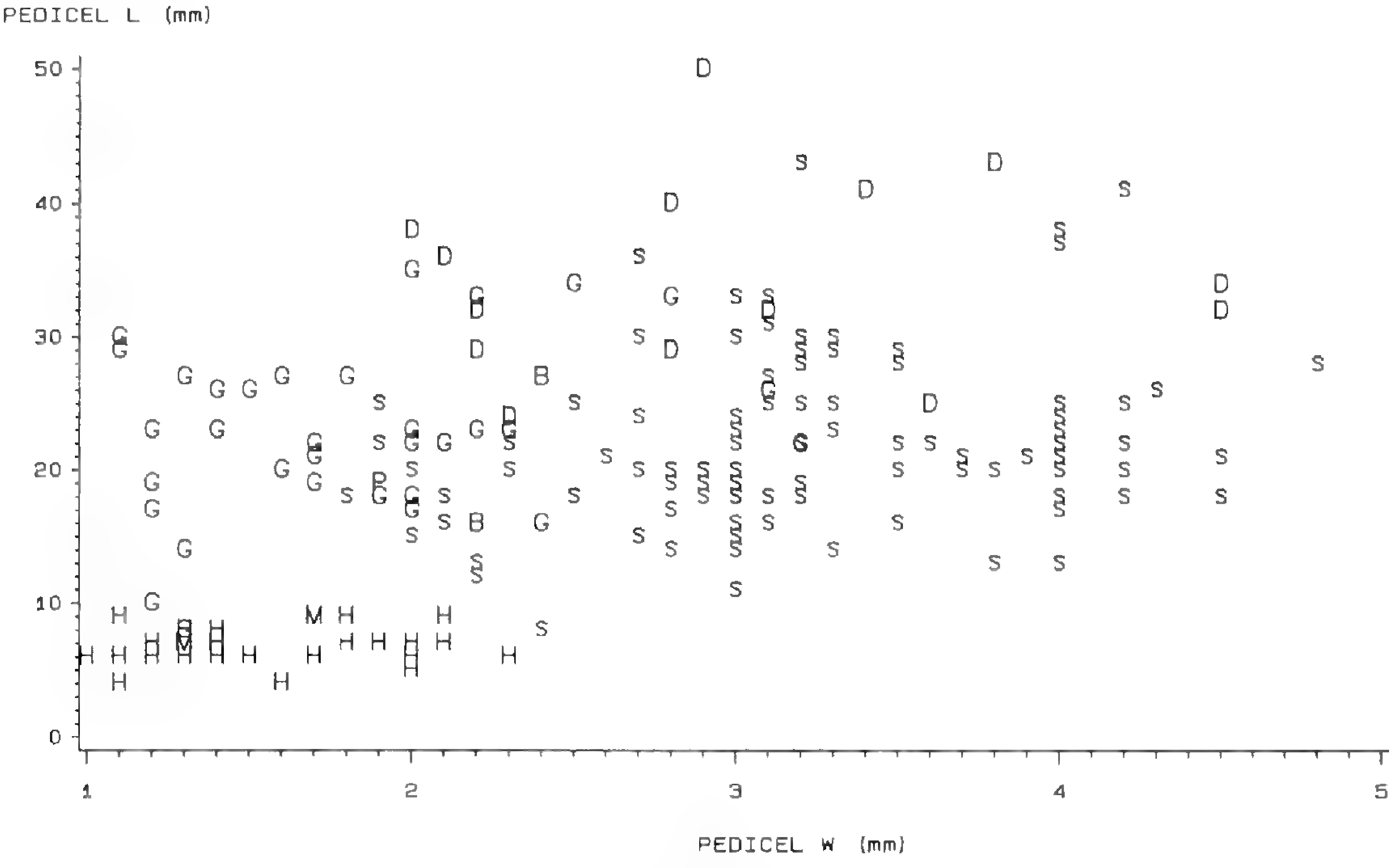


FIGURE 11. Pedicel width vs. length for mature carpels of *P. hypoleuca* complex: B = *P. ovalifolia,* D = *P. discolor,* G = *P. glauca,* H = *P. hypoleuca,* M = *P. multinervis,* S = *P. sumatrana.*

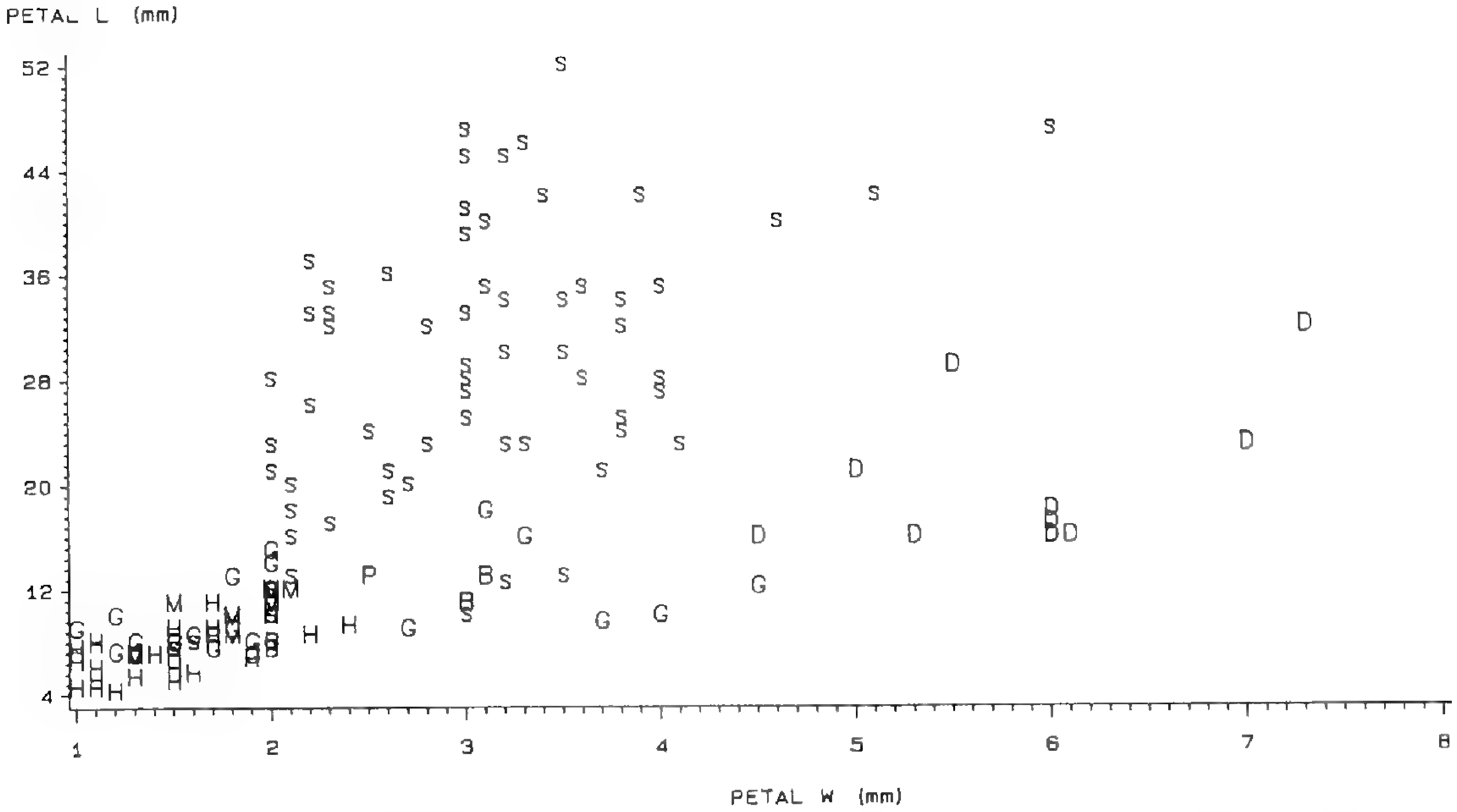


FIGURE 12. Outer petal length vs. width for mature flowers of *P. hypoleuca* complex: B = *P. ovalifolia,* D = *P. discolor,* G = *P. glauca,* H = *P. hypoleuca,* M = *P. multinervis,* S = *P. sumatrana.*

specimens of species that I have included in the *P. hypoleuca* complex, and again, with the possible exception of the *P. discolor* specimens, it is difficult, based on these characters alone, to demarcate any clear groups, let alone find support for Sinclair's proposed differentiation between the two species.

As noted earlier, hundreds of such character comparisons could be presented,

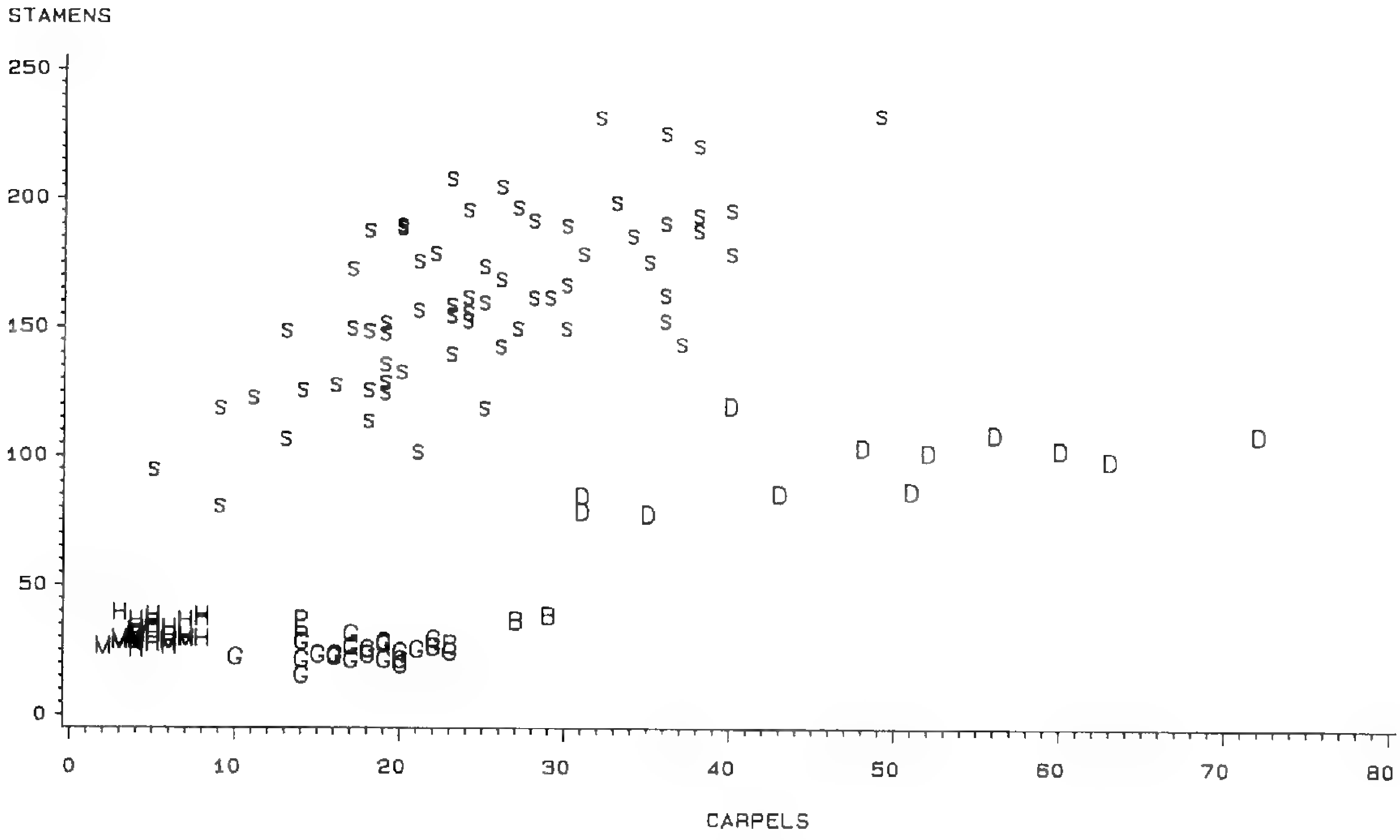


FIGURE 13. Stamen number vs. carpel number for mature flowers of *P. hypoleuca* complex: B = *P. ovalifolia,* D = *P. discolor,* G = *P. glauca,* H = *P. hypoleuca,* M = *P. multinervis,* P = *P. parkinsonii,* S = *P. sumatrana.*

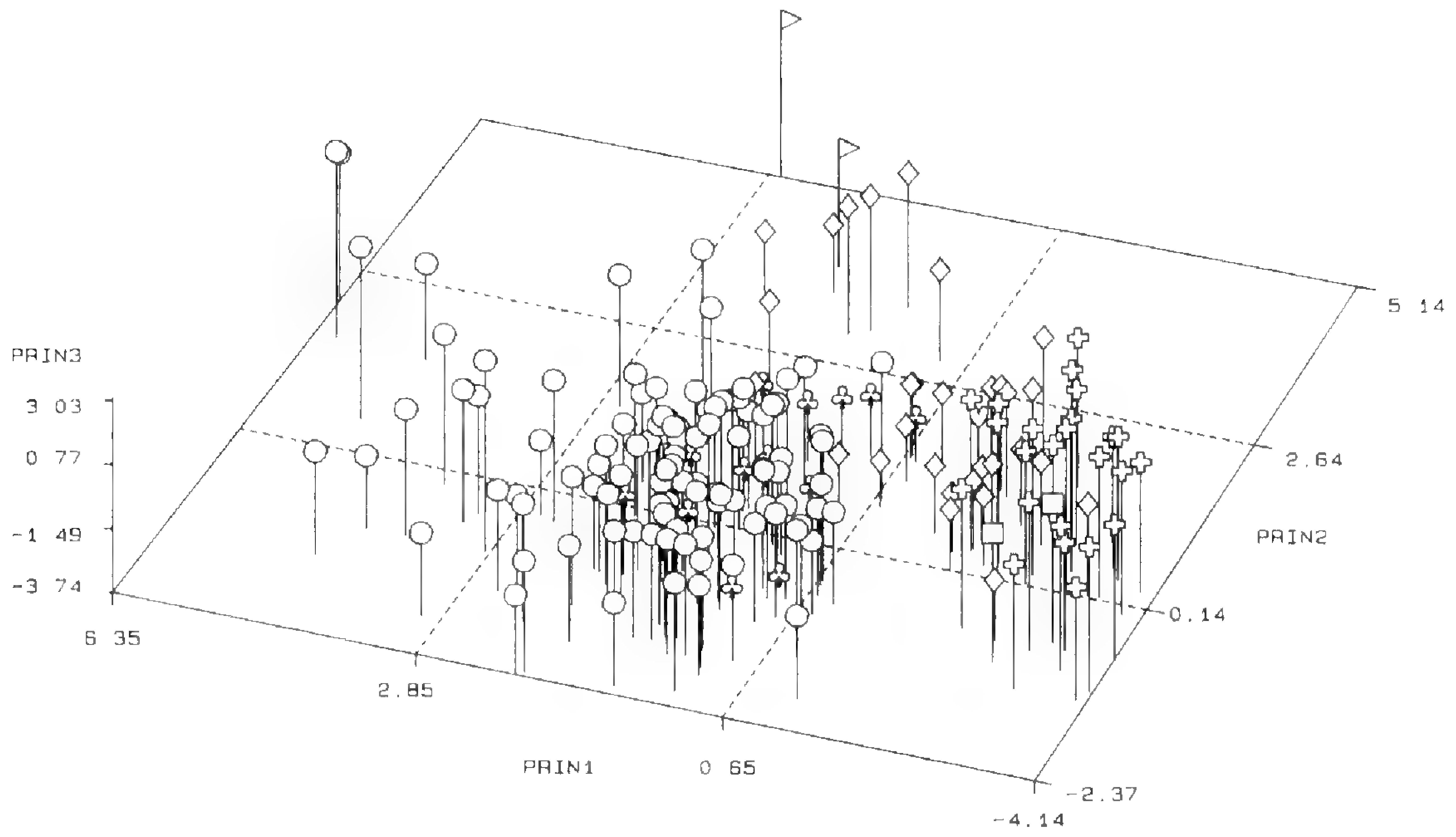


FIGURE 14. PCA results for continuous characters of mature fruits and leaves of *Polyalthia hypoleuca* complex. Each specimen depicted by its score on first 3 principal components ("PRIN") (details given in TABLE 1). *Polyalthia discolor* = clubs, *P. glauca* = diamonds, *P. hypoleuca* = crosses, *P. multinervis* = squares, *P. ovalifolia* = flags, *P. parkinsonii* = hearts, *P. sumatrana* = circles.

and all that I have inspected have shown the same pattern: when univariate or bivariate comparisons are made of mature vegetative, floral, or fruit characters, clear-cut groupings of specimens do not often emerge. In the herbarium the taxonomist examines not only mature specimens (as is the case in all the examples above) but also immature ones, often without any means of distinguishing between them. Obviously, this contributes even more to the uncertainty.

It could be argued that, just as in FIGURE 12 where the *Polyalthia discolor* group of specimens is more or less defined, if one looked at additional plots, other groups could be distinguished, and in this way a set of characters, each defining one taxon or more, could be found. With the present set of specimens, such clear patterns have rarely emerged from this data set, and in any case this procedure is perhaps of dubious general utility. It is more often the case that species show central tendencies with varying degrees of character overlap. As will be seen below, however, such overlap may often not be a problem in searching for groups if specimen data are examined with multivariate statistical techniques that analyze for patterns of characters that covary.

The relationship of stamen number to carpel number (see FIGURE 13) deserves special mention as it unexpectedly emerged as a powerful discriminator of most of the species. Here four rather well differentiated groups (*P. sumatrana, P. discolor, P. hypoleuca–P. multinervis,* and *P. ovalifolia–P. glauca–P. parkinsonii*) can be distinguished. Why these last two groups are composed of more than one species will be explained below. It is important to note that none of these groups is well defined by the number of stamens or carpels alone, but

TABLE 1. **Loadings for first 5 components of continuous and meristic mature fruit and leaf characters* derived from PCA of 195 specimens of Polyalthia hypoleuca complex.****

CHARACTER	COMPONENT LOADINGS 1	2	3	4	5
Leaf L	0.847	0.375	0.130	0.026	0.035
Leaf W	0.744	0.475	0.134	0.187	-0.059
Mature carpel stalk L	0.715	-0.316	-0.288	0.032	0.279
Pedicel W at apex	0.713	-0.474	-0.094	0.128	0.180
Mature carpel L	0.699	-0.401	0.136	-0.263	-0.327
Mature carpel stalk W at apex	0.678	-0.432	0.049	-0.268	-0.234
Pedicel L	0.579	0.128	-0.610	0.112	0.329
Petiole L	0.524	0.492	0.109	0.367	-0.209
Leaf vein number	0.482	-0.134	0.645	0.193	0.019
Mature carpel W	0.317	0.435	-0.515	-0.468	-0.306
Leaf drip-tip L	0.178	0.343	0.472	-0.625	0.445

*Listed in Appendix 3.

**The characters are listed in descending order according to loadings on the first component (L = length; W = width). The scores for each specimen with respect to the first three components are depicted in Figure 14. Of the total variance, the first five components accounted for 38.3, 14.7, 13.1, 9, and 6.5 percent, respectively.

rather the absolute numbers of stamens and carpels plus the quotient of the two must be considered in distinguishing these groups. These characters are not restricted in use to specimens bearing only intact flowers, since stamens and aborted carpels, after abscising, leave scars on the developing fruit. These characters have not generally been utilized by previous systematists working on this group; it is possible that they may also be important in distinguishing species of other species complexes in the Annonaceae.

Because clearly discernible groups were not apparent in the uni- and bivariate character examinations, multivariate statistical analyses were undertaken. Again, only a few of the most representative or meaningful trials will be discussed. All analyses yielded results similar to those selected as examples below. First, PCA was applied to search for possible groups based on suites of correlated characters, and once putative groups were determined, statistical testing of each specimen for membership in its assigned group was conducted utilizing a jackknifed discriminant analysis.

FIGURE 14 presents the scores of each specimen with respect to the first three principle components resulting from the PCA of the continuous mature fruit and leaf characters. These components account for 66.1 percent of the total variance in the data set (TABLE 1 lists the component loadings of each character and the percent of the total variance explained by each of the first five components for this trial). Note that the only specimens in FIGURE 14 that have

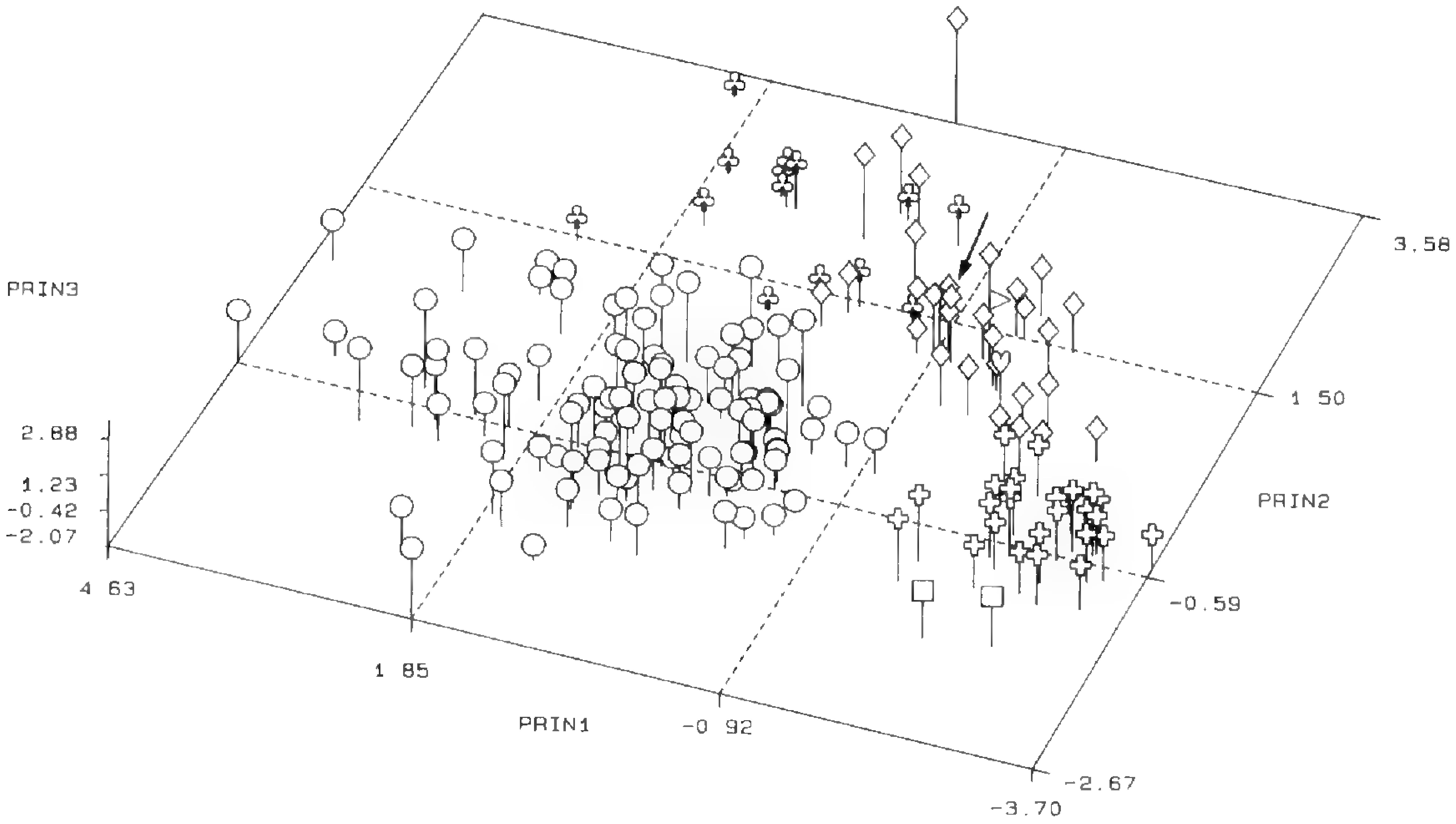


FIGURE 15. PCA results for continuous characters of mature fruits of *Polyalthia hypoleuca* complex. Each specimen depicted by its score on first 3 principal components ("PRIN") (details given in TABLE 2). Arrow points to obscured flag. *Polyalthia discolor* = clubs, *P. glauca* = diamonds, *P. hypoleuca* = crosses, *P. multinervis* = boxes, *P. ovalifolia* = flags, *P. parkinsonii* = hearts, *P. sumatrana* = circles.

densely pubescent pedicels and young shoots are the "flags" (*Polyalthia ovalifolia*) and the "crosses" (*P. hypoleuca*), which makes the "flag" specimens even more distinct.

Inspection of FIGURE 15, which is the PCA of the same data matrix used to generate FIGURE 14 but with the leaf characters removed, shows that fruit data alone yield a clearer grouping of the specimens; the first three components (see TABLE 2) now account for 83.9 percent of the total variance. For example, the *Polyalthia sumatrana* and the *P. hypoleuca* sets of specimens are now more distinct. Inclusion of the leaf characters with the continuous fruit characters, then, generally confounds the clearer clustering of specimens by the continuous fruit characters alone. It is interesting to note, however, that the *P. ovalifolia* specimens sit somewhat apart in the PCA of the fruit and leaf characters (FIGURE 14) but are placed with *P. glauca* when the fruit characters alone are analyzed (FIGURE 15). This difference becomes clear upon inspection of FIGURE 9, where the only two specimens of *P. ovalifolia* having all the fruit and leaf characters required for inclusion in the PCA analyses are set somewhat apart by leaf size.

If one considers some of the noncontinuous characters in conjunction with FIGURE 15, groups become more distinct. For example, only specimens here designated as *Polyalthia sumatrana, P. hypoleuca,* and *P. multinervis* have ellipsoid mature carpels; *P. glauca, P. discolor,* and *P. ovalifolia* have globose ones. Of these species, only *P. hypoleuca* and *P. ovalifolia* have densely pubescent pedicels in both flower and fruit, which further accentuates *P. hypoleuca* as a distinct group in FIGURE 15.

The partial lack of clear grouping by PCA of the continuous fruit characters alone helps explain the confusion that has existed among taxonomists who

TABLE 2. **Loadings for first 5 components of continuous mature fruit characters* derived from PCA of 195 specimens of Polyalthia hypoleuca complex.****

	COMPONENT LOADINGS				
CHARACTER	1	2	3	4	5
Pedicel W at apex	0.822	-0.201	-0.264	0.365	0.164
Mature carpel stalk L	0.821	0.033	-0.307	-0.453	0.113
Mature carpel stalk W at apex	0.781	-0.302	0.301	-0.018	-0.449
Mature carpel L	0.768	-0.298	0.407	0.009	0.257
Pedicel L	0.609	0.609	-0.379	0.124	-0.165
Mature carpel W	0.297	0.779	0.513	0.012	0.090

*Listed in Appendix 3.
**The characters are listed in descending order according to loadings on the first component (L = length; W = width). The scores for each specimen with respect to the first three components are depicted in Figure 15. Of the total variance, the first five components accounted for 50.1, 20, 13.8, 5.9, and 5.7 percent, respectively.

have attempted to classify fruiting specimens with globose mature carpels from New Guinea. Although Diels (1915) described the mature carpels of *Polyalthia discolor* as subglobose (the distal portion is in fact globose), every herbarium specimen from New Guinea with globose ones that I have encountered has been either identified as *P. glauca* or unidentified. This confusion is not difficult to understand since not only do both of these species have distally globose mature carpels, but as can be seen in FIGURE 15, they are not clearly separated by PCA of the continuous characters measured from mature fruit. Note, however, that there are central tendencies to the two groups that do result in some separation based on generalized size factors (see the heavily loaded characters in TABLE 2), since *P. discolor* fruits tend to be larger.

The problem of identifying these specimens has been solved by considering the floral data examined above. Recall that in FIGURE 13 *Polyalthia discolor* is well separated by stamen number from the group including *P. glauca, P. ovalifolia,* and *P. parkinsonii.* In most mature fruits of these two groups from New Guinea, the staminal portion of the torus retains scars of each stamen that it once bore, and these scars can be counted. Every specimen designated *P. discolor* in FIGURE 15 represents a collection with globose mature carpels and more than 60 stamen scars, while those specimens with globose mature carpels and less than 50 stamen scars were assigned to *P. glauca.*

No continuous, presence-absence, or subjectively coded characters were found to separate a specimen described by Hutchinson (1917)—and later recognized by Sinclair (1955)—as *Polyalthia parkinsonii* from the group of specimens assigned to *P. glauca.* Unfortunately, this entity has only been collected once

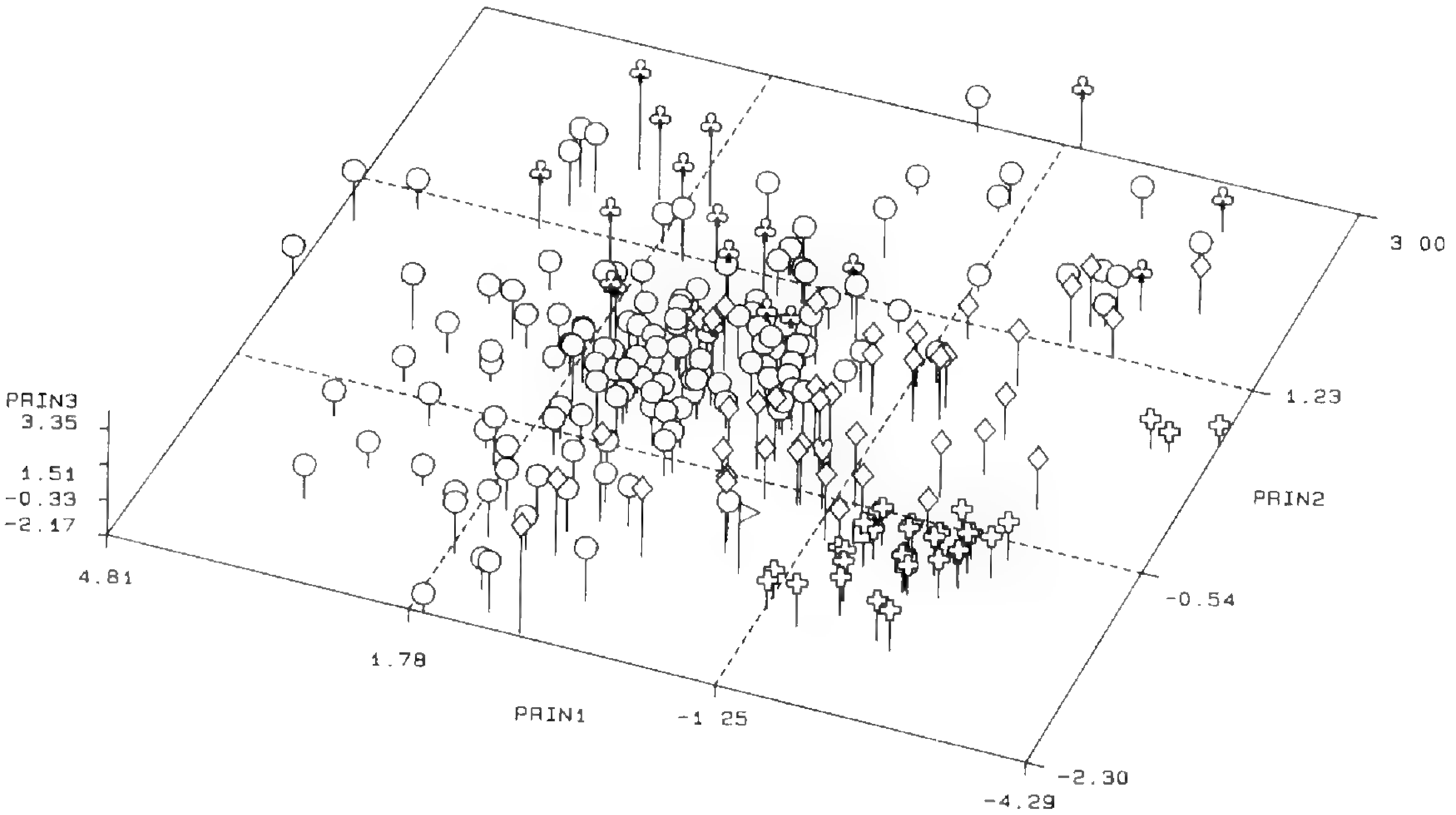


FIGURE 16. PCA results for continuous characters of mature plus immature fruits of *Polyalthia hypoleuca* complex. Each specimen depicted by its score on first 3 principal components ("PRIN") (details given in TABLE 3). *Polyalthia discolor* = clubs, *P. glauca* = diamonds, *P. hypoleuca* = crosses, *P. multinervis* = boxes, *P. ovalifolia* = flags, *P. parkinsonii* = hearts, *P. sumatrana* = circles.

in fruit, from the Andaman Islands, and no label data indicating the maturity of the fruit were available. Perhaps more extensive collection of this entity will demonstrate that it has mature fruit characters distinguishing it from *P. glauca,* but based on current data it cannot be separated.

Another major factor confusing the identity of herbarium specimens, and thus concepts of species in the *Polyalthia hypoleuca* complex, stems from specimens that are immature. The results depicted in FIGURE 16 were calculated by exactly the same PCA method utilized in FIGURE 15, except that data from immature fruit of most of the species have been added to the data set. TABLE 3 indicates that the first three components account for 85.5 percent of the total variance (and includes character loadings for this PCA). These immature fruits (noted as green on the herbarium labels, or obviously very much smaller than normal) have been identified to species by the presence of mature flower or fruit structures on the sheet or by some noncontinuous character specific to a species (e.g., dense pubescence on pedicel, as discussed above; red spots noted as present on green fruits (*P. sumatrana* only)). The inclusion of immature specimens in FIGURE 16 greatly disrupts the group structure recognizable in FIGURE 15. It is easy to understand from this example that using only continuous measurements of fruit characters emphasized by earlier workers may be misleading if immature specimens cannot be (or are not) distinguished from mature ones, a problem common with the Annonaceae.

The results of the multivariate analyses of the floral characters are similarly informative and also support changes of earlier concepts of species within this group. FIGURE 17 presents the scores with respect to the first three components

TABLE 3. **Loadings for first 5 components of continuous mature and immature fruit characters* derived from PCA of 234 specimens of Polyalthia hypoleuca complex.****

CHARACTER	COMPONENT LOADINGS 1	2	3	4	5
Mature carpel L	0.824	0.430	0.099	0.028	0.082
Mature carpel stalk W at apex	0.817	0.214	0.311	0.081	−0.405
Mature carpel stalk L	0.802	−0.326	0.049	−0.493	0.055
Pedicel W at apex	0.785	−0.312	0.307	0.282	0.308
Mature carpel W	0.535	0.532	−0.617	−0.004	0.120
Pedicel L	0.515	−0.596	−0.555	0.168	−0.170

*Listed in Appendix 3.

**The characters are listed in descending order according to loadings on the first component (L = length; W = width). The scores for each specimen with respect to the first three components are depicted in Figure 16. Of the total variance, the first five components accounted for 52.7, 17.9, 14.9, 6, and 5.2 percent, respectively.

resulting from PCA of the continuous floral characters of mature flowers. The character loadings for—and the percent of—the total variance explained by the first five components are given in TABLE 4, wherein 64.5 percent of the total variance is attributable to the first three components. As can be seen in FIGURE 17, the specimens assigned to the six species of the *Polyalthia hypoleuca* complex based on consideration of the total data analyzed are usually "clustered" in closer proximity to other conspecifics when plotted relative to only the first three components. Six rather distinct groups occur: *P. discolor, P. glauca–P. parkinsonii, P. hypoleuca, P. multinervis, P. sumatrana,* and (perhaps least distinct here) *P. ovalifolia.* As with the fruit data, no continuous, presence-absence, or subjectively coded characters could be found to distinguish the two specimens recognized by Hutchinson (1917) as *P. parkinsonii* from the specimens I recognize as *P. glauca.*

These groups are supported by considering the noncontinuous floral characters in conjunction with FIGURE 17. For example, the specimens designated as *Polyalthia ovalifolia* have very densely pubescent pedicels (both flower and fruit) and young shoots and can thus be distinguished from both *P. discolor* and *P. glauca–P. parkinsonii* specimens, which lack this pubescence (rare specimens are very sparsely pubescent). Also, as can be seen in FIGURE 9, specimens assigned to *P. ovalifolia* have larger, more widely elliptic leaves (the width/length quotient is statistically different for these specimens than for either *P. discolor* or *P. glauca* (see comments after the description of *P. ovalifolia,* below)) that set them apart from all of the other groups.

Polyalthia ovalifolia is poorly represented in the PCAs including characters of mature flowers (FIGURE 17) or fruits (FIGURE 15) because individuals with

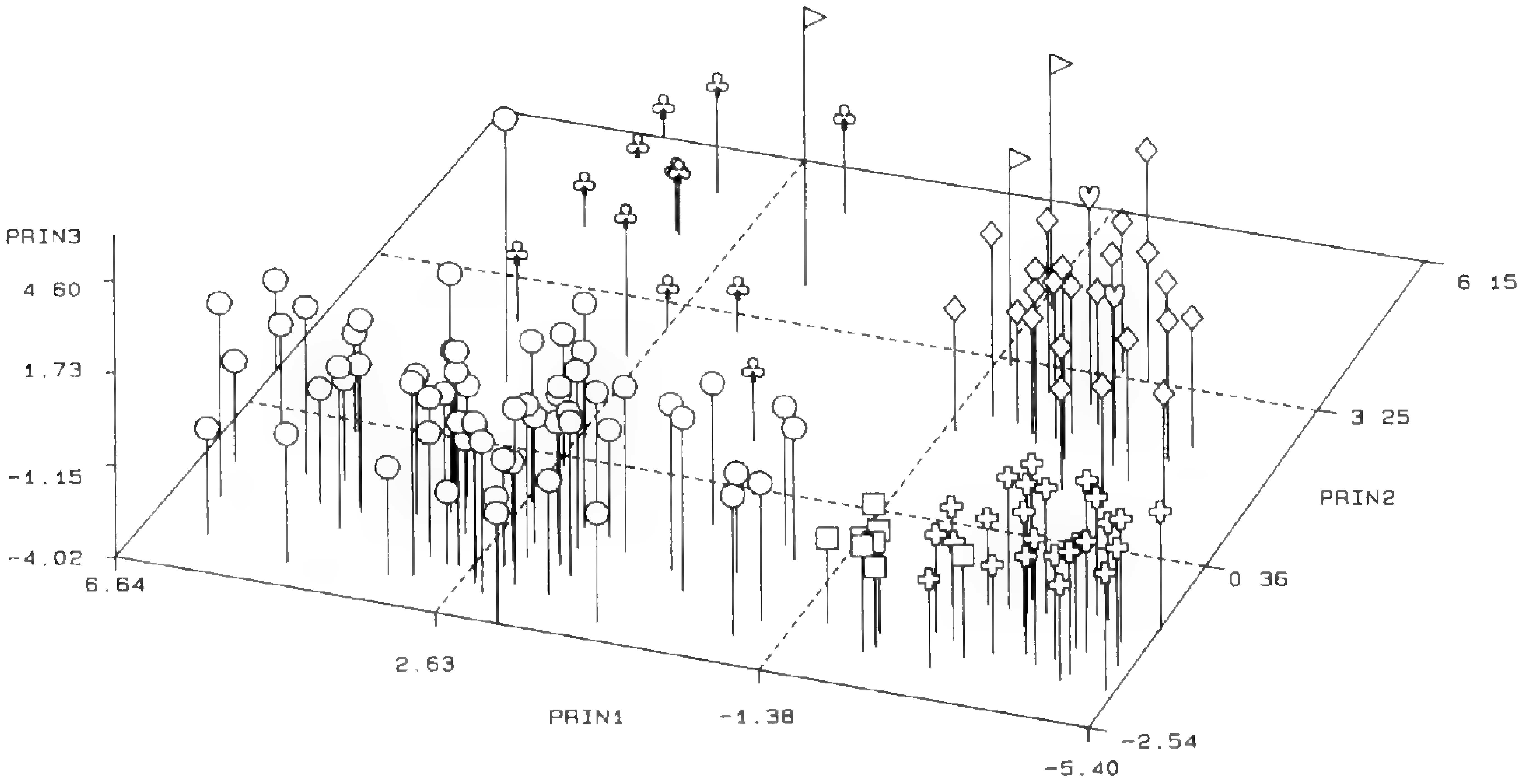


FIGURE 17. PCA results for continuous and meristic characters of mature flowers and leaves of *Polyalthia hypoleuca* complex. Each specimen depicted by its score on first 3 principal components ("PRIN") (details given in TABLE 4). *Polyalthia discolor* = clubs, *P. glauca* = diamonds, *P. hypoleuca* = crosses, *P. multinervis* = boxes, *P. ovalifolia* = flags, *P. parkinsonii* = hearts, *P. sumatrana* = circles.

mature flowers or fruits have rarely been collected. I have visited populations of this species (e.g., Bako Forest Reserve, Kuching, Sarawak; see MAP 1) but was unsuccessful in finding trees with mature flowers or fruits, although fragments of fruits (e.g., pedicels) were observed. Close to 40 individuals were found, and character states were recorded for several vegetative characters (some of these data are included in FIGURE 9). In these surveys and in all of the herbarium specimens I have examined, I have found no intermediates between the group designated as *P. ovalifolia* and the specimens I assign either to *P. glauca* or to *P. discolor*. Specimens of *P. ovalifolia* were previously either unidentified or annotated as *P. glauca*. For example, Sinclair (1955) included them in the latter species (e.g., see collection *S 12401*). However, based upon the distinctness of the sum of the vegetative and reproductive characters, I am recognizing this entity as a separate species, the formal details for which are presented below.

The group denoted as *Polyalthia multinervis* in FIGURE 17 also requires special mention since it can perhaps be argued that the groups I recognize as *P. hypoleuca, P. multinervis,* and *P. sumatrana* are not really distinct but in fact lie along a gradient of continuous character variation. Consideration of noncontinuous characters and field information in conjunction with this graph supports the conclusion that three distinct groups exist. First, all of the *P. multinervis* specimens are from Papua New Guinea, while all of the specimens comprising the *P. hypoleuca* and *P. sumatrana* groups are from Sulawesi or westward, so the variation pattern is not simply clinal. Also *P. multinervis* is very distinct from *P. sumatrana* in stamen and carpel numbers (see FIGURE 13), and from *P. hypoleuca* in having glabrous or very sparsely pubescent (vs. moderately to densely tomentose) pedicels on both mature flowers and fruits.

TABLE 4. **Loadings for first 5 components of continuous and meristic mature flower and leaf characters* derived from PCA of 135 specimens of Polyalthia hypoleuca complex.****

	COMPONENT LOADINGS				
CHARACTER	1	2	3	4	5
Androecium W	0.942	−0.157	0.007	−0.120	0.051
Torus W	0.900	0.155	−0.009	−0.088	0.058
Pedicel W at apex	0.880	−0.213	−0.090	−0.035	0.002
Stamen number	0.874	−0.283	−0.113	−0.211	0.029
Inner petal L	0.854	−0.155	0.018	−0.232	0.078
Outer petal L	0.853	−0.150	−0.009	−0.238	0.138
Androecium H	0.834	−0.390	−0.023	−0.006	0.008
Pedicel W at base	0.822	−0.215	−0.084	0.022	0.001
Stamen L	0.771	−0.140	0.148	0.328	0.030
Gynoecium W	0.752	0.474	0.040	−0.084	0.091
Torus H	0.742	−0.319	0.001	−0.122	0.132
Carpel number	0.733	0.499	0.120	−0.145	0.067
Inner petal W	0.730	0.421	0.303	0.009	−0.081
Inner theca L	0.709	−0.234	0.104	0.353	−0.024
Outer petal W	0.688	0.478	0.300	−0.028	−0.087
Carpel L	0.678	−0.172	0.172	0.303	−0.088
Leaf L	0.525	0.363	−0.683	0.090	−0.060
Pedicel L	0.517	0.621	−0.011	−0.151	−0.207
Leaf vein number	0.457	−0.561	−0.280	0.167	−0.122
Leaf W	0.439	0.444	−0.669	0.090	0.071
Outer theca L	0.434	−0.079	0.248	0.738	−0.022
Stamen W	0.372	0.127	0.002	0.203	0.407
Peduncle L	0.349	0.254	0.421	−0.080	−0.456
Stigma L	−0.319	0.539	−0.081	0.287	0.122
Inflorescence flower number	−0.318	0.671	−0.004	0.006	0.110
Pedicel bract distance	0.284	0.621	0.096	−0.115	−0.341
Petiole L	0.227	0.604	−0.493	0.143	−0.027
Gynoecium emergence	−0.006	0.728	0.169	0.217	0.098
Leaf drip-tip L	0.005	−0.317	−0.374	0.131	−0.628

*Listed in Appendix 3.

**The characters are listed in descending order according to loadings on the first component (H = height; L = length; W = width). The scores for each specimen with respect to the first three components are depicted in Figure 17. Of the total variance, the first five components accounted for 41.4, 16.4, 6.7, 4.8, and 3.7 percent, respectively.

Further, the flowers of *P. multinervis* are generally larger than those of *P. hypoleuca* (thus they cluster almost separately in FIGURE 17), and the mature carpels of *P. multinervis* are more acute at the apex than those of *P. hypoleuca.* Finally, the floral biology of members of *P. multinervis* is distinct from that of *P. hypoleuca,* as will be described in a subsequent article devoted to the comparative floral biology of the complex (Rogstad, in prep. b).

As with the analyses of the fruit data, inclusion of information from immature flowers in the data set used to generate FIGURE 17 (from mature flowers only) has a disruptive effect on the clustering of specimens seen there (results not shown).

The results of the PCA of the floral characters data, in combination with consideration of discontinuous characters and other information, support a hypothesis that the specimens of the *Polyalthia hypoleuca* complex aggregate in six groups. Therefore, a jackknifed discriminant analysis of the same data was undertaken to test the classification of each individual to its proposed group. Only one example of several possible permutations of characters or options chosen is discussed here. This particular example has been selected because it is representative of the general results obtained in all of the discriminant-analysis exploratory trials; it includes all the specimens for which all the characters could be recorded, so there is no bias due to characters that have been deleted prior to the analysis to "improve" the groups; and the procedure used (PROC BMDP DISC JACK) is here computed to reflect the unequal sample sizes (PRIORS).

In this analysis the first three discriminant functions accounted for 96.2 percent of the total dispersion, and the weighting of the coefficients for the (canonical) variables for these functions reflects the pattern found in the PCA analyses described above. Over all the discriminant functions, each species as designated *a priori* from the results of these PCA trials has a class mean that is significantly different (F test; $p < 0.01$ in all comparisons) from those of the other species. All of the specimens assigned to *Polyalthia glauca, P. discolor,* and *P. ovalifolia* from the PCA results were classified similarly in the jackknifed discriminant analysis, while 98.4 percent of the *P. sumatrana* specimens were placed in the latter analysis in accordance with the former (one of the 61 specimens of *P. sumatrana* was placed into *P. multinervis*).

As noted above, *Polyalthia hypoleuca* and *P. multinervis* are very similar to one another with respect to their continuous characters, although *P. multinervis* has slightly larger flowers. These similarities are reflected in the fact that, while the class means of these two species are statistically different, one of the 25 *P. hypoleuca* specimens and one of the eight *P. multinervis* specimens (both as determined by PCA of this data) were placed in the alternate class in the jackknifed discriminant analysis. However, differences in noncontinuous features separate these species (see above), and my decision to recognize them as distinct is founded on the totality of this evidence.

Finally, it should be noted that significant differences exist among these species with regard to vegetative and floral characteristics that could not be included in the above morphometric investigations, and these differences will be discussed in the species descriptions.

SUMMARY AND DISCUSSION

This investigation began with the grouping of a number of specimens possessing a suite of seven characters that distinguishes them from the rest of the Annonaceae.

However, some of the character states found within this monophyletic group conflict with previous attempts at classifying it within the genus *Polyalthia* and even with tribal placement. This conflict demonstrates that just because two species have been recognized as congeneric does not permit the conclusion that they are mutual members of a small monophyletic group, or that the species are "closely related" (see Heywood & Fleming (1986) for an example of TLRF sympatric congeners that are apparently only distantly related). For reasons noted earlier the establishment of monophyletic relationships is essential *before* attempting to utilize such congeners to examine the significance of whether or not sympatric closely related species differ in their niche characteristics.

Univariate, bivariate, and multivariate analyses (including PCA followed by confirmatory discriminant analysis) of morphological data recorded from specimens included in the *Polyalthia hypoleuca* complex determined that, while many of the characters previously used to distinguish these species showed central tendencies, enough overlap existed to cause confusion. In fact, subjective weighting of characters that overlap two or more species appears to have been an important source of previous species identification error.

Further, although PCA of a data set including only the continuous fruit characters revealed the similarity in PCA space of some of the specimens, noncontinuous characters are ultimately crucial in identifying fruiting specimens of this group. Exploration via PCA of covariance patterns of continuous and meristic floral and leaf characters among specimens, complemented with an analysis of the distribution of noncontinuous characters and other information, revealed groups of greater clarity. The statistical significance of these groups was tested and demonstrated through jackknifed discriminant analysis of the same data set. Ultimately, then, these analyses have provided a means to evaluate the characters previously used to define entities in this group, resulting in the rejection of some of these characters, the discovery of new ones, and thus a modification of concepts of the taxa within the *Polyalthia hypoleuca* complex. These characters have been used in constructing the keys to and descriptions of the species presented below.

Perhaps the subjective consideration of large numbers of specimens and characters, and the occasional overlap of character states between otherwise well defined species, partially accounts for the fact that of the 484 specimens examined and identified in accordance with these analyses, 9.7 percent had original identifications and 8.5 percent had subsequent annotations that differed from those presented here. Obviously, the possibility exists that the previous classification protocols and identifications are more correct. However, the analyses presented here utilize explicitly stated and repeatable techniques and character data that future workers can add to or manipulate to examine my conclusions.

The results of the morphometric analyses contribute to the rejection of the first of the three competing hypotheses, specifically that the *Polyalthia hypoleuca* complex is better described as a single polymorphic species. Further, the results support the conclusions that the complex comprises six morphologically distinct entities, and that these distinctions hold over very large geographic areas (see MAPS 2–5; more detailed ones are given in Rogstad, 1986). In other words, no matter what reticulate and clinal variation patterns exist within these species, there are clear morphological discontinuities among them. In subsequent, related articles (Rogstad, in prep. a, b) further evidence will be presented that contributes to the rejection of Hypothesis I and bears on the choice of one of the two remaining hypotheses as the more applicable with regard to the *P. hypoleuca* complex.

One group of specimens that requires further discussion has been designated as *Polyalthia parkinsonii* in the results presented above (see FIGURES 15 and 17, "heart" symbol). As discussed earlier, Hutchinson (1917) and Sinclair (1955) recognized these collections from the Andaman Islands as a separate species. Unfortunately, only three collections with flowers or fruits have been made. With the material available I have been unable to find a single character, much less a suite of them, by which these specimens can be distinguished from those of *P. glauca.* I have therefore recognized *P. parkinsonii* as a synonym of *P. glauca.* Further collections and ecological observations of the Andaman entity may prove these conclusions incorrect.

I did not expect to find that *Polyalthia glauca,* the most widely distributed species of the *P. hypoleuca* complex, shows relatively little variation in comparison to the more-restricted *P. sumatrana* or *P. discolor* (see FIGURES 15, 17; MAPS 2–4). This apparent morphological uniformity in *P. glauca* may be a sampling error, but if it holds as the species becomes better collected, it must be explained in terms of genetic, developmental, and/or selective factors.

In contrast, *Polyalthia sumatrana* shows the greatest range of morphological variation, a finding that I believe to be true based on field examinations of this species (and see the comments under *P. sumatrana,* below). Part of this variation could well be correlated with smaller-scale, intraspecific geographic distribution patterns, a possibility that is currently being explored by a more detailed analysis of the data.

Note that large ecological differences have been found between very similar species, as with the differences in floral biology between *Polyalthia hypoleuca* and *P. multinervis* (Rogstad, in prep. b), and possibly even within what appear here to be morphological species. Thus, individuals of *P. glauca* were found on hilltops in southern Thailand but were restricted to poorly drained sites at Pasoh Forest Reserve, Malaysia. There are also flower-color morphs in *P. sumatrana* (see description of this species below). Such examples serve as a reminder that differentiation of cryptic or sibling species, which are difficult or impossible to distinguish on morphological characters, may be an important constituent of TLRF diversity and evolutionary processes.

The morphological analyses and resultant systematic treatment presented in this study form the foundation for investigations into the comparative autecologies of the designated species of the *Polyalthia hypoleuca* complex. Obviously, a clear concept of species is an absolute prerequisite for the study of sympatric, closely related or very similar entities in the field. While no hypothesis of the phylogeny of the *P. hypoleuca* complex is presented here, analyses using data gathered for this treatment are in progress to provide one. The resultant hypothesis, combined with information concerning the ecological divergence of the species in the complex (Rogstad, in prep. a, b), will be examined in a future article to shed light on the evolution of geographic distribution and niche divergence among the members of this small monophyletic group.

THE POLYALTHIA HYPOLEUCA COMPLEX

General Description

The genus *Polyalthia* Blume (Fl. Javae, 68. 1830) is usually included in tribe Unoneae since the members have two series of petals that are valvate in bud and at maturity are similar or subsimilar and free (but see below). Within the Unoneae, the genus is distinguished by a combination of characters: members are trees or shrubs, with the petals not strongly clawed or basally attenuate, the stamen connectives flat topped or convex, the stigmas globose, rectangular, or irregularly shaped, the mature carpels thin walled (hardly greater than 1 mm) when dry, and the seeds one to five. Three sections have been recognized: sect. *Polyalthia* (formerly *Eu-Polyalthia* Blume), with bisexual flowers and two or more ovules per immature carpel; sect. *Monoon* Miq., with bisexual flowers and only one ovule per immature carpel; and sect. *Afropolyalthia* Engler & Diels, the members being andromonoecious, with compressed stamen connectives and connivent petals (the last section is in dispute; e.g., see Le Thomas, 1969; Verdcourt, 1969).

The *Polyalthia hypoleuca* complex of sect. *Monoon* can be diagnosed as follows: bark white, often mixed with shades of yellow or red on older twigs and branches; leaves with undersides having short, very dense, uniformly distributed papillae, the secondary veins very fine and almost indistinguishable from the tertiary veins, closely spaced and thus dense; pollen monosulcate, boat shaped, the tectum psilate, with medium-sized perforations, the pollen wall with regular columellae and a bipartite foliated basal layer; endosperm with ruminations needlelike. Another potentially useful character is the presence of straight, thickened anticlinal walls in all (or most) cells of the adaxial leaf epidermis.

Although the correct placement of this complex may not be in the genus *Polyalthia,* much more information regarding the possibly related taxa is needed before a clearer determination of the phylogenetic relationships of this group can be made. Until then, I have chosen the conservative option of retaining the complex within *Polyalthia.* I refer to this assemblage as the *P. hypoleuca* complex since *P. hypoleuca* was the first species of this group to be assigned to the genus.

Growth Characteristics

The six species of the *Polyalthia hypoleuca* complex share certain additional characteristics that may be helpful in distinguishing them, either in the field or as herbarium specimens, from other species of the genus. The seedlings are cryptocotylar, the cotyledons not emerging from the seed coats. This distinguishes them from *P. jenkinsii* (Hooker f. & Thomson) Hooker f. & Thomson and *P. rumphii* (Blume) Merr., and perhaps from other species allied with these two, which are phanerocotylar, the cotyledons expanding and remaining green while several true leaves develop after the seed coats have been shed. In the *P. hypoleuca* complex the hypocotyl elongates and becomes erect, bearing the cotyledons and epicotyl still enclosed in the cotyledons, while in *P. lateriflora, P. longifolia,* and *P. sclerophylla* (and perhaps other species allied with them) the hypocotyl does not elongate substantially, and the cotyledons, enclosed in the seed coats, remain at ground level. Above-ground shoot growth in these three species begins with elongation of the basal epicotyledonary internode. In members of the *P. hypoleuca* complex, a few weeks after the hypocotyl has become erect, the epicotyl and the first leaf primordia expand, gradually forcing the seed coats (still bearing the now-abscised cotyledons) to be shed.

The pattern by which seedlings of the *Polyalthia hypoleuca* complex grow (once branching from the axillary buds of leaves of the orthotropic shoot has commenced) appears to be common to seedlings (and saplings and trees) of most or all members of the genus. (The patterns of growth of trees of some Annonaceae—some *Xylopia* species, for example—are somewhat different; Rogstad, unpubl. data.) This pattern most closely agrees—at least for older seedlings—with Roux's model (Hallé *et al.,* 1978). To understand it, one must first realize that the primary phyllotaxy in most or all Annonaceae is distichous. In seedlings of *Polyalthia,* the second true leaf is borne 180° alternate to the first when fully expanded. The mature third leaf is, however, not oriented 180° from the attachment of the second one, but at an angle approximately 50–70° greater or less than this, and so it is not directly above the first leaf. Since these leaves are borne on an orthotropic shoot, such a pattern reduces the shading of the first leaf by the third.

This displacement of the third leaf from its expected position is effected by a "rotation" (presumably caused by differential growth) of the internode immediately below it as that internode and the third leaf expand. As in many Annonaceae, the terminal bud is held nearly horizontally due to the curvature of the internode above the last fully expanded leaf. The rotation of this curved internode occurs simultaneously with its straightening and elongation, and with the growth of the leaf immediately above it. The fourth leaf is usually borne on the orthotropic shoot at an angle of 180° to the third one, but as the third leaf is rotated away from its expected position over the first, so the fourth one is rotated away from its originally expected position over the second. The fifth leaf is again rotated from its expected distichous position relative to the fourth.

This rotation of every odd-numbered leaf (beginning with the third) is the usual initial growth pattern for the species of the *Polyalthia hypoleuca* complex (and for several other species in both this genus and various others). The rotation can be either clockwise or counterclockwise, and the direction appears to be constant in each seedling. It is also often the case in the *P. hypoleuca* complex, and possibly for other taxa as well, that the second true leaf is rotated relative to the first, with the third borne distichous to the second, the pattern described above continuing but offset by one leaf—that is, even-numbered leaves rotating (FIGURE 7A). In young seedlings, and especially in older orthotropic shoots, rotation away from distichy may occasionally occur more frequently, that is, from leaf to leaf. This rotation of leaves continues in vertical shoot growth throughout the life of a tree. It has been observed as the pattern of terminal-bud expansion even in the uppermost shoots of newly fallen 20–34 m mature trees of *P. glauca* and *P. multinervis.*

Whether each leaf or every third leaf is rotated, the result is a more or less spiral leaf arrangement on vertical shoots. Although it appears from a simple inspection of the leaves on vertical shoots as though primary phyllotaxis is other than distichous, this is a secondary phenomenon. Note that as leaves are rotated away from primary distichous orientation, so are their axillary buds and the branches that develop from them—thus the spiral arrangement of the branches of many trees in the Annonaceae.

Another aspect of this growth pattern is not only characteristic for the members of the *Polyalthia hypoleuca* complex but also appears to be widespread in the family. After the third to eighth leaf of the vertical shoot of a seedling expands, further development of the terminal bud is suspended. During this period of suspension, an axillary bud of the latest expanded leaf will grow, forming a plagiotropic branch with fully expanded leaves. Primary distichous phyllotaxy persists on such branches, and the petioles of their leaves twist so that, when fully expanded, the laminas are more or less horizontal. Once such a lateral, plagiotropic branch bears five or more expanded leaves, the basal leaf and the internode immediately below it of the resting terminal bud resume growth. When they have achieved full size, the terminal bud rests again while the axillary bud of the newly expanded leaf is released, generating a new plagiotropic branch.

This rhythmic cycle of vertical-shoot growth, suspension of vertical-shoot growth, and plagiotropic-branch growth, followed by vertical-shoot growth, and so on, is one of the basic growth patterns in the Annonaceae and is common to all members of the *Polyalthia hypoleuca* complex. Above, I noted that this pattern is most consistent with Roux's model for *older* seedlings. This distinction was made because in younger seedlings (up to the stage where three to eight leaves are present on the orthotropic axis), axillary buds usually fail to develop into branches (see FIGURE 7A). In younger seedlings where only one or a few axillary branches have been initiated, the axillary bud of one or more leaves on the orthotropic shoot sometimes fails to develop into a branch, with such branches growing only from higher leaves. This irregular branching pattern, resembling Massart's model (Hallé *et al.,* 1978), is not usually found on older seedlings and saplings where lateral branches develop from the bud of every leaf of the orthotropic shoot (Roux's model). Interestingly, a return to Massart's model often accompanies the early growth of an axillary bud that assumes orthotropic shoot growth after the abortion of the true apical meristem and terminal bud of an orthotropic shoot. This axillary bud usually develops from the axil of the last fully expanded leaf on the orthotropic shoot and may generate two to five fully expanded leaves on the shoot, all with their axillary buds repressed, before a lateral branch is generated from the axil of the next leaf of the shoot to expand, thus resembling Massart's model.

In vertical growth the trees are monopodial, with one axis remaining the "dominant" shoot unless its apical meristem dies, in which case another recently generated shoot takes its place. A few mature individuals of *Polyalthia glauca* have been found that have two major axes. As noted above, the lateral branches are initiated with a strong horizontal orientation, and lower branches are horizontal or initially "swoop" downward before bending upward to a nearly horizontal disposition distally.

General Characteristics

All members of the *Polyalthia hypoleuca* complex are understory to main canopy trees, and although none of them develops large buttresses, boles of larger trees are often slightly fluted. In some species there are pronounced "hoop marks" from branch scars on the lower main bole, while in others such scars are not readily apparent. Although *P. glauca* is unique in this group in developing undulating pneumatophores, none of these species develops extensive stilt roots originating well above the soil surface, as do some Annonaceae (e.g., *Xylopia* spp.).

As noted above, at the very earliest stages of bark development, all the members of the *Polyalthia hypoleuca* complex have a generally smooth, pale white to yellowish white bark; this is mixed with pale reddish spots in some of the species. The greatest departure from this condition occurs in *P. discolor* and *P. glauca,* in which the bark on upper portions of the bole becomes papery and flaking (FIGURE 6C), white in the outermost layer and red underneath. Bark characteristics are usually retained throughout the life of the trees (see FIGURE 6A–C); they can readily be seen on herbarium specimens and provide a useful means of finding and identifying species of this complex in the field. They also distinguish the members of this group from all other species complexes of the genus, including those from Africa and Madagascar, as well as from most other Annonaceae (e.g., see Sinclair, 1955).

The distinctive leaf papillae and venation characteristics (see FIGURES 3 and 4) shared by all members of the complex have been described. Leaf shape, except in *Polyalthia ovalifolia* (elliptic to widely elliptic), is narrowly elliptic, with apices acute to caudate in all species (see FIGURE 3A). The adaxial leaf surfaces (including the sunken midvein) are glabrous and are tan to brown (occasionally olive or gray) when dry. The venation is even less distinguishable adaxially than abaxially. The margins are recurved. All species of this group are evergreen, and most, if not all, are capable of producing two flushes of new leaves a year (Rogstad, in prep. b).

The inflorescences of the *Polyalthia hypoleuca* complex develop in the axils of either present or abscised leaves. In all but one species, I have interpreted the inflorescences as comprising a very short peduncle (usually not longer than 2 mm, and lacking lateral buds and developing flowers) that terminates distally in an articulation subtended by a bract, beyond which an unarticulated pedicel develops. The exception, *P. discolor,* has elongate (up to 11 mm) peduncles that clearly have lateral buds and developing flowers. As in many of the Annonaceae, the members of the *P. hypoleuca* complex often generate serial buds; these give rise to several inflorescences per leaf axil, each with its own peduncle.

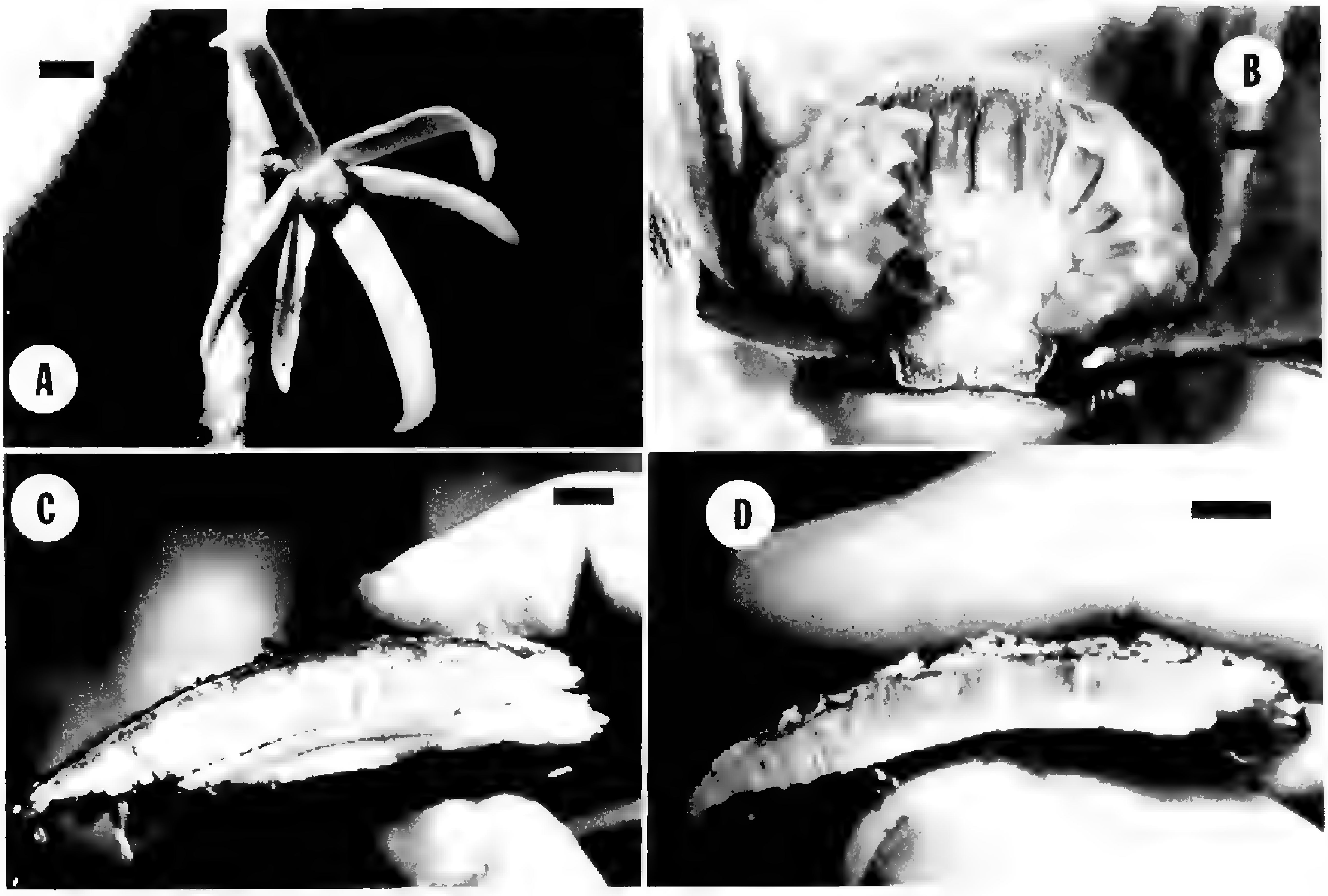


FIGURE 18. A, B, *Polyalthia sumatrana* (*Rogstad 508*), nearly mature flowers; scale bars = 5 mm in A, 0.5 mm in B. C, D, extremes of slash characteristics of mature trees in *P. hypoleuca* complex: C, *P. glauca,* relatively dispersed phloem rays not regularly reaching to epidermis, scale bar = 3 mm; D, *P. hypoleuca,* relatively dense phloem fiber rays regularly extending to epidermis, scale bar = 5 mm.

In species with few serial buds per axil (*P. hypoleuca, P. multinervis,* and *P. sumatrana*), usually no more than five inflorescences, and hence flowers, are found at any one axil (FIGURES 18A; 19A, C), and perennial tubercles built up from the remnant structures of previous flowering rarely develop at points of flowering. At axils where these species bear only one flower, peduncle bracts are perpendicular to the branch axis. In contrast, *P. discolor, P. glauca,* and *P. ovalifolia* all develop massive, perennial, ramiflorous tubercles, often with numerous flowers (more than ten; see FIGURE 20A, C). These tubercles are built up from the remnants of old inflorescences in the axils of abscised leaves. The bracts of the peduncles arising from these tubercles may be oriented in any direction.

Fries (1959) has argued that the presence and nature of pedicel bracts require more investigation as possible indicators of phylogenetic relationships, but in the species of the *Polyalthia hypoleuca* complex, they are very variable even within species. The pedicels are burgundy to blackish red when dry, and their pubescence is a key character for species identification.

The sepals of this group usually resemble equilateral to slightly extended or shortened isosceles triangles with glabrous adaxial and slightly to densely tomentose abaxial surfaces. They are more often caducous in some species (e.g., *Polyalthia hypoleuca*) than in others.

The petals of the two series are approximately equal in size and are always

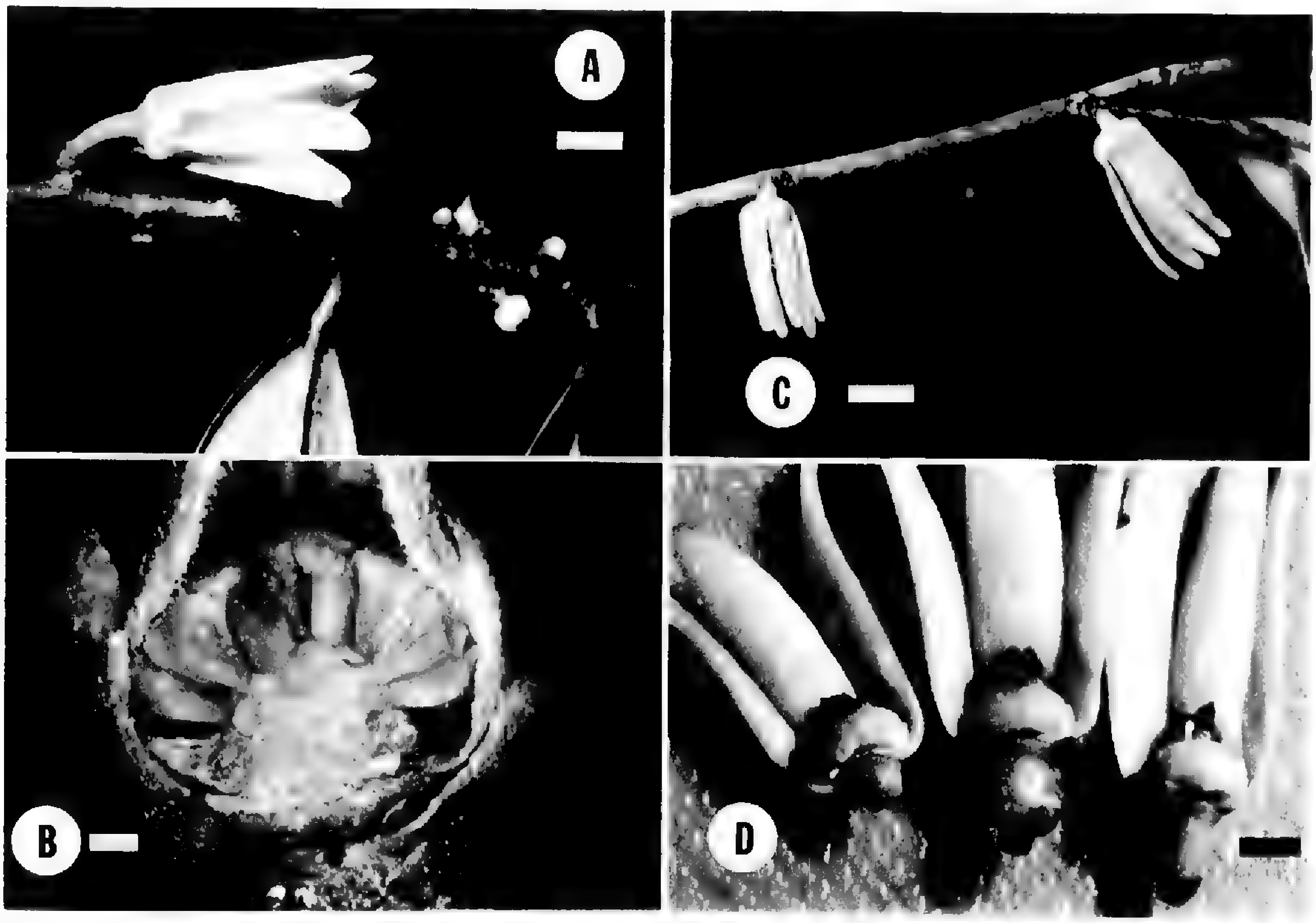


FIGURE 19. Flowers: A, *Polyalthia multinervis* (*Rogstad 813*), at anthesis, scale bar = 1 cm; B, *P. multinervis* (*Rogstad 813*), immature, scale bar = 0.5 mm; C, D, *P. hypoleuca* (*Rogstad 912*), just prior to anther dehiscence (note blackened stigmas in D), scale bars = 1 cm in C, 5 mm in D.

free throughout development. Green in all species until the stigmas become receptive (i.e., glistening with an exudate), they then turn various colors and may become fragrant. Occasional trees of all species of the complex sporadically have a few flowers with seven or eight petals, with two or more that are fused, or with one or more that fail to develop fully. The petals are linear to narrowly elliptic, and in some species they are occasionally flared distally and/or have a slight constriction near the base. Petals in which this constriction is pronounced are referred to as "clawed." The basal adaxial quarter is concave, glabrous, and often somewhat corrugated. The petals are otherwise flat; they are thin throughout, rather than thick and fleshy as in some Annonaceae.

The stamens are normal for the genus, with flat-topped to slightly convex connectives. On the torus each stamen is surrounded by a slightly raised ridge, which remains after the stamen has abscised and often even persists in the mature fruit. The resultant "stamen scars" can usually be counted and are therefore often crucial in species determination (see the discussion about the difficulty of identifying fruiting specimens of *Polyalthia glauca* and *P. discolor* from New Guinea, below). The portion of the torus bearing the stamens is short-columnar, forming a cylinder parallel to the floral axis, while that bearing the carpels may be concave, flat, or convex, varying even within a species (e.g., *P. sumatrana*). Both the androecial and the gynoecial portions of the torus are glabrous in all members of this group. This contrasts with several other species

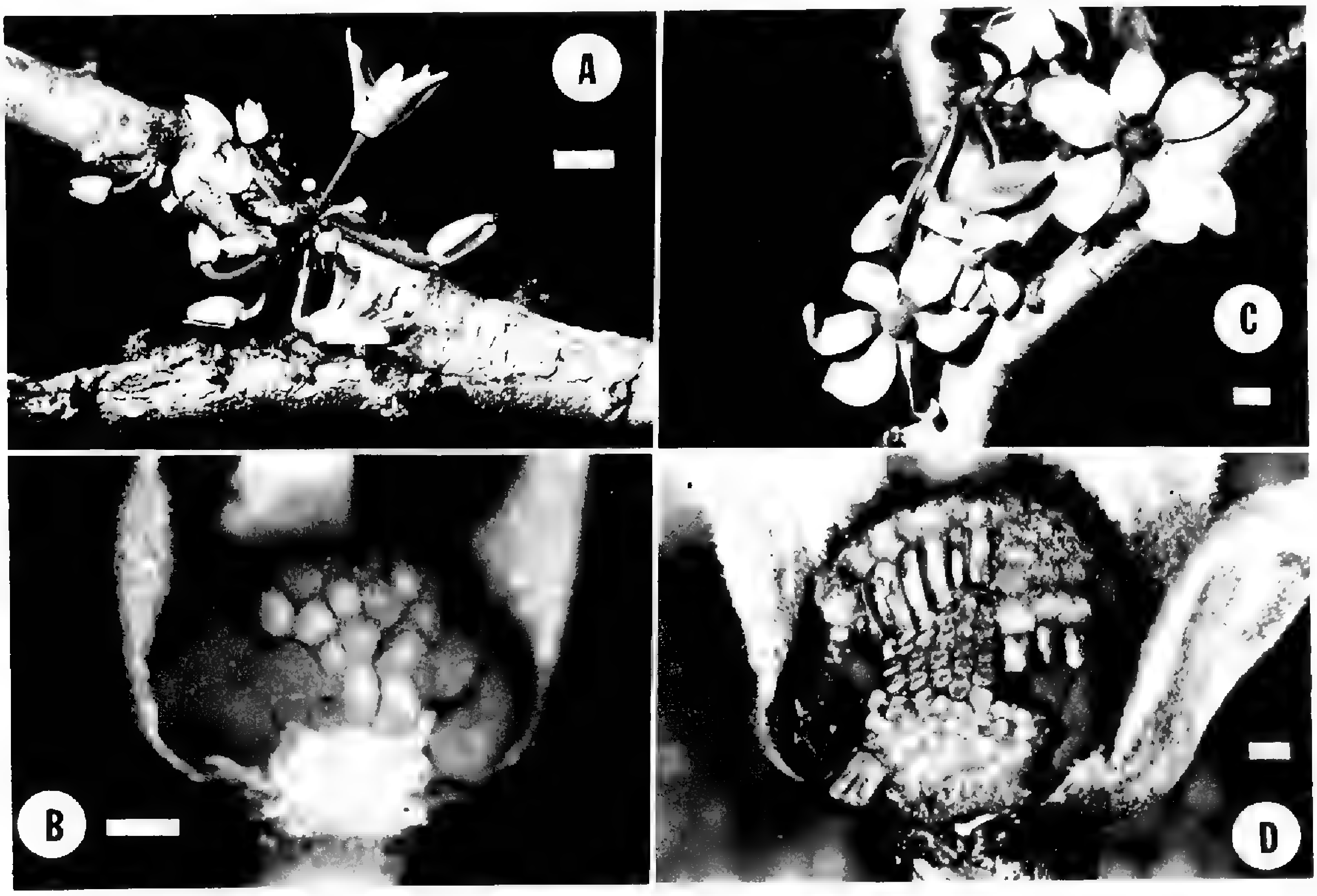


FIGURE 20. Flowers: A, *Polyalthia glauca* (*Rogstad 939*), different stages of development, scale bar = 5 mm; B, *P. glauca* (*Rogstad 939*), immature, few stamens removed, scale bar = 0.5 mm; C, *P. discolor* (*Rogstad 814*), later stages of development, scale bar = 5 mm; D, *P. discolor* (*Rogstad 814*), immature, some stamens and carpels removed, scale bar = 0.5 mm.

of *Polyalthia* (e.g., *P. cinnamomea* Hooker f. & Thomson, *P. lateriflora, P. longifolia, P. sclerophylla*), in which one or both portions are pubescent.

The carpels in the *Polyalthia hypoleuca* complex range from glabrous to tomentose, and all have a clearly visible adaxial stigmatic crest that can be detected even in fruit. The stigmas are always free and densely puberulent. They range from globose to elongate or clavate but are never obviously grooved, as they are in species of many annonaceous genera. The stigmas turn black and are presumably nonfunctional a few hours prior to anther dehiscence. Many of the floral characters described immediately above can be seen in FIGURES 18A and B, 19, and 20.

As the carpels mature, they turn from green to red, and then to purple-black at full ripeness. Within this complex only *Polyalthia sumatrana* has developing carpels that are green streaked with irregular red spots. Either the mature carpels and seeds are both ellipsoid, or they are globose with the seeds biconvex to lenticular. Species in which the mature carpels are ellipsoid have basal placentation and seeds with a strong longitudinal circumferential ridge, a basal micropyle, and a basal "aril scar"; those in which they are globose have ventral placentation and seeds with a longitudinal groove (or a very slight circumferentially raised area with a clear medial groove), a ventral micropyle, and no aril scar. All species of the group have seeds with rumination needles; they have predominantly one-seeded mature carpels (thus their placement in sect.

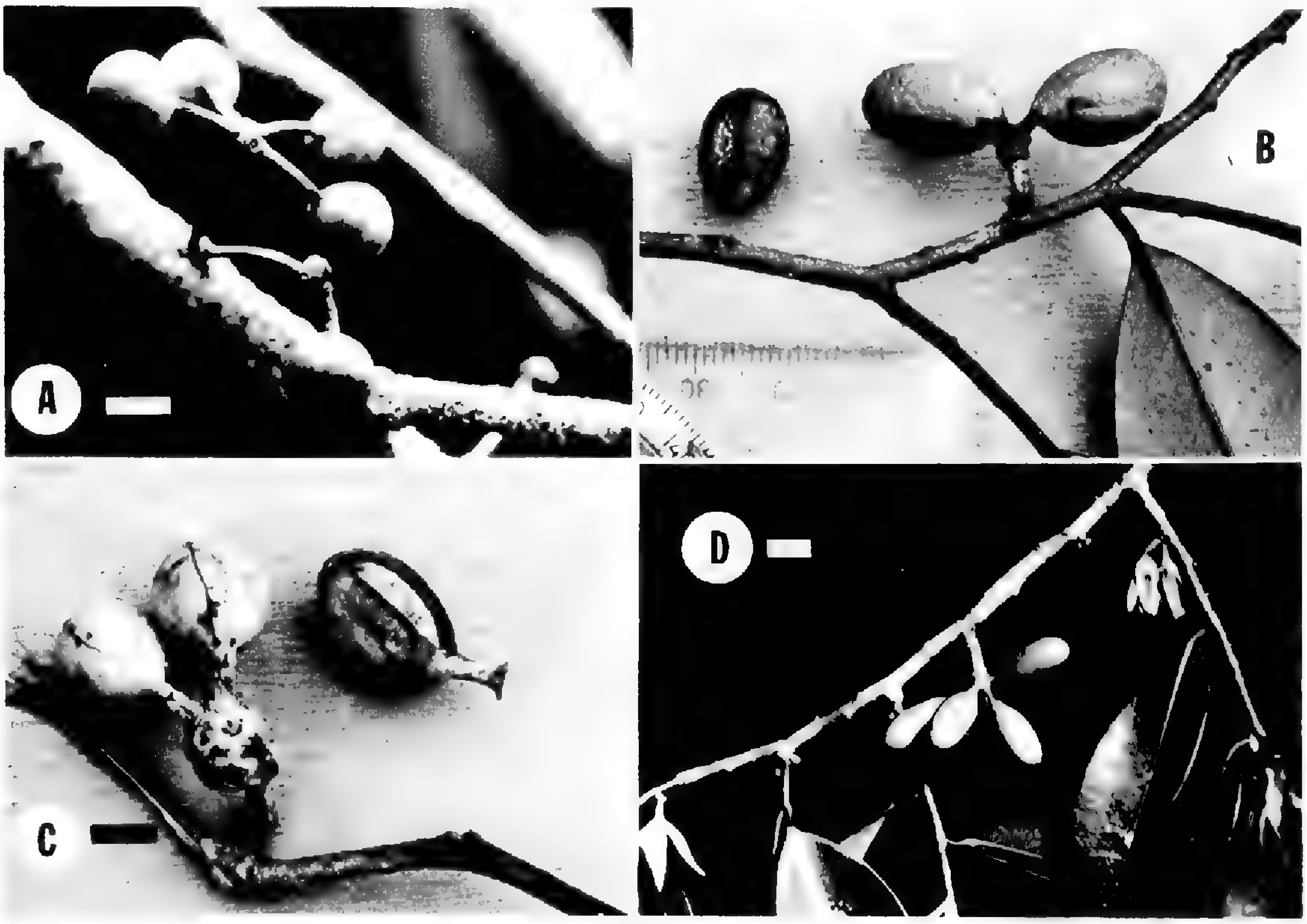


FIGURE 21. Near-mature fruits of members of *Polyalthia hypoleuca* complex: A, *P. glauca* (*Rogstad 939*); B, *P. hypoleuca* (*Rogstad 912*); C, *P. sumatrana* (*Rogstad 508*); D, *P. multinervis* (*Rogstad 813*). Scale bars = 1 cm.

Monoon by most authors), although occasional ones containing two seeds are found. For example, of 183 mature carpels of *P. glauca* sampled at Pasoh, 3.3 percent were two seeded, and most of these seeds germinated. Many of the above-described fruit and seed characters can be seen in FIGURES 7B–D, 8, and 21.

The four species for which chromosomes have been counted (*Polyalthia glauca, P. discolor, P. hypoleuca,* and *P. multinervis*) are all $2n = 18$ (Rogstad, in prep. c).

One gains the impression from the relative number of times that each species of the *Polyalthia hypoleuca* complex has been collected that *P. sumatrana* must grow more abundantly than the others. However, the greater number of sheets of *P. sumatrana* is probably due to the fact that this species is the smallest tree in the group. Kochummen (1972) has stated that *P. glauca* is a rare species, but at Pasoh Forest Reserve, peninsular Malaysia, I found it growing in about equal density to *P. sumatrana,* although in much more restricted habitats and to much greater heights. Drawing conclusions about species distributions and relative abundance from herbarium materials alone can be misleading.

A specimen of *Polyalthia sumatrana* (*Austin Cuadra A 2118,* A) has a black fungus growing in circular colonies on the leaves. An annotation indicates that this fungus is *Meliola polyalthiae* Hansf. I have several times seen this fungus growing on *P. hypoleuca, P. sumatrana,* and most frequently *P. glauca* (in the last species, most of the leaves of an individual can be infected).

Keys to the Species of the Polyalthia hypoleuca Complex

Due to the large amount of overlap of vegetative characters, no strictly vegetative key is presented here.

The morphometric analyses yielded suites of characters by which each species could be distinguished, but their use in entirety would make a key overly complex. I have thus attempted to construct keys based on important, commonly present characters that are relatively easy to determine. Most specimens have only flowers or fruits, so separate keys are provided for each contingency. The ranges of character dimensions have been obtained from the complete data sets that were used in the character-variation analyses reported above.

Although most of the characters used in the keys have been measured from dried herbarium specimens, these keys and the information provided in the species descriptions can also be used on fresh or fixed specimens. For example, the most useful characters for distinguishing fresh material are those unaffected by shrinkage; these include, for flowers, the number of stamens and carpels, the stamen/carpel quotient, the tomentum on the pedicel, the shape of the stigma, and the nature of the inflorescences, and for fruits, the shape of the mature carpels, the shape, circumferential ring, and nature of the aril area of the seeds, the pubescence (or lack thereof) on the pedicel, and the nature of the infructescence. However, it should be noted that mature specimens of *Polyalthia glauca* flowers that were first measured fresh shrank ca. 25–30 percent upon drying, with petals shrinking about 40–45 percent. Herbarium-specimen characters and label-note information that can be used to assess the maturity of flowers and fruits were given above in the discussion of how specimens were chosen for the morphometric analyses.

Key for Flowering Material

1. Stigmas elongate, 65–100% length of carpels, those in outermost ring of carpels bent at least 30° out from floral axis; inflorescences borne on branches, always below the leaves, arising mainly from tubercles, each with 1 terminal flower, this borne on extremely reduced peduncle ($\leq$ 1.1 mm long) bearing no other flowers or buds.
    2. Pedicels glabrous, young shoots glabrous to very sparsely pubescent; laminas narrowly elliptic, 2.5–7 cm wide, width/length quotient 0.24–0.34. .... 1. *P. glauca.*
    2. Pedicels and young shoots moderately to densely tomentose with short, rust-colored hairs; laminas usually elliptic to widely elliptic, 7–11.3 cm wide, width/length quotient 0.34–0.44. .... 2. *P. ovalifolia.*
1. Stigmas usually globose, not exceeding 64% of carpel length, if slightly elongate then those of outermost ring of carpels not strongly bent away from floral axis; inflorescences arising either both at and below present leaves (then lacking well-developed tubercles, with very reduced peduncle bearing only 1 terminal flower) or exclusively below the leaves and from tubercles (then usually with peduncle 1.1–11 mm long bearing lateral flowers or resting buds).
    3. Pedicels 7.5–50 mm long; stamens $>$ 55; carpels $>$ 12 (possibly very rarely $\leq$ 12 in *P. sumatrana*).
        4. Outer petals narrowly elliptic to elliptic (width/length quotient $>$ 0.2), with dense tomentum on adaxial surface beginning on basal ⅓; carpel/stamen quotient $>$ 0.3; inflorescences borne on branches below the leaves, arising from

tubercles, with peduncle bearing lateral developing flowers or resting buds. . . .. 3. *P. discolor.*
   4. Outer petals linear to narrowly elliptic (width/length quotient < 0.2), with moderate to sparse tomentum on adaxial surface absent from at least basal ⅓; carpel/stamen quotient < 0.3; inflorescences both from foliate axils and borne on branches below the leaves, well-developed tubercles lacking, the peduncles extremely reduced, bearing 1 terminal flower and no lateral buds. .... 4. *P. sumatrana.*
  3. Pedicels < 7.5 mm long; stamens < 55; carpels generally < 12.
   5. Pedicels moderately to densely tomentose; collected only west of New Guinea. .... 5. *P. hypoleuca.*
   5. Pedicels glabrous (or very sparsely pubescent); collected only in Papua New Guinea. .... 6. *P. multinervis.*

Key for Fruiting Material

1. Distal portion of mature carpels globose; placentation ventral; seed(s) biconvex-lenticular, often with irregular indentations on surface, with longitudinal circumferential groove (this occasionally running medially within slightly raised circumferential area), no aril scar detectable.
  2. Pedicels and youngest shoots with moderate to dense, short, rusty tomentum; laminas usually elliptic to widely elliptic, 7–11.3 cm wide, width/length quotient 0.34–0.44. .... 2. *P. ovalifolia.*
  2. Pedicels glabrous, youngest shoots moderately pubescent at most; laminas narrowly elliptic, 2.5–7 cm wide, width/length quotient 0.24–0.34.
   3. Stamen scars > 50; mature carpels with stalks > 13 mm long. .... 3. *P. discolor.*
   3. Stamen scars < 45; mature carpels with stalks < 13 mm long. .... 1. *P. glauca.*
1. Distal portion of mature carpels ellipsoid; placentation basal; seeds ellipsoid, never with irregular indentations on surface, with strong longitudinal circumferential ridge, aril scar easily detectable.
  4. Pedicels > 9 mm long; stamen scars > 50. .... 4. *P. sumatrana.*
  4. Pedicels < 9 mm long; stamen scars < 50.
   5. Pedicels moderately to densely tomentose; collected only west of New Guinea. .... 5. *P. hypoleuca.*
   5. Pedicels glabrous (or very sparsely pubescent); collected only in Papua New Guinea. .... 6. *P. multinervis.*

Species Accounts

As with the characters used in the keys, those included in the species descriptions are taken largely from the data sets of mature floral or fruit characters used in the morphometric analyses. These data were collected from dried herbarium specimens (exceptions are noted). The minimum and maximum values of most continuous characters will be given for each species, followed in parentheses by the mean, the standard deviation, and the number of specimens for which the character could be evaluated. For noncontinuous characters, all specimens have the noted trait unless a percentage breakdown is given. In the latter case, the total number of specimens evaluated for the character will be given. Mean values, standard deviations, and number of herbarium specimens used are not reported when the last figure is less than ten.

Rather than listing all of the specimens I have examined, I give only selected ones that illustrate the range of locations and of morphology for each species; all specimens used in the morphometric analyses are included. A "finders list" of all the specimens I have examined is on deposit with the Botany Libraries of Harvard University, and a copy of it will be sent upon request. Most information given for specimens should be self explanatory, with two exceptions. First, where it is not clear whether a label identification number refers to a collector or to the distributing institution, I have given the collector's name or the institutional abbreviation in brackets. Second, a designation as to whether I classified the specimen on the basis of flowers (fl), fruits (fr), or both (fl+fr) is given immediately following the identification number for each specimen; sterile specimens are also indicated (st). If these designations are in capital letters, the specimen has been included in the data sets for the morphometric analyses. Note, however, that different specimens are missing values for different characters or are immature, so all of the specimens included in the data sets are not used in all of the data analyses presented above.

Local or common names applied to the species as recorded by collectors are listed alphabetically for each species. Different spellings that obviously refer to the same name are listed separately. A general location (or locations, if a name is widespread) is given with each name, with more precise information available in the list of selected specimens for each species.

Short descriptions of the habitat ecology are given, but these only very briefly summarize the results of more detailed investigations into comparative habitat ecology, seedling ecology, and floral biology of several species of this group, a full description of which will be detailed subsequently (Rogstad, in prep. a, b).

1. **Polyalthia glauca** (Hassk.) Mueller, Descr. Notes Papuan Pl. App. 95. 1877, non Boerlage (1899); *Uvaria glauca* Hassk. Flora **25**(Beibl. 2): 31. 1842; *Guatteria glauca* (Hassk.) Miq. Fl. Ned. Ind. **1:** 49. 1855; *Monoon glaucum* (Hassk.) Miq. Ann. Mus. Bot. Lugduno-Batavum **2:** 19. 1865. TYPE: *Hasskarl s.n.* (possibly marked "nom. sund. Kaju tinjang" and/or "Arbor in m. Roeboet") (n.v.).
FIGURES 2A, B; 3B, C; 4C; 6C, D; 8D; 18C; 20A, B; 21A.

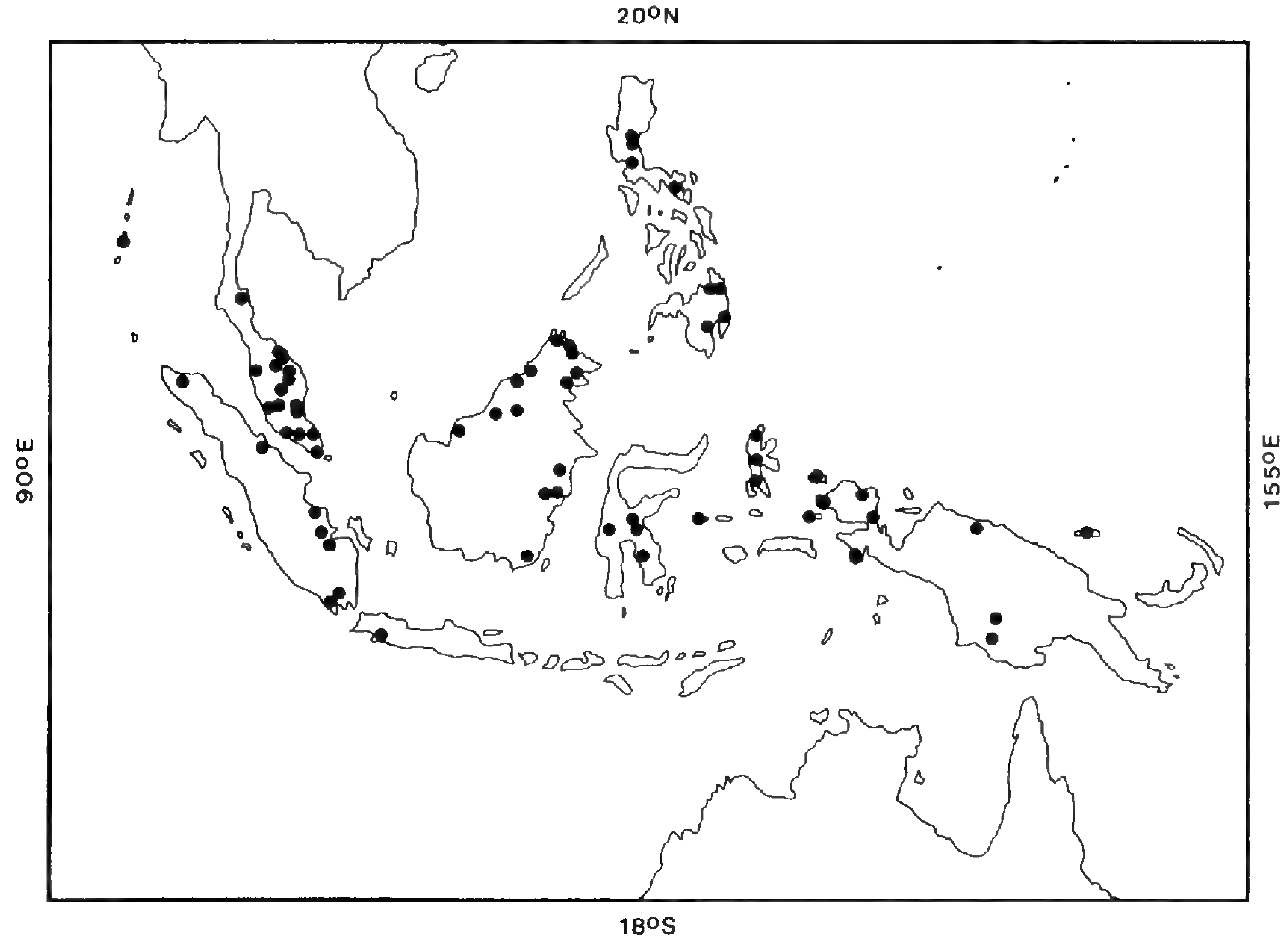
Guatteria hypoleuca Miq. Fl. Ned. Ind., Eerste Bijv. 381. 1861. TYPE: [Sumatra] Priaman, Madang Poelo, *Diepenhorst 2095* (U).

"*Unona hypoglauca* Miq." ex Hooker f. & Thomson, Fl. Brit. India **1:** 63. 1872, nomen nudum.

Unona merrittii Merr. Philipp. J. Sci. C. **1:** 190. 1906; *Polyalthia merrittii* (Merr.) Merr. Philipp. J. Sci. C. **10:** 250. 1915. TYPE: Philippines, Mindoro, Bongabong River, February 23, 1906, *Whitford 1447* (n.v.).

Polyalthia parkinsonii Hutch. Bull. Misc. Inform. **1917:** 25. 1917. SYNTYPES: India, Andaman Islands, Long Island, Feb., *Parkinson 943* (fr) (K); without precise locality, Dec., *Parkinson 765* (fl) (K), *794* (fl) (K).

Tree to 45 m tall, DBH to 56 cm; trunk often fluted at base; pneumatophores (except at drier sites) arising from below soil 0.5–1.5 m from base, ascending up to 0.7 m, then recurving to reenter soil, sometimes emerging again farther away, extending up to 8 m from tree base; bark white, smooth on younger trees and branches but papery and flaking, revealing red, papery and flaking bark above height of 3 m or more on boles of many older trees; hoop marks prominent even on lower portions of bole; slash on larger trees revealing phloem rays separated from surface by 2 mm or more of woody matrix, phloem-ray apices 0.5–1.5 mm apart. Twigs with bark white, often having small red spots throughout, youngest growth glabrous (39%) to slightly tomentose (61%; *n* = 31). Leaves with young petiole 3–8 (5.8, 1.4, 31) mm long, glabrous to moderately tomentose abaxially; lamina narrowly elliptic to elliptic, 9–22 (14.3, 3.3, 31) × 2.5–7 (4.4, 1.1, 31) cm, the apex acuminate to apiculate, 0.3–2.1 (0.9, 0.4, 31) cm long, the base rounded to acute, the secondary veins 13 to 39 (21.5, 6.2, 31) per side, occasionally looping more or less regularly to form weak intramarginal vein; leaves when fresh weakly conduplicate with abaxial surface bright white. Inflorescences borne on branches below leaves, arising predominantly from tubercles, 2 to 15 per tubercle; peduncle extremely reduced, 0.2–1.1 (0.5, 0.3, 23) mm long, usually with only 1 terminal flower developing, lateral floral buds and developing flowers absent; bracts 1 to 3, irregularly oriented with respect to branch axis. Flowers with pedicel 7–29 (18.1, 6, 23) mm long, 0.2–0.8 (0.6, 0.16, 23) mm wide at base and 0.6–1.4 (0.9, 0.19, 23) mm at apex, glabrous (90%) to sparsely pubescent (10%; *n* = 25); bract sometimes (48%; *n* = 23) present, 4–16 (8.3, 3.2, 11) mm above articulation. Sepals triangular, 0.6–1.9 (1, 0.28, 23) mm long, abaxially moderately (22%) to densely (78%; *n* = 23) tomentose, infrequently caducous at floral maturity. Petals linear (91%) to basally clawed with distal portion linear (9%; *n* = 23); outer petals 7–18 (10.4, 3.2, 23) × 1–4.5 (2.2, 1, 23) mm, with the pubescence beginning adaxially on basal (83%) or middle (17%; *n* = 23) ⅓, sparse throughout (9%), moderate throughout (21%), dense throughout (52%), or sparse throughout except abaxially at base where dense (17%; *n* = 23), the midvein generally not visible abaxially; inner petals 6–18 (10.9, 3.5, 23) × 0.9–3.5 (1.8, 0.7, 23) mm; all petals yellow when stigmas become receptive, very fragrant (pleasant-sickly sweet; similar to *Cananga*), turning purplish sepia when anthers dehisce. Torus 0.2–0.8 (0.47, 0.18, 23) × 1.1–2 (1.5, 0.26, 23) mm, gynoecial portion concave (4.4%), flat (56.5%), or convex (39.1%; *n* = 23). Androecium 2–3 (2.5, 0.3, 23) × 0.5–1.4 (1.1, 0.2, 23) mm; stamens 15 to 31 (23.8, 3.6, 23), 0.5–1 (0.78, 0.12, 23) × 0.7–0.9 (0.77, 0.08, 23) mm. Gynoecium 1–2.8 (1.9, 0.4, 23) mm across; carpels 10 to 25 (17.7, 3.1, 23), 0.6–1 (0.78, 0.14, 23) mm long, glabrous (100%; *n* = 23); stigmas elongate, clavate, 0.4–1.1 (0.6, 0.18, 23) mm long, those of outermost ring reflexed at least 30° out from floral axis. Immature carpels green, turning red, finally blackish purple, the pericarp then soft and fleshy (juice laden), with sweet to bitter-sweet taste. Mature, dry fruits with pedicel 8–35 (22.8, 6.4, 33) mm long, 1.1–3.2 (1.8, 0.56, 33) mm in diameter at apex, glabrous (97%) or sparsely pubescent (3%; *n* = 33); stamen scars < 40 (100%; *n* = 21); carpels with the stalk 3–16 (7.9, 2.7, 31) × 1.2–2.7 (1.9, 0.39, 31) mm, the seed-bearing portion globose, 9–25 (15, 3.4, 32) × 11–25 (15.4, 3.3, 32) mm, not ridged, rounded at apex; fruit wall < 1 mm thick, deep red to black. Placentation ventral at maturity. Seed(s) 1 (or 2) per mature carpel, biconvex-lenticular, with circumferential groove (this occasionally within slightly raised area), the aril scar lacking, the testa deep brown to black (often green when fresh), smooth to



Map 2. Distribution of *Polyalthia glauca.*

finely pitted, often irregularly indented in both fresh and dried seeds; rumination acicular.

Distribution. Andaman Islands, southern Thailand, peninsular Malaysia, Sumatra, Borneo, New Guinea, Admiralty Islands (Map 2).

Selected specimens seen. **India.** Andaman Islands: sine loco, *Parkinson 765* (FL) (K), *794* (FL) (K); Bom-ling-la, *Parkinson 943* (FR) (K). **Thailand:** Khao Tha Phet F.R., Surat Thani, 40 m alt., *Rogstad 841* (fr) (A, BKF). **Malaysia.** Trengganu: Kiat, Sungei Nerus, Kuala Trengganu, *SFN 40915* (FR) (KEP, L, SING). Perak: Changkat Jong F.R., 100 m alt., *FRI 5611* (fr) (KEP). Kelantan: Ulu S. Aring, near K. Tapah, *FRI 4485* (FR) (KEP, SAR); Sungai Lebir, Kuala Sepia, *FRI 7038* (FR) (A, KEP, L, SAR). Pahang: Tasek Bera, near Fort Isikandar, 45 m alt., *FRI 3972* (FR) (A, KEP); Taman Negara, 75 m alt., *FRI 14327* (FR) (A, K, KEP, L), *FRI 14438* (FR) (A, KEP, L); Kuala Lompat Game Reserve, Kuala Krau, *FRI 25108* (FR) (KEP). Negri Sembilan: Pasoh F.R., near Simpang Pertang, *Rogstad 939, 944, 945, 966* (all FL) (all A); Perhutian Tinggi(?), *Ridley(?) 10030* (fr) (K); Pasoh F.R., *FRI 27582* (FL+fr) (FRI). Johore: Kuala Sedili, *Kadim & Noor 195* (fr) (A, SING); Sungai Sedili, Mawai, *SFN 29274* (FR) (A, SAR, SING); Ayer Hitam F.R., 50 m alt., *KEP 98248* (A, KEP). Sarawak: Semengoh Arboretum, Kuching, 15 m alt., *Brain anak Tada s.n.* (FR) (A, KEP, L, SAR); Ulu Mayeng, Kakus, 60 m alt., *S 21710* (FR) (SAR, SING). Sabah: Kelumpang Balong, Tawau, 915 m, *SAN 18520* (FR) (L, SAN); 5.5 mi NE of Ranau, 472 m alt., *SAN 28987* (FL) (L, SAN); Biah trail, Sapong Estate, Tenom Distr., 300 m alt., *SAN 50232* [*Sadau*] (FR) (SAN); Crocker Range F.R., Rayoh, Tenom Distr., *SAN 78396* (FR) (KEP, SAN, SAR); Gum-Gum F.R., 16 mi N of Sandakan, 140 m alt., *SAN 90945* (FL) (SAN); Sogo-Sogo, 11 mi from K. Tongod, *SAN 91121* (FR) (SAN). **Singapore:** Mandai Road, *SFN 34448* (FR) (KEP, SING); Mondai Road, *SFN 37120* (FR)

(KEP, SING). **Philippines.** Luzon: Baler, Principe Prov., *Merrill 1031* (FR) (PNH, US). Camarines Prov., *FB 10475* [*Curran*] (FR) (PNH, US); Nueva Vizcaya, Luzon Prov., *FB 28532* (FR) (PNH, US); Casiguran Tayabas Prov., *BS 45271* (FR) (A, K, PNH, US). Sibuyan: Magellanes (Mt. Giting-Giting), Capiz Prov., *Elmer 12449* (FR) (A, US). Mindanao: Mt. Hamiguitan, Davao Prov., 600 m alt., *Edaño 1688* (FL) (A, PNH); Butuan Subprov., *FB 20757* (FR) (PNH, US). **Indonesia.** Sumatra and adjacent islands: Palembang, 20 m alt., *Grashoff 820* (FR) (BO, L); Tg. Djawidjawi, P. Mendol, Selatpandjang, 5 m alt., *bb 21461* (FR) (A, BO, L); Belimbing, 6 m alt., *bb 28490* (FR) (BO, L); Djepara, NE Lampung, 20 m alt., *bb 35755* (FR) (BO, L). Kalimantan: Bangarmassing, *Motley 932* (FL) (K); Tdg. Bangko region, near mouth of Mahakam R., 20 m alt., *Kostermans 7193* (FR) (A, BO, L); Nunukan Is. (northern part), *Kostermans 8954* (FL+fr) (A, BO, K); Sg. Mentawir region, near Mentawir Village, Balikpapan Distr., *Kostermans 10022* (FL) (BO, KEP). Java and adjacent islands: Udjung Kulon Reserve, Mt. Pajung, 300 m alt., *Kostermans c. s.* (UNESCO) *165* (FR) (BO, L). Celebes: En Ond Malili, *Cel./2.-446* (FL+FR) (A, BO); Malili, *Cel./2.-491* (FR) (BO, K). Moluccas: G. Permatang, Sangowo R., Morotai, *Kostermans 927* (fl+FR) (A, BO, LAE); Tiloppe, Weda, 25 m alt., *bb 24853* (FR) (A, BO, L); Morotai, Subdistr. Tobelo Totodokoe, 30 m alt., *bb 33737* (FR) (A, BO, K), *bb 33750* (FR) (BO, L). Irian Jaya: Sorong, Fakal, bank of Kasim R., Misool, *Pleyte 859* (FL+fr) (A, BO, SING); Subdistr. Ransiki, Meos Waar Is., 5 m alt., *BW 1214* (FR) (A, SING); Hollandia [Jayapura], 40 m alt., *BW 4817* (FR) (A, LAE); Radjah Ampat, Lupintol Village, Waigeo Is., 40 m alt., *Van Royen 5481* (FR) (L, SING); Adi Is., Fak-Fak Div., 25 m alt., *BW 10173* (FL+fr) (A, Boswezen); sine loco, *Zippiel* [*Zippelius*] *s.n.* (FL) (A, L). **Papua New Guinea and adjacent islands.** Western Province: Agu R. branch of middle Fly R., near Mipan Village, 30 m alt., *Pullen 7394* (FL+fr) (A, CANB, L); Lake Daviumbu, middle Fly R., *Brass 7622* (FL) (A). Manus Province: above Derimbat Village, Admiralty Islands, 100 m alt., *LAE 59246* (FR) (A, LAE, US).

Regional names. "Lanotan," Ma language, Davao Prov., Philippines, *G. E. Edaño 1688*. "Lulusan sowong," language?, Ranau Distr., Sabah, *SAN 28987*. "Manitan," language?, Selangor, peninsular Malaysia, *KEP 28833*. "Mempisang" (a general name for several Annonaceae), Malay language, SE Kelantan, peninsular Malaysia, *FRI 7038*. "Minakoe," Manikiong language, Meos Waar Is., New Guinea, *BW 1214*. "Paroe," Selogof language, Waigeo Is., New Guinea, *Van Royen 5481*. "Pisang-pisang" (a general name for several Annonaceae), Malay language, Tawau, Sabah, *SAN 18520*. "Saselo," language?, Morotai, Moluccas, *bb 33737*. "Songyu" (a general name for several Annonaceae), (local?) Thai language, Surat Thani, Thailand, *Rogstad 841*.

Local use. *Polyalthia glauca* is thought to be the best source of firewood in the northern region of Sarawak (*Motley 932*). The wood of larger *P. glauca* trees may also be used for crate and toy construction in peninsular Malaysia (Timber Utilization Chart, Forest Research Institute, Kepong, Selangor, Malaysia).

Ecology. Specimens have been collected from sea level to 915 m alt. Of species in the *Polyalthia hypoleuca* complex, *P. glauca* has the widest geographic range. Although occasional specimens of this species are marked as collected from hillsides, the bulk of the herbarium notations, as well as my own observations, indicate that this species most frequently grows in saturated soils along streams, at seasonally or permanently inundated sites, or in peat swamps. It can be quite common (eight to 15 mature individuals/ha) in such habitats. Exceptions to this pattern can be found in drier regions at the boundaries of the species range (e.g., Thailand; *Rogstad 841*). Mature trees of this species occupy the middle to upper canopy. At Pasoh F.R., peninsular Malaysia, flowering can occur, with varying intensity, at least twice per year. Each period is immediately preceded by the initiation of growth of new branches and leaves and may include four (or more?) separate ten- to 14-day waves of flowering.

COMMENTS. I have been unable to locate the type specimen for *Polyalthia glauca* at A, B, BO, F, GH, K, KEP, L, MO, P, SAN, SAR, SING, U, US, or WRSL, and neotypification may be necessary. A type specimen for *P. merrittii* has also not been found at A, B, BO, F, GH, K, KEP, L, LY, MO, P, PNH, SING, U, UC, US, or WRSL.

Miquel's description of *Guatteria hypoleuca,* and the type specimen noted for this name in the synonymy, are both beyond doubt *Polyalthia glauca.* Hooker and Thomson (1872), in describing *Polyalthia hypoleuca,* did not mention *Guatteria hypoleuca* anywhere in the text, but they did compare their newly described species to "*Unona hypoglauca* Miq." This latter name has not been published elsewhere. A syntype of *P. glauca* (at K) is labeled *Unona hypoglauca* in an unidentified hand, and *Guatteria hypoglauca* by Miquel. This specimen must be responsible for the reference of Hooker and Thomson above and is thus the probable source for the *nomen nudum.*

Individuals of *Polyalthia glauca* are often easy to find in poorly drained areas due to the bright red bark that develops on the upper bole of many, but not all, trees (the flaking bark of this species makes it a difficult subject for research because it is often impossible to climb the slippery trunks) and the pneumatophores that may emerge from the soil within a meter or so of the base of the bole, then curve back to and reenter the soil, often again emerging and reentering the soil at a greater distance. A pneumatophore system of one tree may extend up to 8 m from the base of the tree, and because the older pneumatophores have the white bark characteristic of the *P. hypoleuca* complex, they are easily spotted in the field. The extension growth of emergent pneumatophores has an interesting pattern of periodicity marked by annular scars (see FIGURE 6D). Within the *P. hypoleuca* complex, such pneumatophores have been found only in *P. glauca* individuals growing at poorly drained sites.

Sinclair (1955) implicitly recognized *Polyalthia parkinsonii,* although he did not treat it in detail since he thought it occurred outside of the geographic range under consideration. He did suggest, however, that the entity of the *P. hypoleuca* complex found in Burma and the Andaman Islands by Kurz (1874) was actually *P. parkinsonii,* rather than *P. sumatrana,* as the latter author believed. Since Kurz did not list the specimens on which he based his report (and I have been unable to find any specimens of *P. sumatrana* collected in Burma or the Andamans), it is likely that he was dealing with specimens more properly assigned to *P. glauca.* This conclusion finds support in the fact that to date, only *P. glauca* is known from Thailand (*Rogstad 841*), thus being the only species of the complex collected to the north and west of Sumatra and peninsular Malaysia.

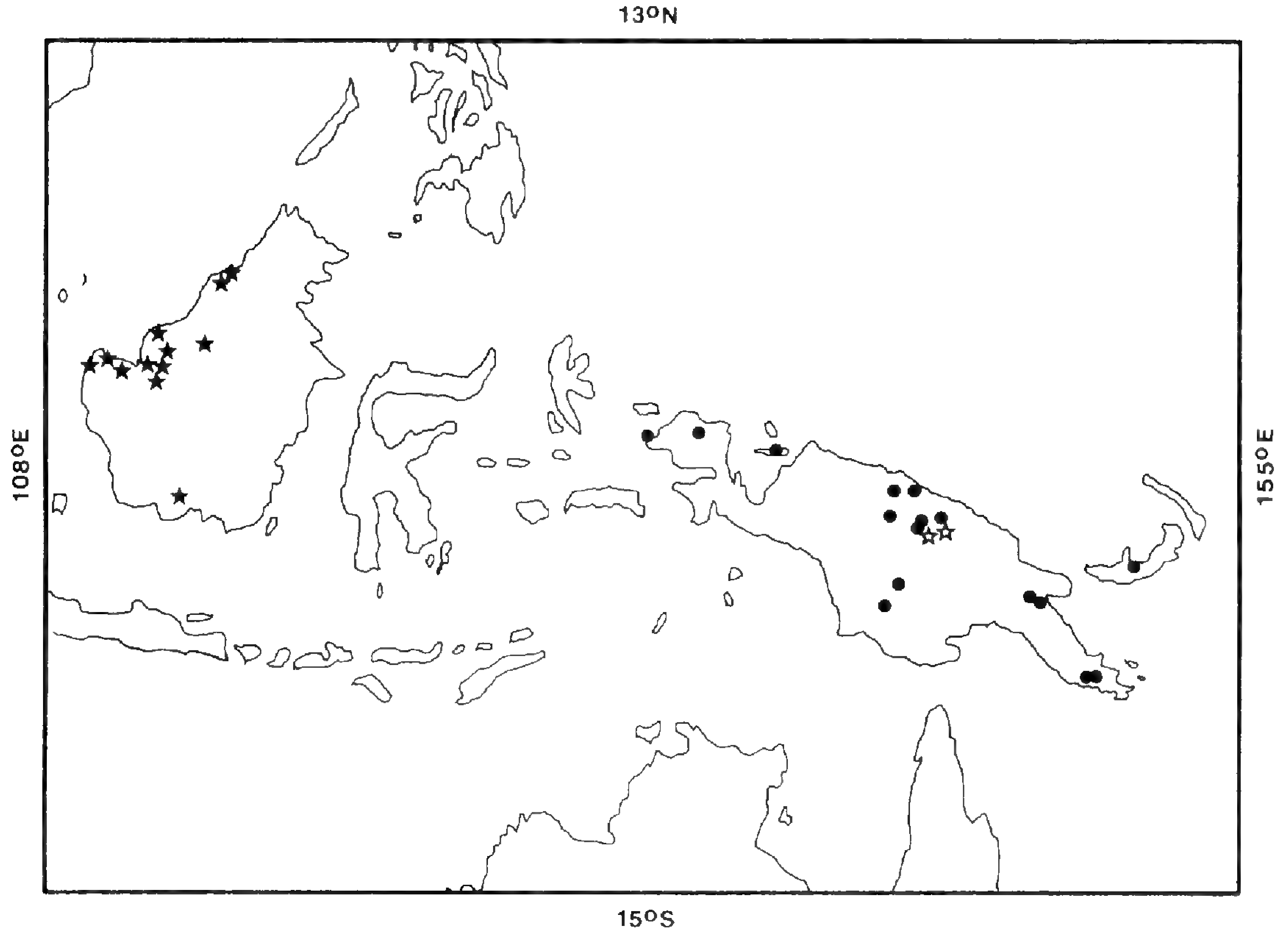
Within the *Polyalthia hypoleuca* complex, specimens of *P. glauca* are most likely to be confused with *P. ovalifolia* (restricted to Borneo) or *P. discolor* (restricted to Papua New Guinea); see the discussion under the latter two species.

The curious irregular indentations of the seed surface often seen in herbarium specimens of this species can also be observed in fresh material (see FIGURE 8D). All of the more than 230 seeds germinated at Pasoh Forest Reserve had them. Such indentations were well developed in all herbarium specimens with mature fruit collected from peninsular Malaysia, Sumatra, and the Andamans, but they are less prominent in collections from Borneo, present in only two of the four collections from the Philippines, and completely lacking in specimens from New Guinea and the Admiralty Islands. In seeds where the indentations are lacking, the rumination needles characteristic of the *Polyalthia hypoleuca* complex occasionally become slightly broadened near the longitudinal circumferential groove.

2. **Polyalthia ovalifolia** S. H. Rogstad, sp. nov. FIGURE 3A.

P. glauca affinis, sed in ramulis novellis et in pedicellis indumento moderate vel dense tomentoso praeditis (haud moderate vel dense tomentoso in P. glauca); foliis grandioribus (19–26 × 7–11.3 cm versus 9–22 × 2.6–7 cm in P. glauca), latioribis (foliis latitudo/longitudo ratio plerumque 0.34–0.44 versus 0.24–0.34 in P. glauca), et magis coriaceis, differt.

Tree to 25 m tall, DBH to 55 cm; trunk often fluted at base; pneumatophores absent; bark white, smooth on younger trees and branches, becoming white mixed with yellow when older; hoop marks prominent even on lower portions of bole; slash on larger trees revealing phloem rays separated from surface by 2 mm or more of woody matrix, phloem-ray apices 0.5–1.5 mm apart. Twigs with bark white to pale yellow-white, youngest growth always with dense, short, rusty tomentum ($n = 20$). Leaves with young petiole 6–10 (8, 1.2, 12) mm long, moderately to densely tomentose abaxially; lamina elliptic to widely elliptic, 19–26 (22.5, 1.5, 12) × 7–11.3 (9.6, 1.1, 12) cm, the apex acuminate to apiculate, 0.8–1.7 (1.1, 0.3, 12) cm long, the base rounded, the secondary veins 21 to 36 (29.6, 4.7, 12) per side, wavering and not forming strong intramarginal vein; leaves when fresh flat, with abaxial surface bright white. Inflorescences borne on branches below leaves, arising predominantly from tubercles, up to 20 per tubercle; peduncle extremely reduced, 0.7–2.1 mm long, usually with only 1 terminal flower developing, lateral floral buds and developing flowers absent; bracts 1 to 3, irregularly oriented with respect to branch axis. Flowers with pedicel 10–18 mm long, 0.7–1.2 mm wide at base and 1–1.5 mm at apex, with dense, short, rusty tomentum; bract 1.1–8 mm above articulation. Sepals triangular, 0.9–1.9 mm long, abaxially densely tomentose, infrequently caducous at floral maturity. Petals linear; outer petals 7.5–13 × 2–3.1 mm, the pubescence beginning adaxially on basal ⅓, moderate throughout except abaxially at base where dense, or dense throughout, the midvein generally not visible abaxially; inner ones 8.5–13 × 2–2.2 mm; all petals (and sepals) pale orange, strongly fragrant (*S 12401*), deep burgundy-red when dry. Torus 0.5–1.1 × 1.8–2.5 mm, gynoecial portion convex. Androecium 0.9–2 × 2.1–2.8 mm; stamens 26 to 36, 0.8–1 × 0.7–0.9 mm. Gynoecium 2–2.1 mm across; carpels 20 to 27, 0.7–1.1 mm long, glabrous or with slight tuft of tomentum only on abaxial apex; stigmas elongate, clavate, 0.5–1.1 mm long, those of outermost ring reflexed at least 30° out from floral axis. Observations



Map 3. Distributions of *Polyalthia discolor* (dots), *P. ovalifolia* (solid stars), and *P. multinervis* (open stars).

on immature carpels lacking. Mature, dry fruits (only 2 available) with pedicel 16–27 mm long, 2.2–2.4 mm in diameter at apex, with dense, short, rusty tomentum; stamen scars < 40; carpels with the stalk 3–4 × 1.7–1.9 mm, the seed-bearing portion globose, 15–19 × 14–18 mm, smooth, rounded at apex; fruit wall < 1 mm thick, deep red to black. Placentation ventral at maturity. Seed(s) 1 (or 2?) per mature carpel, biconvex-lenticular, with circumferential groove, the aril scar lacking, the testa deep brown to black, smooth to finely pitted, not irregularly indented; rumination needles occasionally slightly broadened.

Type. S. and E. Borneo, Sampit, 5 m alt., 09-20-1925, *Buwalda* [sheets may be marked *F. H. Endert*] *7797* (fl) (holotype, A; isotype, BO).

Distribution. To date collected only from northwestern and southern Borneo (see Map 3).

Selected specimens seen. **Malaysia.** Sarawak: Maludan Peninsula, Tj. Keranji, Betong Distr., 3 m alt., *S 12401* [*Anderson*] (FL) (BO, K, SAR); Setapok F.R., Kuching, 15 m alt., *S 12967* [*Zen*] (FR) (SAR); Bako Natl. Park, near Kuching, *Rogstad 842-845* (st) (A). **Brunei:** Badas F.R., 15 m alt., *S 2226* (FL) (FRI, SAR, SING); Badas State Land, Kuala Belait, 13 m alt., *SAN 17439* (FR) (A, KEP, SAN).

Regional names. "Dillah," language?, above Sibu, Sarawak, *S 2342*. "Dilleh," language?, Brunei, *S 2226*. "Riboei," language?, Sampit, Kalimantan, *Buwalda* *(or Endert?) 7797.* "Selaut telor," Malay language(?), Betong Distr., Sarawak, *S 12401* [*Anderson*].

ECOLOGY. The highest recorded altitude for *Polyalthia ovalifolia* is 15 m above sea level, but the species is poorly collected. Rather dense populations (up to ten mature individuals/ha) were observed at Bako F.R., Sarawak, where they appeared to be restricted to areas of stunted forest (the closed kerangas (heath) forests of Brunig (1974); canopy at 20–25 m) that grow on sandy soils covered with a spongy root-humus mat (to 1 m thick). These stunted, closed forests yield black water drainage and are the only habitat where regeneration of this species was found to be occurring at Bako. While this soil formation is reminiscent of peat, it differs in that it appears on flat or gently sloping hilltops and is well drained. However, *P. ovalifolia* has also been collected in peat-swamp forests in Sarawak (*S 12401* [*Anderson*]; *S 12967* [*Zen*]), although I could not find it in the extensive peat swamp formations adjacent to the Baram River, and foresters working in these swamps (e.g., employees of Forescom Sarawak), when presented with leaves of this species, stated that they had not observed it there although they immediately recognized the leaves of *P. hypoleuca,* which grows abundantly in that region.

COMMENTS. There has been some confusion concerning the collector of the type specimen. Sheets at A and BO that agree in collection number, date, and specimen material indicate different collectors (E. H. Endert at A, Buwalda at BO). A comparison of the collecting itineraries (Van Steenis–Kruseman, 1950) indicates that Buwalda was the collector.

This species is most likely to be confused with *Polyalthia glauca*; specimens listed above have usually been identified as *P. glauca* by various workers, including Sinclair. *Polyalthia ovalifolia* differs consistently from *P. glauca* in having moderately to densely tomentose (vs. glabrous) pedicels in flower and fruit, more coriaceous, larger leaves (see FIGURES 3A and 9) that are elliptic to broadly elliptic (vs. narrowly elliptic to elliptic) and usually have a higher width/length quotient (0.34–0.44, $n = 12$, vs. 0.24–0.34, $n = 31$; $P < 0.05$, unbalanced t-test), and young branches always (vs. rarely) with dense, short, rusty tomentum. Although the differences between these two species are not pronounced, they are constant, and no intermediates have yet been found. I have therefore recognized *P. ovalifolia* as a distinct species, although more material and field observations of both *P. ovalifolia* and *P. glauca* in Sarawak and southern Kalimantan are needed.

3. **Polyalthia discolor** Diels, Bot. Jahrb. Syst. **49:** 130, 1913. TYPE: Papua New Guinea, middle April River, Niksek Village area, 4°42′S, 142°32′E, 100–150 m alt., Sept. 16, 1984, *Rogstad 814* (fl+fr) (neotype, A; isoneotypes, K, LAE). FIGURES 2C, D; 4B; 6B; 7B; 8C; 20C, D.

Tree to 35 m tall, DBH to 91 cm; trunk often fluted at base; pneumatophores absent; bark white, smooth on younger trees and branches, with very fine dots of red giving main bole reddish tinge, flaking papery patches scattered on older bark; hoop marks prominent even on lower portions of bole; slash on larger trees revealing phloem rays separated from surface by 2 mm or more of woody matrix, phloem-ray apices 0.5–1.5 mm apart. Twigs with bark white to pale yellow-white, youngest stem growth glabrous (50%) or with moderately dense, short, rusty tomentum (50%; *n* = 20). Leaves with young petiole 3–9 (6.4, 1.7, 14) mm long, glabrous (75%) to moderately tomentose (25%; *n* = 20) abaxially; lamina narrowly elliptic to elliptic, 10.2–15.8 (13.1, 1.3, 14) × 3.3–5.1 (3.9, 0.55, 14) cm, the apex acuminate to apiculate, 0.4–1.1 (0.75, 0.2, 14) cm long; the base rounded to acute, the secondary veins 17 to 28 (23.3, 3.5, 14) per side, occasionally looping more or less regularly to form weak intramarginal vein; leaves when fresh slightly to strongly conduplicate, with abaxial surface bright white. Inflorescences borne on branches below leaves, arising predominantly from tubercles, up to 10 per tubercle; peduncle ca. 1.1–11 mm long, with up to 3 lateral flowers developing or with resting buds; bracts 1 to 7 (often subtending resting or developing bud), distichous, but irregularly oriented with respect to branch axis on different inflorescences of single tubercle. Flowers with pedicel 18–49 (29.2, 8.3, 11) mm long, 0.8–1.2 (0.94, 0.1, 11) mm wide at base and 1.1–2 (1.6, 0.3, 11) mm at apex, glabrous (75%; *n* = 12), occasionally with sparse, short, rusty tomentum; bract always present (*n* = 11), 2–18 (8.8, 4.9, 11) mm above articulation. Sepals triangular, 1.3–2.2 (1.7, 0.36, 11) mm long, moderately tomentose abaxially, infrequently caducous at floral maturity. Petals narrowly elliptic to elliptic to obovate, occasionally with constriction or narrowing in basal ⅓ or with distal portion slightly flared (or both); outer petals 16–32 (20, 5.7, 11) × 4.5–7.3 (5.8, 0.83, 11) mm, the pubescence always beginning adaxially on basal ⅓ (*n* = 20), moderate throughout except abaxially at base where dense, or dense throughout, the midvein often visible; inner petals 14–38 (22.1, 8.8, 11) × 4–9 (5.4, 1.5, 11) mm; all petals red-purple basally, yellow distally, and noticeably sweet smelling when stigmas become receptive, turning purplish sepia, musky, and sickly sweet when anthers dehisce, rusty to deep burgundy-red when dry. Torus 0.8–1.4 (1, 0.16, 11) × 2.3–3.3 (2.8, 0.32, 11) mm, gynoecial portion flat (100%; *n* = 3) or convex (100%; *n* = 8). Androecium 1–2.5 (1.9, 0.4, 11) × 3.6–5.1 (4.5, 0.4, 11) mm; stamens 77 to 119 (95.3, 14, 11), 0.9–1.3 × 0.6–0.9 mm (*n* = 11). Gynoecium 2.3–4 (3.1, 0.5, 11) mm across; carpels 31 to 72 (48.2, 13.6, 11), 1–1.4 (1.14, 0.12, 11) mm long, glabrous (90%) or with slight tuft of tomentum only on abaxial apex (10%; *n* = 20), the outermost ones slightly incurved, distal portion of abaxial surface exposed above androecium, with exposed region slightly swollen and often slightly darker; stigmas globose, 0.2–0.7 mm long (0.45, 0.13, 11) mm in diameter, those of outermost ring not reflexed away from floral axis. Immature carpels green, turning red, finally blackish purple, the pericarp then soft and fleshy (juice laden), with sweet to bitter-sweet taste and often chlorinelike odor. Mature, dry fruits with pedicel 24–50 (34.6, 7.2, 14) mm long, 2–4.5 (3, 0.8, 14) mm in diameter at apex, glabrous (100%; *n* = 14); stamen scars > 40 (100%; *n* = 14); carpels with the stalk 10–24 (17.7, 4.5, 14) × 1.5–2.7 (1.9, 0.36, 14) mm, the seed-bearing portion globose, 15–18 (16.5, 1.3, 14) × 14–19 (16.6, 1.4, 14) mm, smooth, rounded at apex, fruit wall < 1 mm thick, deep red to black. Placentation ventral at maturity. Seed(s) 1 (or 2) per mature carpel, biconvex-lenticular, with circumferential groove, the aril scar lacking, the testa deep brown to black (often greenish when fresh), regular, smooth to finely pitted; rumination acicular, with needles occasionally slightly broadened.

DISTRIBUTION. New Guinea, and probably also the immediately adjacent islands (see MAP 3).

SELECTED SPECIMENS SEEN. **Indonesia.** IRIAN JAYA: Warsamsen R., 25 km E of Sorong, 60 m alt., *BW 2980* (FR) (A, SING); Kebar Valley, Div. W. New Guinea, 450 m alt., *BW 7193* (FR) (BO); Woda, Japen Is., Div. Geelvinkbaai, 50 m alt., *BW 11207* (FR) (K), *BW 11210* (FR) (A, SING). **Papua New Guinea.** WEST SEPIK PROVINCE: Aitape coastal area, coastal alt., *NGF 524* (FR) (L, BRI). EAST SEPIK PROVINCE: Niksek Village, at April R. airstrip, middle April R., 4°42′S, 142°32′E, 50–150 m alt., *Rogstad 814* (FL+fr), *832* (FL+fr), *833* (FL+FR) (all A, LAE, K); Sepik R. near Yellow R., *NGF 3914* (fr) (A, NGF); [Malu region,] Sepik R. region, *Ledermann 6814* (FR) (B, K); Sepik region, *Ledermann 10409* (FL) (B, K, L); Koitaki, 460 m alt., *Carr 12151* (FL) (SING). WESTERN HIGHLANDS PROVINCE: near Ruti E.L.G., Jimi Valley, Mt. Hagen, 450 m alt., *NGF 38825* (FR) (A, BO, L, LAE). MOROBE PROVINCE: Aluki Village (12 km E of Lae), 60 m alt., *Rogstad 782* (FL) (A, LAE, K); 7 mi N of Lae, near Butibum R., 65 m alt., *Hartley 11863* (FR) (A, CANB); Gnalungumbum, 50 m alt., *NGF 25576* (FL) (L, LAE). NORTHERN PROVINCE: Dobodura area, 125 m alt., *NGF 2085* (FR) (L, LAE); between Divinikoari and Horata villages, 50 m alt., *Hoogland 3529* (FR) (A, CANB, US); along Girua R., 1 km NW of Anonda airstrip, 60 m alt., *Hoogland 3776* (FR) (A, CSIRO); Mayu Camp I, jct. of Ugat and Mayu rivers, Mt. Suckling, 305 m alt., *LAE 56049* (FR) (A, K, L, LAE, US). CENTRAL PROVINCE: Mori R., Cape Rodney, Abau Subdistr., 65 m alt., *NGF 38599* (FR) (A, L, LAE); Mori R., Abau Subdistr., 250 m alt., *NGF 41840* (FL) (A, BO, L, LAE). WESTERN PROVINCE: Orovill Camp, Fly R., *Brass 7411* (FR) (A, L). NEW BRITAIN: 7 mi SE of Benim Village, Wariai Subdistr., 300 m alt., *NGF 27395* (FL) (L, LAE).

REGIONAL NAMES. "Adidionga," Orokaiva language (Mumuni), Northern Div., Papua New Guinea, *Hoogland 3529*. "Asiam," Biak language, Japen Is., Irian Jaya, *BW 11210*. "Atim," Bukawa language of the Suling clan, just NE of Lae, Papua New Guinea, *Rogstad 782*. "Fawss" or "pfahss," Niksek language, April R., Papua New Guinea, *Rogstad 814*. "Nimotiet," Kebar language, Div. W. New Guinea, Irian Jaya, *BW 7193*. "Oeloem," Mooi language, Warsamsen R., Irian Jaya, *BW 2980*. "Samoeben," Biak language, Japen Is., Irian Jaya, *BW 11207*.

LOCAL USE. The timber of *Polyalthia discolor* is used for house construction in the April River area (*Rogstad 833*), and for building houses and furniture in the Lae region (*Rogstad 782*).

ECOLOGY. The known altitudinal range is from 35 to 450 m above sea level. Of the 11 collections with details concerning habitat, eight were found on slopes and three at flat sites, but not on constantly inundated soils or those on which a thick root-humus mat had developed, or in peat swamps. This was confirmed by observations on members of a *Polyalthia discolor* population at April River (tributary to the Sepik), Papua New Guinea (Rogstad, in prep. a). Regeneration by seedlings, which was often pronounced, also exhibited this pattern.

Flowering begins when individuals reach the middle canopy but is generally prolific only when they achieve a place in the sun in the upper canopy. This species has the slowest-developing flowers of any species in the group, and individuals can have flowers reaching anthesis more or less continuously over periods of up to 1.5 months. Although the other species of the *P. hypoleuca* complex (except *P. ovalifolia,* for which no observations of pollinators have yet been made) usually attract only one or two pollinators in any numbers, *P. discolor* flowers consistently drew several species of insects as potential pollinators. Pigeons and cassowaries have been observed eating the fruit (*Pullen 8123*).

The Annonaceae are generally known for their weak and somewhat flexible wood, a factor that may have contributed to the observation by Hoogland (*3529,* Northern Div., Papua New Guinea) that *Polyalthia discolor* was the "... most frequent standing tree in a patch of rainforest damaged by a cyclone."

COMMENTS. The type as designated by Diels, *Schlechter 18306,* was destroyed at Berlin, and I have been unable to locate any duplicates at A, B, BO, F, GH, K, KEP, L, MO, P, SAN, SAR, SING, U, or US. I have also been unable to find any collections of this species from the Ramu region of Papua New Guinea. Diels's description very clearly refers to the species recognized here. I have chosen as a neotype a collection that both matches the description by Diels and is representative of this group of specimens.

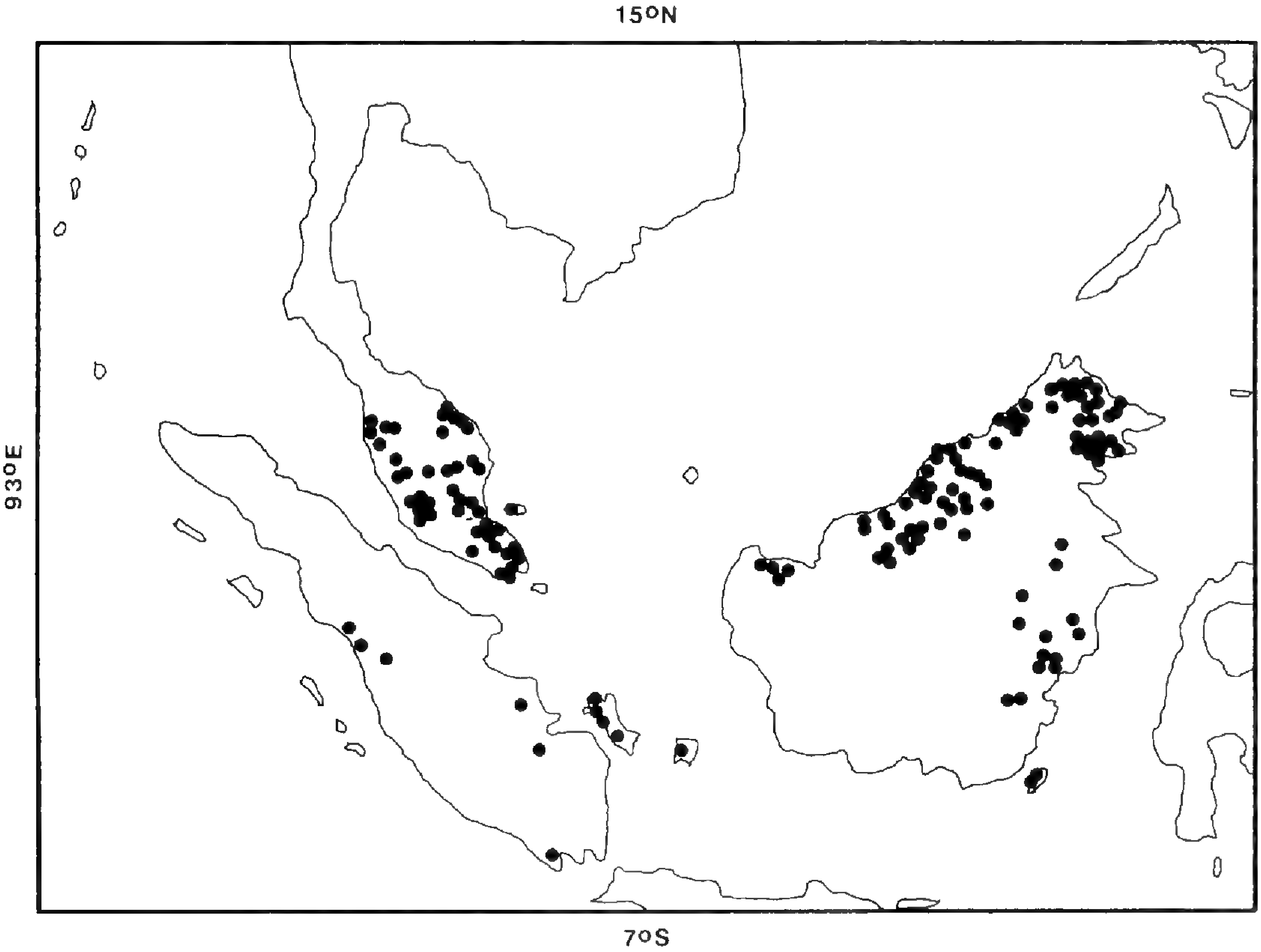
Identification of herbarium specimens of this species has caused much confusion due to their similarity in both flowers and fruits to *Polyalthia glauca,* also from the New Guinea region. This superficial resemblance caused Sinclair to comment (*Carr 12151*), "This is what Diels calls *discolor* but it is probably only a variety of *glauca.*" However, as demonstrated in the morphometric analyses, *P. discolor* consistently has several unique features that distinguish it with a clarity commensurate with species status in this group, and thus I recognize it as such here.

Although *Polyalthia discolor* and *P. glauca* are very similar, the flowers of the former have more than 50 stamens (vs. less than 45 in *P. glauca*), more (vs. always fewer) than 27 carpels, and globose (vs. elongate) stigmas. These two species are much more difficult to distinguish in fruit, as is attested to by the fact that every herbarium specimen of *P. discolor* with fruit that I have seen has been misidentified as *P. glauca.* However, although the seed-bearing portions of the mature carpels are globose in both species, the fruit of *P. discolor* is generally larger than that of *P. glauca.* While the means for pedicel length and (distal) width and mature-carpel stalk length differ significantly ($P < 0.05$, unbalanced t-test, $n = 14$ for *P. discolor,* $n = 31$ for *P. glauca*) for the two species, there is enough overlap to cause confusion. However, specimens (other than immature ones of *P. discolor*) on the upper or lower ends of these scales can be identified. At any stage of development, the best means of separating fruits of these two New Guinean species is to count the scars left by the abscised stamens. Unfortunately, these are sometimes obscured by the expansion of the torus that accompanies fruit growth. Differences in stamen and carpel number and scars between these two species can be seen in FIGURE 20.

Polyalthia discolor and *P. glauca* are to date known to overlap geographically only in the middle Fly River region and possibly in north-central New Guinea (Rogstad, 1986), although with more comprehensive exploration, the area of overlap is likely to expand, especially since *P. glauca* has been found on Manus. Further study of the distribution and possible overlap of these species and comparative investigations of their autecologies are of critical importance to understanding the systematics and evolution of this group.

4. **Polyalthia sumatrana** (Miq.), Kurz, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. **43:** 53. 1874, *pro parte basionymica tantum*; *Guatteria sumatrana* Miq. Fl. Ned. Ind., Eerste Bijv. 380. 1861; *Monoon sumatranum* (Miq.) Miq. Ann. Mus. Bot. Lugduno-Batavum **2:** 19. 1865. TYPE: [Sumatra,] Priaman, *Diepenhorst H.B. 2342* (lectotype, here selected, U: mature fruit and mature flower fragment). FIGURES 3B; 4A, D; 8B, D; 18A, B; 21C.

Tree to 24 m tall, DBH 4–25 cm; trunk rarely fluted at base; pneumatophores absent; bark white on younger trees and branches, remaining white to pale yellowish white on older trees; hoop marks not prominent on lower portion of bole; slash on larger trees revealing phloem rays reaching surface, phloem-ray apices 0.2–0.7 mm apart. Twigs with bark white to pale yellow-white, youngest growth glabrous (88%) or moderately tomentose (12%; *n* = 71). Leaves with young petiole 3–12 (6, 1.5, 105) mm long, glabrous (80%) to moderately tomentose (20%; *n* = 71) abaxially; lamina narrowly elliptic to elliptic, 9.2–28 (15.5, 3.2, 106) × 2.5–9.5 (4.5, 1.1, 106) cm, the apex acuminate to apiculate, 0.1–1.6 (0.9, 0.3, 106) cm long, the base rounded to acute, the secondary veins 19 to 80 (34.8, 10.2, 105) per side, not forming regular intramarginal vein; leaves when fresh flat with abaxial surface dull white (white mixed with gray or brown). Inflorescences in foliate axils, up to 4 per axil, and also borne on branches below leaves, tubercles lacking or poorly developed; peduncle extremely reduced, 0.6–2.5 (1.4, 0.4, 65) mm long, usually with only 1 terminal flower developing, lateral floral buds and developing flowers absent; bracts 1 to 3, oriented perpendicular to branch axis when only 1 flower per axil. Flowers with pedicel 7–25.4 (15.8, 5.4, 65) mm long, 0.6–1.8 (1.2, 0.3, 65) mm wide at base and 0.8–3 (1.9, 0.4, 65) mm at apex, glabrous (78%) to moderately pubescent (22%; *n* = 65); pedicel bract sometimes present (43%; *n* = 65), 4–8 mm above articulation. Sepals triangular, 0.7–3 (1.5, 0.48, 40) mm long, moderately (43%) to very densely (57%; *n* = 40) tomentose abaxially, often caducous (38%; *n* = 65) at floral maturity. Petals linear (97%) to basally clawed with obovate or flared distal portion (3%; *n* = 65); outer petals 7.5–52 (28.4, 10.8, 65) × 1.5–6 (3, 0.8, 65) mm, the pubescence beginning adaxially on basal (11%), middle (49%), or distal (40%; *n* = 65) ⅓, sparse throughout (62%), moderate throughout (11%), dense throughout (9%), or sparse throughout except abaxially at base where dense (18%; *n* = 65), the midvein generally not visible abaxially; inner petals 9–56 (30.8, 11.4, 65) × 1.6–5.7 (2.9, 0.8, 65) mm; all petals turning yellow, or occasionally yellow-white (*S 3020*), yellow-brown (*S 3057*), maroon ([*SAN*] *3626*), cream with pale pink tinge (*Sinclair et al. 9313*) or basal pink flush (*SAN 21222*), red (*SAN 21459*), or gray (*SAN 56203*) at maturity, "astringently fragrant" (*S 38009*; only this collection notes odor), tan to deep burgundy-red when dry. Torus 0.9–2.2 (1.4, 0.38, 62) × 1.3–4.4 (2.6, 0.67, 62) mm, gynoecial portion concave (25%), flat (63%), or convex (12%; *n* = 65). Androecium 1.1–3.1 (2.7, 0.4, 65) × 3–6.2 (5, 0.75, 65) mm; stamens 80 to 232 (160.4, 33.6, 65), 0.8–1.7 (1.1, 0.15, 65) × 0.4–1.1 (0.78, 0.12, 65) mm. Gynoecium 0.9–4.3 (2.2, 0.65, 65) mm across; carpels 5 to 49 (24.8, 8.8, 65), 0.8–2 (1.2, 0.22, 65) mm long, with small distal, abaxial patch of tomentum (65%) or moderately to densely tomentose (35%; *n* = 65); stigmas globose (rarely slightly elongate), 0.2–0.8 (0.3, 0.1, 65) mm in diameter,



MAP 4. Distribution of *Polyalthia sumatrana.*

those of outermost ring not reflexed away from floral axis. Immature carpels firm, green with irregular red spots or streaks appearing 2–4 weeks before full maturity (such streaking diagnostic for this species within the *P. hypoleuca* complex), finally turning deep purple to black, the pericarp then soft and fleshy (juice laden) with sweet to bitter-sweet (pers. obs., Pasoh) or cinnamonlike (W. Kalimantan, *Schut K. 23*) taste or fragrant odor. Mature, dry fruits with pedicel 8–43 (21.7, 6.3, 107) mm long, 1.8–4.8 (3.2, 0.64, 106) mm wide at apex, glabrous (100%; n = 108); stamen scars > 40 (100%; n = 19); carpels with the stalk 5–38 (15.1, 5.4, 105) × 1.3–4.4 (2.7, 0.64, 105) mm, the seed-bearing portion ellipsoid, 13–30 (22, 3.8, 106) × 9–19 (12.6, 2.3, 105) mm, sometimes longitudinally ridged (39%; n = 108), tapered (89%) or blunt or rounded (11%; n = 108) at apex; fruit wall > 1 mm thick, burgundy to deep red-black. Placentation basal at maturity. Seed(s) 1 (or 2) per mature carpel, ellipsoid, with circumferential ridge, the aril scar present, the testa deep brown, finely to moderately pitted, not irregularly indented; rumination needles very fine.

DISTRIBUTION. From peninsular Malaysia to Sumatra, Borneo, and immediately adjacent islands (see MAP 4).

SELECTED SPECIMENS SEEN. **Malaysia.** PERAK: Chior F.R., Sungai Plus–Sungai Siput, 230 m alt., *FRI 5769* (FR) (KEP); sine loco, *Dr. King's collector (Lanit?) 6551* (FL) (K); Gunong Bubu, Ria Trong, 400 m alt., *FRI 11907* (FR) (KEP, L); Maxwell's Hill, 180 m alt., *SFN 38828* (FL) (K, SING); Piah F.R., K. Kangsar, *Rahim Ismail KEPFN 99836* (FR) (KEP). TRENGGANU: Bukit Bauk F.R., 250 m alt., *FRI 2362* (FR) (KEP); near Geram Galong, Ulu Sungai, 65 m alt., *FRI 8357* (FR) (KEP); Ulu S. Trengan, near K. Petang, Ulu

Trengganu, 275 m alt., *FRI 8438* (FR) (A, KEP); Sungai Loh, near K. Datok, 130 m alt., *FRI 10690* (FR) (A, KEP); Sekayu F.R., *FRI 11854* (FR) (KEP, L); along Sungai Pelong, *FRI 14885* (fl+FR) (A, KEP, SAR); Bukit Bauk VJR, Dungun, *FRI 25044* (FR) (KEP); Ulu Brang, 180 m alt., *SFN 33740* (FR) (A, KEP, SING); Jarangau S.L., Dungun Distr., *KEP 76674* (FR) (KEP). KELANTAN: Kuala Lebir Kechil, Sungai Lebir, *FRI 7075* (FR) (A, KEP, L); Sungai Lebir, 2 mi E of Kuala Aring, *FRI 7105* (FR) (KEP). SELANGOR AND KUALA LUMPUR FEDERAL DISTRICT: Gombak Reserve, *Murdock & Hashim 114* (FR) (KEP); Ulu Langat, Bukit Tangkol, K. Pansom, *KL 1360* (FR) (KEP), *KL 1375* (fl+FR) (A, KEP); Bukit Peringkot [Peningkot?], *KL 1494* (FR) (A, KEP); Sungai Buloh Reserve, [*Abu*] *CF Field No. 3335* (FL) (K, KEP); Ginting Simpoh, *Strugnell(?)* [*KEP?*] *11225* (FR) (KEP); Gading F.R., Ulu Selangor, 370 m, *FRI 11229* (FR)(KEP, L); Ulu Gombak F.R., *Symington* [*KEP*] *18162* (FR) (KEP); Bukit Lagong, *FRI 26595* (FR) (KEP); Sungai Buloh, *Walton* [*KEP*] *29737* (FR) (KEP); Bukit Lajong F.R., 450 m alt., *Sow* [*KEP*] *65141* (FR) (KEP); Ulu Gombak F.R., K.L. Distr., *KEP 94038* (FR) (A, KEP), *KEP 98269* (FR) (KEP), *KEP 99610* (FR) (A, KEP). PAHANG: Raub, Sungai Sempam, 920 m alt., *Soepadmo 725* (FL+fr) (KEP, KLU); Ulu Sungai Sepia, near Kuala Aur, *Shah & Noor 1904* (FR) (A, KEP, SING); Taman Negara, Bukit Terom, near K. Keniyum, 150 m alt., *FRI 8538* (FL) (KEP); Panching Forest, ca. 15 km N of Panching, Kuantan, 130 m alt., *Ogata* [*KEP?*] *10432* (FR) (KEP); Raub, 365 m alt., *FRI 14689* (FL) (KEP); Bukit Saup, *Jaamat* [*KEP?*] *16522* (FL) (KEP); Chini F.R., S of Tasek Chini, *FRI 17271* (FR) (KEP, L); Lesong F.R., 115 m alt., *FRI 19835* (FR) (A, KEP); Simpang Pertang, Ulu Tembeling, *SFN 22112* (FR) (A, KEP, SING); Lesong F.R., *FRI 23910, 28028* (both FR) (both KEP); Aur F.R., K. Rompin, 50 m alt., *KEP 75883* (FR) (KEP); Krau Game Reserve, G. Benom, 300 m alt., *KEP 104427* (FR) (A, KEP). NEGRI SEMBILAN: Pasoh F.R., near Simpang Pertang, *Rogstad 508, 509, 527* (all FL) (all at A); Pasoh F.R., 50 m alt., *FRI 23496* (FR) (KEP). JOHORE: road to Sungai Kahang, N to Labis, *Shah & Sanusi 2107* (FR) (A, KEP, SING); path to Gunong Blumut, Kluang, 150 m alt., *Shah & Sanusi 2139* (FR) (A, KEP, SING); Tg. Sedili Kechil, E Johore coast, 30 m alt., *FRI 7688* (FL) (A, KEP); Ulu Endau, Labis F.R., *FRI 7869* (FL) (KEP, L), *FRI 7920* (FL) (KEP), *KEP 110402* (FL) (K, KEP); Kluang F.R., *FRI 8701* (FR) (A, KEP); NW Gunong Blumut, 548 m alt., *FRI 8820* (FR) (KEP, L); Labis F.R., *FRI 14783* (FL+FR) (A, KEP), *FRI 16073* (FR) (A, KEP); Gunong Pulai F.R., 335 m alt., *FRI 17639* (FR) (A, KEP); Tanjong Sedili Kechil, *SFN 28070* (FR) (KEP, SING); Sungai Kayu Ara, Mawai–Jemulang Road, *SFN 29330* (FR) (KEP, SING); Sungai Sedili, below Mawai, *SFN 36979* (FR) (A, KEP, SING); Bukit Mambai F.R., 50 m alt., *KEP 76295* (FL) (KEP, L); near Mersing F.R., 30 m alt., *KEP 77852* (FR) (KEP). SARAWAK: Gunong Mulu, Baram Distr., 550 m, [*Anderson & Keng*] *K 15* (FR) (A, SAR); Sabal Tapang, Ist Div., 130 m alt., *Stevens et al. 174* (FR) (A, SAR?); Gunong Api, Baram Distr., 500 m alt., *Chew Wee-lek 1106* (FR) (A), *1161* (FR) (A, L); Ulu Koyan, Mt. Dulit, IVth Div., 800–1000 m alt., *Richards (native collector) 1918* (FL) (A, K); near Kuching, *Haviland 2218* (FL) (K), *2694* (FL) (SAR); Lambir Hills F.R., Miri Distr., 300 m alt., *Dan bin Haji Bakar 3020* (FL) (A, SAR); upper Plieran, R. Kenaban, 560 m alt., *S 3501* (FR) (SAR, US); 10 km below Belaga, Kapit Distr., IIIrd Div., 500 m alt., *Jacobs 5201, 5351* (both FL+FR) (both L, US); Ulu Pelagus, S. Iran, Kapit(?) Distr., 120 m alt., *Smythies 9469* (FL+fr) (K, SAR); Tatau, Ulu Anap, Sungai Takan, IVth Div., 215 m alt., *S 13763* (FL) (A, K, KEP, SAR); NE Lambir Hills, near Miri, 30 m alt., *S 16439* (FL) (A, SAR); Sabal F.R., Serian Distr., *S 16645* (FR) (A, L, SAR); S Sabal Tapang, Serian Distr., 50 m alt., *S 16990* (FR) (A, L, SAR); Rumah Temenggong, Begrih, Bawan, Balingian, 10 m alt., *S 19484* (FL+fr) (A, L, SAR); Pengiran/Chenaning divide, Ulu Mujong, Balleh, 600 m alt., *S 21161* (FR) (L, SAR); S Ukong, Miri, 10 m alt., *S 21403* (FL) (A, K, KEP, L, SAR); Kakus, Ulu Mayeng, *S 21705* (FL) (A, SAR); Bukit Dam, Ulu Dapoi, Marudi, IVth Div., *S 22955* (FR) (A, KEP, SAR); Long Dapoi, Tinjar, Marudi, IVth Div., 100 m alt., *S 22971* (FR) (A, KEP, SAR); Bok-Tisam, Bukit Mentagai, Marudi, IVth Div., 65 m alt., *S 23099* (FR) (A, SAR); Long Dam, Ulu Tinjar, Marudi, IVth Div., 115 m alt., *S 23373* (FR) (A, KEP, SAR); Ulu Dapoi, Long Kelaby, Tinjar, IVth Div., *S 23464* (FR) (A, KEP, SAR); Bukit Iju, Ulu Arip, Balingian, IIIrd Div., 65 m alt., *S 23623* (FR) (A, SAR); Ulu Sungei Bakong, Miri, 50 m alt., *S 24409* (FR) (A, SAR); Lambir Natl. Park, Miri, *S 25077* (FL) (SAR); Kapit, Balleh, Sg. Mengiong, IIIrd Div., *S 29699* (FR) (SAR); Ulu Kakus, Anap, IVth Div., *S 29974, S 29979* (both FR) (both A, KEP, SAR); Mata Kuching, Ulu Tinjar, S of Dulit Range, Baram Distr., *S 34745* (FR) (KEP, SAR); Bukit Pendam, *SFN 35735* (FR) (A, KEP, SING); Bukit Goram, Ulu Sg. Kapit, VIIth Div., 750 m alt., *S 36184* (FR) (KEP, SAR); Nyabau F.R., Bintulu, IVth Div., *S 37859* (FR) (KEP, SAR); Gunong Mulu Natl. Park, IVth Div., 430 m alt., *S 38009* (FL+FR) (K, KEP, SAR), 425 m alt., *S 38075* (FR) (KEP, SAR); Ulu Sungai Labau, Lambir Hills Natl. Park, IVth Div., 1210 m alt., *S 38429* (FR) (KEP, SAR). SABAH: sine loco, *Agama(?) 550* (FL) (A, PNH); Kinabatangan, *Puasa 1069* (FR) (A, NY); Segaliud, Elopura, *Cuadra A 1090* (FR) (A, K, KEP, SAN, US); Marutai, Tawau, 3 m alt., *Tandom BNBFD 1786* (FL) (A, K); Sepilok F.R., *SAN A 1969* (FR) (A, KEP, SAN); Table Estate, St. Lucia, Tawau, *Kadir A 2103* (FL) (A, KEP, SAN); Gomantong, Elopura, Sandakan, 12 m alt., *Cuadra A 2118* (FL) (A, K, KEP, SAN); Marutai, 8 m alt., *Maidin 2428* (FR) (K); 7 m alt., *Maidin 3057* (FL) (K); Betotan [Bettotan?], 25 m alt., *Orolfo BNBFD 3197* (FR) (A?, SAN), 30 mi WNW of Tawau, 30 m alt., *SAN A 3698* (FR) (A, KEP, SAN); Bettotan, Sandakan, *Puasa BNBFD 4544* (FL) (A, K, US); Apas Road, mi 7, 25 m alt., *Tandom BNBFD 8806* (FR) (A, K); Sepilok F.R., Sandakan, 50 m alt., *Sinclair, Kadim, & Kapis 9313* (FL) (A, K, SING); Beaufort Distr., 1 mi NE of Beaufort Township, 120 m alt., *SAN 15052* (FL) (A, SAN); Kalabakan, 30 mi WNW of Tawau, 200 m alt., *SAN 15263* (FR) (A, KEP, SAN); Sepilok F.R., Sandakan, 15 m alt., *SAN 15488* (FL) (A, K, KEP, L, SAN); Kelumpang Balong, Tawau Distr., 80 m alt., *SAN 17337* (FR) (SAN); Lalangot, ca. 1.5 mi from Pangkalan, Tawau, 40 m alt., *SAN 18718* (FR) (A, KEP, SAN); Sepilok F.R., Sandakan, *SAN 21222* (FL+FR) (K, KEP, SAN), *SAN 21303* (FL) (A, KEP, SAN); Tawao, Elphinstone Prov., B.N.B. *Elmer 20494* (FR) (A, US), *20877* (FL) (A, K, US), *21878* (FR) (A); Apas Road, mi 13, Tawau, *SAN 21459* (FL) (K, KEP, SAN); Membalua F.R., Tawau Distr., *SAN 22752* (FR) (A, KEP, SAN), *SAN 22774* (FR) (KEP, SAN); Bukit Pasil, Lungmanis, Sandakan Distr., *SAN 24238* (FR) (SAN); Lahad Datu Distr., Takun Kennedy Bay, 125 m alt., *SAN 26065* (FL+FR) (SAN); W Sungai Strun, Tawau Distr., 150 m alt., *SAN 26875* (FR) (SAN); Beaufort, Beaufort Distr., 30 m alt., *SAN 28115* (FR) (SAN); Lohan, Ranau Distr., 1200 m alt., *SAN 28758* (FR) (SAN); Mt. Andrassy, Tawau Distr., 300 m alt., *SAN 29430* (FR) (SAN); Quoin Hill, Tawau Distr., 125 m alt., *SAN 29464* (FR) (KEP, SAN); Ulu Sungai, Kalumpang, *SAN 30480* (FL) (KEP, SAN); mi 15, Quoin Hill Road, Tawau, *SAN 30616* (FL) (SAN), *35930* (FL) (K, SAN); Sepilok F.R., Sandakan, 15 m alt., *Brand* [*SAN*] *30983* (FL) (KEP, SAN); Bay Silabukan F.R., Lahad Datu Distr., 160 m alt., *SAN 33432* (FR) (SAN); Halogilot, Beaufort Distr., 300 m alt., *SAN 33754* (FR) (SAN); Sepilok F.R., Sandakan, 20 m alt., *SAN 36709* (FL) (SAN); Lokan F.R., Segaliud, Sungai Munyed, Sandakan, 100 m alt., *Banang* [*SAN*] *36911* (FL) (KEP, SAN); Sepilok F.R., Sandakan, 30 m alt., *P. P. Sam* [*SAN*] *37540* (FL) (SAN); Labuk Road, mi 60, Sandakan Distr., *Meijer* [*SAN*] *37897* (FR) (SAN); Labuk Road trace, mi 81–82, Sandakan Distr., 150 m alt., *Meijer* [*SAN*] *38773* (FR) (K, SAN); Bettotan, Sandakan, *Puasa* [*SAN*] *38920* (KEP); Kabuk [Labuk?] Road, mi 60, Sandakan Distr., 40 m alt., *SAN 39282* (FR) (SAN); Apas Road, mi 7, Tawau, *Tandom* [*SAN*] *44276* (FR) (KEP); Mt. Pock, Pagagau Road, Semporna Distr., 50 m alt., *Singh, Ahmad Talip, & Nordin* [*SAN*] *48900* (FL+FR) (SAN); Montinier Road, mi 12, Kg. Bambangan, 300 m alt., *Madius* [*SAN*] *49259* (FL) (L, SAN); Ulu Sungei Kimanis, Papar Distr., 60 m alt., *Eging Banang* [*SAN*] *49353* (FL) (A, SAN); Elopura Distr., 20 m alt., *Puasa & Enggoh* [*SAN*] *55164* (FL) (KEP); Keningau, mi 8.5, Sook Plain, 350 m alt., *Ahmad Talip* [*SAN*] *55525* (FL) (A, SAN); Beaufort Hill, Beaufort Distr., *SAN 66876* (FR) (L, SAN); Lumaku F.R., Mendalong, Sipitang Distr., *SAN 72361* (fl+FR) (SAN); Telupid, Sandakan Distr., 100 m alt., *SAN 75356* (FR) (L, SAN); Gunong Rara F.R., Kalabakan, 500 m alt., *SAN 75659*; Bengkoka F.R., Kudat Distr., 75 m alt., *SAN 76076* (FL) (A, K, L, SAN); Ulu Sungei Dusun (NE of Sepilok), Sandakan Distr., 60 m alt., *SAN 77357* (FR) (KEP, SAN); Crocker Range F.R., *SAN 78305* (FR) (A, KEP, SAN); Ulu Segama, Tawau Distr., *SAN 79179* (FR)

(KEP, SAN); Sepilok F.R., Sandakan Distr., *SAN 83715* (FL+FR) (A, KEP, SAN); Bukit Tiulon, Nabawan, Keningau Distr., 350 m alt., *SAN 841741* (FR) (KEP, SAN); Kuala Beatrice, Lahad Datu Distr., 270 m alt., *SAN 84916* (FR) (K, KEP, SAN); Denum (Banum?), Ulu Sungai, Lahad Datu Distr., 425 m alt., *SAN 85001* (FR) (KEP, SAN); Tawau Hill F.R., Tawau Distr., *SAN 88228* (FR) (KEP, SAN); Mt. Tawai [Tawau?] F.R., Karamuak (Kuamut?), Sandakan Distr., 500 m alt., *SAN 88722* (FR) (KEP, SAN); Sri Usukan, Tawau Distr., *SAN 88974* (FR) (KEP, L, SAN); Lahad Datu Road, Sandakan Distr., 27 m alt., *SAN 89169, SAN 89177* (both FR) (both KEP, SAN); Kg. Miruru, Mohd. Gan logging area, Ranau Distr., 600 m alt., *SAN 90075* (FL) (A, SAN); Kalabakan, near Tawau, *SAN 91500* (FL) (SAN). **Brunei:** R. Belait at K. Ingei, *BRUN 187* (FR) (BRUN, KEP); Kuala Belalong, Temburong, 300 m alt., *BRUN 465* (FL) (BRUN, KEP, L). **Singapore:** Sebtor [Seletar?], *Ridley 6348* (FR) (A); Bukit Timah Reserve, *SFN 35583* (FL) (A, KEP, SING). **Indonesia.** SUMATRA AND ADJACENT ISLANDS. Selatan: Rawas, Palembang, 200 m alt., *Dumas 1630* (fl+FR) (BO, L); Muelok(?), Velve(?), 550 m alt., *Grashoff 320* (FR) (BO, L); Marbau, Bilah, Bilah Pertama (Parbasir), *Toroes 323* (FR) (A). Tengah: road from Kuala Belilas to Berapit R., Indragiri Uplands, 20 m alt., *Buwalda 6669* (FL) (BO, L). Bangka: Lobok besar, 20 m alt., *Kostermans & Anta 264* (FL) (A, BO, KEP); G. Manghol, 50 m alt., *Kostermans & Anta 783* (FL) (A, BO, K); Lobok-besar, G. Pading, 20 m alt., *Kostermans & Anta 942* (FL) (A, BO, K, L). KALIMANTAN: Kutei, R. Tiram, *Schut K 23* (FR) (BO, K); Sambodja Village, Balikpapan, 60 m alt., *Schut K 33* (FR) (A, BO); Poeloe Lauet, Soengei Paring, 100 m alt., *Verhoeff(?) 80* (FR) (BO, L); Djaro Dam, ca. 10 km NE of Muara Uja, 100 m alt., *Vogel 724, 784* (both FR) (both L); Kecamatan muara Ancalong, Long Lees, 100 m alt., *Wiriadinata 1128* (FR) (A, BO); near Mt. Kemoel, W Koetai, 330 m alt., *Endert 3684* (FL) (A, BO, K); Nunukan Is., 20 m alt., *Kostermans 8629* (FR) (A, BO).

REGIONAL NAMES. "Antoi sembago" ("antoi" is applied to *Cyathocalyx* species in peninsular Malaysia), Indonesian?, Palembang, Sumatra, *Dumas 1630.* "Banetan puteh," language?, reported by Burkill (1966). "Banitan," language?, Lobok Besar, Bangka, *Kostermans & Anta 264* and *942.* "Binhud," Bandjar-Malay language, Balikpapan, Mentawir R., Kalimantan, *Sauveur 99.* "Binhut," Bandjar language, Balikpapan, Kalimantan, *Schut K 33.* "Buah sasak," Malay language(?), E. Kalimantan, *Wiriadinata 1128.* "Dada guan," Malay language(?), Pahang, peninsular Malaysia, *Jaamat* [*KEP*] *16522.* "Delah," Iban language, Brunei, *BRUN 897.* "Delasai," Malay language, Brunei, *BRUN 897.* "Dilah," Iban language, Brunei *BRUN 465.* "Dilasai," Iban language, Kakus, Sarawak, *S 21705.* "Dilleh," Iban language, IVth Div., Sarawak, *S 29979.* "Kalamanjat," Tidong language, Marotai, Sabah, *Maidin 3057.* "Karai," Malay language, Bettotan, Sabah, *BNBFD 3626*; Kedayan and Sungei languages, Bettotan, Sabah, *BNBFD 4544*; dialect?, Kuching, Sarawak, *Zen* [*S*] *13022.* "Karay," Kedayan language, Bettotan, Sabah, *BNBFD 3197.* "Kayu (or "pokok") dada bakok" (= wood or tree of the drug inducing stupor), Temuan language, Selangor, peninsular Malaysia, *KL 690, KL 1360,* and *KL 1375.* "Kerai" (also applied to other species of *Polyalthia* outside of the *P. hypoleuca* complex—e.g., *P. lateriflora*), Malay language, Sandakan region, Sabah, *SAN A 1969.* "Lirap (or sirap?)," Kutei language, R. Tiram, Kutei, Kalimantan, *Schut K 23.* "Medang bentawar," language?, reported by Burkill (1966). "Melada," language?, Pahang, peninsular Malaysia, *F. Gd.(?) & M. Soh(?)* [*KEP*] *15105.* "Melian," language?, Selangor, peninsular Malaysia, *F. gd. Abu CF Field No. 3335.* "Melilin," Malay language(?), Selangor, peninsular Malaysia, *KEP 99610*; Johore, peninsular Malaysia, *Yeob(?) 5873.* "Mempisang," Malay language (a general name referring to several species of Annonaceae), SE. Kelantan, *FRI 7075*; Johore, peninsular Malaysia, *KEP 77852*; Perak, peninsular Malaysia, *KEPFN 29911*. "Nyebulok," Kenyah language, Upper Baram R., Sarawak, *Chin See Chung 2737*. "Pahiding," Kayan language, Upper Plieran, Sarawak, *SAR 3501*. "Pisang-pisang" (pisang = banana), Malay language (a general name referring to several species of Annonaceae), Brunei, *Maidin 3057*; Pahang, peninsular Malaysia, *Hamid* [*KEP*] *10690*; Tawau, Sabah, *SAN 22752*. "Pisang-pisang bukit," Malay language, Lahad Datu, Sabah, *SAN 26065*. "Purda hutan," Malay language, Kuala Belilas, Sumatra, *Buwalda 6669*. "Samukau," Iban language, IVth Div., Sarawak, *S 13763*. "Sarbah," Malay language, Upper Plieran, Sarawak, *SAR 3501*. "Selangan babi," Malay language, Tawau, Sabah, *Kadir A 2106*; Sandakan, Sabah, *A. Cuadra A 2118*. "Selaut," Melanau language, IVth Div., Sarawak, *S 29974*. "Selaut gunong," Malay language(?), Mt. Dulit, Sarawak, *Richards 1918*. "Selmu," language?, Lambir Hills, Sarawak, *Dan bin Haji Bakar 3020*. "Talooto," Sungei language, Elopura, Sabah, *A. Cuadra A 1090*. "Tingo," tidong language, Marutai, Sabah, *Maidin 2428*.

LOCAL USE. Trees of most species of Annonaceae have bark that can be removed in long strips, yielding excellent fiber. This is probably due to the anastomosing bast fibers of the phloem that continue into the bark. Several specimens of *Polyalthia sumatrana* (e.g., *Kostermans & Anta 264* (Bangka), *Tandom BNB 1786* (Sabah)) have notes indicating that the bark is often used as a source of fiber. The wood is used for roof timber in the Upper Plieran region of Sarawak and may deter insects (*Pickles SAR 3501*). Collections by Gadoh anak Umbai (*KL 690, 1360,* and *1375*; peninsular Malaysia) are marked "poisonous" or "stupefying," and the local names, "kayu dada bakok" and "pokok dada bakok" can be loosely translated as "the tree of the drug that induces stupor." *KL 1494* notes that the fruits are intoxicating, while *Chin See Chung 2737* indicates that in the upper Baram River region of Sarawak, *P. sumatrana* is recognized as a good source for blowpipe wood.

ECOLOGY. This species has the highest and widest recorded altitudinal range of any in the *Polyalthia hypoleuca* complex, growing from near sea level to 1200 m alt. (*SAN 28758* from Lohan, Ranau Distr., Sabah). It is found both on drier slopes and in flatter, more poorly drained sites, but apparently not in constantly inundated or peat-swamp habitats. Although occasional individuals are reported to achieve a height of 25 m, *P. sumatrana* rarely reaches the mid-canopy, being primarily a denizen of the lower understory.

The population of *Polyalthia sumatrana* at Pasoh F.R., peninsular Malaysia, puts out new vegetative growth synchronously twice per year but flowers irregularly, and sometimes periods greater than one year intervene between population flowerings. Only one report of floral fragrance exists for this species. However, since the flowers attract beetles thought to feed on rotting fruit, it is probable that they have some fragrance, perhaps one that resembles fermenting fruit, as has been found for other Annonaceae (Rogstad, in prep. b). Observations by M. and D. Leighton (pers. comm.) at Kutei National Park, Kalimantan, Indonesia, indicate that the flesh (not seeds) of mature fruits of *P. sumatrana* is eaten by numerous animals, including primates (*Pongo pyg-*

moides, Hylobates muelleri, Macaca fascicularis), squirrels (*Ratufa affinis, Callosciurves prevostii, C. notatus*), sun bears, hornbills (*Buceros rhinoceros, Ryticeros undulatus, R. corrugatus, Arthrococeros malayanus, Anorrhinus galeritus*), and other birds (*Calyptomena viridis, Calochomphus fuliginosis, Megalaima* sp., *Ducula aenea, Ptilinopus jambu,* and an unidentified bulbul). Hornbills have also been observed feeding on the fruits of *P. sumatrana* in Sabah, Malaysia (*SAN 15263*). The mature fruits of the members of the *P. hypoleuca* complex all have a similar taste and color to humans (pers. obs.), and thus each species may attract the wide array of frugivores (and seed dispersers?) observed for *P. sumatrana.*

COMMENTS. Miquel designated three syntypes: *Teysmann 405* (sterile) and *4007* and *Diepenhorst 2342.* I have chosen the lectotype indicated above because it has diagnostic portions from mature fruit and a flower; a sheet at Kew previously placed with type materials for *Polyalthia sumatrana* (but for which no published reference has been found) bears portions of two Teysmann collections.

This species varies greatly, often on a local basis. For example, two petal forms have been collected from Bangka: the normal linear form (*Kostermans & Anta 264*), and one that is obovate or strongly flared distally (*Kostermans & Anta 942*). The latter shape has also been observed elsewhere (e.g., *Agama 550,* from Sabah). Research is needed to determine the degree to which flower-color variation is correlated with populations and geography and/or with differences in floral biology.

Leaf size provides another interesting example of local variability. In FIGURE 9 the three specimens of *Polyalthia sumatrana* with the largest leaves, as well as several of the smaller-leaved ones (e.g., *S 16645*), all come from Sarawak. The specimen with the largest leaves (*S 29979*) was collected quite near one exhibiting below-average leaf size (*S 29974*) at Ulu Kakus, Anap, IVth Division, Sarawak. Such variation is often observed at a single site and may be due to phenotypic variation.

Kochummen (1972) recognized *Polyalthia sumatrana* var. *macrocarpa,* based upon one specimen (*KEP 104976*; KEP) bearing relatively large fruits. When measurements from this specimen are included in the data set that generated FIGURE 15 and a PCA of this new data set is calculated, this specimen is indeed a very clear outlier (results not shown). However, it may be a mixed collection. The leaves have clearly been taken from some member of the *P. hypoleuca* complex. In contrast, the fruits, which are separate from the leaf-bearing branches, have very wrinkled, unridged mature carpels more like those of *P. clavigera* than the ellipsoid, prominently longitudinally ridged ones of *P. sumatrana.* Further, the seeds from *KEP 104976* have a circumferential groove rather than a ridge and lack an aril scar; although the interior of the seeds has deteriorated somewhat, there are no rumination needles but rather a series of four rumination plates (in cross section) penetrating the endosperm. In addition, the gynoecial portion of the torus bears dense, minute tomentum, in contrast to the glabrous torus characterizing all the members of the *P. hypoleuca* complex. These seed and torus characters, like the external appearance of the fruits, are more consistent with the fruits of the *P. clavigera–P. lateriflora* alliance of species (Rogstad, unpubl. data). Finally, there is only a single collection of this variety (even duplicates are apparently lacking), despite the fact that a few "typical" specimens of *P. sumatrana* have been collected from this region. This all suggests that the fruits from another species of Annonaceae have been mounted with vegetative material of one of the members of the *P. hypoleuca* complex.

Polyalthia sumatrana appears to grow in sympatry with *P. ovalifolia, P. glauca,* and *P. hypoleuca.* The leaves of *P. ovalifolia* are usually much larger and more broadly elliptic than those of *P. sumatrana,* and the two species differ in numerous floral and fruit characters as well. *Polyalthia sumatrana* differs from *P. glauca* in several easily detectable characters, including globose (vs. elongate) stigmas, usually many more than (vs. less than) 50 stamens, the ellipsoid (vs. globose) mature carpels, and circumferentially ridged (vs. grooved) seeds with an easily detectable (vs. undetectable) aril scar. It is less readily distinguished from *P. hypoleuca,* especially if one is examining a specimen of the former with only immature flowers. However, the pedicels of *P. hypoleuca* are usually much shorter (less than 9 mm in fruit) and have dense, short, rusty tomentum in both flower and fruit. If pedicels are not available, *P. hypoleuca* generally has smaller flowers with fewer stamens (< 45) and carpels (usually < 10).

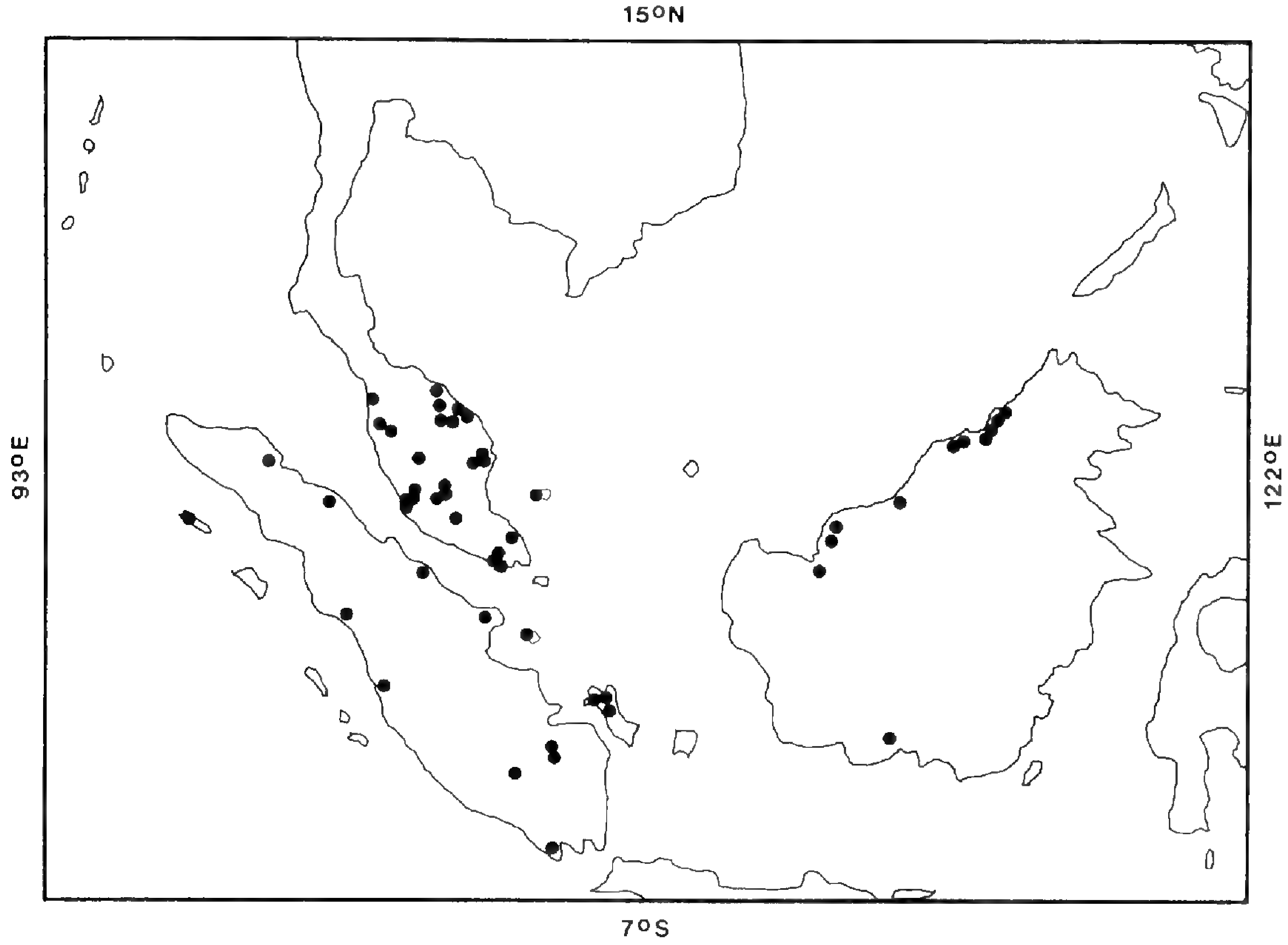
5. **Polyalthia hypoleuca** Hooker f. & Thomson, Fl. Brit. India **1:** 63. 1872, *pro parte florif.,* non *Guatteria hypoleuca* Miq. Fl. Ned. Ind., Eerste Bijv. Suppl. 381. 1861. TYPE: Singapore, [18]67, *Maingay 1516* (Kew Distr. 50) (lectotype, here selected, K, *pro parte*).

FIGURES 3A, B; 6A; 7A; 8D; 18D; 19C, D; 21B.

Tree to 50 m tall, DBH to 40 cm; trunk often fluted at base; pneumatophores absent; bark white to pale yellow, smooth on branches and trunk, with finely fissured or cracked patches appearing irregularly on bole; hoop marks not prominent on lower portions of bole; slash on larger trees revealing phloem rays reaching epidermis, phloem-ray apices 0.1–0.5 mm apart. Twigs with bark pale yellow-white, youngest growth glabrous (6%), or with moderate (39%) to dense (55%; n = 31), short, rusty tomentum. Leaves with young petiole 3–7 (4.7, 1.2, 25) mm long, moderately (45%) to densely (55%; n = 31) tomentose abaxially; lamina narrowly elliptic to elliptic, 6.1–12.5 (9, 1.6, 25) × 2–3.5 (2.6, 0.4, 25) cm, the apex acuminate to caudate, 0.6–1.4 (1.1, 0.2, 25) cm long, the base rounded to acute, the secondary veins 25 to 45 (32, 4.9, 25) per side, not forming regular weak intramarginal vein; leaves when fresh flat with abaxial surface dull white (tinged with brown, tan, or gray). Inflorescences in foliate axils, up to 4 per axil, and also borne on branches below leaves, tubercles absent or poorly developed; peduncle extremely reduced, 0.4–1.8 (0.9, 0.3, 26) mm long, usually with only 1 terminal flower developing, lateral floral buds and developing flowers absent; bracts 1 to 4, oriented perpendicular to branch axis when only 1 flower per axil. Flowers with pedicel 1–7.5 (2.7, 1.2, 26) mm long, 0.5–0.9 (0.7, 0.1, 26) mm wide at base and 0.5–1.2 (0.9, 0.4, 26) mm at apex, with dense, rust-colored tomentum (100%; $n = 26$); bract occasionally present (8%; $n = 26$), 1–2 mm above articulation. Sepals triangular, 0.7–1.2 (1, 0.14, 16) mm long, very densely tomentose abaxially (100%, $n = 16$), often (38%; $n = 26$) caducous at floral maturity. Petals linear; outer petals 4–11 (7.1, 1.8, 26) × 1–2.4 (1.4, 0.4, 26) mm, the pubescence beginning adaxially on basal (42%), middle (54%), or distal (4%; $n = 65$) ⅓, sparse to moderate throughout (58%), to sparse throughout except abaxially at base where dense (42%; $n = 26$), the midvein not visible abaxially; inner petals 4–12 (7.5, 2.2, 26) × 0.8–1.9 (1.2, 0.3, 26) mm; all petals turning yellow at maturity, with perfumelike scent, deep burgundy-red when dry. Torus 0.3–0.8 (0.58, 0.12, 26) × 0.6–1.5 (1, 0.2, 26) mm, gynoecial portion concave (7.7%), flat (57.7%), or convex (34.6%; $n = 26$). Androecium 0.7–1.8 (1.3, 0.3, 26) × 1.8–2.8 (2.3, 0.3, 26) mm; stamens 25 to 39 (32.3, 4, 26), 0.7–1.1 (0.8, 0.13, 26) × 0.5–0.8 (0.7, 0.07, 26) mm. Gynoecium 0.5–1.5 (1, 0.23, 26) mm across; carpels 3 to 9 (5.4, 1.4, 26), 0.5–1.2 (0.9, 0.17, 26) mm long, glabrous (4%) or moderately to densely tomentose (96%; $n = 26$); stigmas globose to moderately elongate, 0.2–0.7 (0.4, 0.16, 26) mm long, those of outermost ring not reflexed away from floral axis. Immature carpels green, slowly turning red 2–4 weeks before full maturity, finally deep purple to black, the pericarp then soft and fleshy (juice laden), with sweet or bitter-sweet taste. Mature, dry fruits with pedicel 4–9 (6.5, 1.4, 25) mm long, 1–2.3 (1.5, 0.4, 25) mm in diameter at apex, with dense, short, rusty tomentum (96%) or only moderately tomentose (4%; $n = 25$); stamen scars < 40 (100%; $n = 21$); carpels with the stalk 2–5 (3.8, 0.9, 25) × 1.2–2.4 (1.5, 0.3, 25) mm, seed-bearing portion ellipsoid, 10–20 (15, 2, 25) × 9–14 (11, 1.1, 25) mm, not ridged, apex blunt or rounded (100%; $n = 25$); fruit wall < 1 mm thick, deep burgundy to black. Placentation basal at maturity. Seed 1 per mature carpel, ellipsoid, with circumferential ridge, the aril scar present, the testa deep brown, finely to moderately pitted, not irregularly indented; rumination needles very fine.

DISTRIBUTION. Peninsular Malaysia, Sumatra, Borneo, and immediately adjacent islands (see MAP 5).

SELECTED SPECIMENS SEEN. **Malaysia.** KELANTAN: Ulu Lebir Kechil, SE Kelantan, near Trengganu border, 370 m alt., *FRI 4413, FRI 4414* (both FR) (both KEP); Ulu Lebir F.R., *KEP 11695* (fl+FR) (KEP); G. Rabong, 610 m alt., *FRI 20623* (FL+FR) (A, K, KEP). TRENGGANU: Ulu S Trengan, Kg. Melaka, 150 m alt., *FRI 10538* (fl+FR) (A, KEP); Bukit Bauk F.R., Dungun Distr., 25 m alt., *G. H. S. Wood 76094* (FR) (KEP). PAHANG: near Ulu Sungai Sepia, *Shah & Noor MS 2008* (FR) (A, KEP, SING); Lesong F.R., *FRI 25181* (FL) (KEP); Bukit Kajang F.R., Raub, *Jinal* [*KEP*] *20351* (FR) (KEP); Pelican Road, T. Lapah Tempwiang, Kuantan-Pahang, *Jaamat & Sow* [*KEP*] *43190* (FR) (KEP). SELANGOR AND KUALA LUMPUR FEDERAL DISTRICT: Telok F.R., *Rogstad 934, 947* (both FL) (both A); Bangi, *Balgooy 2199* (fl+fr) (KEP, L); Telok F.R., near Klang, *Hamid & Yeop (Yeob?)* [*KEP*] *3267* (fl) (KEP); Bukit Changgang, Klang, *SFN 33955* (FR) (A, KEP, SING); near Kuala Lumpur, *Sudin* [*KEP*] *41882* (FL+FR) (KEP); Telok F.R., Klang, *KEP 45808* (FR) (KEP). NEGRI SEMBILAN: Pasoh F.R., near Simpang Pertang, *Rogstad 912, 933, 942* (all FL) (all A); Tampin F.R., 540 m alt., *FRI 14216* (FR) (KEP); Gunong Angsi F.R., 400 m alt., *FRI 14631* (FL) (A, KEP). JOHORE: Segamat Wildlife Reserve, *FRI 17148* (fl+FR) (A, KEP); Sungai Kayu, *SFN 32189* (FR) (A, KEP, SING); Pengkalan Raja, Pontian, *SFN 36644* (fl+FR), *SFN 36697* (FL+FR) (both A, KEP, SING). SARAWAK: Buglgan(?), Tj.



Map 5. Distribution of *Polyalthia hypoleuca.*

Kelepis(?), *S 690* (FR) (KEP, SAR); S Entulang, Simanggang, *S 13120* (FR) (SAR). Sabah: Kimanis F.R., Papar Distr., 3 m alt., *SAN A 4600* (FR) (KEP, L, SAN); K. Klias Saratok, Beaufort Distr., *SAN 27307* (FR) (KEP, SAN, SAR); Melaliah N.F. Reserve, Sipitang Distr., 15 m alt., *SAN 27953* (FR) (KEP, L, SAN); Seratok Camp, Beaufort Distr., 10 m alt., *SAN 35236* (FL) (K, SAN); along rail line Lumat, Beaufort Distr., *Binideh* [*SAN*] *58445* (FR) (SAN). **Brunei:** Seria peat swamp, 8 m alt., *S 5892* (fl) (BRUN, FRI); Badas swamps, *Sinclair & Kadim 10460* (fr) (A, SING); Kuala Belait, Badas State Land, 7 m alt., *SAN 17457* (FL) (A, KEP, L, SAN). **Singapore:** Jurong Road, *SFN 26163* (FL+fr) (A, FRI, SING). **Indonesia.** Sumatra and adjacent islands: Riouw en Ond., Koeantan Distr., Sei Rambei [Sumatra?], 70 m alt., *bb 23472* (FR) (A, BO, L). Utara: Masihi F.R., Asahan, E coast, *Krukoff 4095* (FR) (A, L, US). Tengah: Bengkalis, Sekoedi [E coast], 5 m alt., *bb 21285* (fl) (A, BO, L); Pulau Gelang, 4 m alt., *bb 29166* (fl+FR) (A, BO, L). Selatan: Palembang, 15 m alt., *Zwan WF(?) 1172* (FR+fl) (BO, L); Belimbingan, 6 m alt., *bb 28536* (FL) (A, BO, K). Bangka: Lobok-besar, 20 m alt., *Kostermans & Anta 148* (FL+FR) (A, BO, KEP?), *199* (fl+FR) (A, BO), *1072* (FL+FR) (A, BO, LAE), *1171* (FR) (A, BO, K, KEP). Kalimantan: near Sampit, 5 m alt., *Kostermans 8134* (FL) (A, BO, L).

Regional names. "Ban aan aandoel," Indonesian?, Palembang, Sumatra, *Zwan 1172.* "Banittan," Indonesian?, Sumatra, *L. B. 72.* "Kayu selaut," Malay language? (kayu = wood, laut = sea), Sarawak, *S 690.* "Mahawai," language?, Sampit, S. Kalimantan, *Kostermans 8134.* "Manitan," language?, Pahang, peninsular Malaysia, *KEP 78666.* "Melian," language? (in Burkill, 1966). "Melilin," language? (in Burkill, 1966). "Mempisang," Malay language (a general name for several species of Annonaceae), Kelantan, peninsular Malaysia, *KEP 11695.* "Pisang-pisang," Malay language (pisang = banana) (a general name for several species of Annonaceae), Pahang, peninsular Malaysia, *Jinal* [*KEP*]

20351; Papar Distr., Sabah *SAN A 4600*. "Ridis," language?, Lobok Besar, Bangka, *Kostermans & Anta 1072*. "Selaut," Iban language?, Simanggang, S. Sarawak, *S 13120*. "Telinga basing," language?, Beaufort Distr., Sabah, *SAN 27307*. "Usai," language?, Lobok Besar, Bangka, *Kostermans & Anta 148*.

LOCAL USE. As in many Annonaceae, the bast fibers of the phloem and bark anastomose to yield a bark that can be removed in strips and makes excellent rope or fiber. This quality is noted by J. A. R. Anderson (*S 690*), who indicated that the natives of southern Sarawak use the bark of *Polyalthia hypoleuca* to make string and the wood to make bows. Burkill (1966) noted that this fiber withstands sea water. The wood of larger *P. hypoleuca* trees may also be used for crate and toy construction in peninsular Malaysia (Timber Utilization Chart, Forest Research Institute, Kepong, Selangor, Malaysia). In addition, Burkill (1966) reported that a decoction of the roots of this species is given after childbirth in peninsular Malaysia.

ECOLOGY. Altitudinal range is recorded as from near sea level to 610 m alt. Although Sinclair (1955) indicated that *Polyalthia hypoleuca* attains a height of 15 m, I have observed several individuals at Pasoh F.R., peninsular Malaysia, that have grown to over 30 m; flowering is generally most pronounced in tall individuals with exposed crowns. At Pasoh this species is restricted to drier slopes and does not appear to grow at seasonally or constantly inundated sites with little or no peat development. It is somewhat puzzling, therefore, that it (or a cryptic sibling species?) does grow in peat-swamp forests, but only where a thick peat mat has developed; *P. hypoleuca* is unable to grow in inundated bare clay soils. Possible reasons for this will be suggested in a subsequent article (Rogstad, in prep. a).

Ten distinct waves of flowering of varying intensity divided into two main periods were observed at Pasoh over the period of a year. Each main period was immediately preceded by the initiation of a flush of vegetative growth. The waves are very synchronized among the members of the population. Pollination appears to be effected, in both the Pasoh and Telok populations, primarily by the same species of beetle.

COMMENTS. Unfortunately, the type designated by Hooker and Thomson (1872) is a mixed specimen consisting of flowering and fruiting branches of *Polyalthia hypoleuca* and fruiting ones of *P. sumatrana*. Sinclair (1955) noted this mixed specimen, and here I lectotypify *P. hypoleuca* based on it.

Polyalthia hypoleuca grows in sympatry with *P. glauca*, *P. ovalifolia*, and *P. sumatrana*. Characters separating *P. hypoleuca* from *P. sumatrana* are included in the comments under the latter species. It can be distinguished from *P. glauca* and *P. ovalifolia* because the latter two species have elongate, clavate stigmas more than 64 percent of the length of the carpels, stigmas of the outermost ring bent outward at an angle greater than 30°, short (usually less than 10 mm) pedicels in fruit, and seed-bearing portions of the carpels globose at maturity.

Due to a very close morphological resemblance, *Polyalthia hypoleuca* is the species most likely to be confused with *P. multinervis*. As indicated in the PCA analyses of characters (e.g., see FIGURE 17), *P. multinervis* does differ slightly from *P. hypoleuca*: it has slightly larger flowers, glabrous or very sparsely pubescent (vs. densely tomentose) pedicels, and mature carpels acute to acuminate (rather than blunt) at the apex. These two species also differ in floral biology. Populations of *P. hypoleuca* studied in peninsular Malaysia had very fragrant flowers from the time of stigma receptivity until the petals abscised at anther dehiscence. Flowers at the equivalent stage from numerous individuals of *P. multinervis* studied at April River, Papua New Guinea, lacked detectable fragrance. The main pollinator of *P. hypoleuca* in peninsular Malaysia is of a strikingly different morphology than the main pollinator of *P. multinervis* in Papua New Guinea (Rogstad, in prep. b). *Polyalthia hypoleuca* has not been collected east of Borneo, while *P. multinervis* is thus far known only from the April River region of the Sepik River drainage in Papua New Guinea.

The sum of the evidence at hand indicates that slight but constant morphological differences exist between these two entities, that biological differences exist between them such that if they were to grow sympatrically, gene exchange might well not occur, and that they are geographically isolated. The two entities thus appear to conform to the evolutionary species concept defined above, and I therefore recognize them as such here.

6. **Polyalthia multinervis** Diels, Bot. Jahrb. Syst. **52:** 178. 1915. TYPE: [Papua New Guinea,] Sepik River region, April River, Sept. 1912, *Ledermann 8835* (fl) (holotype, B; isotypes, K, SING).

FIGURES 3D; 4E; 8A; 19A, B; 21D.

Tree to 30 m tall, DBH to 30 cm; trunk often fluted at base; pneumatophores absent; bark white to pale yellow, smooth on branches and trunk, with finely fissured or cracked patches appearing irregularly on bole; hoop marks not prominent on lower portions of bole; slash on larger trees revealing phloem rays reaching epidermis, phloem-ray apices 0.1–0.5 mm apart. Twigs with bark pale yellow-white, youngest growth glabrous (18%) or with moderate short, rusty tomentum (82%; $n = 11$). Leaves with young petiole 4–5 (4.6, 0.5, 8) mm long, glabrous (9%) to moderately tomentose (91%; $n = 11$) abaxially; lamina narrowly elliptic to elliptic, 8.4–10.6 (9.4, 0.7, 8) × 2.3–3.4 (2.8, 0.4, 8) cm, the apex acuminate to caudate, 0.5–1.1 (0.8, 0.2, 8) cm, the base rounded to acute, the secondary veins 16 to 29 (25, 4.1, 8) per side, not forming regular weak intramarginal vein; leaves when fresh flat with abaxial surface dull white (tinged with brown, tan, or gray). Inflorescences in foliate axils, up to 4 per axil, or borne on branches below leaves, tubercles absent or poorly developed; peduncle extremely reduced, 0.4–1.4 (0.8, 0.3, 8) mm long, usually with only 1 terminal flower developing, lateral floral buds and developing flowers absent; bract(s) 1 to 4, oriented perpendicular to branch axis when only 1 flower per axil. Flowers with pedicel 2–7 mm long, 0.6–1 mm wide at base and 0.9–1.2 mm at apex, glabrous or rarely with very sparse pubescence; bract always absent. Sepals triangular, 1–1.2 mm long, very densely tomentose abaxially, often caducous at floral maturity. Petals linear (100%, $n = 18$); outer petals 7–12 × 1.3–2.1 mm, the pubescence always beginning adaxially on basal ⅓, sparse to moderate throughout, the midvein not visible abaxially; inner petals

6.6–13 × 1.3–2 mm; all petals turning yellow at maturity, detectable fragrance absent, deep burgundy-red when dry. Torus 0.5–1.1 × 0.9–1.1 mm, gynoecial portion convex. Androecium 1.3–2.4 × 2.5–3.2 mm; stamens 26 to 32, 0.9–1.2 × 0.8–1 mm. Gynoecium 0.7–1 mm across; carpels 2 to 7, 1.1–1.3 mm long, moderately to densely tomentose; stigmas globose to moderately elongate, 0.3–0.6 mm long, those of outermost ring not reflexed away from floral axis. Immature carpels slowly turning red 2–4 weeks before maturity, finally deep purple to black, with soft, fleshy (juice-laden) pericarp tasting sweet or bittersweet. Mature, dry fruits with pedicel 6–10 mm long, 1.2–1.9 mm in diameter at apex, glabrous or with very sparse, short pubescence; stamen scars < 40; carpels with stalk 2–5 × 1.4–1.9 mm, seed-bearing portion ellipsoid, 18–22 × 7–12 mm, not ridged, acutely tapering at apex; fruit wall < 1 mm thick, burgundy to black. Placentation basal at maturity. Seed 1 per mature carpel, ellipsoid, with circumferential ridge, the aril scar present, the testa deep brown, finely to moderately pitted, not irregularly indented; rumination needles very fine.

DISTRIBUTION. Sepik River basin of Papua New Guinea in middle to lower April River region (see MAP 3).

SELECTED SPECIMENS SEEN. **Papua New Guinea.** EAST SEPIK PROVINCE: Niksek Village, April River airstrip, middle April R. (tributary to Sepik R.), 4°42′S, 142°32′E, 50–150 m alt., *Rogstad 813* (FL+fr), *817, 818, 819* (all FL), *820* (FL+FR), *828* (FL+fr), *829* (FL+FR) (all A, LAE); [April R. region, Sepik Valley, ca. 15–20 km upriver from Ambunti,] *Ledermann 8835* (fl) (B, K, SING).

REGIONAL NAMES. "Fawss" or "pfahss," Niksek language, April R., Papua New Guinea (*Rogstad 829*).

LOCAL USE. Timber of this species is used for house construction in the April River region of Papua New Guinea (*Rogstad 829*).

ECOLOGY. *Polyalthia multinervis* is thus far known only from 80 to 200 m alt. since it has only been collected from the April River region. More information on all aspects of this species is obviously needed. In the forests around Niksek Village (April River airstrip), flowering individuals are generally small to medium-size trees. However, their crowns are at or near canopy level because they grow almost exclusively in somewhat stunted forest on a thick, "peaty" humus mat (mat depth may exceed 1 m) that develops mostly in flatter areas and yields black water drainage. Areas with this root-humus mat are not true peat swamps; they are well drained and are not even intermittently inundated. Tracts on which the mat develops may be ecologically similar to the closed kerangas (heath) forests of Sarawak described by Brunig (1974), but this can only be determined by comparative investigations. *Polyalthia multinervis* appears to be a late secondary species, not growing in the full sun of open gaps but also not regenerating in the deepest forest. The most prolific regeneration can be found on well-developed root mats on banks well above the April River. As in *P. hypoleuca,* flowering in this species appears to occur in several distinct waves each year. Although mature individuals vary in the number of waves in which they flower, flowering of all plants within a wave is highly synchronized (see also *P. hypoleuca,* and Rogstad, in prep. b).

COMMENTS. Diels (1915) was apparently not familiar with *Polyalthia hypoleuca* since he made no mention of its similarity to *P. multinervis*. Despite this close resemblance, I have maintained the two as distinct species (see comments under *P. hypoleuca*). The New Guinea region is very poorly collected, and thus this classification scheme may require review as more information accumulates.

The type material designated by Diels (1915) that I have seen bears only immature flowers. However, enough characters are present to distinguish this entity clearly from *Polyalthia discolor* and to confirm its identity with specimens I have collected in the April River region. Diels also mentioned the only other collection of this species previous to mine, *Ledermann 9843*, stating that it bore fruit. I have been able to locate but one fruiting sheet of this collection (at L), and it bears only an apparently mature fruit pedicel with the developed carpels missing. The stamen scars number less than 50, and the pedicel agrees with *P. multinervis* as found at April River.

Uncertain Taxa

The possibility that a putative variety of *Polyalthia sumatrana*, var. *macrocarpa*, may be based on a mixed collection has been discussed above under that species.

Two specimens from the Andulau Forest Reserve, Kuala Belait District, Brunei (*Sinclair & Kadim 10454, SAN 17486*), and one from R. Belait at K. Ingei, Brunei (*BRUN 187*), are most closely allied, on the basis of flower and fruit characters, with *Polyalthia sumatrana*. However, they differ in their pedicels that are moderately tomentose and are occasionally fully articulated about 8–11 mm above the articulation here interpreted as separating the peduncle from the pedicel. The latter character is variable, however, even on a single specimen. Since "typical" specimens of *P. sumatrana* can also be found in this region (e.g., *BRUN 465, BRUN 897*), and since no population has been found that exhibits constant and discrete variation in these characters (as has been seen in *P. ovalifolia*, for example), I have not recognized this variation formally.

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APPENDIX 1. **Specimens examined for leaf papillae* and for seeds with spiniform endosperm ruminations.†**

Anaxagorea javanica Blume var. *tripetala* Corner: *Elmer 21131* (A).
A. luzonensis Gray: *Ramos BS 13623* (A).
A. petiolata R. E. Fries: *A. C. Smith 3192* (MO).
A. phaeocarpa Martius: *Anderson 12139* (MO).
A. rufa Timmerman: *Gentry & Tillett 10883* (MO).
A. sylvatica R. E. Fries: *Mexia 5053* (MO).
Annona muricata L. and *A. squamosa* L.: specimens from living collections at Fairchild Tropical Garden, Coral Gables, Florida.
Artabotrys harmandii Finet & Gagnep.: *Pierre 423* (A).
A. siamensis Miq.: *Rogstad 959*; *Sargent s.n.,* 16 Oct. 1903 (MO).
A. suaveolens Blume: *Maxwell 81-206* (MO); *Rogstad 831.*
A. trichopetalus Merr.: *Elmer 20489* (A).
A. zeylanicus Hooker f. & Thomson: *Saldanha 16365* (A); *Waas 934* (A).
Asimina triloba (L.) Dunal: specimen in living collection at Arnold Arboretum, Jamaica Plain, Massachusetts.
Bocageopsis canescens (Spruce) R. E. Fries: *Prance et al. 5929, 8792* (both MO).
B. mattogrossensis (R. E. Fries) R. E. Fries: *Maas et al. 6242* (MO).
B. multiflora (Martius) R. E. Fries: *Prance et al. 22714, 25798* (both MO); *Silva & Rosario 5849* (A).
Cleistochlamys kirkii (Bentham) Oliver: *Pereira & Correia 2351* (MO); *De Carvalho 1045* (MO).
Cleistopholis glauca Pierre ex Engler & Diels: *Leeuwenberg 6467* (MO); *Louis 12459, 12563* (both MO).
C. patens (Bentham) Engler & Diels: *Darko 732* (MO); *Louis 7993* (MO).
C. staudtii Engler & Diels: *Bates 1568* (MO).
Cremastosperma anomalum R. E. Fries: *Correa & Dressler 887, 1060* (both MO); *Stern et al. 107* (A).
C. cauliflorum R. E. Fries: *Bristan 1341* (MO); *Diaz & Jaramillo 1229* (MO); *Lleras et al. 16879* (MO).
C. macrocarpum Maas: *Liesner & González 9763* (MO).
C. pedunculatum (Diels) R. E. Fries: *Klug 3726* (A).
Desmos cochinchinensis Lour. and *D. dasymaschalus* (Blume) Safford: specimens in living collections at Kebun Raya, Bogor, Indonesia.
Enantia chlorantha Oliver: *Bates 1959* (MO); *Leeuwenberg 7355* (MO); *Zenker 441* (MO).
E. polycarpa (DC.) Engler & Diels: *Baldwin 10696* (MO).

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*See also APPENDIX 2.

†For most species several specimens have been examined, but usually only one representative collection is noted. *Rogstad* collections are deposited at A.

Ephedranthus amazonicus R. E. Fries: *Prance et al. 11555, 18787* (both MO).
E. guianensis R. E. Fries: *Gentry et al. 29075* (MO).
E. pisocarpus R. E. Fries: *Schatz et al. 732* (MO).
Goniothalamus giganteus Hooker f. & Thomson: *Rogstad 985.*
G. tortilipetalus Henderson: *Rogstad 566.*
Lettowianthus stellatus Diels: *Seuisei S1027* (MO).
Malmea depressa (Baillon) R. E. Fries: *Croat 24646* (MO); *Lundell 4852* (MO).
M. obovata R. E. Fries: *Riedel s.n.* (A).
Meiocarpidium lepidotum Engler & Diels: *De Wilde 1942 A, 2735* (both MO); *Zenker 3602* (MO).
Melodorum fruticosum Lour.: *Scortechini 1946* (SING).
Monocarpia marginalis (Scheffer) James Sincl.: *De Vogel 4492* (MO).
Monodora myristica Dunal: specimen growing at the Forest Research Institute, Kepong, Selangor, Malaysia.
Oncodostigma monosperma (Hooker f. & Thomson) James Sincl.: *Rogstad 920.*
Oncodostigma sp.: *Rogstad 957.*
Onychopetalum krukoffii R. E. Fries: *Krukoff 5326* (MO).
O. lanceolatum R. E. Fries: *Krukoff 6909* (MO).
O. lucidum R. E. Fries: *Krukoff 8214* (MO).
Oxandra acuminata Diels: *Croat 19729* (MO).
O. asbeckii (Pulle) R. E. Fries: *Mori & Boom 15170* (MO).
O. eneura Diels: *Croat 18738* (MO).
O. espintana (Spruce) Baillon: *Gentry, Aronson, & Ramírez 26744* (MO).
O. laurifolia Rich.: *Duss 4180* (MO).
O. leucodermis (Spruce) Warm.: *Liesner 6983* (MO); *Liesner & Clark 8949* (MO).
O. longipetala R. E. Fries: *Holdridge 6313* (MO).
O. xylopioides Diels: *Huashikat 1257* (MO).
Phaeanthus sp.: *Rogstad 938.*
Piptostigma fasciculata (Wilde) Boutique: *Germain 2396* (MO); *Toussaint 2151* (MO).
P. glabrescens Oliver: *Thomas 510* (MO).
P. pilosum Oliver: *Thomas 4726, 4755* (both MO).
Platymitra siamensis Craib: *Rogstad 796.*
Polyalthia angustissima Ridley: specimen in living collections at Singapore Botanical Garden.
P. brunneifolia James Sincl.: *James Sinclair 24179* (A).
P. bullata King: *FRI 11643* (KEP).
P. capuronii Cavaco & Keraudren: *Capuron SF 11795* (P).
P. cf. *cauliflora* Hooker f. & Thomson: *Rogstad 997.*
P. cinnamomea Hooker f. & Thomson: *Rogstad 936.*
P. clavigera King: *Curtis 2444* (SING).
P. discolor Diels: *Rogstad 814, 832.*
P. emarginata Diels: *Capuron 20977-SF* (P).
P. gigantifolia Merr.: *Ramos & Edaño 36966* (SING).
P. glauca (Hassk.) Mueller: *Rogstad 939, 944, 945, 966.*
P. gracilis Burck: *Versteeg 1408* (BO).
P. heteropetala Diels: *Ghesquier 4942* (P).
P. hypoleuca Hooker f. & Thomson: *Rogstad 912, 916, 942.*
P. jenkinsii (Hooker f. & Thomson) Hooker f. & Thomson: *Rogstad 968.*
P. lateriflora (Blume) King: *Rogstad 931.*
P. longifolia (Sonn.) Thwaites: *Rogstad 960.*
P. macropoda King: *Kostermans 7360* (SING).
P. michaelii C. T. White: *NGF 77111* (LAE).
P. multinervis Diels: *Rogstad 813, 817–819, 829.*
P. obliqua Hooker f. & Thomson: *Rogstad 935.*

P. oblongifolia Burck: *Ramos 1595* (A).
P. oligosperma (Danguy) Diels: *Thouvenot 62* (P).
P. oliveri Engler & Diels: *Baldwin 10394* (MO); *Enti 1701* (MO); *Oldeman 856* (MO).
P. ovalifolia Rogstad: *Buwalda 7797* (A).
P. pedicellata A. C. Smith: *A. C. Smith 647* (BO).
P. rumphii (Blume) Merr.: *Rogstad 922.*
P. sclerophylla Hooker f. & Thomson: *Rogstad 930.*
P. stenopetala (Hooker f. & Thomson) Ridley: *Dev 165* (KLU).
P. stuhlmannii (Engler) Verdc.: *Harris 3635* (MO).
P. suaveolens Engler & Diels: *Gilbert 8500* (MO); *Leeuwenberg 5082, 7322* (both MO).
P. suberosa (Roxb.) Thwaites: specimens from living collections at Fairchild Tropical Garden, Coral Gables, Florida.
P. sumatrana (Miq.) Kurz: *Rogstad 508, 509, 527.*
P. thorelii Finet & Gagnep.: *Pierre 1506* (SING).
Polyalthia sp.: *Rogstad 987.*
Polyceratocarpus gossweileri (Exell) Paiva: *Breyne 752* (MO).
P. microtrichus (Engler & Diels) Ghesq. ex Pellegrin: *Zenker 478* (MO).
P. parviflorus (Engler & Diels) Ghesq.: *Bos 6684* (MO); *Jacques-Georges 16832* (MO).
Pseudephedranthus fragrans (R. E. Fries) Aristeg.: *Maguire et al. 60189* (MO).
Pseudoxandra coriacea R. E. Fries: *Prance, Steward, Ramos, & Pinheiro 11468* (MO).
P. cuspidata Maas: *C. C. Berg et al. 757* (MO); *Prance & Sylva 58673* (MO).
P. guianensis R. E. Fries: *A. C. Smith 2665* (MO).
P. lucida R. E. Fries: *Steyermark & Delascio 129373* (MO).
P. polyphleba (Diels) R. E. Fries: *Gentry, Vasquez, Andrade, Horna, & Stern 28807* (MO); *Krukoff 8409* (MO).
Pseuduvaria spp.: *NGF 77112* (LAE); *Rogstad 924.*
Ruizodendron ovale (Ruiz & Pavón) R. E. Fries: *Begazo 61* (MO); *Klug 3798* (MO).
Stelechocarpus cauliflorus (Scheffer) R. E. Fries: *Rogstad 998.*
Unonopsis floribunda Diels: *Gentry 7452* (MO).
U. panamensis R. E. Fries: *Johnston 1643* (MO).
U. pittieri Saff.: *Contreras 10031* (MO); *Lent 2289* (MO).
U. spectabilis Diels: *Maas et al. 6229* (MO).
Uvaria boniana Finet & Gagnep.: *W. T. Tsang 23823* (MO).
U. calamistrata Hance: *Lau 468* (MO).
U. confertiflora Merr.: *Elmer 21081* (A).
U. grandiflora Roxb.: *Rogstad 629.*
U. javana Dunal: *Elmer 20857* (MO).
U. littoralis Blume: *De Vogel 3895* (MO).
U. lucida Bentham: *Faden 74/1251* (MO); *Pawek 12051* (MO).
U. mendesii J. Paisa: *Mendes 639* (MO).
U. muricata Pierre & Engler: *Gentry & Pilz 32795* (MO).
U. osmantha Diels: *Mendes 673* (MO).
U. ovata A. DC.: *Jacques-Georges 5850* (MO).
U. poggei Engler & Diels: *Robyns 4227* (MO).
U. sabrida Oliver: *Gossweiler 10417* (MO).
U. sofa Elliot: *Jacques-Georges 14602* (MO).
Xylopia elliptica Maingay ex Hooker f. & Thomson: *Yeob 5037* (SING).
X. ferruginea (Hooker f. & Thomson) Hooker f. & Thomson: *Rogstad 703.*
Xylopia sp.: *Rogstad 816.*
Unidentified species: *Rogstad 928, 961, 969.*

APPENDIX 2. Species of Polyalthia examined for leaf papillae* and for thickened, straight anticlinal walls in adaxial epidermal peels.†

P. amygdalina (A. Gray) Gillespie: *E. H. Bryan, Jr. 509.*
P. borneensis Merr.: *Elmer 21733.*
P. cauliflora Hooker f. & Thomson (sensu lato): *Kiah 32101; Mohd. Shah 167; S 16620.*
P. celebica Miq.: *bb 17290.*
P. cinnamomea Hooker f. & Thomson: *Henderson 35168.*
P. clemensorum Ast: *Poilane 29657.*
P. consanguinea Merr.: *Chun & Tso 44029.*
P. corticosa Finet & Gagnep.: *Poilane 19623.*
P. debilis Finet & Gagnep.: *Pierre 289.*
P. evecta (Pierre) Finet & Gagnep.: *Poilane 17313.*
P. flagellaris (Becc.) Airy-Shaw: *Chew Wee Lek 1177.*
P. jenkinsii (Hooker f. & Thomson) Hooker f. & Thomson: *Chun & Tso 43798.*
P. lateriflora (Blume) King: *Elmer 21013.*
P. littoralis Boerl. (sensu lato): *Poilane 19707.*
P. longifolia (Sonn.) Thwaites: *Wight 35.*
P. micrantha Boerl.: *Buwalda 7241.*
P. microtus Miq.: *SAN A 3668.*
P. modesta Finet & Gagnep.: *Poilane 17782.*
P. motleyana (Hooker f.) Airy-Shaw: *Chew Wee Lek 1008.*
P. nemoralis DC.: *Pételot 5955.*
P. obliqua Hooker f. & Thomson: *Hallier 1774.*
P. oligosperma (Danguy) Diels:** *Capuron 20030.*
P. oliveri Engler: *Thomson 109.*
P. parviflora Ridley: *Poilane 704.*
P. plagioneura Diels: *Poilane 29564.*
P. rumphii (Blume) Merr.: *FRI 14190.*
P. simiarum (Hooker f. & Thomson) Hooker f. & Thomson: *Khant D.R. 1174.*
P. stenopetala (Hooker f. & Thomson) Ridley: *Kiah 36162.*
P. suaveolens Engler & Diels:** *Kennedy 1544.*
P. subcordata (Blume) Blume: *Korthers s.n.*
P. suberosa (Roxb.) Thwaites: *Poilane 5185.*
P. tenuipes Merr.: *Richards 2306.*
P. venosa Merr.: *Ramos & Edaño 36558.*

*See also APPENDIX 1.

†Papillae similar in structure and distribution to those of the *Polyalthia hypoleuca* complex were lacking in all species listed; the two species with similar thickened anticlinal walls are marked with double asterisks. All specimens are at A.

APPENDIX 3. Characters used in the morphometric analyses of the Polyalthia hypoleuca complex.*

I. Floral and vegetative characters.
  A. Continuous (measured; in mm unless noted) and meristic (counted) characters used in multivariate data sets.
    1. Androecium width.
    2. Torus width.

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*For measurements of mature leaves, an average-size leaf on older growth was subjectively chosen.

3. Pedicel distal width.
4. Stamen number.
5. Carpel number.
6. Inner-petal length.
7. Outer-petal length.
8. Androecium height.
9. Pedicel basal width.
10. Stamen length.
11. Gynoecium width.
12. Torus height.
13. Inner-petal width.
14. Outer-petal width.
15. Stamen inner theca length.
16. Carpel length.
17. Pedicel length.
18. Distance of gynoecium emergence above androecium.
19. Flower number per leaf axil.
20. Distance from distal peduncle articulation to base of pedicel bract.
21. Stigma length.
22. Outer theca length.
23. Peduncle length.
24. Stamen width.
25. Lamina length (in cm).
26. Lamina maximum width (in cm).
27. Leaf drip-tip length (measured from inflection point of distal lamina border and border of drip-tip; in cm).
28. Leaf primary vein number (counting only largest class of veins branching directly from mid-vein).
29. Petiole length.

B. Characters used in conjunction with results of multivariate analyses.
   1. Number of latest flush of vegetative growth bearing flowers.
   2. Flowers in axils: of present leaves = 1; of abscised leaves = 2.
   3. Tree height (in m).
   4. Bole diameter at breast height (in cm).
   5. Inflorescence type: flowers with reduced peduncles (< 2 mm long), lateral buds and flowers lacking, large tubercles built up of old inflorescence scars lacking = 1; similar to 1, but tubercles present = 2; peduncles generally longer than 2 mm, lateral buds (and/or developing lateral flowers) and tubercles present = 3.
   6. Peduncle bract number.
   7. Lowest peduncle bract position with respect to stem bearing inflorescence: abaxial = 0; adaxial = 1; abaxial and adaxial on same specimen = 2; all angles (as on tubercle) = 3.
   8. Medial pedicel bract: present = 0; lacking = 1.
   9. Pedicel color: tan-brown = 1; dark red-black = 2.
   10. Peduncle and pedicel pubescence: lacking = 0; present only on peduncle = 1; tomentum = 2.
   11. Sepal pubescence (abaxial surface): lacking = 0; present on margins only = 1; present over entire surface = 2.
   12. Outer petal shape: no constriction, linear = 1; basal portion clawed, distal portion linear = 2; basal portion clawed, distal portion obovate or flared = 3; no constriction, ovate-obovate or elliptic = 4.
   13. Portion of inner petal where pubescence begins on adaxial surface: basal ⅓ = 1; middle ⅓ = 2; distal ⅓ = 3.

14. Color of adaxial, glabrous (basal) portion of inner petal: light tan-brown = 1; brownish red to wine red = 2; dark reddish black = 3; deep purple = 4.
15. Inner petal pubescence: sparse throughout = 1; moderate throughout = 2; dense throughout = 3; sparse throughout except dense on abaxial surface at base = 4.
16. Mid-vein of outer petal on abaxial surface: not detectable = 0; easily seen = 1.
17. Gynoecium emergence: all stigmas depressed below androecium = 0; stigmas level with androecium = 1; stigmas emergent above androecium = 2; stigmas and portion of carpels emergent above androecium = 3.
18. Stigmas: central ones depressed = 1; all level = 2; central ones raised = 3; all separate, radiating = 4.
19. Gynoecial area of torus: concave = 0; level = 1; convex = 2.
20. Apices of stamen connectives: concave = 0; flat = 1; mixed = 2.
21. Inner thecae of stamens: not touching = 0; touching = 1.
22. Color of carpel: all tan = 0; distal, abaxial surface deep red-brown, becoming tan basally = 1; all red-brown = 2; all dark reddish black = 3.
23. Carpel pubescence: lacking = 0; present on abaxial apex only = 1; present on abaxial apex with some on ridged sides and/or stigmatic crest = 2; present throughout = 3.
24. Shape of stigma: spherical = 0; elongate = 1.
25. Outer ring of carpels with very strongly curved carpels: no = 0; yes = 1.
26. Pubescence on youngest stems: lacking = 0; sparse = 1; moderate to heavy = 2.
27. Pubescence on petiole of smallest leaf: lacking = 0; sparse = 1; moderate to heavy = 2.

II. Fruit and vegetative characters.
  A. Continuous (in mm unless noted) and meristic characters used in multivariate data sets.
    1. Pedicel length.
    2. Pedicel distal width.
    3. Mature carpel stalk length.
    4. Mature carpel stalk distal width.
    5. Mature carpel length, including only seed-bearing portion above stalk.
    6. Mature carpel width.
    7. Lamina length (in cm).
    8. Lamina maximum width (in cm).
    9. Leaf drip-tip length (measured from inflection point of distal lamina border and border of drip-tip; in cm).
    10. Leaf primary vein number (counting only largest class of veins branching directly from mid-vein).
  B. Characters used in conjunction with multivariate data analyses.
    1. Pedicel pubescence: lacking = 0; sparse or irregular = 1; dense tomentum = 2.
    2. Mature carpel apex: rounded or blunt = 0; acute = 1.
    3. Dried mature carpels with longitudinal ridges: no = 0; yes = 1.
    4. Stamen scars: < 40 = 0; > 40 = 1.
    5. Tree height (in m).
    6. Bole diameter at breast height (in cm).

THE GENERA OF PINACEAE IN THE SOUTHEASTERN UNITED STATES[1]

ROBERT A. PRICE[2]

PINACEAE Lindley, Nat. Syst. Bot. ed. 2. 313. 1836, nom. cons.

(PINE FAMILY)

Evergreen [or deciduous], monoecious trees (occasionally shrubs), usually pyramidal in form. Leaves linear to acicular [rarely lanceolate], spirally arranged (often apparently 2-ranked), sessile or short-petiolate; foliage leaves either borne on long-shoots or clustered tightly on short-shoots. Pollen cones (microsporangiate strobili) bearing spirally arranged, bilaterally symmetrical microsporophylls; microsporangia 2 on the abaxial surface of each sporophyll, longitudinally or transversely [or obliquely] dehiscent; pollen grains bisaccate, or less commonly with the saccae reduced to a frill (in *Tsuga* sect. TSUGA) [or nonsaccate in *Larix* and *Pseudotsuga*]; prothallial cells 2. Ovulate cones with

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I thank Carroll Wood and Norton Miller for the opportunities afforded by participation in the Generic Flora project and for their guidance and editorial help in the study. I am grateful to Ihsan Al-Shehbaz for his generous help during my visits to Harvard University; to William Critchfield, M. Thompson Conkle, and Eugene Zavarin for sharing insights and prepublication manuscripts on the Pinaceae; and to Rudolf Schmid for bibliographic assistance. Library and herbarium collections associated with Harvard University and the University of California, Berkeley, were consulted in this study, and I wish to thank the librarians and curatorial staffs of these institutions. Elizabeth Schmidt and Stephen Spongberg added their editorial expertise to the manuscript.

The illustrations were drawn by Karen Stoutsenburger in 1977 under the supervision of Carroll Wood, who also made the dissections. Living, liquid-preserved, and some of the dry materials used were variously collected by Walter Judd, Norton Miller, and Carroll Wood. Herbarium materials include an unattributed sheet [A] with mature seeds of *Pinus Strobus* utilized by C. E. Faxon for the illustration in Sargent's *Silva of North America,* as well as specimens collected by Adams & Wherry (*2252* [GH]), R. M. Harper (*2023, 2027* [GH]), and J. D. Smith (*s.n.,* Aug. 1881 [GH]). The diagrammatic cross sections of leaves of *Pinus* are after J. W. Lanyon's *A Card Key to Pinus Based on Needle Anatomy.* The pollen grain of *P. Strobus* is after a photograph made by Norton Miller.

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spirally arranged, strongly flattened bract-scale complexes; bracts included or exserted, separate from the scales for most of their length; mature ovuliferous scales relatively thin to strongly thickened and woody (in *Pinus*); ovules 2 on the adaxial surface of each scale, the micropyles directed toward the cone axis; archegonia few per ovule, not clustered. Seeds with an elongate terminal wing partially folded around the seed body [wing short or absent in some species of *Pinus*]; embryo straight, cotyledons 2–12[–18]. Chromosome number $2n = 24$ [26 and 44 in one species each]. (Including Abietaceae Walpers; Abietineae Rich.) TYPE GENUS: *Pinus* L.

The largest and most economically important family of conifers, with ten genera and approximately 220 species, the Pinaceae are restricted almost entirely to the Northern Hemisphere[3] both at present and as fossils (Florin, 1963). Three small genera are confined to eastern Asia: *Keteleeria* Carr., a genus of perhaps nine species (Cheng & Fu) much in need of further study, and the monotypic *Cathaya* Chun & Kuang (described in 1958 from southern China) and *Pseudolarix* Gordon (golden larch, false larch). *Cedrus* Trew, comprising the true cedars, consists of four closely related species occurring disjunctly in North Africa, the Near East, Cyprus, and the Himalayas and is widely cultivated in temperate areas, including the southeastern United States. All six remaining genera are represented by species native to the United States. Only two of them have no species indigenous to our area: *Larix* Miller, larch, with about ten species in northern North America and Eurasia, and *Pseudotsuga* Carr., Douglas fir, with seven or eight species in western North America and eastern Asia.

The family Pinaceae is a well-defined natural group, distinguished particularly by characters of its ovulate cones. These have well-developed scales that are distinct from the subtending bracts, two inverted ovules per scale, and a prominent terminal seed wing developing from the cone scale. It is supported as a monophyletic group by shared features unique among the gymnosperms, including the pattern of proembryogeny (Doyle, 1963; Singh), protein-type sieve-cell plastids (Behnke), and the absence of biflavonoid compounds (Geiger & Quinn).

On the basis of morphological comparisons (e.g., Eckenwalder; Hart), immunological comparisons of seed-protein extracts (Price & Lowenstein), and phloem polypeptide profiles (Alosi & Park), there is no evidence that the Pinaceae are closely related to any of the other extant families of conifers. Rather, the family has a long fossil history as a distinct lineage, probably dating to the Triassic (Miller, 1977), as is also the case for such other major extant coniferous groups as the Araucariaceae, the Podocarpaceae, and the Cupressaceae-Taxodiaceae lineage. The combination of apparently primitive characters (bisaccate pollen with two prothallial cells, chromosome number $2n = 24$, and lack of bract-scale fusion) and uniquely derived features characteristic of the Pinaceae suggests that its origin should be sought among early conifer groups preceding the extant families (see Florin, 1951). Thus a number of European workers

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[3] One species, *Pinus Merkusii* Jungh & De Vries, is native from Indochina south of the Equator to Sumatra.

(e.g., Emberger; Lebreton & Sartre; Norin) have placed the Pinaceae in the unifamilial order Pinales.

The monotypic *Sciadopitys* Sieb. & Zucc., Japanese umbrella pine (Sciadopityaceae), has sometimes been associated with the Pinaceae on the basis of its unusual "double-needles." These superficially resemble longitudinally fused pairs of *Pinus* needles but in fact differ from them considerably in pattern of development (see Roth). Other morphological and cytological evidence suggests that *Sciadopitys* diverged at an early time from the cupressaceous-taxodiaceous lineage, since *Sciadopitys*—as well as the Cupressaceae *sensu lato* (including Taxodiaceae)—differs from the Pinaceae in having nonsaccate pollen without prothallial cells, substantial fusion of bract and scale in the mature ovulate cone, multiple ovules per scale, and lateral seed wings derived from the seed coat (Florin, 1951; Singh; Sporne). In its proembryogeny *Sciadopitys* appears to be more primitive than either group (Doyle & Brennan; Singh). Immunological comparisons of seed-protein extracts (Price & Lowenstein) and overall patterns of secondary-product chemistry (Hegnauer, 1962, 1986) also indicate that *Sciadopitys* is quite isolated from the Pinaceae.

The ten genera of Pinaceae are clearly delimited, but subfamilial groupings have been controversial. *Pinus,* in recognition of its unusual short-shoots (needle fascicles) and its distinctive, usually highly thickened cone scales, is often placed by itself in subfam. Pinoideae. Vierhapper and a number of later authors (e.g., Florin, 1931, 1963; Krüssmann; Pilger & Melchior) divided the remaining genera into two groups based on presence or absence of strongly condensed vegetative short-shoots that bear the majority of the foliage leaves. The genera with marked shoot dimorphism (*Cedrus, Larix, Pseudolarix*) have been placed in subfam. Laricoideae Pilger & Melchior, with the remaining genera (long-shoots only) in subfam. Abietoideae Ascherson & Graebner *emend.* Pilger & Melchior or in equivalent groups of lower rank. The relatively recently discovered genus *Cathaya,* which has less-marked shoot dimorphism (see photo in Chun & Kuang, 1958), was placed by Florin (1963) in the Abietoideae. However, other morphological characters show little concordance with shoot dimorphism, so division of the family on this basis alone is highly artificial.

Another subfamilial division, first proposed by Van Tieghem (1891), placed together those genera with resin canals in the primary root adjacent to each protoxylem pole (*Pinus, Picea, Larix, Pseudotsuga* (and *Cathaya*; see Hu & Wang), comprising the Pinées or Epixylocèles of Van Tieghem, here termed the pinoid group) and those with a single central resin canal in the primary root (*Cedrus, Tsuga, Abies, Keteleeria,* and *Pseudolarix,* comprising the Cedrées or Myélocèles of Van Tieghem, here termed the abietoid group). This classification appears to be a natural one, based on the concordance of root anatomy with other morphological features. Each of the pinoid genera regularly exhibits both vertical and horizontal resin canals in the wood and lacks resin vesicles in the seed coat, while the abietoid genera have much more localized resin canals in the wood following wounding ("traumatic resin canals," usually in the vertical system) and have resin vesicles in the seed coat (Jeffrey; Phillips; Price *et al.*). Immunological comparisons of seed-protein extracts have also yielded precisely the abietoid and pinoid groups of Van Tieghem (Prager *et al.*;

Price *et al.*). Thus recognition of two subfamilies, the Pinoideae and the Abietoideae, corresponding to the groups of Van Tieghem—or of three subfamilies, with *Pinus* placed in a monogeneric Pinoideae and the remaining pinoid genera in the Laricoideae—seems to be the most reasonable alternative.

Within the pinoid group, *Larix* and *Pseudotsuga* appear to be closely related sister-genera on the basis of their shared possession of nonsaccate pollen, a highly modified micropylar apparatus at time of pollination, fiber-sclereids in the bark, and similar, relatively asymmetric karyotypes, all of which seem to be derived characters within the family. They also group together in immunological comparisons of seed proteins (Prager *et al.*; Price *et al.*).

Chromosome counts have been obtained for all ten genera and approximately 75 percent of the species of Pinaceae (see particularly Khoshoo, 1961). The number $2n = 24$, which is apparently primitive for the conifers,[4] has been found in all but two species (*Pseudotsuga Menziesii* (Mirbel) Franco, $2n = 26$, and *Pseudolarix amabilis* (Nelson) Rehder, $2n = 44$). Counts are available for six of the remaining seven species of *Pseudotsuga*; all have $2n = 24$ (Doerksen & Ching; El-Kassaby *et al.*). Karyotypes have been obtained for all genera of the Pinaceae (see particularly Chu & Sun; Khoshoo, 1962; Kuo *et al.*; Sax & Sax; see also Saylor, 1964, 1972, 1983, cited under *Pinus*); they vary from largely symmetrical (11 of 12 chromosomes metacentric or submetacentric in *Pinus, Cathaya,* and *Cedrus*; nine of 12 metacentric in *Picea* and *Tsuga*) to extremely asymmetric in *Pseudolarix*. *Pseudotsuga* and *Larix* both have asymmetric karyotypes—six metacentric and six subtelocentric chromosomes, with one metacentric chromosome replaced by a subtelocentric and an additional short telocentric chromosome in *P. Menziesii*. *Pseudolarix amabilis* has a particularly unusual karyotype, with two metacentric and 20 shorter subtelocentric chromosomes (Sax & Sax), implying an aneuploid increase involving fission of ten of the original 12 chromosomes (Ehrendorfer; Khoshoo, 1959). Given their long fossil record, the Pinaceae have shown remarkably little change in chromosome number, a situation shared with the other conifer families except the Podocarpaceae (Ehrendorfer; Khoshoo, 1962), but one differing markedly from most angiosperm groups. Individuals or cells with polyploid chromosome numbers have occasionally been reported in the Pinaceae (Khoshoo, 1959), but polyploid plants apparently seldom survive under natural conditions.

The Pinaceae are characterized by a specialized variant of the coniferous pattern of proembryogeny (Dogra, 1980; Doyle, 1963; Singh). Two free-nuclear mitotic divisions yield four nuclei that come to lie in a more or less planar arrangement. A third mitotic division yields two tiers of four nuclei that rapidly become separated by transverse walls. The Pinaceae differ from the other conifers in that the lower of the two tiers produced by vertical division of the original upper or "open" tier does not elongate to form the suspensor. Instead, the tier of cells below this, produced by vertical division of the lowest original tier, forms the suspensor, while only the lowest of the four tiers forms the embryonal mass. In *Pseudotsuga* (at least in *P. Menziesii*) apparently only the

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[4] This number is also found in *Taxus* (Taxaceae), *Cephalotaxus* (Cephalotaxaceae), some Podocarpaceae, and the outgroup *Ginkgo* L. (see discussions in Ehrendorfer, and Khoshoo, 1962).

lower of the original two tiers divides, yielding a three-tiered proembryo (Allen & Owens; Singh).

Although only a single embryo usually matures in each seed, polyembryony is characteristic of many conifers, including all genera of Pinaceae. Simple polyembryony, where embryos are formed in more than one archegonium per ovule, occurs relatively frequently. Cleavage polyembryony, where multiple embryos are formed by the splitting up of the products of a single zygote, is also a regular feature in *Pinus, Cathaya, Cedrus, Tsuga,* and *Keteleeria* (Doyle & Brennan; Wang & Chen). It also occurs in a limited percentage of embryos in some species of *Abies* but has not been found in *Pseudolarix, Picea, Larix,* or *Pseudotsuga.* In the last two genera, unequal growth rates often cause two of the units to overtop the others (although the four embryonal units do not separate from one another, a situation termed "incipient cleavage" by Doyle & Brennan).

The Pinaceae have the highest average number of cotyledons and the greatest range in this number of any family of seed plants (Butts & Buchholz). The highest numbers are found in *Pinus,* which has the entire range of numbers for the family (2–18, with intraspecific averages ranging from ca. 4 to 14), and in *Cedrus* (5–14, averaging ca. 9 or 10). Detailed discussions of the vascular-bundle patterns in the cotyledons and embryos are presented in Boureau (1939) and Ferré (1952).

Ovulate-cone anatomy in the Pinaceae has been studied by Aase, Miller (1976), Radais, and Van Tieghem (1869), with emphasis on distribution of the vasculature and resin canals. *Pinus* appears to be unusual in having partial fusion of the bract and scale traces at their bases. The arrangement of the resin canals associated with these traces seems to be fairly specific to each genus (Miller, 1976; Radais), with those in the cones of *Pinus* restricted to the area abaxial to the scale trace, perhaps because of the basal fusion of the traces. The axial vascular cylinder of the cone is reduced in thickness and much dissected in the genera with abscising cone scales (*Abies, Cedrus, Pseudolarix*; Miller, 1976).

Pollen grains are bisaccate in the Pinaceae, except in *Larix* and *Pseudotsuga,* where they are spheroidal and nonsaccate, and *Tsuga* sect. TSUGA, where the saccae are reduced to a subequatorial frill (G. Erdtman, 1957, 1965; Ueno). Saccate pollen is evidently the primitive state both in the Pinaceae and among the conifers generally (see Florin, 1951; Millay & Taylor), but the saccae have been lost in all other extant coniferous groups except the Podocarpaceae, where pollen may be bi-, tri-, or nonsaccate.

The Pinaceae are wind pollinated, as are the other conifers, and often release huge volumes of pollen. Specific mechanisms of pollination have been reviewed by Dogra (1964), Doyle (1945), and Singh and have recently been elegantly demonstrated through scanning electron, as well as light, microscopy for a number of western North American taxa by Owens and coworkers (Allen & Owens; Owens & Molder; and additional references cited under the individual genera). A pollination-drop mechanism has been substantiated only in *Pinus* and *Picea* and is lacking in the other genera examined to date (*Cathaya, Keteleeria,* and *Pseudolarix* are unstudied in this regard). It is found in most other gymnosperms and is presumably the primitive state for the Pinaceae (see Doyle, 1945; Singh).

In *Pinus* and *Picea,* pollen is caught on a sticky film on the inner surfaces of the two integumentary arms and, when contacted by the pollination drop, is then drawn into the micropylar canal, after which it floats or is pulled up to the nucellus (Owens *et al.,* 1981, 1987, cited under *Pinus* and *Picea,* respectively). *Pseudotsuga* and *Larix* have a highly specialized mechanism in which the unwinged pollen is caught between hairs on the highly expanded outer-integument lip and then drawn into the micropylar canal by collapse of the surface of the lip (Allen & Owens; Owens & Molder). In *Cedrus* and *Abies,* pollen is caught on the inner surface of the funnel-shaped integumentary area around the micropyle, and the nucellus grows out to the pollen (Doyle, 1945; Owens & Molder, 1977, cited under *Abies*). In *Tsuga Mertensiana* (Bong.) Carr., of sect. HESPEROPEUCE, the situation is similar, but the integument tip is very asymmetric; in sect. TSUGA the pollen lands primarily on the bract surfaces rather than the ovule tip, and then the pollen tubes grow over to the nucellus (Doyle & O'Leary). This unusual situation is otherwise seen only in the Araucariaceae and in *Saxegothaea* Lindley (Podocarpaceae), which also have unwinged pollen (Doyle, 1945). Doyle (1945) related the pollination mechanisms of Pinaceae to the groupings of Van Tieghem (1891) in an evolutionary diagram, showing series leading from *Pinus* and *Picea* to *Larix* and *Pseudotsuga* on the one hand, and *Cedrus, Abies,* and *Tsuga* on the other. *Cathaya* might be expected to have a mechanism similar to that of *Pinus* and *Picea,* and *Keteleeria* and *Pseudolarix* to have ones similar to those of the other abietoid genera.

A characteristic feature of the Pinaceae is the formation of ectomycorrhizal associations with a variety of fungi, including a number of basidiomycetes, such as *Armillaria matsutake* and *Boletus edulis,* that are highly sought for their edible mushrooms. The presence of mycorrhizae appears to help buffer the plants against various types of environmental stress, and thus mycorrhizal associations have been much investigated in regard to commercial tree production.

Because of the economic importance of the Pinaceae, numerous studies of the chemical composition of the leaves, wood, and bark have been made on many species (see reviews by Hegnauer, 1962, 1986; Norin; Squillace; Von Rudloff), with particular emphasis on *Pinus, Picea, Abies,* and *Pseudotsuga.* The chemistry of *Cedrus* has recently been reviewed by Agrawal & Rastogi. Significant gaps remain in our knowledge of the chemosystematics of even the best-known genera, however.

The Pinaceae contain a diversity of terpenoid compounds in the bark, wood, leaves, and cones, particularly in the characteristic oleoresins of the resin canals or vesicles. The bulk of the volatile portion of the stem and leaf oleoresins is usually a complex mixture of monoterpenes. These impart much of the characteristic fragrance associated with Pinaceae. Terpenoid and hydrocarbon profiles of the oleoresins or turpentines (the steam-distillable portion thereof) often show significant differences among species and have been widely used in chemosystematics of the Pinaceae (see particularly the reviews by Squillace and

Von Rudloff and the papers by Mirov, Von Rudloff, Zavarin, and their coworkers cited under the individual genera).

Sesquiterpenoid compounds have received much less attention than monoterpenoids, although the former may also be of considerable chemosystematic utility. *Cedrus* is particularly notable for its array of unusual structural types including the atlantones, himachalenes, and allohimachalenes (Agrawal & Rastogi; Norin).

Diterpene resin acids are major constituents of the "rosin" remaining after removal of the volatile components of pinaceous oleoresin by steam distillation (Hegnauer, 1962, 1986; Norin). Resin acids of the abietane and pimarane types have been reported from woods of *Pinus, Picea, Larix, Pseudotsuga,* and *Abies* (H. Erdtman, 1963; Norin) and from the cone oleoresins of *Cedrus* (Norin). These compounds are to be expected in the other genera if appropriate oleoresins are examined. Both pimarane and abietane terpenoids occur widely in the conifers (Hegnauer, 1986), although the abietane type was once thought to be specific to the Pinaceae (H. Erdtman, 1963). Several other types of diterpenoids have also been found in the Pinaceae, including labdane terpenoids in various species of *Pinus, Picea, Larix,* and *Abies,* and macrocyclic compounds of the thunbergene type in *Pinus, Picea, Larix,* and *Pseudotsuga* (Norin). Pseudolaric acids, a very unusual structural class of diterpenes, have been isolated from the roots of *Pseudolarix amabilis*; these constitute the active components of antifungal medicines in traditional use in China (Zhou *et al.*).

Serratene triterpenoids are characteristic bark components of *Pinus* and *Picea* (Hegnauer, 1962, 1986; Norin) and the morphologically similar *Cathaya* (He *et al.*) but have not been found in the other genera. Unusual lanostane triterpenoids have been isolated from the bark or needles of a few species of *Abies* (Hegnauer, 1962, 1986; Norin), while other tetracyclic triterpenes have been found in *Larix, Pseudotsuga, Pinus,* and *Picea.*

Alkaloids do not occur frequently in the Pinaceae but have been detected in some species of *Pinus, Picea,* and *Keteleeria* (Hegnauer, 1962; Willaman & Schubert). The pyridine alkaloids pinidine and α-pipecoline have been isolated from needles of several species of *Pinus* but are apparently absent in many others.

The Pinaceae are unusual in their almost total lack of biflavonoid compounds, otherwise ubiquitous among the conifers and *Ginkgo* (Geiger & Quinn). A single biflavonoid compound, abiesin, has recently been reported to occur in low concentration in the needles of *Abies spectabilis* (D. Don) Spach (Hegnauer, 1986).

Anthocyanins (3-glucosides of cyanidin (red) and delphinidin (blue), either singly or in combination) are important in the coloration of the young pollen and seed cones of the Pinaceae (Santamour, 1966). They are also involved in the transient spring coloration of *Picea* needles (Santamour, 1967).

Cyclitols (sugar 5-methyl ethers) such as sequoyitol and pinitol occur widely among the conifers, including the Pinaceae, and are of interest in that pinitol is the sugary substance exuded from the trunk of sugar pine (*P. Lambertiana* Douglas) and the related *P. Ayacahuite* Ehrenberg (Hegnauer, 1962). The related compound D-1-O-methylmucoinositol occurs widely in the leaves of the other families of conifers but is apparently absent in those of the Pinaceae (Dittrich *et al.*).

Jamieson & Reid surveyed the fatty acids of conifer leaves, including representatives of seven genera of the Pinaceae. These uniformly exhibited a series of 18-carbon polyunsaturated acids that were absent in the other conifers examined.

Many species of Pinaceae are of great economic importance, with the family supplying over half of the world's timber (Sporne). *Pinus, Pseudotsuga, Picea, Larix, Abies, Tsuga,* and *Cedrus* are all of major significance in this regard. These genera are important sources of ornamental trees, and numerous horticultural varieties have been developed (L. H. Bailey; Dallimore & Jackson; Den Ouden & Boom; Krüssmann). The attractive golden larch (*Pseudolarix amabilis*), grown as an ornamental in China, is suitable to much of our region. Species of *Abies* (e.g., *A. balsamea* and *A. Fraseri*), *Picea,* and *Pinus* are frequently used as Christmas trees. The Pinaceae, particularly *Pinus,* are also economically important as the source of turpentine, pitch, and rosin used in shipbuilding (often termed "naval stores"), as well as in other industries. In addition, the leaf and stem resins of several genera have been used by native peoples of the United States and Canada in treating respiratory ailments and aiding wound healing, as well as for other medicinal purposes (Arnason *et al.*; Krochmal & Krochmal).

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KEY TO THE GENERA OF PINACEAE IN THE SOUTHEASTERN UNITED STATES

General characters: *monoecious evergreen* [*or winter-deciduous*] *trees (rarely shrubs); leaves alternate, linear to acicular, containing resin canals; pollen cones with spirally arranged, flattened microsporophylls; sporophylls with 2 abaxial microsporangia; pollen bisaccate (sometimes nonsaccate); ovulate cones erect or pendent at maturity; bract-scale complexes spirally arranged, flattened; bracts largely free from cone scales, included or exserted; ovules 2 per cone scale, adaxial, with micropyles facing the cone axis; seeds with 1 terminal wing (rarely wingless).*

- A. Foliage leaves in fascicles of 2–5, each fascicle subtended by a scale leaf; cone scales thickened at apex, often armed with a prickle. .... 1. *Pinus.*
- A. Foliage leaves borne singly, without subtending scale leaves; cone scales not thickened at apex, unarmed.
  - B. Twigs roughened by persistent leaf bases (sterigmata); ovulate cones not erect at maturity, falling as a unit.
    - C. Leaves squarish in cross section, acute tipped, not abruptly narrowed at base; leading shoot erect. .... 2. *Picea.*
    - C. Leaves flattened, blunt tipped, abruptly petiolate at base; leading shoot drooping. .... 3. *Tsuga.*
  - B. Twigs not roughened by leaf bases; leaf scars circular, flush with twig; ovulate cones erect at maturity, cone scales shed individually. .... 4. *Abies.*

1. **Pinus** Linnaeus, Sp. Pl. **2**: 1000. 1753; Gen. Pl. ed. 5. 434. 1754.

Evergreen trees (or less commonly shrubs). Bark deeply furrowed to thin and scaly. Wood with axial and radial resin canals and ray tracheids regularly present; axial parenchyma absent. Primary leaves spirally arranged; secondary (foliage) leaves borne in fascicles of 2, 3, or 5 [rarely to 8 or solitary] on highly condensed short-shoots subtended by a scale leaf and surrounded at base by a sheath of bud scales or their remnants; foliage leaves acicular [to linear or rarely lanceolate], entire or minutely serrulate, usually much elongated ([2–]3–50 cm); fibrovascular bundle single (subg. STROBUS) or double (subg. PINUS); resin ducts 2 to several. Pollen cones (microsporangiate strobili) cylindrical, clustered around the bases of the current year's leafy shoots, each borne in the axil of a bract; microsporophylls many per strobilus; microsporangia longitudinally dehiscent; sporophyll apex prolonged into a crest; pollen bisaccate. Ovulate cones terminal or subterminal (sometimes appearing to be lateral) on young lateral shoots, borne singly or more commonly clustered, maturing in the second year [less commonly in the third year, or after ca. 1 year in the tropics]; mature cones usually ovoid to cylindrical, radially symmetrical to oblique, sessile or short stalked, pendulous; bracts much smaller than scales at maturity; ovuliferous scales persistent, obovate to oblong, very woody (or only slightly lignified in some members of subg. STROBUS), with exposed portion (apophysis) thickened and bearing in a terminal or abaxial position the remnant of the exposed portion (umbo) from the first year's development. Seeds with a terminal wing [this sometimes short or absent]; body rounded on the sides and usually acute at base; seed coat hard and somewhat thickened, without resin vesicles. Cotyledons ca. 4–11 [2–18], denticulate or entire. Chromosome number $2n = 24$. (Including *Strobus* Opiz, *Ducampopinus* A. Chev.) LECTOTYPE SPECIES: *P. syl-*

vestris L.; see Britton, N. Am. Trees, 5. 1908. (Classical Latin name for pine.) —PINE.

Pinus, with approximately 100 species, is the largest genus of conifers and the most widespread and economically important genus of trees in the Northern Hemisphere (Critchfield & Little; Mirov, 1967). It occurs from arctic or subarctic areas of North America and Eurasia to subtropical and even tropical areas of Central America and Asia, with a few species reaching approximately 12°N latitude in the highlands of Nicaragua and Vietnam. The range of one species, *P. sylvestris* L., extends north of the Arctic Circle in Scandinavia, while that of *P. Merkusii* Jungh & De Vries crosses the equator in Sumatra. The greatest number of species (ca. 65) are native to North America, with particular concentrations in Mexico, California, and the southeastern United States. Thirty-four species are native to Eurasia, with three of these ranging into North Africa, and one (*P. canariensis* C. Smith) endemic to the Canary Islands. Several species are now widely grown in the Southern Hemisphere.

The complex history of classification within *Pinus* has been reviewed by Mirov (1967) and Little & Critchfield. Many of the currently recognized subdivisions date to the important 1838 classification of Loudon, which divided the genus into three sections based on number of needles per fascicle, and then into 15 groups corresponding to subsections. The division of the genus into two main groups based on the number of vascular bundles in the needle (one vs. two), which has been central to most recent classifications, dates to 1893, when Koehne treated these groups as sections *Haploxylon* and *Diploxylon* (= subg. STROBUS (D. Don) Lemmon and subg. PINUS, respectively).

Shaw's (1914) worldwide monograph has been the basis from which most modern classifications of the genus have been developed. He utilized characters from a diversity of plant parts—including morphology of the shoots, leaves, ovulate cones, ovuliferous scales, and seeds, and also data on wood anatomy derived from the research of I. W. Bailey (1910). Shaw's treatment is notable in emphasizing proposed evolutionary transformation series for seed and cone characters in the formulation of the classification. Some of the assignments of character polarity are open to question, and not enough attention was given to character conflict and the possibility of convergence, but many of his groups appear to be natural ones. Shaw divided the genus into sections *Haploxylon* and *Diploxylon,* under which he recognized two subsections each and thirteen "groups" designated by names and roman numerals. He later (1924) merged the related white-pine groups *Strobi* and *Flexiles* under the former name. The yellow pines (subg. PINUS) from our region, along with a diversity of species from elsewhere in North and Central America and a few from Europe, were placed in his groups *Australes* and *Insignes,* depending on the degree of serotiny and cone asymmetry.

More recent treatments, beginning with Pilger's in 1926 and including that of Little & Critchfield (1969), which is used here, have raised Shaw's infrageneric groups in rank so that his sections now correspond to subgenera, his subsections to sections, and his groups to subsections. Later classifications have diverged most from Shaw in their treatment of groups in subg. PINUS. Duffield's studies of crossability among species in Shaw's subsect. *Pinaster* (comprising the bulk of subg. PINUS) have resulted in important rearrangements reflected in Little & Critchfield's classification. Further study of the diverse Mexican pine flora has also resulted in the publication of a number of new species in both subg. PINUS (see particularly Martínez, 1948) and subg. STROBUS, where classification of the piñon pines has recently been in great flux (see Eguiluz Piedra, 1988; Zavarin, in press).

Little & Critchfield's classification recognizes three subgenera, PINUS, STROBUS, and DUCAMPOPINUS (A. Chev.) Ferré. The last includes only the unusual Vietnamese *Pinus Krempfii* Lecomte, which has two strongly flattened needles per fascicle but otherwise fits well into subg. STROBUS (see Erdtman *et al.*; Van der Burgh). Little & Critchfield rigorously applied the rules of botanical nomenclature in their choice of names and ranks and utilized information on crossability and, to some degree, chemistry and karyotype in recognizing five sections (essentially the subsections of Shaw plus a new section for *P. Krempfii*) and fifteen subsections, three of which are represented in our area. Another recent classification that strongly emphasizes characters of wood anatomy, along with more traditional morphological characters, is presented in Van der Burgh. It has been modified somewhat by Farjon. Van der Burgh did not split the genus into two main groups representing haploxylon and diploxylon pines but instead implied (see his *fig. 1*) that various groups of diploxylon pines have been derived separately from primitive haploxylon pines (see also Farjon, *fig. 1*, p. 202). He thus divided the genus into eight sections, two among the haploxylon pines and six among the diploxylon pines, and 21 subsections. Many of the sections and subsections are similar to those recognized by Little & Critchfield, but

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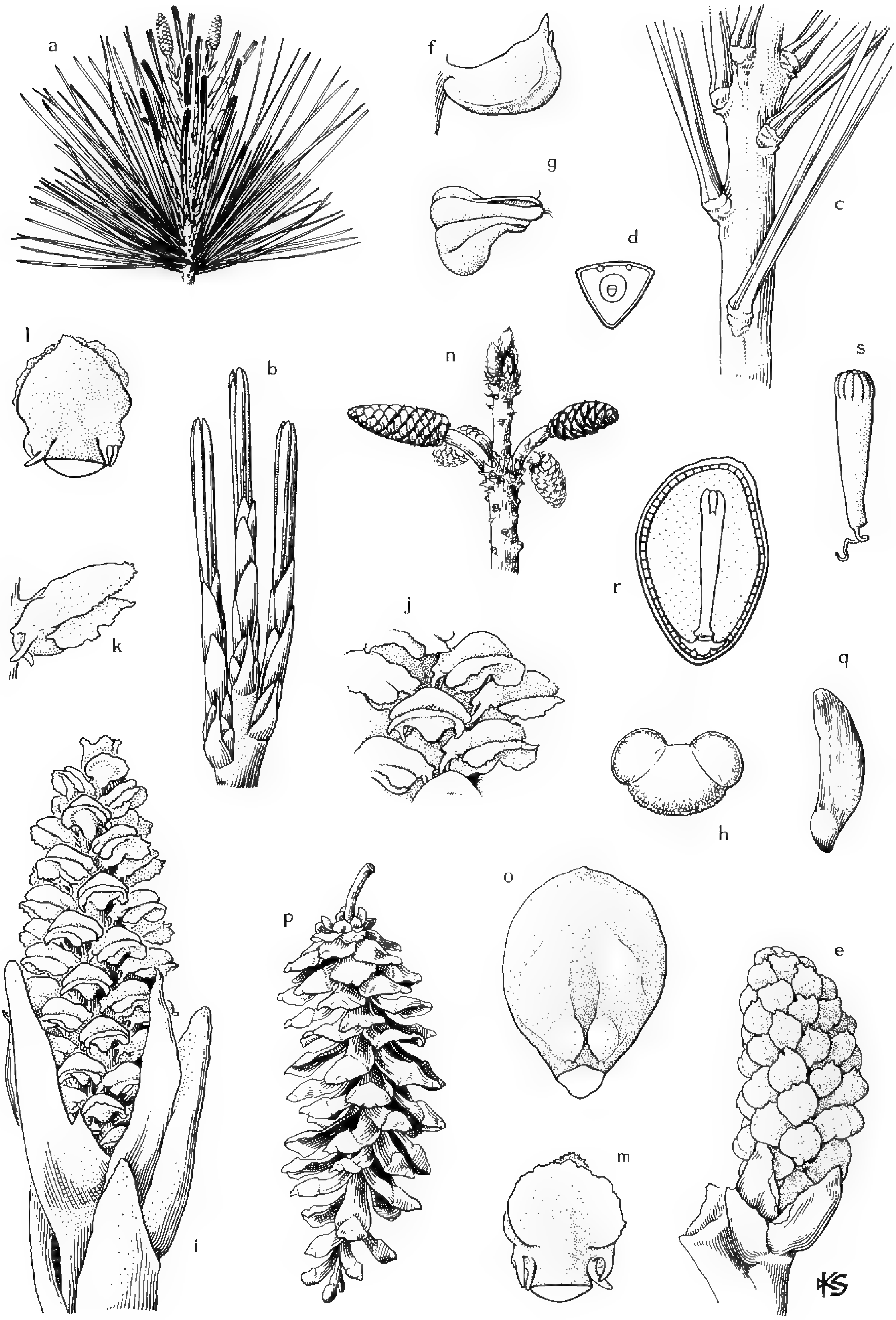
FIGURE 1. **Pinus** subg. STROBUS sect. STROBUS subsect. STROBUS. a–s, *P. Strobus*: a, tip of shoot with last season's leaves, new growth, and 2 ovulate cones at time of pollination, × ½; b, short-shoots, each showing subtending bract, scale leaves, and 5 developing needle leaves, × 2; c, detail of bases of mature short-shoots, the bracts and scale leaves having abscised, × 2; d, diagrammatic cross section of needle leaf, showing single fibrovascular bundle, endodermis enclosing transfusion tissue, and 2 resin ducts, × 15; e, microsporangiate strobilus (pollen cone) just before sporangial dehiscence, × 4; f, g, lateral and abaxial views of microsporophyll, showing the 2 abaxial sporangia and their dehiscence, × 10; h, pollen grain, showing the 2 saccae, × 250; i, ovulate cone at time of pollination, × 6; j, detail of ovulate cone, showing scales with ovules and subtending bracts, × 10; k, detail in lateral view of single cone scale and subtending bract at time of pollination, 1 ovule with 2 micropylar appendages visible, × 12; l, m, adaxial and abaxial views of cone scale and bract at time of pollination, showing micropylar appendages on the 2 ovules, × 12; n, "whorl" of 4 cones at end of first growing season, all surrounding fascicles of leaves removed, lateral and terminal buds visible, × ½; o, cone scale with 2 developing seeds at time of pollination of the next year's cones, showing remnants of the micropylar appendages and development of wings, × 3; p, mature cone, pendent on tree, seeds already shed, × ½; q, mature seed, after wing has separated from cone scale, × 1; r, longitudinal section of seed, wing removed, showing embryo surrounded by tissue of megagametophyte (stippled), micropyle facing base, × 5; s, embryo, showing suspensor and numerous cotyledons, × 6.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some—particularly in the heterogeneous sections PARRYA Mayr and PINEA Endl.—have been divided more finely. Another quite different classification that emphasizes resin-canal distribution in the needles, cotyledonary formulae (see Ferré, 1953, 1965), and pollen size is given by Gaussen.

Pinus is readily distinguished from the other genera of Pinaceae by its elongate foliage leaves borne in tight clusters of two to five [one to eight] needles on extremely reduced short-shoots, and its distally thickened, woody, often spine-tipped cone scales. As discussed under the family, *Pinus* is linked to the other pinoid genera (*Picea, Cathaya, Larix, Pseudotsuga*) by features of wood and primary root anatomy. *Pinus* shows the greatest overall similarity to *Picea* and *Cathaya,* which are the only other Pinaceae containing serratene triterpenoids. *Pinus* has the longest well-established fossil record of any of the extant genera of Pinaceae, dating back to the Lower Cretaceous. Miller (1976, 1977) has observed that early fossil cones of the Pinaceae are often similar to those of *Pinus* in form and anatomy. This led him to suggest that early evolution of the family was distinctly *Pinus*-centered. Immunological comparisons of seed proteins (Prager *et al.*; Price *et al.*), however, do not provide evidence that *Pinus* diverged before the other nine genera and instead place it within the pinoid group of genera.

The 11 species native to our region fall into two of the subgenera recognized by Little & Critchfield. Subgenus STROBUS (subg. *Haploxylon* (Koehne) Rehder) is characterized by leaves with a single fibrovascular bundle, five needles per fascicle [one to five in sect. PARRYA Mayr] with a deciduous sheath at the base [rarely persistent in sect. PARRYA], and a nondecurrent subtending bract. Members of sect. STROBUS, including the white pines (subsect. STROBUS) and the stone pines (subsect. CEMBRAE Loudon), have five needles per fascicle and cone scales with the umbo terminal and lacking an apical point or bristle.

Subsection STROBUS, which differs from subsect. CEMBRAE in having seed cones that are dehiscent at maturity and winged seeds, comprises 14 species in North and Central America and Eurasia (Little & Critchfield). Our only species, *Pinus Strobus* L. (*Strobus Strobus* (L.) Small), eastern white pine, white pine, $2n = 24$, occurs broadly in the northeastern United States and the Great Lakes states, in southern Canada from extreme southeastern Manitoba to Newfoundland, and south in the Appalachian Mountain region to northern Georgia and South Carolina (Little, 1971, *maps 73N, E*). This species, characteristic of areas with a cool, moist climate, occurs most commonly on well-drained sandy soils, although it also grows on a number of other soil types (Fowells). Huge numbers of these trees were cut for timber in the last two centuries, so few large first-growth individuals, which may reach 40–50 m in height, remain (Peattie). In our area the species occurs up to 1500 m altitude in the Appalachian Mountains of Tennessee, the Carolinas, and Georgia. Disjunct populations are also found in central North Carolina (Chatham and Lee counties; Coker & Totten) and central Tennessee (Cheatham County).

A related taxon from highland areas of southern Mexico and Guatemala has often been treated as *P. Strobus* var. *chiapensis* Martínez (see, for example, Sharp). Andresen (1964, 1966) has treated it as a distinct species, *P. chiapensis* (Martínez) Andresen, on the basis of quantitative studies indicating that the taxon is less similar to *P. Strobus* than is the western white pine (*P. monticola* Douglas ex D. Don). According to Andresen (1966), *P. chiapensis* differs quantitatively from *P. Strobus* in having longer leaves with a greater number of serrations per unit length, ovulate cones with longer stalks and more scales per cone, and qualitatively in having undulate, truncate cone-scale apices and in lacking recurved cone scales adjacent to the stalk. Chemical comparisons of these taxa will be of great interest in providing independent assessments of relationship.

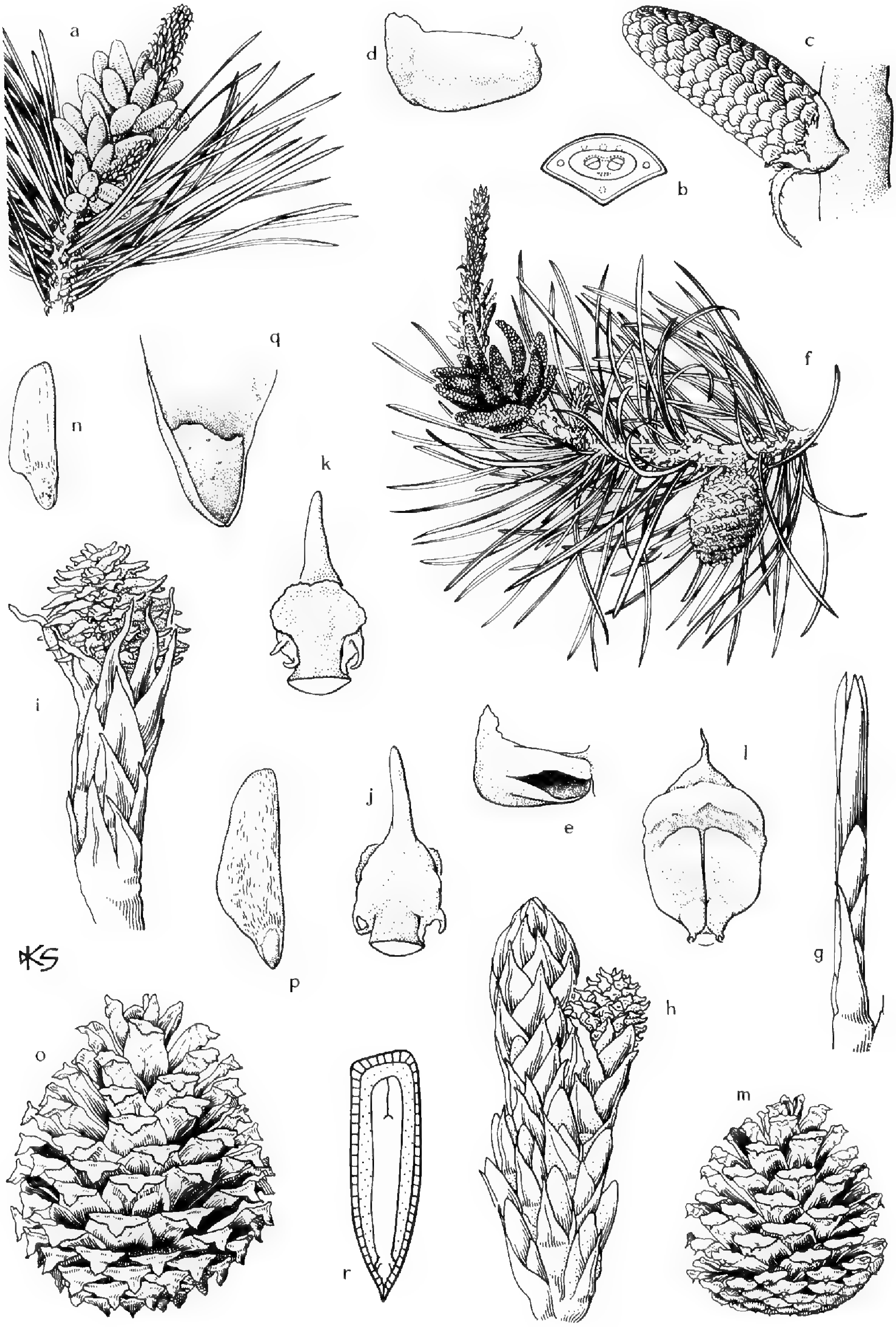
Subgenus PINUS (subg. *Diploxylon* (Koehne) Rehder, subg. *Eupitys* (Spach) Rehder) (leaves two or three [rarely four to eight] per fascicle, fibrovascular bundles two per needle, basal sheath of fascicle persistent [rarely deciduous], the subtending bract decurrent; seed cones symmetrical or oblique; cone scales with umbo abaxial, often armed with a sharp prickle) comprises at least 62 species (Little & Critchfield) distributed throughout virtually the entire range of the genus. Two subsections of sect. PINUS (seeds with a long [or rarely short] detachable wing, leaf fascicles with a persistent basal sheath) have species native to our area.

Subsection AUSTRALES Loudon (leaves two or three per fascicle, resin ducts internal or medial; seed cones symmetrical, generally opening at maturity; cone scales usually with persistent prickles) comprises 11 species in the eastern United States, the Caribbean islands, and adjacent Central America; eight of them are native to our region. *Pinus palustris* Miller (*P. australis* Michx. f.), longleaf pine, longstraw pine, Georgia pine, yellow pine, $2n = 24$, is found on well-drained sandy soils of the Atlantic and Gulf coastal plains and sometimes up to 600 m altitude on foothills of the adjacent Piedmont, from southeastern Virginia to south-central Florida and west to eastern Texas (Little, 1971, *map 65E*). The species has been heavily exploited for timber and turpentine production, and it has been estimated that by 1930 only ten percent of its original volume of timber remained (Snyder *et al.*). Young trees of *P. palustris* are highly fire tolerant, so the species is often found in pure stands on burned areas.

Pinus palustris is a large tree (to ca. 30 m) with the longest leaves (ca. 25–45 cm) and largest cones (ca. 15–25 cm long) of any pine in the eastern United States. Leaves are three per fascicle, and cones are nonserotinous and have small prickles on the cone scales. The winter buds are distinctively large and whitened. This is one of very few pine species in which the seedlings go through an unusual "grasslike" stage. The stem thickens but elongates very little during the first few years, and the densely overlapping needles protect the growing point (see discussion in Mirov, 1967). This form of seedling development is restricted to a few subtropical or tropical pines and conveys substantial fire resistance.

Natural hybrids between *Pinus palustris* and *P. Taeda* (*P.* ×*Sondereggeri* Chapman) occur with some regularity when the species grow in mixed populations (Snyder *et al.*), but the two species nevertheless remain quite distinct overall. Hybrids of *P. palustris* and *P. Elliottii* var. *Elliottii* occur less frequently in southern Georgia and northern Florida (Mergen, 1958a; Snyder *et al.*).

Pinus Taeda L., loblolly pine, oldfield pine, North Carolina pine, $2n = 24$, is found on the Coastal Plain and Piedmont from southern New Jersey south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to central Florida and west to southern Arkansas, eastern Texas, and extreme southeastern Oklahoma (Little, 1971, *map 75E*). It is a common tree in South Carolina, Georgia, Alabama, and eastern Mississippi, and north to southern Tennessee. It grows in both poorly drained clay (the name "loblolly" means mud puddle; Little, 1980) and well-drained sandy soil. It rapidly invades abandoned fields on the Coastal Plain, but to a much lesser degree in the Piedmont, where *P. echinata* is the characteristic oldfield pine (Fowells; Little, 1980). Loblolly pine increases in size very rapidly and is the most widely utilized commercial pine in the southeastern United States, being very widely grown in plantations.

Loblolly pine is a large tree (up to 45 m) with stout but relatively flexible needles ca. 15–25 cm long, usually three per fascicle, and cones ca. (5–)7–13 cm long, with short, stout prickles. It differs from the related *Pinus rigida* Miller and *P. serotina* Michx. in having larger, more readily deciduous cones with larger prickles (ca. 2–3 mm long) and wider cone scales (ca. 12–15 vs. 6–10 mm), and nonresinous winter buds (Little *et al.*). In addition to the hybrids with *P. palustris* noted above, *P. Taeda* forms natural hybrids with *P. rigida, P. serotina,* and *P. echinata* (Dorman & Zobel; Little *et al.*; Smouse & Saylor, 1973b), but the species remains relatively distinct even in areas of narrow sympatry.

Pinus echinata Miller, shortleaf pine, yellow pine, $2n = 24$, is the most widely distributed of the southern yellow pines, occurring from New Jersey and extreme southeastern New York south to northern Florida and west to eastern

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FIGURE 2. **Pinus** subg. PINUS sect. PINUS subsect. AUSTRALES. a–n, *P. rigida*: a, tip of shoot with last season's leaves, microsporangiate strobili (pollen cones) before shedding of pollen, and new vegetative lateral and terminal shoots, the fascicles just beginning to expand, the subtending bracts evident, × ½; b, diagrammatic cross section of needle leaf, showing the 2 fibrovascular bundles, nearby sclerenchyma (dotted), and 6 resin canals outside the endodermis, × 15; c, single microsporangiate strobilus and subtending bract before sporangial dehiscence, × 2; d, e, ¾ view of abaxial side of microsporophyll, showing 2 microsporangia, before and after dehiscence, × 10; f, shoot tip after shedding of pollen, showing persistent fascicles, cone of preceding season, new lateral and terminal growth (fascicles only beginning to expand), and microsporangiate strobili just after shedding of pollen, × ½; g, expanding fascicle of 3 foliage leaves with scale leaves and subtending bract (decurrent on stem) below, × 2; h, tip of shoot with terminal bud, lateral shoot with terminal cone (just before pollination), and new fascicles of leaves just beginning to expand, × 2; i, ovulate cone (terminating lateral shoot) at time of pollination, × 3; j, k, adaxial and abaxial views of cone scale with 2 ovules (each with 2 micropylar appendages) and subtending bract at time of pollination, × 12; l, cone scale with 2 developing seeds (from second year's cone in "f") at time of pollination of new cones, showing shriveled micropylar appendages and evident wing of seed, × 3; m, mature cone with seeds shed, × ½; n, seed with wing (abaxial view), × 1. o–r, *P. pungens*: o, mature cone with seeds shed, × ½; p, seed with wing (adaxial view), × 1; q, detail of seed and base of wing (abaxial view), × 3; r, diagrammatic longitudinal section of seed, the seed coat hatched, megagametophyte stippled, embryo (showing 2 cotyledons) unshaded, × 6.

Texas, eastern Oklahoma, Arkansas, and southern Missouri (Little, 1971, *map 52E*). It grows at moderate elevations (to ca. 1000 m) in the Appalachian Mountains and commonly invades abandoned fields on the Piedmont. It is less common on the Coastal Plain (Coker & Totten). The species can grow on many kinds of soils but is best developed on fine sandy loam with good drainage (Fowells). Young plants are capable of surviving repeated fires by sprouting from the root collar (Fowells; Mattoon).

Pinus echinata is a large tree (ca. 20–30 m) with two or occasionally three slender, flexible needles ca. 7–13 cm long per fascicle, small (ca. 4–6 cm), conical or narrowly ovoid cones that open at maturity but are long persistent, and cone scales with a small, slender prickle.

Pinus glabra Walter, spruce pine, cedar pine, Walter's pine, $2n = 24$, one of the least common of the southern yellow pines, grows in moist lowland areas of the Coastal Plain from eastern South Carolina south to northern Florida and west to southern Alabama and eastern Louisiana, particularly along river courses (Little, 1971, *map 58E*). It is a large tree (to ca. 30 or more m high) with relatively slender and short needles (ca. 4–10 cm long) in fascicles of two, and small, conical to narrowly ovoid cones (ca. 3–6 cm long) with small, easily shed, slender scale prickles. The characteristic bark is smooth and grayish, in contrast to that of the related *P. echinata,* which is irregularly flaking and reddish brown.

Pinus serotina Michx. f. (*P. rigida* Miller var. *serotina* (Michx. f.) Loudon, *P. rigida* subsp. *serotina* (Michx. f.) R. T. Clausen), pond pine, marsh pine, pocosin pine, $2n = 24$, occurs in somewhat surprising habitats for a pine—sandy swamps and shallow ponds—along the Coastal Plain from southern New Jersey and Delaware south to central and northwestern Florida, often forming nearly pure stands (Little, 1971, *map 74E*). It is a medium-sized tree (generally 10–20 m high) with flexible needles ca. 15–20 cm long and usually three per fascicle. It is characterized by short (ca. 4–6 cm), rounded to ovoid cones that remain unopened on the tree for several years and cone scales that have only a weak prickle. It intergrades morphologically with the closely related *P. rigida,* from which it differs modally in ecology.

Pinus rigida Miller, pitch pine, $2n = 24$, is a small to medium-sized tree that occurs from southern Maine and extreme southern Quebec and Ontario through New England and the mid-Atlantic states and south, mostly in the Appalachian Mountains, to northern Georgia and South Carolina. It is tolerant of dry, rocky soils but also occurs on sands and sometimes in swampy soils. The needles are usually three per fascicle, stout, and ca. 7–13 cm long; the cones are ovoid, 3–7 cm long, long persistent, occasionally serotinous, and generally with sharp, slender prickles. Pitch pine is highly resistant to fire and other forms of injury and sprouts from roots and stumps after damage, becoming very irregular in form (Ledig & Fryer, 1974; Little, 1980). Dwarfed plants of the species are characteristic of parts of the Pine Barrens of New Jersey, where the high incidence of fire may have selected for cone serotiny, a feature otherwise not typical of the species (Givnish; Ledig & Fryer, 1972).

A number of authors have discussed the geographic variation of *Pinus rigida* in relation to that of *P. serotina,* with which it intergrades in New Jersey, Delaware, and Maryland (Clausen; Ledig & Fryer, 1974; Smouse & Saylor, 1973a, b). The two are largely allopatric and differ modally in ecology and morphology but show clinal variation in a number of characters. Smouse & Saylor (1973a, b) found pond and pitch pines to group much more closely in multivariate analyses than loblolly and shortleaf pines did (all of these taxa being subject to natural hybridization) and suggested that *P. serotina* should be treated as a subspecies of *P. rigida.* Other recent authors (Ledig & Fryer, 1974; Little, 1980) have continued to treat them at the level of species.

Pinus pungens Lamb., Table Mountain pine, prickly pine, hickory pine, $2n = 24$, is a small to medium-sized tree of the Appalachian area from southeastern Pennsylvania south to extreme northeastern Georgia and eastern Tennessee, and also locally in New Jersey, Delaware, and the District of Columbia (Little, 1971, *map 66E*). In our area the species occurs on dry, rocky slopes and ridges of the Appalachians up to ca. 1200 m altitude. The species has two stiff, usually twisted needles per fascicle and ovoid, long-persistent cones that differ from those of the other eastern pines in their very stout, incurved prickles. The cones are at least sometimes serotinous (C. E. Wood, pers. comm.). *Pinus pungens* is named "hickory pine" because of its tough, hickorylike branches.

Pinus Elliottii Engelm. (*P. caribaea* sensu Small, non Morelet; *P. palustris* sensu Small, non Miller; *P. heterophylla* (Ell.) Sudw., 1893, non K. Koch, 1849), slash pine, swamp pine, $2n = 24$, occurs along the Coastal Plain from central South Carolina to southern Florida and west to southern Mississippi and eastern Louisiana. It is also naturalized in eastern Texas. Little & Dorman (1952b, 1954) distinguished two geographic varieties: var. *densa* Little & Dorman, of central and southern Florida, differs from var. *Elliottii* in having a grasslike seedling stage and a lower average number of needles per fascicle. Rangewide geographic variation in morphological and physiological traits was thoroughly examined by Squillace (1966), who used both field and common orchard studies. There are significant differences between the varieties in the means of several characters, but the patterns of variation are largely continuous within and between them, and there is no increase in variability in the area of transition in central Florida. Variety *Elliottii* was originally largely confined to ponds, pond margins, and other poorly drained habitats (Fowells), but it has become more widespread in its range because natural fires have been suppressed. South Florida slash pine (var. *densa*) occurs in dryish flatwoods and on thin soil over limestone (Hardin; Squillace, 1966). Because of its thicker stems and better protected growing points in young plants, it shows a greater degree of fire tolerance than does var. *Elliottii* (Squillace, 1966).

Pinus Elliottii is a medium-sized to large tree (to 30 m or more) with stout, stiff needles ca. 15–30 cm long, both two and three per fascicle, and narrowly ovoid cones ca. 6–15(–18) cm long with relatively short prickles. It is closely related to *P. caribaea* Morelet, of the Caribbean Islands and Central America, under which it was formerly treated, but differs in having longer (1–2 vs. < 1 mm) cone-scale prickles, broader seeds with more readily detachable wings, and needles in fascicles of two and three, rather than consistently three or more (Little & Dorman, 1954). *Pinus Elliottii* can be crossed artificially with several species including *P. caribaea* in subsect. AUSTRALES, and also with *P. clausa* in subsect. CONTORTAE (Critchfield, 1963; Saylor & Koenig), but under natural conditions it hybridizes only occasionally with *P. palustris* (Mergen, 1958a).

Subsection CONTORTAE Little & Critchfield (leaves two per fascicle, short (2–8 cm), often twisted, with mostly medial resin ducts; seed cones small (3–8 cm long), symmetrical [or oblique], often serotinous, long persistent; cone scales with [or without] a persistent prickle) is quite similar in morphology to subsect. AUSTRALES, and the two subsections may be more appropriately combined once their evolutionary relationships are better understood. Subsection CONTORTAE comprises four species native to the United States and Canada, of which two, *P. clausa* (Engelm.) Vasey ex Sarg. and *P. virginiana* Miller, are native in our region. A third species, *P. Banksiana* Lamb., jack pine, which now has a native range north of our region in Canada and the Great Lakes states, occurred in parts of the southeastern United States during the Late Pleistocene (Watts, 1970, 1980).

Pinus clausa, sand pine, scrub pine, spruce pine, $2n = 24$, occurs on well-drained sandy soils from extreme southwestern Alabama east through the panhandle of northwestern Florida, as well as in scattered localities through much of peninsular Florida, except in the extreme south (Little, 1971; Ward, 1963). It often forms dense pure stands and is the dominant tree in some 200,000 acres in Marion Co., Florida (Ward, 1963). Two geographic races have been defined: the Ocala race (var. *clausa*), with serotinous cones, including almost all of the peninsular populations, and the Choctawhatchee race (var. *immuginata* Ward), with cones opening at maturity, encompassing most of the northwestern populations (Little & Dorman, 1952a; Ward, 1963; Wheeler *et al.*). The two cone morphs occur intermixed in several areas of northwestern Florida (Ward, 1963), and no other obvious morphological differences are present, so formal designation as varieties seems unwarranted.

The closely related *Pinus virginiana* Miller, Virginia pine, scrub pine, poverty pine, Jersey pine, $2n = 24$, geographically separated by over 100 km from *P. clausa,* occupies a broad area from Long Island and New Jersey west to Ohio and southern Indiana and south to northern South Carolina and Georgia, central and northern Alabama, and northeastern Mississippi (Little, 1971, *map 77E*). In our region it is found primarily in the Piedmont and at moderate elevations (usually below 1000 m) in the Appalachians. It occurs very occasionally on the Coastal Plain in the Carolinas and Georgia (Coker & Totten). Tending to grow on dry, shallow soils, including clay, loam, or (less commonly) sandy soils near the coast, it often invades old fields on the Piedmont as a pioneer species (Kellison & Zobel). It is a medium-sized tree with relatively short (ca. 4–8 mm), stout needles and narrowly ovate, persistent but nonserotinous cones. It differs from *P. clausa* primarily in having longer (ca. 5 mm), more slender cone-scale prickles, and stouter, more often twisted needles (Coker & Totten; Little, 1980), as well as in its edaphic tolerances.

Pinus virginiana is very similar in isozyme profiles to *P. clausa* (Wheeler *et al.*), with which it is readily crossable (Critchfield, 1963; Kellison & Zobel). Both show strong cross-incompatibility with the two remaining species of subsect. CONTORTAE (*P. contorta* Douglas ex Loudon and *P. Banksiana*). The electrophoretic evidence is consistent with the hypothesis that *P. virginiana* is a relatively recent derivative of an ancestor similar to *P. clausa,* and Wheeler *et al.* have suggested that the two taxa be treated as ecogeographic subspecies. Preliminary data on turpentine composition (Mirov, 1961) indicating differences in terpenoid profiles between these species need further confirmation.

Chromosome numbers have been reported for approximately 90 species of *Pinus*; with the exception of occasional aberrant individuals, all have $2n = 24$ (see particularly Khoshoo, 1961; Santamour, 1960; Sax & Sax; Saylor, 1964, 1972, 1983; Styles & Khosla). Karyotypes have been reported for 87 species in the systematic surveys of Saylor (1964, 1972, 1983), and chromosome constriction patterns have been examined in detail by Pederick for a much smaller sample of species. The smallest chromosome is definitely heterobrachial (with a submedian centromere) in *Pinus,* while the other 11 are approximately isobrachial, except in subsect. PINUS (subsect. *Sylvestres* of Saylor, 1972), in which the second smallest chromosome is also somewhat heterobrachial. Patterns of arm lengths and arm-length ratios are reasonably concordant with the Little & Critchfield classification of subg. PINUS and lend some support to the separation of the southern yellow pines into subsects. AUSTRALES and CONTORTAE. Patterns are more variable within some subsections in subg. STROBUS, particularly among the white and stone pines of sect. STROBUS.

As noted in the species discussions above, natural hybridization occurs between a number of species of pines within the subsections recognized by Little & Critchfield. In many cases, however, interspecific hybridization is greatly restricted or prevented by a combination of phenological and physiological barriers (see discussions in Critchfield, 1963, and Mirov, 1967). Natural hybrids between species in closely related subsections occur only infrequently (Mirov, 1967)—for example, between *Pinus Coulteri* D. Don and *P. Jeffreyi* Grev. & Balf. (Zobel). Zones of hybridization between certain species—for example, *P. Banksiana* and *P. contorta* in western Canada (Dancik & Yeh; Mirov, 1956b; Moss; Wagner *et al.*; Zavarin *et al.,* 1969)—have been studied intensively through a number of biochemical techniques, as well as morphological comparisons.

Thorough investigations (see particularly Critchfield, 1963, 1966, 1967, 1977, 1986; Duffield) of artificial crossability among pine species have had a major impact on the systematics of the genus. These results have been particularly important in evaluating relationships among the diploxylon pines (see Critchfield, 1963; Duffield; Little & Critchfield) and have led to the treatment of the southern yellow pines under subsections AUSTRALES and CONTORTAE, rather than intermixed with the western North American closed-cone pines of subsect. OöCARPAE Little & Critchfield as in the classifications of Shaw (1914) and Pilger (1926). The species in subsect. AUSTRALES are all linked directly or indirectly by successful crosses (Critchfield, 1963), although some individual combinations (e.g., *P. palustris* × *P. echinata*) seem to be highly cross-incompatible. Crossability within a number of other subsections (e.g., among the pines in sect. STROBUS; Critchfield, 1986) is much more restricted and may sometimes show unpredictable geographic patterns. No successful crosses between species representing different subgenera have ever been made.

Pinus is notable for the great diversity in the size of its cones and the form of its cone scales (Sargent, 1897; Shaw, 1914). The morphological complexity of the cone-scale apex relates directly to the multi-year development of the ovulate cone, with the areas left exposed in the first-year conelet (the umbo) and in the mature cone (the apophysis) both being evident. The extremely stout prickles seen in several species of subg. PINUS (e.g., *P. pungens* and *P. Sabiniana* Douglas ex D. Don) presumably act as a deterrent to seed predation (McCune).

Klaus (1980), who has surveyed cone-scale form and ornamentation in relation to the systematics of *Pinus,* emphasized the central position of sect. PARRYA in the evolution of the genus. This section of subg. STROBUS (which includes the lacebark, bristlecone, and piñon pines) has an abaxial ("dorsal") umbo, often with an apical point or bristle, and thus provides a morphological link with subg. PINUS, which invariably has an abaxial umbo. The same pattern of relationship is seen in wood anatomy (Hudson; Van der Burgh). The amount of toothing on the walls of the ray tracheids is greater in subg. PINUS than in sect. STROBUS, while the species of sect. PARRYA span most of the range in denticulation of the genus. Other types of characters separate the haploxylon (subg. STROBUS) and diploxylon (subg. PINUS) pines more sharply. Pollen grains of species in subg. STROBUS have a strongly ornamented germinal zone, while those of species in subg. PINUS have a relatively smooth one (Sivak). The profiles of heartwood phenolic compounds (H. Erdtman, 1959; Norin), discussed below, also separate the haploxylon pines (including *P. Krempfii*) from the diploxylon ones.

Pinus shows great diversity in seed size and in the degree of seed winging. Loss of a seed wing in the stone pines (subsect. CEMBRAE) and the piñon pines (subsect. CEMBROIDES) is part of a morphological syndrome related to seed dispersal by corvid birds, especially jays and nutcrackers, or to a lesser degree by rodents (Lanner, 1982; McCune).

Cone serotiny occurs in a number of North American species in subg. PINUS (particularly in subsects. CONTORTAE and OÖCARPAE, but also in a few species of subsects. AUSTRALES and SABINIANAE Loudon (McCune; Mirov, 1967)). Many such species are polymorphic for serotiny, so some seed dispersal can occur in the absence of major fires (McCune). A simple genetic basis for polymorphism in this character has been demonstrated in some species (Sittmann & Tyson). Many of the serotinous species have asymmetric cones, a character that may have been overemphasized in Shaw's (1914) classification, given its potential for convergence.

Mirov (1958, 1961) did a preliminary survey of turpentine composition for the majority of species of *Pinus.* Most species have a steam-distillable oleoresin fraction composed predominantly of various monoterpenoids, but in some it is made up almost entirely of hydrocarbons such as n-heptane. Turpentine composition does not separate major groups such as subgenera but is often valuable in the determination of interspecific hybrids, since closely related species (e.g., *P. Banksiana* and *P. contorta* in subsect. CONTORTAE) may differ considerably in their profiles. Leaf-oil composition is reviewed for a number of North American species by Von Rudloff, and wood or leaf oleoresins have been studied for a number of groups in subg. STROBUS by Zavarin and coworkers (see, for example, Zavarin *et al.* (1982) on subsect. BALFOURIANAE, and Zavarin (in press) and Zavarin & Snajberk (1980, 1987) on subsect. CEMBROIDES).

The composition of heartwood phenolics has been surveyed for over 80 species of *Pinus* and has proved to be very useful in distinguishing the haploxylon and diploxylon pines (H. Erdtman, 1959, 1963; Norin). Members of subg. PINUS have a characteristic, relatively simple pattern that includes the stilbene compound pinosylvin and its methyl ethers and the flavanone derivatives pinocembrin and pinobanksin. The members of subg. STROBUS also have these compounds, as well as dihydropinosylvin and various flavone derivatives. Some groups within subg. STROBUS also contain C-methylated flavonoids. It is postulated that the enzymatic capabilities needed to produce these additional groups of compounds have been lost in the common ancestor(s) of subg. PINUS (H. Erdtman, 1959; Norin). *Pinus Krempfii,* although treated as a separate subgenus by Little & Critchfield, has a pattern of compounds characteristic of subg. STROBUS (Erdtman *et al.*).

Results of allozyme or isozyme electrophoresis have been used in systematic or evolutionary studies in several species groups of *Pinus* (e.g., Conkle *et al.* on the *P. brutia–P. halepensis* complex; Millar *et al.* on the California members of subsect. OÖCARPAE; Steinhoff *et al.* on *P. monticola*; Wheeler *et al.* on subsect. CONTORTAE), and a number of similar studies are now in progress. Levels of within-population variation for electrophoretic alleles are generally high in pines and other long-lived, wind-pollinated trees (Hamrick *et al.*), but they are extremely low in some species—for example, *P. resinosa* Aiton (Fowler & Morris) and *P. Torreyana* Parry (Ledig & Conkle).

Pines are of exceptional economic importance for their timber, which is used for construction, pulpwood, and numerous other purposes. Among the eastern North American species, *Pinus Elliottii, P. palustris,* and *P. Strobus* yield particularly high quality lumber for construction, although *P. Taeda* is now more widely available. The rapid-growing *Pinus radiata* D. Don (a narrow endemic in coastal California and nearby islands) is now one of the most widely cultivated timber trees in the Southern Hemisphere. Several species (e.g., *P. echinata, P. Elliottii,* and *P. palustris* in our area) are tapped for stem oleoresin, from which commercial turpentine, tar oils, rosin, and pitch are obtained by distillation (Dallimore & Jackson; Mirov, 1961, 1967). Pine-leaf oil, utilized medicinally, is also obtained from various species by distillation. Highly esteemed edible seeds (pine nuts) are obtained from large-seeded species (e.g., *P. Pinea* L., umbrella pine; *P. edulis* Engelm., piñon; and *P. Gerardiana* Wallich) in Mediterranean Europe, North America, and Asia. Many species are of horticultural importance, and several are prized for bonsai.

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2. **Picea** A. Dietrich, Fl. Gegend Berlin, 794. 1824.

Pyramidal evergreen trees (or shrubs under harsh conditions) with slender, more or less whorled branches. Branchlets pubescent with simple trichomes or glabrous, roughened by persistent leaf bases. Bark thin and scaly or sometimes furrowed. Wood with axial and radial resin canals and ray tracheids regularly present; axial parenchyma absent. Leaves spirally arranged, linear, 4-sided and then stomatiferous on all sides [or dorsiventrally flattened and stomatiferous on the lower—but morphologically adaxial—surface], acute to acuminate, often sharply pointed [or sometimes obtuse or emarginate]; fibrovascular bundle apparently single [or often double]; resin canals 2 [rarely 1], laterally placed; leaf bases persistent, ultimately woody. Pollen cones (microsporangiate strobili) subsessile [or stalked], borne singly in axils of leaves of previous year; microsporophylls many per strobilus, each with apex prolonged into a broad, nearly circular crest; microsporangia longitudinally dehiscent; pollen bisaccate. Ovulate cones borne at tips of previous year's growth, maturing in 1 year, before pollination erect on short stalks; mature cones ovoid to cylindrical, 2–7[–15] cm long, sessile or short stalked, pendulous; bracts much smaller than scales at maturity; ovuliferous scales persistent, obovate to oblong, with apex rounded [to rhombic], entire to denticulate [erose]. Seeds with thin terminal wing; body rounded on the sides and usually acute at base; seed coat without resin vesicles. Cotyledons ca. 6 [4–15], denticulate or entire. Chromosome number $2n = 24$. TYPE SPECIES: *Picea rubra* A. Dietr., *nom. illeg.*, = *P. Abies* (L.) Karst.; see Britton, N. Am. Trees, 54. 1908. (Classical Latin name for a conifer, from *pix,* pitch.)—SPRUCE.

A well-defined genus of approximately 35 species, *Picea* occurs widely in the boreal and temperate areas of the Northern Hemisphere, from the arctic of North America and Eurasia south to the higher mountains of Mexico and southern China. The greatest number of species (ca. 24) occurs in eastern and central Asia, where the taxonomic situation is particularly complex (see Cheng & Fu; Rehder, 1940; Schmidt-Vogt, 1977; Wright). Seven species are native to the United States and Canada; three of these occur in the eastern part, with only one, *P. rubens* Sarg., ranging south into our region.

Sections within *Picea* are not easily distinguished on the basis of overall morphology, chemistry, or crossability. Willkomm divided the genus into two sections, *Eupicea* Willk. (= sect. PICEA) and OMORIKA Willk., based on the cross-sectional form and stomatal arrangement of the needles. Mayr divided the genus into three sections, *Morinda* (= sect. PICEA), CASICTA, and OMORIKA, on the basis of cone-scale shape and texture, in addition to the needle characters noted above. A number of later authors (Bobrov, 1970; Dallimore & Jackson; Gaussen, 1966; Krüssmann; Rehder, 1940) have used this three-section classification, but there has been considerable disagreement over the placement of several species (see comparisons in Schmidt-Vogt, 1977). Wright, in a worldwide treatment utilizing both crossability data and comparisons of overall morphological similarity, found no clear-cut groups among the species. Thus neither his treatment nor the more recent monograph by Schmidt-Vogt (1977) divided the genus into sections. Preliminary comparisons of monoterpene profiles (Schantz & Juvonen; Von Rudloff, 1975), leaf phenolics (Wellendorf & Kaufmann), and electrophoretic alleles (Wellendorf & Simonsen), as well as further crossability data (Fowler; Mikkola, 1969, 1972), also did not yield groups concordant with the earlier morphological sections. Smaller groups of morphologically similar species recognized as series by Bobrov (1970) seem to be of greater utility.

Our only species, *Picea rubens* (*P. australis* Small; *P. rubra* (Du Roi) Link, non *P. rubra* A. Dietr.), red spruce, yellow spruce, he-balsam, $2n = 24$, a prominent forest tree of the cooler parts of northeastern United States and adjacent Canada, occurs from eastern Ontario east to Nova Scotia, south to Pennsylvania, northern New Jersey, and Delaware, and locally south in the Appalachians to the higher mountains of eastern Tennessee and western North Carolina (Little, 1971, *maps 41N, E*). The species occurs most commonly on well-drained, rocky slopes, as compared to the closely related black spruce (*P. mariana* (Miller) BSP.), which is generally found on wet, boggy soils where it overlaps the range of the red spruce in the northeastern United States and southeastern Canada (Gordon, 1976; Manley & Ledig).

Red spruce differs from black spruce in having lustrous dark or bright green (rather than glaucous) leaves and ovoid-cylindrical, reddish brown, ovulate cones that are usually deciduous at maturity (vs. ovoid, dull gray ones that persist for several years). Both red and black spruce have sharply pointed four-sided leaves and pubescent branchlets, and both are unusual in the genus in having terminal buds with awl-shaped points on their outer scales. Monoterpene profiles are also very similar for the two species (Von Rudloff, 1967a, b; Wilkinson & Hanover). Reports of *P. mariana* in the southern Appalachians (e.g., by Small) are erroneous and based on material of *P. rubens*.

Hybridization between red and black spruces is well documented (Gordon, 1976; Manley; Morgenstern & Farrar) in areas where the two come in contact in southern Canada, but the prevalence of intermediate plants is apparently limited by the habitat differences between the species, relatively low crossability between them (Gordon, 1976), and natural selection against hybrids and hybrid derivatives. Manley & Ledig reported a lack of heterosis and found that photosynthetic rates of hybrids and backcrosses were significantly lower than those of the parental species under all environmental regimes examined. Khalil, however, did find heterosis in hybrids from the lowlands of New Brunswick. The significant geographic variation in morphological and physiological characters within *Picea rubens* found in Khalil's long-term provenance studies appears to reflect selection along latitudinal and altitudinal gradients, as well as effects of hybridization and backcrossing.

During late Pleistocene times additional species of *Picea* occurred in the southeastern United States (Watts). Large cones (up to 10 cm long) that appear to represent an undescribed species similar to *P. glauca* (Moench) Voss, white spruce, have been found as fossils at sites in Louisiana, Tennessee, and Georgia (Critchfield; Delcourt & Delcourt).

Picea comprises a natural group, as is indicated by the overall similarity and crossability among its species (Wright), and is appropriately treated as a distinct genus. It differs from the other pinoid genera primarily in lacking their unusual derived features, as detailed in the family treatment. It also differs from each of these genera in having leaves that are squarish in cross section and with prominent, persistent bases. As noted in the family treatment, *Picea, Cathaya,* and *Pinus* are apparently the only genera in the Pinaceae that produce the unusual serratene triterpenoids (He *et al.*; Hegnauer, 1986). *Pinus* and *Picea* are quite similar in the details of their pollination mechanisms. *Picea* differs from *Pinus* and *Cathaya* in lacking cleavage polyembryony (Doyle & Brennan) and in having a more asymmetric karyotype.

Chromosome numbers have been reported for 22 of the 36 species of *Picea* recognized by Schmidt-Vogt (see particularly Kuo *et al.*; Santamour, 1960; Sax & Sax; Seitz), with all species having $2n = 24$. Aneuploid and polyploid seedlings have been found at very low frequency in nursery plantings of *P. Abies* (Kiellander), but these presumably would not survive in nature. Supernumerary (B) chromosomes have been reported from some populations of *P. sitchensis* (Bong.) Carr., *P. glauca,* and *P. obovata* Ledeb. (*P. Abies* var. *obovata* (Ledeb.) Fellm.) but are lacking in others (Herzog; Moir & Fox; Pravdin *et al.*). Increase in nuclear-DNA content with latitude has been reported for *P. glauca* and *P. sitchensis* by Miksche (1968, 1971), but this has not been confirmed in wider sampling by Teoh & Rees.

Intergradation or more limited hybridization among species is an important factor in the taxonomic complexity seen in *Picea.* Wright proposed that a number of Asian taxa of uncertain status were the variable products of interspecific hybridization. Among the North American species, *P. glauca* and *P. Engelmannii* Parry show an extensive zone of intergradation in western Canada and Montana (Daubenmire; La Roi & Dugle; Ogilvie & Von Rudloff; Roche), leading some authors (e.g., T. M. C. Taylor, 1959) to treat these taxa as ecogeographic subspecies. Relatively frequent hybridization in regions of sympatry is also seen between the more obviously distinct species *P. sitchensis* and *P. glauca* (Daubenmire; Nienstadt & Teich; Roche), as well as *P. rubens* and *P. mariana,* discussed above. In contrast, the widely sympatric *P. glauca* and *P. mariana* only rarely hybridize (Little & Pauley) and are very difficult to cross artificially (Fowler). The closely related *P. Engelmannii* and *P. pungens* Engelm. may hybridize to a limited degree in areas of sympatry in the southern Rocky Mountains, but no evidence for this was seen in the electrophoretic study of Mitton & Andalora.

Extensive programs of artificial interspecific crossing have been undertaken in *Picea* (Bongarten & Hanover; Fowler; Gordon, 1976; Mikkola, 1969, 1972; Wright), resulting in a substantial number of verified hybrid combinations, including several involving species from different continents. The infrageneric groupings proposed by Mikkola (1969) and Fowler on the basis of crossability agree poorly with those based on leaf anatomy. For example, *P. mariana* and *P. rubens* are more readily crossable with the morphologically dissimilar *P. omorika* (Pančić) Purkyne than they are with one another (Gordon, 1976), perhaps because of selection against hybridization in the two partially sympatric species (Fowler). Prezygotic barriers to hybridization (e.g., failure of the pollen tube to penetrate the nucellus) and early postzygotic barriers have been detailed for a number of interspecific combinations by Mikkola (1969).

Detailed expositions of the comparative leaf anatomy of *Picea* are given by Marco and Colleau. Species assigned to sect. OMORIKA have needles dorsiventrally flattened to varying degrees and are unusual in generally having stomata only on the adaxial leaf surface, which faces downward due to twisting of the leaf base. *Picea sitchensis,* however, often has stomata on all four sides of the leaf (Marco). Colleau attempted to limit sect. OMORIKA to those species with a foliar stomatal density greater than 80 per mm^2, but it is unclear that this yields a more natural group. Resin canals in species of sect. OMORIKA are near the abaxial leaf surface, while those in the other species are usually adjacent to the lateral angles of the leaf. The leaf mesophyll is differentiated into palisade and mesophyll cells in some species with flattened needles and in some with quadrangular ones (Marco). Another interesting feature of the leaves is the variation in color from bluish to greenish in some species—for example, *P. pungens* (Colorado blue spruce)—due to differences in the amount and structure of the surface wax (Hanover & Reicosky).

Leaf-terpenoid patterns in *Picea* have been critically reviewed by Von Rudloff (1975), following the earlier treatment of Schantz & Juvonen. Von Rudloff found relatively minor differences between some of the species assignable to sects. OMORIKA (*P. omorika* and *P. Breweriana* S. Watson) and PICEA (*P. rubens* and *P. mariana*), but greater ones among other species assignable to the latter section or to sect. CASICTA. Schantz & Juvonen also found differences in leaf- and stem-terpenoid composition to be greater within than among the sections of *Picea.* The degree of geographic or intrapopulational variation in leaf-terpene composition is quite limited in some species (e.g., *P. mariana* and *P. rubens*; Von Rudloff, 1975) but quite variable in others (such as *P. Engelmannii*).

Leaf-stilbene spot patterns and their intensities were surveyed for 23 species of *Picea* by Wellendorf & Kaufmann, who found no clear-cut subgroups within the genus. It has been alleged that sect. OMORIKA is distinct in its leaf-stilbene profile, but this has not been substantiated (Hegnauer, 1962, 1986). Overall leaf-phenolic profiles have proved useful in differentiating *Picea* species in the western United States and Mexico (La Roi & Dugle; R. J. Taylor & Patterson).

A number of species of *Picea* are heavily utilized for pulpwood, lumber for construction, and specialized wood products, with *P. Abies* in Europe, and *P. sitchensis* and *P. glauca* in North America, being of particular economic importance. Acid rain has recently had serious effects on spruce forests in central Europe (e.g., the Black Forest in Germany) and is also adversely affecting *P. rubens* populations from northern Vermont southward in the Appalachian Mountains. Wood of *P. Abies* and *P. glauca* has been valued for violins and for the sounding boards of keyboard instruments, while the high strength-to-weight ratio of the wood of *P. sitchensis* made it particularly valuable for aircraft construction (Dallimore & Jackson). Spruces are frequently grown as ornamentals in the cooler parts of the North Temperate Zone, with Norway spruce (*P. Abies*) and Colorado blue spruce (the glaucous form of *P. pungens*) the most widely cultivated in the United States. Spruce beer, prepared from *P. rubens* and *P. mariana* in the United States and *P. Abies* in Europe by boiling the leafy shoots with flavorings and sugar, was used as an antiscorbutic on sea voyages, while spruce chewing gum was obtained from the resin of the former two species before chicle became widely utilized (Dallimore & Jackson; Little, 1980). The purified resin of *P. Abies,* known as Burgundy pitch, has been used in medicinal plasters (Dallimore & Jackson), and the pitch of *P. rubens* was similarly utilized in the United States (Krochmal & Krochmal).

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3. **Tsuga** (Endlicher) Carrière, Traité Conif. ed. 1. 185. 1855.

Evergreen trees with pendulous leading shoots and branches. Bark usually furrowed and scaly. Wood pale, without normal resin canals; ray tracheids and axial parenchyma regularly present. Leaves spirally arranged (often appearing 2-ranked due to twisting of leaf bases), linear, flattened and bearing 2 whitened abaxial stomatiferous bands [or quadrangular and bearing stomata above and beneath], narrowing abruptly to a short petiole, abscising at maturity from the ultimately ligneous leaf bases; apex obtuse and often notched, or acute; margin entire or minutely serrulate; fibrovascular bundle double; resin canal single, abaxial to the vascular cylinder. Pollen cones (microsporangiate strobili) small (ca. 1 cm long), subglobose, stalked, borne singly in leaf axils of previous year; microsporophylls prolonged at tip into a short crest or knob; microsporangia subglobose, transversely dehiscent; pollen grains with saccae reduced to a circular "frill" [or bisaccate in sect. HESPEROPEUCE]. Ovulate cones terminal on short branches, maturing the first year; mature ovulate cones relatively small (1–4[–7] cm long), usually pendulous [rarely erect], with cone scales persistent; bracts shorter than scales [to somewhat protrusive in *T. longibracteata*]; ovuliferous scales suborbicular to oblong, entire or minutely lacerate. Seeds with delicate, obliquely oblong terminal wings; seed coat thin, bearing resin vesicles; cotyledons 2–7. Chromosome number $2n = 24$. LECTOTYPE SPECIES: *Tsuga Sieboldii* Carr.;[5] see Britton & Brown, Illus. Fl. No. U.S. & Canada, ed. 2. **1:** 62. 1913. (Name in Japanese for one of the species.)—HEMLOCK.

A genus of ten or more species of forest trees in the Temperate Zone of eastern and western North America and eastern Asia west to the Himalayas, both at low elevations and in mountain areas up to near timberline. Four well-marked species occur in the United States, including two in our region, and at least six grow in Asia. Over ten species have been described from China (Downie; Flous, 1936b, 1937), of which several are doubtfully distinct and have been placed in synonymy by Cheng & Fu. Thorough study of their patterns of variability is badly needed. Fossils indicate that the genus was more widespread and diverse in the past, having occurred in Europe well into the Tertiary (Florin, 1963; Kirchheimer; Sivak, 1973).

The species of *Tsuga* have generally been divided into two sections: TSUGA (sect. *Eutsuga* Engelm., sect. *Micropeuce* (Spach) Schneider), with pollen saccae reduced to a frill and stomata only on the lower (abaxial) leaf surface, and HESPEROPEUCE Engelm., with bisaccate pollen and less-flattened, amphistomatic leaves. Section HESPEROPEUCE consists of only two extant species, *T. Mertensiana* (Bong.) Carr. in western North America and *T. longibracteata* Cheng in southern China. The latter species, which is unusual in the genus in having the ovulate cones strongly ascending at maturity and the cone-scale bracts exserted, has otherwise been treated in sect. *Heopeuce* Keng & Keng, and in subg. *Paleotsuga* Miki, which was based on fossil material. French workers of the Toulouse school, beginning with Campo-Duplan & Gaussen, have proposed that the two species of sect. HESPEROPEUCE are actually stabilized intergeneric hybrids, as discussed below.

Section TSUGA is represented in our area by two species. *Tsuga canadensis* (L.) Carr. (*T. americana* (Miller) Farw.), Canada hemlock, eastern hemlock,

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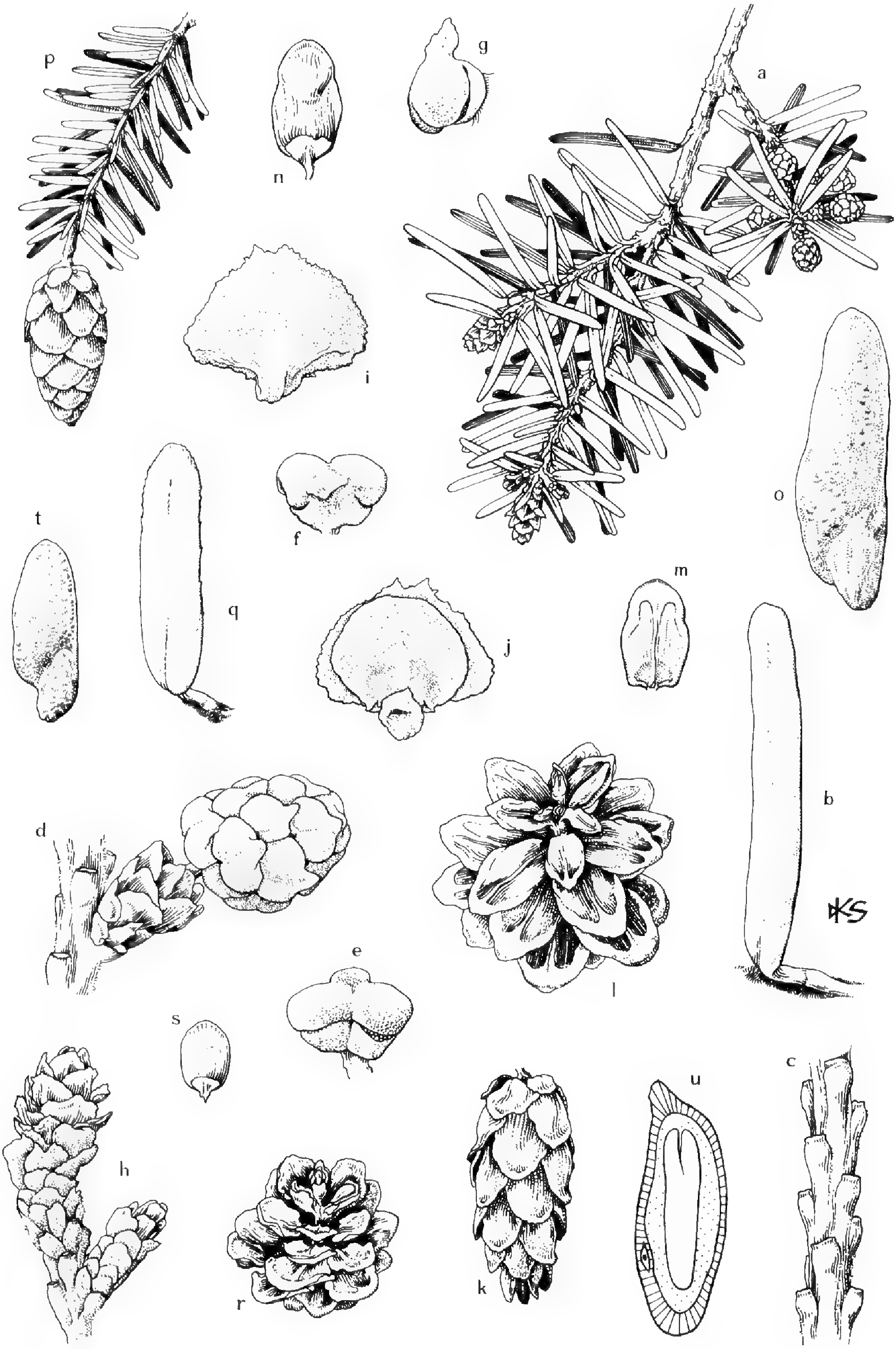
[5] *Abies Araragi* Sieb., Verh. Batav. Genootsch. **12:** 12. 1830 (*Tsuga Araragi* (Sieb.) Koehne), is an earlier name for *T. Sieboldii*. It was published without a usable description, illustration, or type and was only secondarily validated by Siebold & Zuccarini, Fl. Jap. **2:** 15. 1842, under *Abies Tsuga* Sieb. & Zucc. I thus accept the widely used name *T. Sieboldii* Carr. as correct.

hemlock-spruce, $2n = 24$, is a widely distributed species in the northeastern United States and adjacent Canada (Little, 1971, *maps 91N, E*) that occurs west to Wisconsin, eastern Minnesota, eastern Ohio, and southern Indiana. It is widely distributed in the Appalachian region of our area, ranging south to northern Georgia and northwestern Alabama and west to central Tennessee. It occurs in moist valleys and ravines and sometimes on steep, usually north-facing slopes at lower elevations in the northern part of its range, and on moist slopes and streamsides up to 1500 m altitude in our region. Ecogeographic variation in physiological and morphological features is pronounced between northern and southern provenances of the overall range and between north and south of the Tension Zone in Wisconsin (Eickmeier *et al.*; Ruth), although discrete infraspecific taxa have not been proposed on this basis. *Tsuga canadensis* is characterized by distichous, minutely serrulate leaves with rounded apices, pubescent young branchlets, and short-stalked, brownish to grayish ovulate cones with suborbicular scales. It differs from the rather similar western North American *T. heterophylla* (Raf.) Sarg. in having a broader tree crown and narrower, more sharply defined white stomatal bands on the abaxial leaf surface.

Tsuga caroliniana Engelm., Carolina hemlock, crag hemlock, southern hemlock, $2n = 24$, is a much more narrowly distributed species, occurring locally on dry slopes and ridges and along streamsides in the Appalachian Mountains from western Virginia and northeastern Tennessee south to extreme northeastern Georgia and northwestern South Carolina (Little, 1971, *map 94E*), generally at higher elevations than *T. canadensis.* It differs from the latter in having clearly spirally arranged, entire leaves (see FIGURE 3b) and larger (2–3.5 cm long), yellowish, early-deciduous cones with oblong (vs. broadly rounded) scales (see FIGURE 3k, l, r). Although the two species are reported occasionally to occur sympatrically (e.g., in Stokes County, North Carolina, and Roanoke County, Virginia; Coker & Totten; C. E. Wood, pers. comm.), despite differences in habitat preference, they are very distinct morphologically, and hybridization between them has not been reported.

Tsuga is distinguished from all other genera of the Pinaceae by its abruptly petiolate leaves with only a single resin canal abaxial to the vascular tissue. The genus has often been treated as similar to *Picea* because the twigs of both are roughened by the persistent leaf bases, the cones are usually pendulous at maturity, and prominent short-shoots are lacking. The two genera differ, however, in embryogeny and in their pollination mechanisms (Owens & Blake; Owens & Molder), as well as in the characters of root, stem, and seed anatomy that separate *Tsuga* and the other abietoid genera from *Picea* and the other pinoid genera.

Campo-Duplan & Gaussen and subsequent workers of the Toulouse school in France have proposed that *Tsuga Mertensiana* is an intergeneric hybrid of the western North American *T. heterophylla* and *Picea sitchensis* (Bong.) Carr., and that *T. longibracteata* is a hybrid of *Tsuga* and *Keteleeria.* These hypotheses were based primarily on purported intermediacy for a series of morphological characters and irregularities in the bisaccate pollen of the two hemlock species. No case of natural or artificial hybridization has been confirmed for either of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the pairs of genera, however, and it is far more likely that the two taxa involved are merely surviving species that have retained primitive states (e.g., bisaccate pollen) instead of the derived ones seen in sect. TSUGA. Comparison of leaf-terpenoid profiles (Von Rudloff, 1975a, b), immunological distances from seed proteins (Prager *et al.*; Price *et al.*), and patterns of embryological development (Owens & Molder) all show *T. Mertensiana* to be quite similar to other species of *Tsuga* but not to *Picea.*

Chromosome numbers, all $2n = 24$, are known for six species, including all four North American ones (Kuo *et al.*; Sax & Sax; Vabré-Durrieu, 1954b). The karyotype of nine approximately isobrachial and three heterobrachial chromosomes is similar to that of *Picea* (see Khoshoo, 1962; Sax & Sax).

Interspecific hybridization is extremely infrequent among the North American species. *Tsuga* ×*Jeffreyi* (Henry) Henry is a cultivated plant of unknown origin that is morphologically intermediate between *T. Mertensiana* and *T. heterophylla.* Attempts at artificial hybridization between these taxa have been unsuccessful (Meagher; Taylor), but a portion of the infrequent morphological intermediates from areas of near sympatry have proved to be intermediate in leaf-phenolic profile (Taylor).

Comparative pollen morphology of *Tsuga* has been treated in detail by Campo, G. Erdtman (1957, 1965), Sivak, and Ueno (1957). The species of sect. TSUGA are unique in the Pinaceae in having the pollen saccae reduced to a circular frill and in often having spinules atop the verrucate surface ornamentation (G. Erdtman, 1957, 1965; Sivak, 1973). The spinules are apparently absent in *T. canadensis* and are relatively small in *T. caroliniana* and *T. heterophylla* (Sivak, 1973). The size of the two saccae is quite variable within the species of sect. HESPEROPEUCE (Campo; Ho & Sziklai), and fossil *Tsuga* pollen

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FIGURE 3. **Tsuga.** a–o, *T. caroliniana*: a, branchlet at time of shedding of pollen, microsporangiate strobili at upper right, 2 ovulate strobili terminating branches below, × 1; b, leaf, showing characteristic entire margin, × 5; c, part of twig after leaf abscission, showing persistent leaf bases, × 6; d, microsporangiate strobilus with bud scales at base, × 6; e–g, microsporophyll with dehisced sporangia, viewed from below, from above, and from side, × 10; h, twig (leaves removed) with terminal ovulate cone (subtended by bud scales), very young leaves beginning to show at tip of short twiglet at right, × 3; i, cone-sale bract (abaxial view) at time of pollination, the smaller ovuliferous scale above completely hidden, × 10; j, adaxial view of ovuliferous scale and bract at time of pollination, micropyles of the 2 ovules below, × 10; k, mature cone in moist condition, cone scales appressed, × 1; l, mature dry cone, seeds already shed, impressions of seed wings conspicuous on ovuliferous scales, × 1; m, n, mature cone scale, adaxial and abaxial views, bract showing at base in n, × 1; o, seed with wing, adaxial view, × 3. p–u, *T. canadensis*: p, branchlet with mature unopened cone (compare leaf arrangement with "a," noting especially the smaller appressed leaves on upper side), × 1; q, leaf, showing serrulate margin and abrupt narrowing to petiole, × 5; r, mature dry cone with seeds shed (compare to "l"), × 1; s, mature cone scale, abaxial view, with bract at base, × 1; t, seed with wing, adaxial view, × 3; u, diagrammatic longitudinal section of seed, with seed coat hatched, megagametophyte stippled, and embryo (with 2 cotyledons) unshaded, × 10.

has been reported to show a wide range of variation between saccate and frilled forms (Kirchheimer; Wodehouse).

In accord with the differences in pollen form, the pollination mechanisms of *Tsuga Mertensiana* and members of sect. TSUGA are quite dissimilar, although both lack the pollination-drop mechanism of *Picea* and *Pinus*. The relatively smooth pollen of *T. Mertensiana* is caught on microdroplets on the integumentary flaps (Owens & Blake). In contrast, the spinulose pollen surface of species such as *T. heterophylla* apparently aids in its adherence to the waxy surface of the bracts, which are much more prominent than the cone scales at this stage of development (Colangelli & Owens; Owens & Blake). Although this unusual pollen-capture mechanism has also been reported in *T. dumosa* (D. Don) Eichler, it needs to be documented in other species of sect. TSUGA (Doyle & O'Leary).

Leaf anatomy of *Tsuga canadensis* has been studied in detail by Gambles & Dengler. Crystals, presumably of calcium oxalate, on the outer surfaces of the leaf-parenchyma cells are an unusual feature to be sought in other species of the genus.

Relatively few comparative chemical studies of *Tsuga* have been made (see Hegnauer, 1962, 1986). Von Rudloff (1975a, b), comparing leaf-terpene profiles of each of the North American species except *T. caroliniana*, found *T. Mertensiana* to be more or less intermediate between *T. heterophylla* and *T. canadensis* and not at all similar to *Picea sitchensis*. Leaf-phenolic pigments of seven species of *Tsuga* were compared by Taylor, yielding a cluster diagram agreeing rather poorly with morphological data. Immunological comparisons of seed-protein extracts (Prager *et al.*; Price *et al.*) indicate that *T. heterophylla* and *T. Mertensiana* are more similar to one another than to representatives of any other pinaceous genus.

Both of our species of *Tsuga* are utilized as ornamentals in the eastern United States, and numerous cultivars of *T. canadensis* have been selected (Den Ouden & Boom; Krüssmann). Bark of *Tsuga* is rich in tannins, and that of *T. canadensis* has been heavily exploited for use in the tanning industry. Wood of most *Tsuga* species is relatively soft and is used most often for crates and paper pulp, while that of *T. heterophylla* is often employed for construction purposes.

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4. **Abies** Miller, Gard. Dict. abr. ed. 4. Vol. 1 (alph. ord.). 1754.

Pyramidal evergreen trees (rarely shrubs at high elevation or latitude) with well-separated "whorls" of branches. Bark with frequent resin blisters, smooth on younger trunks, becoming fissured with age. Wood pale, without normal resin canals (occasionally with traumatic ones); ray tracheids only occasionally present; axial parenchyma present. Leaves spirally arranged (often appearing 2-ranked due to twisting of the leaf bases), linear to linear-lanceolate, flattened and bearing 2 whitened abaxial stomatal bands [less often triangular or quadrangular in cross section and with stomata frequent above, as well as below], obtuse and often notched at apex or acute [to sharply pointed in *Abies bracteata*]; fibrovascular bundle double; resin canals 2 [rarely to 12], in the medial parenchyma [or near the leaf margin]; leaf scars circular, nearly flush with twig [to somewhat raised]. Pollen cones (microsporangiate strobili) short stalked, pendent, borne singly in axils of leaves of previous year; apex of microsporophyll prolonged into a short knob; microsporangia opening transversely; pollen bisaccate. Ovulate cones borne on upper side of topmost branches, maturing the first year; mature cones erect, ovoid [to cylindrical], short stalked or sessile; bracts fimbriate, with apiculate to long-attenuate tips, exserted [or more commonly included]; ovuliferous scales fan shaped, with margin deeply indented near base; bracts and scales abscising from the persistent cone axis. Seeds compressed; body triangular with acute base, the thin terminal wing broadest and often oblique at apex, partially folded over open surface of seed; seed coat thin, with large resin vesicles. Cotyledons [2–]4 or 5[–8 or rarely 14]. Chromosome number $2n = 24$. LECTOTYPE SPECIES: *Abies alba* Miller (*Pinus Picea* L., not *A. Picea* Miller); see Britton, N. Am. Trees, 74. 1908. (Classical Latin name for fir or related conifers.)—FIR, SILVER FIR.

A genus of approximately 40 species, *Abies* is widely distributed in temperate and boreal portions of the Northern Hemisphere, with the largest number of species in mountainous areas. The centers of distribution are in eastern and central Asia (ca. 17 species), southern Europe and North Africa (ca. eight), the western United States and Canada (eight), and Mexico and Guatemala (ca. six). *Abies sibirica* Ledeb. ranges north of the Arctic Circle in the U.S.S.R., while *A. lasiocarpa* (Hooker) Nutt. and *A. balsamea* (L.) Miller extend well into the subarctic of North America. *Abies balsamea* and *A. Fraseri* (Pursh) Poiret occur in eastern North America, but only the latter is native to our region.

Infrageneric groups in *Abies* are based on a limited number of morphological characters, which are probably subject to considerable homoplasy, and thus a number of conflicting classifications have been proposed (see comparisons in Critchfield, 1988; Liu). Liu's recent monographic treatment, which is followed here, recognizes two subgenera, PSEUDOTORREYA (Hickel) Franco (including only the unusual California endemic *A. bracteata* D. Don) and ABIES, continuing the precedent of Franco (1942, 1950). Within subg. ABIES, Liu recognized 14 sections based on ovulate-cone, leaf, and branchlet characters. Each of these sections is quite restricted in geographic range, usually to part of a continent. Franco (1950) divided subg. ABIES into seven sections and seven series, with the 11 terminal taxa very similar in composition to those of Liu. The North and Central American species of subg. ABIES fall into three sections (one including two series) in Franco's classification and five in Liu's. The less-formal classification of Gaussen, in which the genus is divided into five sections (one for *A. bracteata* only) and 14 species groups, differs in having sections that include both American and Eurasian species. A significantly different classification by Matzenko (1964, 1968) split the genus into four sections and 18 series based largely on relative size and form of the bracts and scales in the ovulate cone. This treatment often agrees poorly with the preponderance of morphological data and utilizes names without regard to nomenclatural priority. The terminal groups recognized by Liu, Franco, and Gaussen for the North American taxa have proved useful in predicting additional character states such as crossability and distribution of wood crystals. The sectional classifications of the entire genus seem to be fairly arbitrary, however, and should be evaluated using further data on crossability and biochemistry.

Subgenus ABIES is characterized by emarginate to acute (vs. acuminate and callose-tipped) leaf apices, ovate to globose (vs. fusiform) winter buds, and included or exserted bracts without a long-aristate middle lobe. Section BALSAMEAE Engelm. *emend.* Liu (leaves with median resin canals; fibrovascular bundles distinct; ovulate cones oblong to ovoid) comprises three species of the United States and Canada: *A. balsamea, A. lasiocarpa,* and the sole species in our region, *A. Fraseri* (*A. balsamea* var. *Fraseri* (Pursh) Spach), Fraser fir, southern balsam fir, she-balsam. Fraser fir is restricted to higher elevations (ca. 1200–2040 m) in the Appalachian Mountains of southwestern Virginia, eastern Tennessee, and western North Carolina. It occurs in pure stands on cool, moist slopes above 1500 m altitude on Mount Rogers, Roan Mountain, Grandfather Mountain, Mount Mitchell, and Clingman's Dome, and in mixed stands with red spruce (*Picea rubens*) and various hardwoods at lower elevations (Coker & Totten; Liu). In recent years several populations of *A. Fraseri* (e.g., on Mount Mitchell) have declined significantly in size, possibly as a result of the effects of acid rain.

Abies Fraseri is closely related to *A. balsamea,* differing most prominently in having the bracts of the ovulate cone strongly exserted and reflexed (vs.

included or somewhat exserted but not strongly reflexed). *Abies Fraseri* tends to have more lines of stomata per band on the leaves (Fulling, 1934; Rehder, 1940), and its young branchlets pubescent with generally reddish (vs. grayish) hairs. Plants of *A. balsamea* from New England and eastern Canada with somewhat exserted bracts were treated by Fernald as var. *phanerolepis.* Although bract/scale ratio is apparently positively correlated with elevation, it exhibits considerable variation within the northeastern populations (Jacobs *et al.*; Lester, 1968; Myers & Bormann), making this variety not very distinct. Similar plants with a tendency toward exserted bracts are also found scattered in the mountains of West Virginia and northern Virginia in the area between the allopatric ranges of *A. balsamea* and *A. Fraseri.* Several studies (Jacobs *et al.*; Robinson & Thor; Thor & Barnett) have compared these populations to *A. Fraseri* and eastern *A. balsamea* and have found intermediacy but no significant increase in variability in regard to morphological features, terpenoid profiles, or electrophoretic alleles. This is consistent with the hypothesis that these populations are remnants of a previous continuum from which *A. Fraseri* has diverged, rather than products of hybridization. *Abies Fraseri* shows significant differences from *A. balsamea* in the percentage composition of several monoterpenes in the wood and balsam oleoresins (Thor & Barnett; Zavarin & Snajberk, 1972), but only minimal divergence in electrophoretic alleles (Jacobs *et al.*). The two taxa are highly crossable (Hawley & DeHayes, 1985a, b) but are kept distinct by geographic isolation. Given the number of other species in the genus that are subject to partial intergradation, *A. Fraseri* is treated here as a separate species, albeit presumably a recent derivative of *A. balsamea.*

Abies is a distinct genus characterized by a unique combination of characters that separate it from the other abietoid genera of Pinaceae. *Cedrus* and *Pseudolarix* differ from *Abies* in their pronounced shoot dimorphism; *Keteleeria* and *Tsuga* differ in their ovulate cones with persistent scales; and *Tsuga* differs in its cones that are terminal and usually pendulous at maturity. *Abies, Keteleeria,* and *Pseudolarix* all have cone scales that are strongly indented at the base, with the seed apex extending beyond the cone scale and the seed wing consequently partially folded over the abaxial surface of the seed, a condition most pronounced in *Abies. Abies* and *Keteleeria* are also similar in having circular, only slightly raised leaf scars, but *Keteleeria* differs in its clustered pollen cones, along with its persistent cone scales. Immunological comparison of seed proteins indicates that *Abies* is most similar to *Cedrus* and *Keteleeria* (Price *et al.*).

While the genus is a distinct one, species delimitation within *Abies* is often problematic. Intergradation in morphology and chemistry occurs in a number of areas where related species are geographically adjacent. This could be due to incomplete evolutionary differentiation of taxa or to hybridization between distinct ones, and both of these situations probably occur in *Abies* (Critchfield, 1988). In addition to the *A. balsamea–A. Fraseri* complex discussed above, intermediate populations have been documented in other North American species pairs: *A. concolor–A. grandis* in sect. GRANDES Engelm. (Hamrick & Libby; Von Rudloff, 1976; Zavarin *et al.*, 1977a), *A. balsamea–A. lasiocarpa* in sect. BALSAMEAE Engelm. (Hunt & Von Rudloff; Parker *et al.*; Von Rudloff, 1975a), and *A. magnifica–A. procera* in sect. NOBILES Engelm. (Liu). Intermediate populations between related species are also known in Europe—for example, involving *A. alba* and *A. cephalonica* (Mitsopoulos & Panetsos)—and Asia (Jain; Liu). Disagreements persist as to the distinctness of several Chinese taxa (cf. Cheng & Fu; Gaussen, 1964; Liu; Rushforth, 1983, 1984). Studies of morphological and chemical variation in the Chinese firs are badly needed.

Several artificial interspecific hybrids have been reported in *Abies* (Critchfield, 1988; Hawley & DeHayes, 1985a, b; Klaehn & Winieski; Mergen *et al.*), but many of the early reports were not verified using F_1 morphology or chemistry. Critchfield's (1988) recent review indicates that at least for the North American taxa, interspecific hybrids can frequently be produced within the sections of Liu, but seldom between them. None of the crosses of American and exotic species attempted by Critchfield succeeded, except for that of *A. concolor* with Mexican *A. religiosa,* although earlier reports of unverified crosses of American and Eurasian species need further investigation. In some cases failure of crosses due to embryo abortion or pollen-tube inhibition have been documented (Kormutak; Kormutak & Dubovsky).

Chromosome counts (all $2n = 24$) have been obtained for 22 of the 39 species recognized by Liu and for one putative interspecific hybrid (see especially Khoshoo; Mergen & Burley); *Abies Fraseri* apparently has never been counted. Natural polyploidy within species seems to be very rare. Karyotypes have been investigated by several authors (e.g., Mehra & Khoshoo; Mergen & Burley; Sax & Sax). According to Mergen & Burley, who compared six species of diverse taxonomic affinities and analyzed the effects of different chemical treatments, the three chromosomes with the smallest short arm are clearly heterobrachial and the two with the next longest ones are sometimes heterobrachial. This compares to earlier reports of five heterobrachial chromosomes by Mehra & Khoshoo and Sax & Sax. Secondary constrictions were found by Mergen & Burley to be variable in position and number, even within individual trees.

The pollination mechanism of *Abies* entails adherence of the pollen to microdroplets on the funnel-shaped integument tip, followed by slight infolding of the tip (Doyle & Kane; Owens & Molder; Singh & Owens, 1981, 1982). The pollen is then dormant for up to two months before germinating and growing into the nucellus (megasporangium). Syngamy occurs within a week of pollen germination in the North American species studied by Owens and coworkers. Inefficiencies in the pollination mechanism may be a factor in the high frequency of unfilled seeds seen in several species of firs (Franklin; Owens & Molder). Seed crops also tend to vary substantially in size over two- to several-year cycles (Franklin).

Variation in the form of the bracts and their length relative to the scales in the mature ovulate cones is particularly marked among—and sometimes within—species of *Abies* (Liu). The color of young cones at the time of pollination also varies strikingly, ranging from green or yellowish to various shades of purplish, bluish, or reddish among and sometimes within species (Liu; Sturgeon & Mitton).

Features of leaf anatomy, including number and position of resin canals, presence and distribution of hypodermal cells, degree of separation of the fibrovascular bundles, and distribution of stomata, are often useful in separating species of *Abies* (Fulling, 1934; Liu), although care must be taken to assure sufficient and comparable samples, since there can be considerable intraspecific variability.

Distribution of calcium-oxalate crystals in the ray parenchyma of the wood has been compared among the nine species of *Abies* native to the United States (Kennedy *et al.*). Rhomboid and elongate crystals are both regularly present in wood samples from five of the western species but are sparse or absent in the western *A. amabilis* (Douglas) Forbes and in the three species of sect. BALSAMEAE (except for elongate crystals in some samples of *A. lasiocarpa*). Rhomboid or elongate crystals have also been reported from the wood of several Asian species (Greguss, 1955, 1972).

Terpenoid profiles from leaf, wood, or bark oleoresins have been used in a number of systematic comparisons among or within species of *Abies* (e.g., Von Rudloff, 1976; Von Rudloff & Hunt; Zavarin & Snajberk, 1965, 1972; Zavarin *et al.*, 1973, 1977a, b, 1978), with emphasis on the North American taxa (see reviews by Critchfield, 1984; Giannasi & Crawford; Von Rudloff, 1975a). These studies have been particularly useful in assessing intergradation among species and in highlighting geographic races within such widespread species as *A. concolor, A. balsamea,* and *A. lasiocarpa.* A survey of cortical terpenoids in the Japanese and Taiwanese firs (Zavarin *et al.*, 1978) yielded a diversity of monoterpenoid and sesquiterpenoid compounds and showed partial agreement with previous morphological classifications.

A particularly interesting sesquiterpenoid derivative isolated from the wood of *Abies balsamea* is juvabione, the "paper factor," which exhibits juvenile hormone activity in certain hemipteran insects (Williams). Juvabione and related todomatuic-acid derivatives with juvenile hormone activity have been found in several other *Abies* species and appear to be produced in response to woolly-aphid attack in some (Puritch & Nijholt). This group of compounds has also recently been found in the wood of *Cedrus Deodara* (see Hegnauer, 1986), which is of interest in light of the morphological similarities between these genera. Himachalene sesquiterpenoids characteristic of *Cedrus* have also been found in *Abies* (Zavarin *et al.*, 1978).

Several species of *Abies* are important as ornamental trees, particularly in cool-temperate areas. *Abies balsamea* and others, including *A. Fraseri,* are highly sought after as Christmas trees. Several species of *Abies* are important sources of pulpwood, and fir wood is used for a variety of purposes not requiring great durability. "Canada balsam," employed as a mounting medium in microscopy and as an optical cement, is an oleoresin obtained from the bark blisters of *A. balsamea,* while "Strasbourg turpentine," used in varnishes and artists' paints, is a refined oleoresin from *Abies alba.* Bark and leaf oleoresins from *Abies* have also been utilized medicinally by native peoples in North America to treat colds and to aid wound healing, among other purposes (Arnason *et al.*; Krochmal & Krochmal).

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JOURNAL OF THE ARNOLD ARBORETUM

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THE GENERA OF SUBORDER APOCYNINEAE (APOCYNACEAE AND ASCLEPIADACEAE) IN THE SOUTHEASTERN UNITED STATES[1]

THOMAS J. ROSATTI[2]

Suborder Apocynineae L. Benson ex Rosatti,[3] comprising the Apocynaceae Juss. and Asclepiadaceae R. Br., is recognized here as a compromise between conflicting traditional and more recent views about the systematics of these plants. Although most botanists have maintained the "apocynads" and the

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[1] Prepared for the Generic Flora of the Southeastern United States, a long-term project made possible by grants from the National Science Foundation and at this writing supported by BSR-8303100 and BSR-8415637 (Norton G. Miller, principal investigator), under which this account was prepared, and BSR-8415769 (Carroll E. Wood, Jr., principal investigator). This treatment, the 128th in the series, follows the format established in the first one (Jour. Arnold Arb. **39**: 296–346. 1958) and continued to the present. The area covered by the Generic Flora includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with information about extraregional members of a family or genus in brackets. References I have not verified are marked with an asterisk.

Norton Miller and Carroll Wood deserve recognition for maintaining the Generic Flora project, and for their many contributions to this treatment in particular. Gordon C. Tucker should be canonized for having calmly endured my almost daily practice of dribbling ideas around him and then slam-dunking them into the computer without even a passing acknowledgment of the integral role he played in their development. Ihsan A. Al-Shehbaz, at Harvard, and George K. Rogers, now at the Missouri Botanical Garden, have continued to be valuable colleagues in matters regarding the Generic Flora and otherwise. Walter S. Judd provided a good deal of critical information about species not native to but occurring without cultivation in Florida. Donald J. Drapalik freely shared his knowledge about species of *Matelea* and *Gonolobus* in the Southeast and provided liquid-preserved material of special importance to these investigations. Warren D. Stevens conveyed helpful insights regarding taxonomic concepts at and above the level of genus. I thank Li Ping-T'ao for sending a copy of the treatment of the Apocynaceae and Asclepiadaceae he coauthored for the *Flora of the People's Republic of China*; the many fine illustrations considerably enhanced my otherwise meager knowledge about these plants in that part of the world. Elizabeth A. Shaw helped with the Latin diagnosis.

This manuscript, as well as the others I have authored in the Generic Flora series, has benefited from the editorial expertise of Elizabeth B. Schmidt and Stephen A. Spongberg. In Berkeley James M. Affolter, Robert A. Price, and Toni M. Rosatti helped with the considerable task of reading proof,

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"asclepiads" as distinct families since Robert Brown first separated them early in the nineteenth century, an increasing number (e.g., Hallier; Judd, pers. comm.; Stebbins; Stevens; Thorne, 1976, 1981) believe that the two groups grade into each other so gradually that it would be more appropriate to treat them as a single family; in addition, the peculiar gynoecium (carpels free in the ovule-bearing region but connate above) present nearly throughout is nearly unknown in other flowering plants. Despite these facts, even botanists (including this author) supporting unification of the two families usually continue to recognize them as distinct for reasons of practicality and tradition; each is a

and William J. Stone provided technical computing assistance. These investigations were based on collections of the libraries and/or herbaria associated with the New York State Museum, Harvard University, the University of California at Berkeley, and the University of Florida.

The illustrations were prepared by Karen Stoutsenberger (KS) and Rachel A. Wheeler (RAW), variously under the direction of Kenneth R. Robertson, Carroll Wood, and George K. Brizicky, from materials collected by Robertson, Wood, Brizicky, A. H. Curtiss, R. A. Howard, N. G. Miller, H. B. Parks, G. V. Nash, E. Prichard, and R. J. Eaton.

This treatment is published as Contribution Number 600 of the New York State Science Service.

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[3]Article 16.1 of the International Code of Botanical Nomenclature (ICBN, 1988) states that "names of taxa above the rank of family are automatically typified if they are based on generic names," which this name is, and that "for such automatically typified names, . . . the name of a suborder which includes the type of the adopted name of an order" is to be "based on the generic name equivalent to that type, but without the citation of an author's name." The ordinal name adopted here is Gentianales, not Apocynales, so in this case author citation is necessary. Benson proposed the Apocynineae in 1979, but his name was not validly published because it was not accompanied either by a Latin description or diagnosis or by a reference to a previously and effectively published one (i.e., it was not published in accordance with Art. 36.1 [ICBN, 1988], the effective date of which is January, 1935). The following is presented to correct this situation.

Apocynineae L. Benson ex Rosatti (Apocynineae L. Benson, Pl. Classification, ed. 2. 263. 1979, nomen invalidum).

Herbae vel frutices lactiferi; folia simplicia, opposita; flores actinomorphi, hermaphroditi, pentameri; calyx partitus persistens; corolla sympetala; stamina 5, epipetala; carpella 2, supera, ad basim plerumque libera, ad apicem connata; placentae marginales, rare parietales vel axiales; fructus plerumque folliculus, rare drupa vel capsula; semina apice plerumque comosa.

Trees to herbs with latex. Leaves simple, usually opposite, entire [rarely toothed or lobed], often with colleters basally. Inflorescences terminal but often appearing interpetiolar, cymose, or flowers sometimes solitary. Flowers perfect [rarely carpellate or staminate functionally], actinomorphic or nearly so, 5- [rarely 4-]merous except carpels 2 [sometimes to 8]; sepals nearly free, often with squamellae basally; corollas variously sympetalous; tubes often appendaged adaxially, lobes often overlapping; stamens epipetalous, alternating with corolla lobes, filaments free and short or connate around gynoecium, unappendaged or bearing abaxially 1, 2, [or more] coronas; coronas discoid or comprising 5 free or connate, variously shaped segments, each sometimes appendaged adaxially; anthers free, variously agglutinated to each other and to style-stigma head, or connate into anther head around style-stigma head; pollen released as individual grains or tetrads, or in pollinia; nectaries external to ovaries, absent, or within stigmatic chambers; carpels free or sometimes connate in ovule-bearing region, free or connate in stylar region, and connate apically into variously modified style-stigma head; ovaries superior to subinferior, placentae marginal when ovaries free, parietal [or axile] when connate; ovules 1 to many per carpel. Fruits follicles, sometimes drupes, capsules, [or berries]; seeds in follicles glabrous, each with a tuft of trichomes at apex [or sometimes at both ends] [or arillate], those in drupes [or berries] naked, those in capsule winged.

very large and complex group (i.e., one in which many infrafamilial taxa have been recognized) that has long been accepted at the level of family.

Recognition of the Apocynineae as proposed here is essentially consistent with Stevens's (p. 67) assertion that "almost everyone . . . would agree that what is represented by Apocynaceae and Asclepiadaceae (including Periplocaceae) is a single taxon at some classificatory level; the cumulative similarities far outweigh the differences." However, acceptance here within a single taxon, the Apocynineae, of only two families, the Apocynaceae and the Asclepiadaceae, is at odds with his belief that there are five groups involved (which he recognized as subfamilies) and that the greatest discontinuity lies not between the Apocynaceae and the Asclepiadaceae, as is implied by the arrangement adopted here, but between the Plumerioideae K. Schum. and the Apocynoideae, the two subfamilies of Apocynaceae recognized here.

Two other alternatives to unification of the Apocynaceae and the Asclepiadaceae into a single family would also reflect the close relationship between the two, but in my view they are not as acceptable as the one adopted here. The better of these would involve establishment of a superfamily but is undesirable because there is no recommended name termination for such a taxon in the International Code of Botanical Nomenclature, and its implementation therefore could cause confusion. The other alternative would consist of including the two families in their own order, the Apocynales, as was adopted by Hutchinson (1926), among others. However, such an arrangement would impart nothing about the relationships between these two and the other families usually included in the Gentianales, an order of relatively consistent circumscription by most modern authors; therefore, it, too, is undesirable.

In summary, recognition of the Apocynineae as a suborder within the Gentianales is adopted here not only because it allows a rather commonly accepted order to be maintained but also because it conveys the closeness of relationship between the Apocynaceae and the Asclepiadaceae in a way that has been specifically addressed by the International Code of Botanical Nomenclature.

As indicated above, there appears to be nearly uniform agreement among modern systematists regarding the circumscription and, to a lesser extent, the infraordinal structuring of the Gentianales. Dahlgren, Takhtajan, Thorne (1976, 1981), and Wagenitz each included at one level or another and in various sequences groups recognizable as the Apocynaceae, Asclepiadaceae, Gentianaceae, Menyanthaceae, Loganiaceae, Buddlejaceae, Rubiaceae, and various other taxa. A most notable exception to this uncharacteristically high degree of conformity is the view of Cronquist, who considered the Rubiales to be a link between his Gentianales (excluding the Buddlejaceae and Menyanthaceae but otherwise delimited as above) and Dipsacales, but too large to be included as a peripheral group in either. Benson placed the Rubiales even farther away, in the fourth of four "groups" of dicotyledons, and included the Adoxaceae, Caprifoliaceae, Dipsacaceae, Rubiaceae, and Valerianaceae in the order. The Gentianales (including the Oleaceae but otherwise delimited as above) consisted of the suborders Gentianineae, Oleineae, and Apocynineae, the last as defined here.

The Gentianales, in the usual sense and as accepted in this treatment, may be defined as Asteridae (according to Cronquist, a subclass in which more than 99 percent of the species are distinguished from other dicotyledons by sympetalous flowers and stamens equal in number to and alternate with, or sometimes fewer than, the corolla lobes) that are characterized by a combination of traits including diversity of habit, although the plants are commonly woody and usually nonglandular; simple, entire, opposite or whorled leaves; colleters associated with petiole bases, leaf axils, and/or adjacent areas of the stem; five or sometimes four sepals, petals, and stamens but only two carpels; corolla lobes that overlap and are twisted either to the right or left, at least in aestivation; epipetalous stamens; and superior or inferior ovaries. According to Wagenitz, the order occupies an isolated position among other sympetalous groups and is of unknown ancestry.

As accepted here, the Apocynineae can be distinguished most readily from the rest of the Gentianales by their laticifers, which usually produce a white liquid and are lacking in the rest of the order, including the Rubiaceae. Otherwise, the suborder is generally set apart by a combination of character states including funnelform, salverform, or urceolate corollas, sometimes with strongly reflexed lobes; anthers that are adherent to or fused with the apical portion of the gynoecium (except in the Plumerioideae); carpels that are free in the ovule-bearing region (except in some Plumerioideae) but variously united above and often enlarged and elaborated terminally; superior ovaries; and follicular fruits (except in some Plumerioideae) containing comose seeds (except in most Plumerioideae).

The Apocynaceae and Asclepiadaceae also share a number of other features, including those having to do with morphology, embryology, anatomy, and chemistry; many of the frequently cited differences may not hold after the plants are more thoroughly known. These similarities and differences are summarized below, and in some cases they are discussed more fully in the treatments of the individual families and genera.

Several traits commonly used to separate the Apocynaceae and Asclepiadaceae, including the widely presumed absence or presence, respectively, of special structures for pollen transport (see below), in fact represent continua or involve a number of exceptions. As pointed out by Cronquist, in various aspects of floral morphology there are evolutionary progressions from the Plumerioideae to the Apocynoideae of the Apocynaceae, and from there into the Asclepiadaceae, in which the sequence proceeds from the Periplocoideae R. Br. ex Endl. to the Secamonoideae Endl. and the Asclepiadoideae.

The most characteristic features of the Asclepiadaceae are related to pollination, the specialized mode of which is usually cited in attempts to explain the large number of species in the family. Within the Apocynaceae, however, a comparable number of species exists in which pollination is less specialized. According to Cronquist, the equal numbers of species in the two families are not due to equal levels of pollination-mode effectiveness, but instead to the fact that the number of species in the Periplocoideae has remained small because the mechanism of mass pollen transfer (particularly the pollinia) is imperfectly developed in the group.

The extensive elaborations and the various fusions characterizing the flower in the Asclepiadaceae appear to represent, at least in some cases, culminations of evolutionary trends apparent in the Apocynaceae. The coronas in the Apocynaceae generally arise as relatively simple appendages in the throat of the corolla, while those present in most Asclepiadaceae are more complex structures derived from the abaxial side of the staminal filaments or from the area of fusion between the filaments and the corolla. In the Plumerioideae anthers are completely fertile, unappendaged, and free from each other as well as from the style-stigma head,[4] whereas in the Apocynoideae they are characteristically fertile only in the apical half or so, variously appendaged (at the base and sometimes also apically), and adherent to one another as well as agglutinated to the style-stigma head. Anthers in the Periplocoideae are mostly unappendaged and usually free but are sometimes adherent to one another and appressed against the style-stigma head, a condition comparable to that described for the Apocynoideae; in the Secamonoideae and the Asclepiadoideae they, as well as other floral parts including the filaments, are elaborate (and hence only partially fertile) and fused to each other as well as to the style-stigma head, thereby contributing to formation of the so-called gynostegium of the Asclepiadaceae.

Anther dehiscence is longitudinally introrse (and sometimes slightly latrorse) throughout the Apocynaceae and in some Asclepiadaceae (Periplocoideae, Secamonoideae) and apical in the majority of the Asclepiadaceae (i.e., most Asclepiadoideae). According to Woodson (1930), anthers are essentially four-locular (tetrasporangiate) in the Apocynaceae. However, whereas they remain so throughout development in most of the family, in *Apocynum* L., *Poacynum* Baillon, and *Trachomitum* Woodson (recognized here as the tribe Apocyneae, see below) the partition between adaxial and abaxial pairs ruptures by maturity, yielding a seemingly bilocular anther. This condition was considered by Woodson (1930) to be indicative of an affinity with the Asclepiadaceae, in which anthers are tetrasporangiate but bilocular in the Periplocoideae and Secamonoideae, and bisporangiate and bilocular in the Asclepiadoideae (see primarily Cronquist; Davis; and Maheswari Devi, 1964). The account of Safwat differs from the foregoing in stating that anthers are four-locular in the Periplocoideae and Secamonoideae (see discussion of the Asclepiadaceae).

The apparent lack in the Apocynaceae and universal presence in the Asclepiadaceae of special structures for pollen transport out of the flower has been widely believed to be the single most reliable difference between the families, and it may indeed be. However, Schick (1980) has suggested that in the Apocynaceae secretions of the style-stigma head that were at one point in evolution (i.e., before development of the concealed stigma) stigmatic presently hold pollen in place and perhaps even contribute to its attachment to insect visitors. This possibility, together with the fact that it is now known that pollen-transporting structures of the Asclepiadaceae are actually hardened, acellular secre-

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[4] Several terms including "stigma," "stigma head," "stigmatic head," and "style head" have been used for this structure, primarily because it is usually elaborated to various degrees and is only partially stigmatic. "Style-stigma head" is used here to reflect the idea that it appears to be precisely homologous to neither the style nor the stigma, as these terms are usually used, but to both the stigma and the apical portion of the style.

tions of the style-stigma head, suggests that even in this regard the families are indistinct. (For more detailed accounts, see family discussions.)

The two meiotic divisions of pollen mother cells are simultaneous in most Apocynaceae, Periplocoideae, and Secamonoideae, whereas only the successive type has been reported in the Asclepiadoideae (see Safwat in the discussion of the Asclepiadaceae, to follow). Pollen is released as individual grains in most of the Apocynaceae, but as tetrahedral, isobilateral, or decussate tetrads in *Apocynum, Poacynum,* and *Trachomitum*; although grains or tetrads in the family are sometimes loosely coherent (Cronquist), they do not form pollinia. In the Asclepiadaceae, pollen is released as linear (or sometimes tetrahedral, isobilateral, rhomboid, or T-shaped) tetrads that are loosely coherent in the Periplocoideae but firmly enclosed in pollinia in the Secamonoideae and Asclepiadoideae.

According to Brewbaker, the pollen is binucleate when shed in some genera of both families (e.g., *Allamanda* L., *Catharanthus* G. Don, *Nerium* L., *Rauvolfia* L., *Urechites* Mueller-Arg. [= *Pentalinon* Voigt], *Vinca* L. in the Apocynaceae; several extraregional genera of Asclepiadaceae) and trinucleate in others (e.g., *Amsonia* Walter, *Apocynum, Carissa* L., *Thevetia* L.; *Asclepias* L.); such reports are not consistent with the accounts of Cronquist, Davis, and others, who have indicated that the grains in both families are in all cases trinucleate.

According to Cronquist, pollen in the Apocynaceae is tricolporate or bi- or triporate, sometimes with granular instead of the usual columellar infratectal structure. It is notable that such aspects of pollen morphology and structure evidently have not been reported for the Asclepiadaceae.

Inflorescences in both families are essentially cymose (for discussion of those of the Apocynaceae, see Woodson, 1935b; for those of the Asclepiadaceae, see Nolan), but while they are usually raceme- or panicle-like in the Apocynaceae, they are often umbel-like in the Asclepiadaceae.

Flowers in both families display most of the features generally associated with insect pollination. They are perfect throughout the suborder, except that those in the Asclepiadaceae are rarely imperfect and are five-merous with respect to the number of sepals, petals, and stamens, although some Apocynaceae are in this sense four-merous. The gynoecia are bicarpellate in all but the tribe Pleiocarpeae K. Schum. (Apocynaceae), in which they are usually three- to five- (but sometimes two-, six-, seven-, or eight-)carpellate. Anthers are held within the fused portion of the corolla in parts of both families, but they are exserted in tribe Parsonsieae K. Schum. of the Apocynaceae and in most of the Asclepiadaceae. In some Apocynaceae, including *Apocynum,* and many Asclepiadaceae the corolla lobes are strongly reflexed. Filaments are distinct in the Apocynaceae and Periplocoideae but are usually connate into a short sheath around the style (to which they are coherent) in the Asclepiadoideae; filaments are unappendaged in the Apocynaceae but are variously elaborated in the Asclepiadaceae.

Nectaries are present in most Apocynaceae and, according to Good, especially frequent in the Apocynoideae. Although they may number either two or five and vary from completely free to totally fused into an unlobed, annular structure, they are always located around the base of the gynoecium (see V. S. Rao & Ganguli). Nothing comparable exists in the Asclepiadaceae, where nectar is produced in the stigmatic chambers and sometimes held in the corona (see discussion of Asclepiadaceae).

While some apocynaceous flowers (i.e., those of most members of the tribe Pleiocarpeae) are unique within the suborder in having three or more carpels, others qualify as such by virtue of their compound (yet bicarpellate) ovaries: those in the Melodininae K. Schum. are bilocular and have axile placentae, while those in the Landolphiinae K. Schum. and the Allamandeae Pichon are unilocular with parietal placentae. The ovule-bearing region in the asclepiadaceous gynoecium is uniformly composed of two free carpels. Ovaries are wholly superior throughout both families, with the exception that they are partially sunken into the receptacle in some members of each (e.g., *Plumeria* L., *Himatanthus* Willd. ex Schultes, Apocynaceae). The non-ovule-bearing region of the gynoecium is more or less completely united throughout the Apocynaceae (except, for example, in double flowers of *Tabernaemontana divaricata* (L.) R. Br.; see Raghuvanshi & Chauhan), although the styles of many genera are bilobed in transverse section. In the Apocynineae there is a progression from a generally typical style and a small, relatively simple, stigmalike style-stigma head in more primitive Apocynaceae to an enlargement and elaboration of the style-stigma head in more advanced members of the Apocynaceae and all Asclepiadaceae. In *Apocynum* the region may represent an evolutionary diversion in the sense that it is not differentiated into a style and a style-stigma head but into a single massive, sessile, rhomboid structure, the clavuncle (see FIGURE 5e, i). The non-ovule-bearing region of the gynoecium in the Asclepiadaceae appears to be generally free in the stylar region (i.e., there are two distinct styles), a condition in sharp contrast to that described for the Apocynaceae. This distinction between the two families is not often made and needs to be investigated further.

Ovules are usually numerous in each ovary or locule and are commonly pendulous throughout the Apocynineae but may be reduced to as few as two or even one in the Apocynaceae and Asclepiadaceae, respectively. Whereas some authors (e.g., Corner, Davis) have indicated that the ovules are anatropous and massively unitegmic in both families, Cronquist stated that they are amphitropous, anatropous, or hemianatropous in the Apocynaceae but anatropous in the Asclepiadaceae. They are tenuinucellar in the Apocynaceae in all accounts I have seen, but "pseudocrassinucellar" in the Asclepiadaceae, according to Davis. That is, although the archesporial cell in investigated Asclepiadaceae functions directly as the megaspore mother cell, as in tenuinucellate ovules, the megaspore mother cell is deeply embedded in a thick nucellar cap; except that no primary parietal cell is formed, this condition is comparable to that seen in the crassinucellate ovule.

In members of the Apocynineae, cytokinesis accompanies meiosis in the megaspore mother cell, and the chalazal megaspore of the resulting linear (or, in some Asclepiadaceae, T-shaped) tetrad develops into a Polygonum-type megagametophyte. The synergids are pyriform throughout the suborder, and an associated filiform apparatus has been reported in at least one (extraregional) species of Asclepiadaceae. In the megagametophytes of both families, the polar nuclei fuse before fertilization, the antipodals are ephemeral (except in *Ceropegia* L. and *Cynanchum* L., of the Asclepiadaceae, in which they simulate the egg apparatus), and starch grains are commonly present. Accessory megagametophytes have been reported in ovules of several extraregional genera of Apocynaceae (Rau).

Endosperm formation is nuclear throughout the suborder (but see Maheswari Devi, 1964), although cell walls form centripetally early in the development of the embryo. In the Apocynaceae a central cavity free of endosperm develops, but in the Asclepiadaceae the tissue remains cellular throughout. According to Cronquist, the endosperm is oily in both families, and copious to scanty in the Apocynaceae but uniformly scanty in the Asclepiadaceae. Endosperm haustoria in the Apocynaceae have been reported in species of *Carissa* and *Catharanthus* (Maheswari Devi, 1971, 1974). Evidently throughout the suborder, embryogeny does not commence until after large numbers of endosperm nuclei have formed. It is of the Caryophyllad type in the Apocynaceae and conforms to the Solanad type in the Asclepiadaceae by Davis's account, although Asterad, Caryophyllad, Chenopodiad, Onagrad, and Solanad types have been indicated in the former, according to Maheswari Devi (1974). Davis also stated that polyembryony has been reported for members of both families—in one species of the extraregional genus *Kopsia* Blume (Apocynaceae) and commonly in (unspecified members of) *Vincetoxicum* (author not indicated, see discussion of *Gonolobus*) (Asclepiadaceae).

The Apocynaceae are more diverse than the Asclepiadaceae both in fruit type and in the shapes and sizes of seeds. Follicles are most common throughout the suborder and in fact are the only types represented in the Apocynoideae and Asclepiadaceae. Capsules, berries, and drupes are produced only by certain members of the Plumerioideae.

Seeds appear to be larger when fruits are drupes (e.g., in *Ochrosia* Juss., *Thevetia*, *Vallesia* Ruiz & Pavon) or berries (e.g., in *Carissa*). Seeds in capsules (e.g., in *Allamanda*) and follicles tend to be smaller, are usually flattened, and are sometimes winged (e.g., in *Allamanda*); those in capsules and those in follicles of the Plumerioideae lack the apical tufts of long silky trichomes that characterize the Apocynoideae and Asclepiadaceae; and those in follicles in the Plumerioideae are sometimes arillate (e.g., in *Tabernaemontana* L.) or have tufts of short hairs at both ends (e.g., in *Alstonia* R. Br.). Seeds in follicles seem to be generally more elongate in the Apocynaceae and rounder in the Asclepiadaceae. Seed coats are multiplicative[5] in the Apocynaceae, but only sometimes in the Asclepiadaceae. Such seed coats are generally more characteristic of larger seeds.

A woody habit occurs in both families of the Apocynineae but is more prevalent in the Apocynaceae, the more primitive and more tropical of the two. A clear majority of the species in this family are trees, erect to scrambling

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[5] A term used by Corner for the condition in which cell layers are produced in the integument by periclinal divisions; this usually occurs in addition to the more widespread mechanism by which the number of cells in each layer is increased through anticlinal divisions.

shrubs, or woody vines; only some are herbaceous, and succulents are rare (except in parts of Africa, in, for example, *Adenium* Roemer & Schultes and *Pachypodium* Lindley). Woody members of the Asclepiadaceae constitute a minority and are usually scrambling shrubs or vines (rarely erect shrubs or trees); a larger number of species are erect herbs, and succulents are relatively common.

Other than differences in the extent to which secondary growth occurs, the Apocynaceae and Asclepiadaceae are quite similar in stem anatomy. In both families the pericycle almost always includes white, sometimes mucilaginous, unlignified cellulosic fibers (slight lignification reported in an extraregional species of *Vincetoxicum*), either in a continuous ring or as separate strands according to Cronquist, but either isolated or in groups according to Metcalfe & Chalk (1950, 1983) (not detected in material of *Rhazya orientalis* A. DC., an extraregional member of the Apocynaceae); the cork cambium is superficial (but substantially deeper within the stem in *R. orientalis*); and wood rays are one to several cells wide. Vessel elements have simple perforations in both families, except that scalariform plates (the more primitive condition) with only a few cross bars (more advanced than many cross bars) have been reported in several genera of Apocynaceae, including an extraregional species of *Rauvolfia*. Intervascular pitting in both families is alternate; the pits are generally vestured in both families but are evidently smaller in the Apocynaceae. According to Cronquist, imperforate tracheary elements (i.e., tracheids) in both families have simple or bordered pits. (The foregoing material is summarized primarily from Cronquist and Metcalfe & Chalk (1950, 1983); see also below.)

The most outstanding anatomical features of the Apocynineae are the laticifers and the internal phloem present in nearly all species (see primarily Metcalfe & Chalk (1950, 1983)). The former are well developed, nonarticulated (or possibly sometimes articulated), branched or unbranched, and with variously colored (e.g., greenish in *Trachelospermum* Lem., bright yellow or pale red in some extraregional genera of Apocynaceae, according to Metcalfe & Chalk (1950, 1983)) but usually white contents. They evidently permeate most of the stem in both families; they have been reported, at least in the Apocynaceae, from the primary cortex, pericycle, phloem, pith, and medullary rays. Laticifers in leaves are associated with vascular bundles and frequently (in genera including *Echites* P. Br., *Catharanthus, Thevetia,* and *Vinca* in the Apocynaceae, and *Asclepias* in the Asclepiadaceae) extend into the mesophyll and sometimes even to the epidermis (in taxa of Apocynaceae, including *Carissa grandiflora* (E. Meyer) A. DC. and an extraregional species of *Allamanda*) as well. Laticiferous canals have been reported in the root cortex of *Apocynum androsaemifolium* L. and an extraregional species of *Thevetia* and may also occur in other taxa in both families. Internal phloem (the so-called intraxylary phloem of older literature) has been detected in all examined members of both families (except *Pachypodium,* a highly specialized, extraregional genus usually assigned to the subfam. Apocynoideae of the Apocynaceae) either as a continuous ring or as isolated bundles around the pith.

Datta & Maiti (1971) listed a number of anatomical similarities between the Apocynaceae and Asclepiadaceae (e.g., in the secondary xylem of both: medium-sized to small vessel members, simple perforation plates, alternate and relatively large pits, bordered pits on fibers; see also above). However, the Apocynaceae can be distinguished from the Asclepiadaceae by generally diffuse-porous wood, with a tendency toward the ring-porous condition in some genera (including *Allamanda*), and markedly heterogeneous rays containing latex tubes. (Although not explicitly stated, the implication is that in the Asclepiadaceae the wood is ring-porous, and the rays are homogeneous and without latex tubes.)

Leaves throughout the Apocynineae are usually opposite or whorled, simple, and entire; rarely, and only in the Asclepiadaceae, are they either lobed or toothed. True stipules occur in neither family, although colleters[6] and/or colleterlike structures are found in the Apocynaceae and, probably to a lesser extent, in the Asclepiadaceae. Stomata are usually paracytic, sometimes anomocytic, and less frequently actinocytic, anisocytic, brachyparacytic, or cyclocytic in the Apocynaceae (Chandra *et al.*, 1969, 1972; Dolph & Young; Kapoor & Mitra; Kapoor *et al.*; Sharma *et al.*; and Trivedi & Upadhyay, 1976, 1977); they are usually paracytic and less often anomocytic or anisocytic in the Asclepiadaceae (see Cronquist). In both families the vascular bundles of the petiole and midrib are evidently bicolateral and arc shaped, and in at least some genera of each there are sometimes small peripheral bundles as well. Nodes are unilacunar throughout the suborder (Metcalfe & Chalk, 1950, 1983).

The most common, and therefore presumably ancestral, base chromosome number in the Apocynineae is $x = 11$, although $x = 8$, 9, 10, and 12 are also known. These and other cytological data have been of some use systematically and are discussed more thoroughly in the treatments of the families and some of the genera. The abundance of latex and the generally small chromosomes have evidently impeded cytological investigations of many taxa.

With respect to chemistry, there are probably more similarities than differences between the Apocynaceae and the Asclepiadaceae (see also discussion of the Apocynaceae). A diversity of iridoid compounds, cardiotonic (cardiac) glycosides (see below), and alkaloids has been found in both families, although the two latter may be more numerous and widespread in the Apocynaceae (e.g., see Lewis & Elvin-Lewis for cardiac glycosides; Dahlgren *et al.*, Raffauf (1964, 1970), Raffauf & Flagler, Willaman & Li, and Willaman & Schubert for alkaloids). Indole, pyrrolizidine, and steroid (including tropane) alkaloids occur in the Apocynaceae (see also family discussion), whereas pyridine and phe-

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[6] A term that has not always been used precisely, "colleter" has been applied at one time or another to many kinds of secretory structures of plants, from the simplest few-celled glandular trichomes to much more complex, multicellular appendages derived from both epidermal and subepidermal layers. The term is used here in the latter sense. In the Apocynineae the structures may be homologous to stipules. They are often quite conspicuous, are located on the base of the petiole and/or on adjacent areas of the stem, are often root-, finger-, and/or leaf-like, and are reportedly epidermal and subepidermal in derivation, at least in some species of some genera including *Carissa, Nerium, Thevetia,* and *Tabernaemontana* (Jain *et al.*). Fjell reported that those of *Allamanda neriifolia* Hooker and *Thevetia peruviana* (Pers.) K. Schum. consist of parenchyma cells covered with an epidermis of elongate, palisadelike cells and a cuticle, and that while those of *Vinca minor* L. are similar in structure, they were not observed to be secretory and therefore would not qualify as colleters. (See also Guédès.)

nanthro-indolizidine types are found in—and so-called tylophorine types are reportedly unique to—the Asclepiadaceae; Cronquist is seemingly alone in attributing indole alkaloids to the Asclepiadaceae as well.

Crystals of calcium oxalate are often present in both families, while tannins, proanthocyanins, and saponins are variously absent or relatively uncommon throughout the suborder. Cyanogenic compounds are present, but uncommon, in both families. Whereas the major component fatty acids in the Apocynineae include linoleic and oleic, palmitic acid is apparently found only in the Apocynaceae (see Alston & Turner).

The comparative distribution of phenolic compounds in the two families is difficult to assess. For example, although delphinidin, ellagic acid, and myricetin were indicated for neither family by Bate-Smith, Farnsworth (in Taylor & Farnsworth, 1973) listed delphinidin for *Vinca minor,* and Hrazdina indicated hirsutidin, petunidin, and malvinidin for *Catharanthus roseus,* as well as cyanidin for two extraregional genera of Asclepiadaceae.

Cardenolides, one of two groups of naturally occurring cardiotonic glycosides, have been reported in at least 12 plant families (see Hoch), including the Apocynaceae and the Asclepiadaceae. Still used as arrow poisons, they are now firmly established for various uses in clinical medicine. The increase in force and the decrease in rate of heart-muscle contractions brought on by cardenolides improves circulation and consequently a number of other aspects of metabolism. As with most drugs, toxic and therapeutic doses are nearly equal.

Whereas some reports have indicated that the Apocynaceae are richer in cardiotonic glycosides than the Asclepiadaceae, others suggest that the two are more or less comparable in this regard. According to Kingsbury, about 400 cardiac glycosides had been isolated and characterized by the early 1960's, mostly from the Apocynaceae, Liliaceae, and Scrophulariaceae. In a later review Singh & Rastogi indicated that these compounds were about equally numerous in ten genera each of Apocynaceae and Asclepiadaceae. Even more recently, Lewis & Elvin-Lewis declared that the compounds are known in more genera of Apocynaceae than any other plant family, although Huber (p. 26) later stated that the "Cerberoideae [included here in the Plumerioideae] and Apocynoideae are distinguished [presumably from other Plumerioideae as recognized here] by the frequent presence of cardiotoxic [i.e., cardiotonic] glycosides, which indicates a strong affinity of these two subfamilies with Periplocaceae [treated here as the Periplocoideae of the Asclepiadaceae] and the tribe Asclepiadeae of Asclepiadaceae." Regardless of the foregoing, the story of the monarch butterfly (*Danaus plexippus*) and the cardenolides of *Asclepias* (Brower *et al.*) is perhaps one of the best known in biology (see discussion of that genus).

The close relationship between the Apocynaceae and the Asclepiadaceae is not, and to my knowledge has never been, in question. However, the taxonomic history of these families has been relatively complex, at least in part because the plants have been familiar to humans for such a long time. Although the name *Apocynum* is present in herbals dating back to the fourth century B.C., it is not thought to have been unequivocally and exclusively applied to plants now included in the genus until the seventeenth century. Before that time, practically all plants with milky juice, including those now placed in the Apocynaceae, the Asclepiadaceae, and even the Euphorbiaceae, were referred to one monstrous assemblage.

Taxonomic refinement of this unnatural group was a gradual and sometimes halting process. The "Apocinae" of De Jussieu, on which the family name is based, represented a considerable advance in this direction but nevertheless included as one of four unnamed and unnatural groups a nonlaticiferous one comprising five genera now placed in other families (including the Loganiaceae, see below). Of the three remaining groups, two included genera now assigned to both the Apocynaceae and Asclepiadaceae, although the third was composed only of those now placed in the former. Thus, the system of De Jussieu failed not only to restrict the group to these two families but to distinguish between them as well. Credit for these advancements belongs instead to Robert Brown, who at least tacitly excluded the nonlaticiferous group of De Jussieu and removed the "Asclepiadeae" from the rest on the basis of "the singular structure of the stamina," which at present remains the only consistent difference between the Apocynaceae and the Asclepiadaceae. (For additional taxonomic history, see discussions of the Apocynaceae, *Apocynum,* and the Asclepiadaceae.)

The closest link between the Apocynineae and other Gentianales appears to lie between the Apocynaceae and the putatively more primitive and possibly ancestral Loganiaceae. Probably the least specialized and most diverse family in the order, the Loganiaceae were considered by Takhtajan and by Thorne (1976) to be transitional to the Apocynaceae through *Plocosperma* (three species; trees and shrubs; opposite or subwhorled leaves; Mexico and Guatemala). This genus is strikingly similar to some Apocynaceae in its elongate, fusiform fruits and apically comose seeds. However, the fruits are capsular, open along two sutures, and usually contain only a single, stalked seed; the ovary is bicarpellate and unilocular, usually with two basal, erect ovules on one parietal placenta and two subapical, pendulous ovules on the other. Carr & Carr implied that *Plocosperma,* with its apically twice bifid styles, might be considered primitive within the Apocynaceae.

Solereder indicated possible connections between *Plocosperma* and the Apocynaceae (the Hydrophyllaceae were also mentioned in this regard), although he actually placed the genus in the Loganiaceae. However, he was uncertain of its placement, mostly because it lacks internal phloem (in contrast to the Loganiaceae and Apocynaceae) and, presumably, because it has laticifers (lacking in the Loganiaceae; present in the Apocynaceae). A unigeneric Plocospermatoideae was recognized in the Loganiaceae by Takhtajan (tentatively) and Thorne (1976). Stating that the plants combined features of the Apocynaceae, Loganiaceae, Convolvulaceae, and Ehretiaceae, Airy Shaw (in Willis) recognized the Plocospermataceae of Hutchinson (1973), who had included the family with the Apocynaceae, Periplocaceae, and Asclepiadaceae in his Apocynales. Cronquist included the Plocospermataceae in the Apocynaceae, although his description of the latter does not appear to have been adjusted accordingly. *Plocosperma* is here excluded from the Apocynineae.

As summarized by Rogers, the Apocynaceae and the Loganiaceae both have internal phloem, vestured pits, nuclear endosperm, and colleters but differ in that members of the former are laticiferous (although in the latter, latex is present in the fruits of *Fagraea* Thunb.), generally lack stipules, and frequently have specialized androecia and/or gynoecia. As pointed out by Hutchinson (1973), the Loganiaceae also differ from the Apocynaceae in that the gynoecium is stigmatic at the apex or within apical lobes (vs. at the base of the style-stigma head), the fruits are not follicular, and the embryos are smaller.

According to Datta & Maiti (1971), the Apocynaceae have more aspects of wood anatomy in common with the Loganiaceae, Oleaceae, and Salvadoraceae (very small to medium-sized pores and axial parenchyma in all four families) than with the Gentianaceae, Linaceae, Menyanthaceae, and Plocospermataceae. Each of these families has been proposed by one systematist or another as ancestral to the Apocynaceae, although the basis for inclusion of the Plocospermataceae in this group is unclear because the wood anatomy of *Plocosperma* appears not to have been studied. Pores and fibers of equal diameter (as in the Gentianaceae), exclusively solitary pores (Linaceae), and scalariform or spiral lateral pitting of vessels (Menyanthaceae) are all indicated as lacking in the Apocynaceae (but see Record). Wood characteristics of the Loganiaceae considered to be more specialized than those of the Apocynaceae include dendritic grouping of vessels, mostly paratracheal parenchyma, and a predominance of exclusively uniseriate rays; additionally, members of the Loganiaceae lack the vasicentric tracheids that have been reported in the Apocynaceae. Datta & Maiti (1971) also indicated that wood of the Apocynaceae is most similar to that of the Salvadoraceae: in each there are both upright and square cells in the rays, a greater frequency of simple pits on radial walls of fibers, and internal phloem.

Paleobotanical evidence seems, for the most part, to be consistent with the phylogenetic relationships between the Loganiaceae, Apocynaceae, and Asclepiadaceae discussed above. According to Cronquist, pollen assignable to the Apocynaceae has been recovered from Paleocene sediments, while that of the Asclepiadaceae has not been found earlier than the Oligocene. Apparently, fossil pollen assignable to the Loganiaceae has not been found. Macrofossil evidence places the Apocynaceae and Loganiaceae in the Eocene and the Asclepiadaceae no earlier than the Oligocene. (See also Mildenhall; Muller, 1970, 1981.)

The economic significance of the Apocynineae lies primarily in the considerable medicinal value of cardenolides (discussed above) and of several alkaloids, especially those isolated from two genera of Apocynaceae, *Catharanthus* and *Vinca* (see Taylor & Farnsworth, 1973, 1975). Two in particular from *C. roseus* (L.) G. Don, vincaleucoblastine and leurocristine, have been extensively applied in chemotherapeutic treatment of various forms of cancer in humans. Often considered to be of "miracle drug" status, leurocristine has been effective against brain tumors, acute leukemia in children, various types of lymphomas including Hodgkin's disease, and carcinomas of the breast, cervix, and prostate. Experimental evidence has indicated that these two and other related alkaloids may be effective in lowering excessive levels of sugar in the blood and in increasing the flow of urine in humans as well. Many other applications involving plants in the suborder have had long histories in folk medicine but have not been much evaluated scientifically.

The latex of these plants has been used to make rubber, while the bark has yielded fibers. The woods are employed in heavy construction, in the building of cabinets, and in carving. Many species are grown for ornamental purposes, including several that in the southeastern United States have either escaped from or persisted beyond cultivation without having become truly naturalized. (For further details, see discussions of families and genera.)

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Candolle, A. de. Apocynaceae. Prodr. **8:** 317–489. 1844. [Addenda et corrigenda, 675–677; for treatment of Asclepiadaceae in the Prodromus, see Decaisne.]

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Chittenden, F. J., ed. Dictionary of gardening. ed. 2. 4 vols. 2316 pp. Oxford. 1951. [Many genera of Apocynaceae and Asclepiadaceae included, in alphabetical order.]

Clapham, A. R., T. G. Tutin, & E. F. Warburg. Flora of the British Isles. ed. 2. xlviii + 1269 pp. Cambridge. 1962. [Probably no native Apocynaceae or Asclepiadaceae; only *Vinca herbacea, V. major,* and *V. minor* of Apocynaceae treated.]

Clewell, A. F. Guide to the vascular plants of the Florida Panhandle. viii + 607 pp. + inside front and back covers. Tallahassee. 1985. [*Apocynum cannabinum,* 15 species of *Asclepias.*]

Corner, E. J. H. The seeds of dicotyledons. Vol. 1. xii + 311 pp. Vol. 2. viii + 522 pp. Cambridge, London, New York, and Melbourne. 1976. [Apocynaceae described (**1:** 70–73) and illustrated (**2:** 13–16); Asclepiadaceae described (**1:** 74, 75).]

Correll, D. S., & H. B. Correll. Aquatic and wetland plants of southwestern United States. xvi + 1777 pp. Water Pollution Control Res. Ser., Environ. Protect. Agency. Washington, D. C. 1972. (Reissued in 2 vols. by Stanford Univ. Press. 1975.) [Apocynaceae, 1331–1338; Asclepiadaceae, 1339–1350; numerous southeastern taxa represented.]

——— & M. C. Johnston. Manual of the vascular plants of Texas. xv + 1881 pp. Renner, Texas. 1970. [Apocynaceae (including *Amsonia, Apocynum, Nerium, Trachelospermum, Vinca*), 1211–1218; Asclepiadaceae (including *Asclepias, Cynanchum, Matelea, Periploca, Sarcostemma*), 1219–1241.]

Cronquist, A. An integrated system of classification of flowering plants. *Frontisp.* + xviii + 1262 pp. New York. 1981. [Apocynaceae, 876–879; Asclepiadaceae, 879–882.]

Dahlgren, R. M. T. A revised system of classification of the angiosperms. Bot. Jour. Linn. Soc. **80:** 91–124. 1980.

———, S. Rosendal-Jensen, & B. J. Nielsen. A revised system of classification of the angiosperms with comments on correlation between chemical and other characters. Pp. 149–204 *in* D. A. Young & D. S. Seigler, eds., Phytochemistry and angiosperm phylogeny. New York. 1981. [Tropane and pyrrolizidine alkaloids in three genera of Apocynaceae, including *Urechites* (= *Pentalinon*), but not in Asclepiadaceae.]

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Decaisne, J. Asclepiadeae. DC. Prodr. **8:** 490–665. 1844. [For treatment of Apocynaceae in the Prodromus, see De Candolle.]

Demeter, K. Vergleichende Asclepiadeenstudien. Flora **115:** 130–176. 1922. [Translators no longer unique to Asclepiadaceae, since structures in *Apocynum* considered related; other interpretations regarding inflorescences and flowers offered.]

Dormon, C. Wildflowers of Louisiana. xix + 172 pp. + *24 colored pls.* Garden City and New York. 1934. [Apocynaceae, 93, including *Amsonia salicifolia* (= *A. Tabernaemontana*); Asclepiadaceae, 94–96, including *Asclepias incarnata, A. rubra, A. tuberosa, A. variegata* (line drawing), *Vincetoxicum carolinense.*]

Duke, J. A. On tropical tree seedlings I. Seeds, seedlings, systems, and systematics. Ann. Missouri Bot. Gard. **56:** 125–161. 1969. [Apocynaceae, Asclepiadaceae, 158, 159; first few seedling leaves with green, expanded blades said to be alternate in Apocynaceae (although opposite in examples given), opposite in Asclepiadaceae.]

DUNCAN, W. H. Woody vines of the southeastern United States. Sida **3:** 1–76. 1967. [Key to genera, brief comments, illustrations, maps. Apocynaceae, 34, *Trachelospermum difforme,* 45, 71; Asclepiadaceae, 34, *Cynanchum scoparium,* 46, 71, *Periploca graeca,* 46, an escape in Knox Co., Tennessee.]

——— & J. T. KARTESZ. Vascular flora of Georgia. An annotated checklist. xii + 147 pp. Athens, Georgia. 1981. [Apocynaceae, 105; Asclepiadaceae, 105, 106.]

EICHLER, A. W. Blüthendiagramme. Erster Theil. 348 pp. Leipzig. 1875. [Apocynaceae, 251–253; Asclepiadaceae, 253–259.]

ENDLICHER, S. L. Apocynaceae. Gen. Pl. **8:** 577–586. 1838. Asclepiadaceae. *Ibid.* 586–599. [Suppl. 1, 1841: Apocynaceae, 1395–1397; Asclepiadaceae, 1397–1399.]

ENDRESS, P. K., M. JENNY, & M. E. FALLEN. Convergent elaboration of apocarpous gynoecia in higher advanced dicotyledons (Sapindales, Malvales, Gentianales). Nordic Jour. Bot. **3:** 293–300. 1983. [*Mortoniella Pittieri* Woodson (Apocynaceae) and *Asclepias physocarpa* Schlecter; scanning electron micrographs of carpel-fusion process.]

ERDTMAN, G. Pollen morphology and plant taxonomy. Angiosperms. *Frontisp.* + xii + 539 pp. Uppsala. 1952.

FERNALD, M. L. Gray's manual of botany. ed. 8. lxiv + 1632 pp. New York (and several other cities). 1950. [Apocynaceae, 1167–1169; Asclepiadaceae, 1169–1177.]

GIBBS, R. D. Chemotaxonomy of flowering plants. 4 vols. 2372 pp. Montreal and London. 1974. [Vol. 4 includes bibliography, index, and addendum.]

GLEASON, H. A. The new Britton and Brown illustrated flora of the northeastern United States and adjacent Canada. Vol. 3. iii + 596 pp. New York and London. 1963. [Apocynaceae, 69–72; Asclepiadaceae, 72–84.]

——— & A. CRONQUIST. Manual of vascular plants of northeastern United States and adjacent Canada. li + 810 pp. New York (and several other cities). 1963. [Apocynaceae, 554–556; Asclepiadaceae, 556–560.]

GODFREY, R. K., & J. W. WOOTEN. Aquatic and wetland plants of southeastern United States. Dicotyledons. x + 933 pp. Athens, Georgia. 1981. [Apocynaceae (*Amsonia, Rhabdadenia, Trachelospermum, Urechites* [= *Pentalinon*]), 538–543; Asclepiadaceae (*Asclepias, Cynanchum, Sarcostemma*), 543–554.]

GOLDBERG, A. Classification, evolution, and phylogeny of the families of dicotyledons. Smithson. Contr. Bot. **58.** iv + 314 pp. Washington, D. C. 1986. [*Table 1* indicates ordinal assignments of dicotyledonous families by 12 recent authors; 11 of these included the Apocynaceae and Asclepiadaceae in the Gentianales (one used the name Contortae), HUTCHINSON alone placed them in the Apocynales.]

GOOD, R. Features of evolution in the flowering plants. x + 405 pp. New York. 1974. [Corrected version of a work originally published in London, 1956; chapters 7 and 8 are lengthy discussions of the Apocynaceae and Asclepiadaceae.]

GRAY, A. Synoptical flora of North America. Vol. 2. Part 1. 1878. [Apocynaceae, 79–85; Asclepiadaceae, 85–106.]

GREENE, W. F., & H. L. BLOMQUIST. Flowers of the South, native and exotic. xv + 208 pp. *26 pls.* Chapel Hill, North Carolina. 1953. [Line drawings of native Apocynaceae and Asclepiadaceae, plus exotic Apocynaceae (*Allamanda cathartica, Carissa grandiflora, Ervatamia coronaria, Nerium Oleander, Trachelospermum jasminoides*) and Asclepiadaceae (*Cryptostegia grandiflora, Hoya carnosa, Stephanotis floribunda*); also other references.]

GUÉDÈS, M. Stipules et ligules vraies chez quelques Apocynacées et Asclépiadacées. Compt. Rend. Acad. Sci. Paris **274:** 3218–3221. 1972. [Structures associated with leaf bases in Apocynaceae (e.g., *Ervatamia divaricata* [*E. coronaria*], *Vinca major, V. minor*) and Asclepiadaceae (e.g., *Vincetoxicum officinale*) said to include stipules, ligules, and colleters.]

GUIGNARD, L. L'ovule chez les Apocynacées et Asclépiadacées. Mém. Acad. Roy. Sci. Inst. France **55:** 1–34. 1917a. [Illustrations representative of genera of Apocynaceae (e.g., *Amsonia, Apocynum, Catharanthus, Vinca*) and Asclepiadaceae (e.g., *Asclepias, Vincetoxicum*).]

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HARBORNE, J. B., & C. A. WILLIAMS. Flavone and flavonol glycosides. Pp. 261–311 *in* J. B. HARBORNE & T. J. MABRY, eds., The flavonoids: advances in research. London and New York. 1982.

HARVILL, A. M., JR., T. R. BRADLEY, & C. E. STEVENS. Atlas of the Virginia flora. Part 2. Dicotyledons. 148 pp. Farmville, Virginia. 1981.

HEGNAUER, R. Chemotaxonomie der Pflanzen. Band 3. Dicotyledoneae: Acanthaceae–Cyrillaceae. 743 pp. Basel and Stuttgart. 1964. [Apocynaceae, 124–163; Asclepiadaceae, 199–223.]

HESLOP-HARRISON, Y., & K. R. SHIVANNA. The receptive surface of the angiosperm stigma. Ann. Bot. II. **41:** 1233–1258. 1977. [*Strophanthus* (Apocynaceae) with unicellular papillae on dry stigmas; *Asclepias, Vincetoxicum* (Asclepiadaceae) with nonpapillate, dry stigmas; *Carissa, Mandevilla, Vinca* (Apocynaceae) with low to medium papillae on wet stigmas; *Apocynum, Oncinotus* (Apocynaceae), *Asclepias* (possibly heterogeneous), *Strophanthus* (Asclepiadaceae) with nonpapillate, wet stigmas; bi- and trinucleate pollen, wet and dry stigmas in each family.]

HEYWOOD, V. H., ed. Apocynaceae. *In:* T. G. TUTIN *et al.*, eds., Fl. Europaea **3:** 68, 69. 1972. [*Nerium* and *Trachomitum* by F. MARKGRAF, *Vinca* by W. T. STEARN.] Asclepiadaceae. *Ibid.* 70–73. [*Asclepias, Cynanchum, Vincetoxicum* by F. MARKGRAF.]

HITCHCOCK, C. L., A. CRONQUIST, & M. OWNBY. Vascular plants of the Pacific Northwest. Part 4: Ericaceae through Campanulaceae. vi + 510 pp. Seattle and London. 1959. [Second printing, 1969; Apocynaceae, 77–82; Asclepiadaceae, 82–85.]

HOCH, J. H. A survey of cardiac glycosides and genins. South Carolina. 1961.* [Cited by SINGH & RASTOGI.]

HRAZDINA, G. Anthocyanins. Pp. 135–188 *in* J. B. HARBORNE & T. J. MABRY, eds., The flavonoids: advances in research. London and New York. 1982.

HUBER, H. Apocynaceae. *In:* M. D. DASSANAYAKE & F. R. FOSBERG, eds., A revised handbook to the flora of Ceylon **4:** 25–72. 1983. Asclepiadaceae. *Ibid.* 73–124.

HUMBOLDT, F. W. H. A. VON, A. J. BONPLAND, & C. S. KUNTH. Apocyneae. Nov. Gen. Sp. Pl. **3:** 188–233. 1818 [1819].

HUTCHINSON, J. The families of flowering plants. Vol. 1. Dicotyledons. ed. 1. xiv + 328 pp. London. 1926. [Apocynales, 279–282.]

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JENSEN, S. R., B. J. NIELSEN, & R. DAHLGREN. Iridoid compounds, their occurrence and systematic importance in the angiosperms. Bot. Not. **128:** 148–180. 1975.

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JOLIVET, P. Les Eumolpinae (Col. Chrysomelidae) des Apocynaceae et des Asclepiadaceae (Gentianales). Bull. Mens. Soc. Linn. Lyon **51:** 214–222. 1982. [Food plants of several leaf beetles, which are often monophagous, belong to these families.]

JONES, S. B., JR., & N. C. COILE. List of Georgia plants in the University of Georgia herbarium. 53 pp. Athens, Georgia. 1979. [Apocynaceae, 18; Asclepiadaceae, 19.]

JUSSIEU, A. L. DE. Apocineae. Gen. Pl. 143–151. 1789.

KINGSBURY, J. M. Poisonous plants of the United States and Canada. xiii + 626 pp. Englewood Cliffs, New Jersey. 1964. [Apocynaceae, 262–267; Asclepiadaceae, 267–271.]

KNOBLOCH, I. W. Intergeneric hybridization in flowering plants. Taxon **21:** 97–103. 1972. [Combined number of interspecific and intergeneric hybrids reported in literature: Apocynaceae, 4; Asclepiadaceae, 39.]

KNUTH, P. Handbuch der Blütenbiologie 2(2): 1–27. 1899. (English translation, Handbook of flower pollination **3:** 1–27. 1909, by J. R. AINSWORTH DAVIS.) [Insect visitors for numerous species and genera.]

KUNZE, H. Typologie und Morphogenese des Angiospermen-Staubblattes. (English summary.) Beitr. Biol. Pflanzen **54:** 239–304. 1978 [1979]. [Apocynaceae, including illustrations and photographs of *Nerium Oleander, Ochrosia elliptica, Vinca minor,* 269–272; Asclepiadaceae, including *Ceropegia Woodii* and *Cynanchum vincetoxicum,* 272–275.]

LAKELA, O., R. W. LONG, G. FLEMING, & P. GENELLE. Plants of the Tampa Bay area. rev. ed. vi + 192 pp. Sarasota, Florida. 1975. [Apocynaceae, 118; Asclepiadaceae, 118, 119.]

LAWRENCE, G. H. M. Taxonomy of vascular plants. xiii + 823 pp. New York. 1951. [Apocynaceae, 672, 673; *Vinca minor* and *Allamanda neriifolia* illustrated; stigma of *Vinca* shown in wrong position on style-stigma head. Asclepiadaceae, 673–675; *Asclepias curassavica* and *Stapelia variegata* illustrated.]

LÉGER, V. Recherches sur la structure anatomique du tégument séminal des Apocynacées et des Asclépiadacées. Thèse de docteur de l'Université de Paris. 1913. [Includes descriptions and illustrations of many genera represented in the Southeast.]

LEÓN [J. S. SAUGET] & ALAIN [E. E. LIOGIER], HERMANOS. Apocynaceae. Fl. Cuba **4:** 170–197. 1957. Asclepiadaceae. *Ibid.* 198–217.

LEWIS, W. H., & M. P. F. ELVIN-LEWIS. Medical botany. Plants affecting man's health. xvii + 515 pp. New York, London, Sydney, and Toronto. 1977. [Partial list of cardiac glycosides in the Apocynaceae, 184.]

LI, H.-L. Floristic relationships between eastern Asia and eastern North America. Trans. Am. Philos. Soc. Phila. **42:** 371–429. 1952. [Apocynaceae (*Amsonia,* but not *Trachelospermum*); no Asclepiadaceae.]

LINDLEY, J. A natural system of botany. ed. 2. xxvi + 526 pp. London. 1836. [Apocynaceae, 299–302; Asclepiadaceae, 302–305.]

LONG, R. W., & O. LAKELA. A flora of tropical Florida. xvii + 962 pp. Coral Gables, Florida. 1971. [Apocynaceae, 697–703; Asclepiadaceae, 703–711.]

LUBBOCK, J. A contribution to our knowledge of seedlings. Vol. 2. iv + 646 pp. London. 1892. [Fruits and seeds also; Apocynaceae, 216–222, descriptions include *Echites umbellata* (illustrated) and species of *Plumeria, Tabernaemontana, Thevetia*; "Asclepiadeae," 223–233, descriptions include species of *Asclepias, Periploca, Sarcostemma* (the last illustrated).]

MACFARLANE, J. M. The evolution and distribution of flowering plants. Vol. 1. The Apocynaceae and Asclepiadaceae. xi + 181 pp. *2 foldout charts.* 1933. [A great deal of interesting speculation, although much of the information is outdated.]

MACROBERTS, D. T. The vascular plants of Louisiana. Bull. Mus. Life Sci. Louisiana State Univ. **6.** 165 pp. Shreveport, Louisiana. 1984. [Apocynaceae, 58, 59; Asclepiadaceae, 60.]

MAHESWARI DEVI, H. Embryological studies in Asclepiadaceae. Proc. Indian Acad. Sci. **60:** 52–65. 1964. [Reports of both nuclear and cellular endosperm formation in *Calotropis procera* need confirmation.]

MARTIN, A. C. The comparative internal morphology of seeds. Am. Midl. Nat. **36:** 513–660. 1946. [Apocynaceae, 602, 603; Asclepiadaceae, 614, 615.]

METCALFE, C. R., & L. CHALK. Apocynaceae. Anat. Dicot. **2:** 905–917. 1950. Asclepiadaceae. *Ibid.* 917–925.

——— & ———. Anat. Dicot. ed. 2. **2:** 74. 1983. [Numerous references to the Apocynaceae and Asclepiadaceae: e.g., intraxylary phloem, 54; laticifers, 72, 73.]

Mildenhall, D. C. New Zealand Late Cretaceous and Cenozoic plant biogeography: a contribution. Palaeogeogr. Palaeoclimatol. Palaeoecol. **31:** 197–233. 1980. [Pollen of two species of *Parsonsia* in Quaternary constitutes first appearance of Apocynaceae; Asclepiadaceae not mentioned.]

Morton, J. F. Plants poisonous to people in Florida and other warm areas. iii + 116 pp. Miami. 1971. [Color photographs of *Nerium Oleander* and *Thevetia peruviana*; grazing on *Cryptostegia madagascariensis* Bojer suspected in sudden death of a donkey and a pony in South Florida in 1970.]

———. Folk remedies of the low country. 176 pp. Miami. 1974. [*Apocynum cannabinum,* 27, 28; *Asclepias tuberosa,* 33, 34.]

Muller, J. Palynological evidence on early differentiation of angiosperms. Biol. Rev. **45:** 417–450. 1970. [Earliest pollen appearances of Apocynaceae include *Alyxia* Banks ex R. Br. (Lower Paleocene), *Parsonsia* R. Br. (Lower Oligocene), *Alstonia* (lower Upper Miocene) (Asclepiadaceae not mentioned); earliest macrofossils of Apocynaceae are Eocene, those of Asclepiadaceae are Oligocene.]

———. Fossil pollen records of extant angiosperms. Bot. Rev. **47:** 1–142. 1981. [Apocynaceae: *Alyxia* from Paleocene of Borneo, *Rauvolfia* from Upper Eocene of Cameroon, *Alstonia* from Upper Miocene of Borneo, *Dyera* Hooker from Upper Miocene of Borneo, and *Trachomitum* from Upper Miocene of Spain supported; *Parsonsia* from Oligocene of New Zealand retracted, that from Upper Eocene of southeastern North America questionable; *Nerium* from Lower and Middle Eocene of western Europe questionable; *Trachelospermum* from Middle Eocene of U. S. A. possible. Asclepiadaceae: *Tacazzea* Dcne. from Oligocene and Lower Miocene of Cameroon supported; *Periploca* L. and/or *Myriopteron* Griff. from Miocene of Hungary and Soviet Union possible.]

Munz, P. A. A California flora. vii + 1681 pp. Berkeley, Los Angeles, and London. 1959. [Apocynaceae (including *Amsonia, Apocynum, Vinca*), 449–452; Asclepiadaceae (including *Asclepias, Cynanchum, Matelea, Sarcostemma*), 452–457; see also pp. 82, 83 in Supplement (224 pp.). 1968.]

Netolitzky, F. Anatomie der Angiospermen-Samen. Handb. Pflanzenanat. II. Archegon. 10. vi + 365 pp. 1926. [Apocynaceae, 268–270; Asclepiadaceae, 270, 271.]

Nevling, L. I., Jr. A catalogue of the published works of Robert E. Woodson, Jr. Ann. Missouri Bot. Gard. **52:** 229–233. 1965. [At least 65 references to Apocynaceae and/or Asclepiadaceae.]

Nolan, J. R. Developmental morphology of the asclepiadaceous inflorescence. 177 pp. Unpubl. Ph.D. dissertation, Cornell Univ., Ithaca, New York. 1967.* (Diss. Abstr. B. **28**(3): 802. 1967.)

Ohwi, J. Apocynaceae. Pp. 743, 744 *in* F. G. Meyer & E. H. Walker, eds., Flora of Japan. (English translation.) Washington, D. C. 1965. Asclepiadaceae. *Ibid.* 744–751. [Editorial assistance by R. E. Woodson, Jr.]

Palton, J. E., & W. S. Judd. Vascular flora of Paynes Prairie Basin and Alachua Sink Hammock, Alachua County, Florida. Castanea **51:** 88–110. 1986. [No Apocynaceae; *Asclepias perennis* Walter, uncommon at edge of basin, *Cynanchum scoparium* Nutt. occasional at edge of hammock.]

Philipson, W. R. Ovular morphology and the major classification of the dicotyledons. Bot. Jour. Linn. Soc. **68:** 89–108. 1974.

Plouvier, V. Distribution of aliphatic polyols and cyclitols. Pp. 313–336 *in* T. Swain, ed., Chemical plant taxonomy. London and New York. 1963.

Pobedimova, E. G. Apocynaceae. *In:* B. K. Shishkin, ed., Flora URSS (in Russian) **18:** 645–662. 1952; Flora of the U.S.S.R. (English translation by N. Landau) **18:** 474–487. 1967. Asclepiadaceae. Flora URSS, 663–718; Flora of the U.S.S.R., 487–527. [Addenda to English translation include *Cynanchum,* 561.]

RADFORD, A. E., H. E. AHLES, & C. R. BELL. Manual of the vascular flora of the Carolinas. lxi + 1183 pp. Chapel Hill, North Carolina. 1968. [Apocynaceae (*Amsonia, Apocynum, Trachelospermum, Vinca*), 845–847; Asclepiadaceae (*Asclepias, Cynanchum, Matelea*), 847–858.]

RAFFAUF, R. F. A simple field test for alkaloid-containing plants. Econ. Bot. **16:** 171, 172. 1962. ["False positives" obtained for plants in laticiferous families including Apocynaceae and Asclepiadaceae; no clearly positive plants missed by the field assay.]

———. A handbook of alkaloids and alkaloid-containing plants. xi + several hundred unnumbered pp. New York, London, Sydney, and Toronto. 1970. [First part, organized alphabetically by plant family, includes about 32 pages for Apocynaceae and less than one for Asclepiadaceae (alkaloids, genera, and references).]

RAGHUVANSHI, S. S., & A. K. S. CHAUHAN. Evolution within certain species of Apocynaceae. Pp. 231–235 *in* P. KACHROO, ed., Advancing frontiers in cytogenetics. Delhi. 1974. [Variety of *Tabernaemontana divaricata* with normal flowers diploid, $2n = 22$; variety with double flowers triploid, $2n = 33$, in some cases with separate style and style-stigma head for each ovary.]

RECORD, S. J. Classifications of various anatomical features of dicotyledonous woods. Trop. Woods **47:** 12–27. 1936. [Vessel elements of Apocynaceae and Asclepiadaceae characterized by simple perforation plates on end walls and vestured pits, in Apocynaceae occasionally with scalariform or (e.g., in *Vinca*) spiral thickenings; wood fibers of Apocynaceae characterized by conspicuous bordered pits; *Allamanda, Periploca* with ring-porous wood.]

——— & R. W. HESS. Timbers of the New World. xv + 640 pp. *58 pls.* New Haven and London. 1943. [Apocynaceae, 56–68; Asclepiadaceae not included.]

RICKETT, H. W. Wildflowers of the United States. Vol. 2. The Southeastern States. Part 2. Pp. i–vi + 323–688. New York. 1966. [Includes color photographs of many of our species of both Apocynaceae and Asclepiadaceae.]

ROBERTSON, C. Flowers and insects. 221 pp. Carlinville, Illinois. 1928. [Visitors listed by plant species. Apocynaceae, 27, 28; Asclepiadaceae, 28–36.]

ROGERS, G. K. The genera of Loganiaceae in the southeastern United States. Jour. Arnold Arb. **67:** 143–185. 1986.

SAFWAT, F. M. The floral morphology of *Secamone* and the evolution of the pollinating apparatus in Asclepiadaceae. Ann. Missouri Bot. Gard. **49:** 95–129. 1962.

SCHNARF, K. Vergleichende Embryologie der Angiospermen. vii + 354 pp. Berlin. 1931. [Apocynaceae, 199, 200; Asclepiadaceae, 200–203; review of literature; illustrations representative of both families.]

SCHUMANN, K. Apocynaceae. *In:* ENGLER & PRANTL, Nat. Pflanzenfam. IV. **2:** 109–189. 1895. Asclepiadaceae. *Ibid.* 189–306.

SEIGLER, D. S. Terpenes and plant phylogeny. Pp. 117–148 *in* D. A. YOUNG & D. S. SEIGLER, eds., Phytochemistry and angiosperm phylogeny. New York. 1981. [Apocynaceae, but not Asclepiadaceae.]

SHARP, A. J., R. E. SHANKS, J. K. UNDERWOOD, & E. MCGILLIARD. A preliminary checklist of dicots in Tennessee. Mimeographed. 114 pp. 1960. [Apocynaceae and Asclepiadaceae, 74, 75.]

SINGH, B., & R. P. RASTOGI. Cardenolides—glycosides and genins. Phytochemistry **9:** 315–331. 1970. [Apocynaceae (e.g., *Carissa, Nerium, Thevetia*) and Asclepiadaceae (e.g., *Asclepias, Periploca*).]

SMALL, J. K. Flora of the southeastern United States. ed. 2. xii + 1394 pp. New York. 1913. [Asclepiadales, 933–956, with 19 species and 11 genera of Apocynaceae, and 67 species and 12 genera of Asclepiadaceae.]

———. Manual of the southeastern flora. xxii + 1554 pp. New York. 1933. [Asclepiadales, 1057–1078.]

SMITH, E. B. An atlas and annotated list of the vascular plants of Arkansas. 592 pp.

Published by the author, Fayetteville, Arkansas. 1978 [1979?]. [Apocynaceae, 9–12; Asclepiadaceae, 15–20.]

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KEY TO THE FAMILIES OF APOCYNINEAE IN THE SOUTHEASTERN UNITED STATES

Filaments not connate, unappendaged; anthers free or variously agglutinated to each other and to style-stigma head; pollen released as individual grains or as tetrads; nectaries external to ovaries or absent; ovaries free or sometimes connate; fruits follicles or drupes when ovaries free, capsules [or berries] when ovaries connate; seeds in follicles glabrous, each with a tuft of trichomes at apex [or at both ends] [or arillate], those in drupes [and berries] glabrous, those in capsules winged. .... Apocynaceae.

Filaments connate around gynoecium, bearing abaxially 1 or 2 coronas; anthers connate into an anther head around style-stigma head; pollen released in pollinia, 2 from adjacent anthers united by 2 translator arms and 1 corpusculum into 1 pollinarium; nectaries within stigmatic chambers; ovaries free; fruits follicles; seeds each with a tuft of trichomes at apex. .... Asclepiadaceae.

APOCYNACEAE A. L. de Jussieu, Gen. Pl. 143. 1789, "Apocineae," nom. cons.

(DOGBANE FAMILY)

Terrestrial to aquatic (emergent; sometimes in brackish water), erect, ascending, decumbent, scandent, and/or twining, annual or perennial herbs or subshrubs, or shrubs or trees [or succulents, at least in *Pachypodium*] with usually white or sometimes nearly colorless latex; axes and leaves glabrous or with various amounts of nonglandular, but sometimes viscid, pubescence [glandular trichomes (other than colleters, see below) reported but not confirmed in *Rauvolfia tetraphylla*]. Leaves simple, usually opposite or sometimes subopposite, less frequently alternate, whorled, or subwhorled; blades broad to linear [or panduriform], apices often mucronate, margins entire, usually revolute, sometimes undulate, bases attenuate to obtuse or truncate, sometimes oblique; petioles distinct, sometimes very short and/or indistinct (especially when leaves linear), without lateral appendages (except in *Vinca*), bases and/or adjacent areas of stem often and variously appendaged, usually with colleters (see footnote 6) [or possibly stipular spines in *Pachypodium*]. Inflorescences terminal or axillary, pedunculate to sessile, 1- to many-flowered, then variously cymose [or racemose]; bracteate or ebracteate; pedicels bracteolate or ebracteolate. Flowers perfect, often large, actinomorphic or nearly so; sepals, petals, and stamens 5 [or sometimes 4], carpels 2 [to 8]. Calyx synsepalous but usually divided nearly to the receptacle, persistent in fruit; lobes with or without squamellae (small, usually scalelike, glandular or nonglandular projections in axils and/or between bases), commonly imbricate basally to various degrees, variously shaped, equal or unequal. Corolla sometimes double (e.g., in *Nerium*), basal $\frac{1}{3}$–$\frac{2}{3}$ united, sometimes with nonglandular pubescence adaxially and/or rarely abaxially, urceolate, campanulate, funnelform, salverform (then tube sometimes widened in 1 or more places) [or infrequently rotate]; tube or throat sometimes with corona (see filaments); lobes alternating with those of calyx, all overlapping either to right or to left in aestivation, and to a lesser extent at anthesis as well [rarely valvate], erect, spreading, or slightly recurved. Stamens alternating with corolla lobes. Filaments distinct, basally adnate to corolla tube, short to very short, terete to flat, straight or curved; corona (i.e., abaxial appendages) sometimes present, basally adnate to and indistinguishable from corolla tube and/or throat, apically free and laminate. Anthers basifixed and usually somewhat movable on filaments; either distinct from one another and free or only slightly adherent to style-stigma head (in Plumerioideae) or adherent to one another and agglutinated to and often forming a cone over style-stigma head (in Apocynoideae), completely fertile[7] (in Plumerioideae, except *Vinca*) or partially sterile (in Apocynoideae, and *Vinca*), more or less introrsely dehiscent, sometimes with apical appendages (most prominently in *Pentalinon*). Pollen tricolporate or sometimes bi- or triporate, released as single grains or tetrads (each type sometimes cohering loosely). Nectaries either absent (or appearing so) or adjacent to ovaries externally; 10 (e.g., in *Echites,* 5 larger, external, and alternating with stamens, and 5 smaller, internal, and opposite stamens), 5 (alternating with stamens and free to variously connate), or 2 (either alternating with carpels and widely spaced or, as in *Allamanda,* opposite them and forming a shallowly 2-notched annulus). Carpels united to various degrees; ovule-bearing region superior to partially inferior [almost completely inferior, for example, in *Plumeria, Himatanthus*], sometimes united to form a unilocular ovary with intrusive, parietal placentae (e.g., in *Allamanda*) [or a bilocular ovary with axile placentae, as in *Carissa*], but much more commonly free, resulting in 2 distinct, unilocular ovaries each with a marginal placenta; non-ovule-bearing region generally united, either differentiated into a single style and often basally umbraculiform style-stigma head (see footnote 4) or (as in *Apocynum*) comprising a clavuncle (see Figure 5e, i). Ovules 1 to many per locule, sometimes pendulous, more or less anatropous, tenuinucellar, and with a single, massive integument; megagametophyte of the Polygonum type. Fruits capsular (e.g., in *Allamanda*) [or baccate, as in *Carissa*] when carpels basally connate, drupaceous (e.g., in *Vallesia,* [*Ochrosia, Rauvolfia, Thevetia*]) or follicular (in remainder of our genera) when carpels basally free; usually 1 carpel developing in *Vallesia* [2 developing and fusing during fruit maturation in *Thevetia*], and 2 developing in remainder of our genera. Seeds 1 to many per developed carpel, variously shaped, those in capsules winged, those in drupes [and berries] naked, and those in follicles glabrous (*Amsonia, Catharanthus, Vinca*) or each with a tuft of trichomes at apex [or at both ends, as in *Alstonia*] [or arillate, as in *Tabernaemontana*]; endosperm nuclear, sometimes with starch (e.g., in *Apocynum*); embryo usually straight, its development of the Caryophyllad type. (Emeticaceae Dulac, Plumeriaceae Horan., and Vincaceae S. F. Gray, "Vincae," are superfluous; excluding Plocospermataceae Hutchinson; including Willughbeiaceae J. G. Agardh, "Willughbejieae.") Type genus: *Apocynum* L.

A family, here considered in the traditional sense (i.e., distinct from the Asclepiadaceae), of perhaps as many as 200 genera and 2000 species distributed primarily throughout the tropics of the world but with some subtropical and

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[7] "Completely fertile" and "partially fertile" or "incompletely fertile" are used here instead of the more commonly used "connective not expanded" and "connective expanded" (or something comparable), respectively, in part because "expanded" parts (and appendages) may not always be derived completely from tissues of the connective (see V. S. Rao & Ganguli).

temperate representatives as well. The plants grow in a variety of habitats including deciduous and rain forests, mangrove and other types of swamps, hammocks, thickets, and fields. A diversity of habits characterizes genera represented in the southeastern United States by plants that are native, naturalized, or escaped from or persistent beyond cultivation (see below and at end of this discussion).

Alstonia (naturally distributed throughout the Old World tropics) is one of a number of genera in the family that consist mostly of large trees, while others including *Carissa* (throughout the Old World tropics and subtropics), *Tabernaemontana* (pantropic), *Nerium* (Mediterranean region), *Ochrosia* (Indonesian region), *Rauvolfia* (pantropic), *Thevetia* (Mexico to Paraguay), and *Vallesia* (New World tropics and subtropics) are composed of smaller trees and shrubs. In many genera most of the species are woody vines. Of these, *Allamanda, Angadenia* Mueller-Arg., *Echites, Rhabdadenia* Mueller-Arg., and *Pentalinon* (*Urechites*) are confined to tropical and subtropical America; *Trachelospermum* includes one species indigenous in the Southeast, while the rest are native to southeastern Asia. Principally herbaceous, temperate and/or subtemperate genera of annuals or perennials include *Amsonia* (southern United States and northern Mexico; one species in Japan and possibly adjacent areas), *Catharanthus* (originally endemic to Madagascar; one species possibly native to India), *Vinca* (mostly Mediterranean), and *Apocynum* (northern Mexico to southern Canada).

The taxonomic history of the Apocynaceae was intertwined with that of the Asclepiadaceae, at least until Robert Brown first established the "Asclepiadeae" on the basis of staminal characters (see discussion of suborder). Brown divided his resulting restricted "Apocineae" into three unnamed divisions on the bases of seed attachment and pubescence (presence or absence and distribution on the seed), but two genera included in two of these are now lumped under *Wrightia* R. Br. Lindley, who was evidently the first to use the family name in its present form, accepted the group as defined by Brown but adopted the infrafamilial classification of Bartling, who established three divisions based on fruit and seed characters. Endlicher refined this approach and subdivided the family on the bases of ovary structure and fruit type into three somewhat rearranged assemblages (each a "subordo" or subfamily), one of which was further divided into four groups (each a "tribus") differing primarily in seed attachment and pubescence (as above). To characters that had been used previously in grouping genera, De Candolle added ones such as placentation, ovule type, and the presence or absence of squamellae in recognizing seven tribes and several subtribes within the family.

Mueller-Argoviensis was evidently the first to incorporate the degree of anther fertility and the direction of corolla-lobe overlap in classifying the Apocynaceae. He divided the family into two unnamed groups primarily on the basis of such characters, and each of these groups into tribes based on a number of others that had been previously used; completely fertile anthers and corolla lobes (mostly) overlapped to the left were indicated for four of the six tribes, while partially sterile anthers and corolla lobes overlapped to the right in part defined the other two. Bentham (in Bentham & Hooker) may have been the first to suspect the importance of anther agglutination to the style-stigma head, although he actually placed less emphasis on the anthers than did Mueller-Argoviensis in the sense that in two of the three tribes he recognized the anthers were said to be completely fertile and free from the style-stigma head (the corolla lobes usually overlapped to the left), while in the third they were partially sterile and agglutinated to this structure (the corolla lobes usually overlapped to the right). The three tribes seemed unnatural, in part because one included both unilocular and bilocular ovaries, another both fleshy and dry fruits, and the third both fused and free carpels (but see Trivedi & Upadhyay, 1977).

In his treatment of South American Apocynaceae, Miers recognized three "classes," one of which was in part characterized by partially fertile, "connivent" anthers; the condition in the other two classes was not specified. On the basis of a wide range of characters, he further divided the family into 21 tribes, a classification that is for the most part unnatural. Asa Gray, on the other hand, was more in line with the trends begun by Mueller-Argoviensis and Bentham (in Bentham & Hooker); he was the first to recognize the full taxonomic value of the anther characters they introduced. Gray established two tribes in the family in his treatment of North American plants, the Plumerieae Gray,[8] with completely fertile anthers free from each other and from the style-stigma head (and corolla lobes overlapped to the left in bud), and the Echiteae Gray (as "Echitideae" [= Apocyneae]), with partially sterile anthers adherent to each other and to the style-stigma head (and corolla lobes almost always overlapped to the right). Division of the family along these lines is generally, but not universally, accepted at present.

Baillon, seemingly unaware of Gray's classification, recognized six "séries" within the Apocynaceae. In five of these the anthers were indicated to be free from the style-stigma head, although they were specifically said to be completely fertile in only three; in the sixth they were reportedly sterile at the base and agglutinated to the style-stigma head.

Schumann elevated Gray's tribes to the level of subfamily, as the Plumerioideae (see footnote 8) and the Echitoideae K. Schum. (= Apocynoideae). The Plumerioideae included three tribes: the Arduineae K. Schum.,[9] with compound ovaries of two carpels; the Pleiocarpeae, with apocarpous ovaries and more than two carpels; and the Plumerieae (as the "Plumiereae"), with apo-

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[8] This name is based on *Plumeria* L., the spelling of which has been variable. Although Linnaeus (Critica Botanica, p. 94. 1737; p. 77 in A. Hort, English translation, 1938) indicated that "*Plumieria*" commemorated the French botanist Charles Plumier, "*Plumeria*" was used in both the first edition of Species Plantarum (**1**: 209. 1753) and the fifth edition of Genera Plantarum (p. 99. 1754), the simultaneous, original places of publication of this name. Therefore, it appears that the alteration in spelling to "*Plumeria*" by Linnaeus was intentional and that it should not be considered an orthographic or typographic error. This being the case, Linnaeus's original spelling (from a nomenclatural point of view, i.e., "*Plumeria*") must be retained (Art. 73.1, ICBN, 1988), even though several authors have used "*Plumieria*," as well as "*Plumiera*."

[9] *Carissa* L. (1767), listed as a synonym of *Arduina* Miller ex L. (1767) by Schumann, is conserved (against *Carandas* Adanson, 1763). The two (*Carissa* and *Arduina*) are based on different types according to *Index Nominum Genericorum*, yet there appears to be no reason why the correct name for the tribe proposed by Schumann should not be Arduineae, as indicated by Schumann, even though most authors have taken up Carisseae for the group, following Pichon.

carpous ovaries and two carpels. Whereas the Arduineae and the Plumerieae were further divided, the Pleiocarpeae were not.

The Arduineae included two subtribes: the Melodininae, with bilocular ovaries, includes 11 genera (one of which, *Arduina* Miller ex L., included *Carissa,* as sect. *Carissa* K. Schum., see footnote 9), and the Landolphiinae, with unilocular ovaries, has nine (including *Allamanda*). The Plumerieae included four subtribes, in the following order: the Alstoniinae K. Schum. (many seeds from each carpel, unappendaged calyces, dry fruits), with 21 genera (e.g., *Alstonia, Amsonia, Catharanthus, Vinca*); the Tabernaemontaninae K. Schum. (many seeds from each carpel, appendaged calyces, fleshy fruits), with six genera (e.g., *Tabernaemontana*); the Rauvolfiinae K. Schum. (as the "Rauwolfiinae") (two or rarely as many as six seeds from each carpel; placentae thin, not intrusive; seeds not peltately attached), with eight genera (e.g., *Rauvolfia, Vallesia*); and the Cerberinae K. Schum. (two or rarely as many as six seeds from each carpel; placentae thick, intrusive; seeds peltately attached), with eight genera (e.g., *Ochrosia, Thevetia*).

It is notable that on the basis of evidence from cytology and stem anatomy involving species in seven genera (including *Alstonia, Catharanthus, Tabernaemontana, Rauvolfia,* and *Thevetia*), Datta & Maiti (1971, 1972) concluded that the subtribes of Plumerieae recognized by Schumann are distinct, and that within this group the Tabernaemontaninae and Rauvolfiinae are the most primitive and the most advanced, respectively; the Cerberinae and the Plumeriinae (= Alstoniinae) were considered intermediate groups, derived from the main line of evolution.

Schumann divided the Echitoideae K. Schum. (= Apocynoideae) into two tribes: the Echiteae (as the "Echitideae," = Apocyneae, anthers not exserted from corolla), with 50 genera (e.g., *Echites, Trachelospermum, Rhabdadenia* [including *Angadenia,* as sect. *Glandulosae* K. Schum.], *Pentalinon, Apocynum, Nerium*); and the Parsonsieae (anthers exserted from corolla), with 12.

Woodson (1930) retained the Plumerioideae (but see below) of Schumann but removed to the Echitoideae all genera of Apocynoideae except *Apocynum* and the closely related *Poacynum* and *Trachomitum.* Hence, he recognized within the Apocynaceae the Echitoideae (calyces rarely, if ever, without squamellae; anthers four-locular at maturity; pollen released as individual grains), the Apocynoideae (calyces always without squamellae; anthers two-locular at maturity; pollen released as tetrads), and the Plumerioideae, in that order.

Although other differences between the Echitoideae and the Apocynoideae were indicated by Woodson (1930), only those having to do with pollen and anther locularity appear to be absolute, and the two subfamilies seem to be more closely related to each other than either is to the Plumerioideae. In addition, the Apocynoideae seem to be most advanced within the Apocynaceae, instead of intermediate and more primitive than the Plumerioideae, especially if release of pollen as tetrads is considered to represent a condition transitional to that seen in the Asclepiadaceae. (Pollen grains are aggregated into and released as pollinia in the Asclepiadaceae, and evidently throughout the family they are arranged as tetrads.) Furthermore, it seems reasonable to suggest that the character states by which the Apocyneae and Parsonsieae of Schumann differ—nonexserted vs. exserted anthers, respectively—are of comparable significance, since the latter condition is also widespread in the Asclepiadaceae.

In view of the foregoing, it would seem most reasonable to retain two subfamilies within the Apocynaceae, the Plumerioideae and the Apocynoideae. If development of persistent tetrads and anther exsertion are considered to be comparable advancements toward the Asclepiadaceae, then it is also reasonable to propose three groups, as tribes, within the Apocynoideae. The Echiteae (pollen released as individual grains, anthers held within united part of corolla) constitutes the most primitive assemblage and includes *Angadenia, Echites, Nerium, Pentalinon, Rhabdadenia, Trachelospermum,* and all the other genera of Schumann's tribe except the three removed by Woodson. Each of the two other tribes is characterized by one of the advancements. The Apocyneae, with persistent tetrads but nonexserted anthers, includes *Apocynum, Poacynum,* and *Trachomitum,* the three genera Woodson removed from Schumann's Echiteae. The Parsonsieae, with exserted anthers but nonpersistent tetrads, corresponds completely to the tribe of the same name as recognized by Schumann. Although additional research is necessary to assess these proposals more rigorously, this classification of the Apocynoideae is adopted here.

Woodson (1930) also rearranged the Plumerioideae of Schumann, recognizing within the subfamily four tribes and two subtribes, instead of three tribes and six subtribes, and employing characters in a slightly different way. Thus, he recognized—in order—the Plumerieae (as the "Plumiereae"; ovaries apocarpous, follicles two), including the Tabernaemontaninae (calyces with squamellae, fruits pulpy) and the Alstoniinae (calyces without squamellae, fruits dry); the Pleiocarpeae (ovaries apocarpous, follicles more than two); the Rauvolfieae Woodson (as the "Rauwolfieae"; ovaries compound, bilocular, and with axile placentation); and the Arduineae (ovary compound, unilocular, and with parietal placentation). Woodson's (1930) treatment is confusing to the extent that he did not list included genera. This is especially significant in the case of the Rauvolfieae, since Schumann's Rauvolfiinae were said to be apocarpous (although in some genera, including *Rauvolfia,* the carpels often fuse during fruit maturation [see A. S. Rao]).

Woodson (1930) not only redefined several of Schumann's groups but, as indicated above, presented a nearly opposite view of the direction of evolutionary changes within the Apocynaceae. Schumann had considered plants with free, completely fertile anthers (the Plumerioideae) to be more primitive than those with fused (to each other and to the style-stigma head), partially sterile ones (the Apocynoideae), while Woodson (1930) held the opposite view. In addition, Schumann had considered members of the Plumerioideae with compound ovaries to be more primitive and those in which the carpels are free to be more advanced, again in contrast to the opinion of Woodson (1930). Debate over the latter issue (summarized below), based primarily on evidence from *Allamanda* provided by Woodson (1930) and more recently by Fallen (1985), seems to have led to better understanding of the course of evolution within the Plumerioideae and throughout the family.

The most recent classification of the Apocynaceae was presented by Pichon in a series of papers appearing over several years (primarily between 1947 and

1953). According to Wagenitz, who adopted the system for his treatment of the family in Engler's *Syllabus der Pflanzenfamilien,* Pichon recognized three subfamilies, thirteen tribes, and many more subtribes in the family. Among the more significant departures from earlier systems was Pichon's recognition of the Cerberoideae Pichon and the Allamandeae. *Cerbera* L., *Ochrosia, Thevetia,* and five other genera had been included by Schumann in the Cerberinae, a group that corresponds only partially to the Cerberoideae of Pichon. Among other differences, the Cerberoideae were defined by a different set of characters, and such genera as *Ochrosia* and *Kopsia,* which were referred by Pichon to the Rauvolfieae, were excluded. As defined by Pichon, the Cerberoideae appear to differ most substantially from the Plumerioideae in relatively minor characters of the anthers (e.g., slightly latrorse vs. clearly introrse dehiscence). The Cerberinae of Schumann were completely ignored in the system of Woodson (1930), and the subfamily of Pichon is not recognized here. Pichon recognized the Allamandeae as a monogeneric, isolated tribe, the most advanced in the Plumerioideae. Although his reasons for doing this were not entirely clear, his treatment presaged the later conclusions of Fallen (1985; discussed below). Also interesting were Pichon's inclusion of *Pleiocarpa* Bentham in the Carisseae (= Arduineae), which was placed first in his system (see below), and his division of the Apocynoideae (as it is circumscribed here) into three tribes (not recognized here) differing in construction of the retinaculum.

The sequence of genera in most early systems, as well as in Schumann's, suggested that in the Apocynaceae simple (i.e., free) ovaries were considered to have been derived from compound (i.e., fused) ones. However, citing as evidence the compound, unilocular ovary of *Allamanda,* Woodson (1930) proposed that the free condition is primitive, that the compound, bilocular ovary with axile placentation is intermediate, and that the compound, unilocular ovary with two parietal placentae along the lines of carpel fusion, as seen in *Allamanda,* is advanced. He suggested that the parietal placentae in *Allamanda* were sterile toward the center of the ovary because they were derived from the evolutionary degeneration of the central part of the septum in a compound, bilocular ovary with axile placentation. That the former type evolved from the latter in the Apocynaceae was also indicated, according to Woodson (1930), by the fact that the ovary in *Allamanda* is bilocular and the placentae axile during early stages of development.

Without reference to Woodson's earlier discussion of *Allamanda,* Woodson & Moore (p. 151) stated that "in frequent instances [taxa unspecified] one finds that a compound ovary is bilocular at both base and apex, where placentation is axile, but unilocular in the middle where placentation is parietal." It is also notable that Woodson & Moore provided micrographic evidence of a unilocular ovary with parietal placentae in *Lacmellia edulis* Karsten, apparently unaware that Schumann had included the genus in his Melodininae, in which the ovaries are supposedly bilocular. These and other considerations suggest that gynoecial evolution within the Apocynaceae could be clarified by careful substantiation of the basic data involved.

Fallen (1985) argued that neither of the contrasting evolutionary sequences outlined above for the Apocynaceae (i.e., ovaries simple to compound, or the reverse) is entirely correct. She demonstrated that in the ovule-bearing region in flowers of *Allamanda Schottii* Pohl, epidermal cells can be recognized where the two carpels meet and are fused, and the carpels in this region are actually free in the earliest stages of their differentiation, suggesting that at least in this case simple (free) ovaries are (more immediately) ancestral. However, in other Apocynaceae with compound ovaries, such cells have evidently not been reported, and in addition, the carpels in the ovule-bearing region are fused even in the earliest stages of their development, suggesting that in these groups the ovaries either are primitively compound or are further evolved from their ancestors with simple ovaries. Thus, she considered gynoecial evolution in the Apocynaceae to have proceeded from a primitively compound ovary to one in which the carpels are free in the ovule-bearing region, and from there to an advanced compound condition in *Allamanda.* The ovary in *Allamanda* is not comparable to that seen in other Apocynaceae with compound ovaries, as is further evidenced by the fact that, at least in *A. Schottii,* the carpels fuse in the ovule-bearing region without ever closing; while such a developmental pattern is common in the Gentianaceae, it has not been reported in other Apocynaceae.[10] The absence in other genera of Apocynaceae of the gynoecial features summarized above for *Allamanda* needs to be substantiated.

An alternative and at least potentially more reasonable interpretation of the course of gynoecial evolution within the Apocynaceae—one that has not been specifically presented in this debate—is suggested by conditions in the Pleiocarpeae and the Asclepiadaceae. It is to some extent surprising that the former group, with more than two simple (free) ovaries, is placed in an intermediate position in the treatments of both Schumann and Woodson (1930); it seems more consistent with modern concepts to regard such a condition as less specialized than the others seen in the Apocynaceae. In addition, it would seem that if the Asclepiadaceae, with two simple ovaries, are considered to have been derived from the Apocynaceae, such a condition should characterize the more advanced groups within the latter. It is notable in this regard that Pichon (1948a) placed *Pleiocarpa* in the Carisseae, the first (i.e., presumably most primitive) tribe of Apocynaceae treated, and that Corner regarded *Lepina* Dcne., included in the Pleiocarpeae by Schumann, to be one of the more primitive genera of Apocynaceae on the basis of its gynoecium, which consists of three or four carpels that separate widely in the ovule-bearing region during fruit maturation.

Rather than proposing—in an attempt to explain an independent origin of compound ovaries in *Allamanda*—that evolution of the ovary within the Apocynaceae proceeded from compound to simple, and from there to an advanced compound condition in *Allamanda,* it is more parsimonious to suggest that the main line of evolution within the family was from gynoecia with more than

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[10] An isolated position within the Apocynaceae for *Allamanda* is also suggested by its unique fruit type (a capsule), as well as by evidence from chemistry and androecial morphology (see discussion of *Allamanda*). That it in particular does not belong with other members of Schumann's Arduineae (i.e., other Apocynaceae with compound ovaries) is perhaps suggested by cytological and geographic evidence summarized by Van der Laan & Arends (see discussion of cytology below).

two simple ovaries, as in the Pleiocarpeae, to those with two simple ovaries, as seen in advanced Plumerioideae, Apocynoideae, and the Asclepiadaceae. The compound, bilocular ovary with axile placentation present in the Melodininae of Schumann and the compound, unilocular ovary with parietal placentation characterizing *Allamanda* (and perhaps other genera in Schumann's Landolphiinae; see Monachino, 1945) then might be viewed as two distinct branches from the main line, separately derived from a gynoecium of two simple ovaries within the Plumerioideae. (Even though the gynoecium of *Allamanda* may have passed through an intermediate condition of bilocularity and axile placentation, that intermediate appears not to have been related to the Melodinineae.) Additional research aimed toward assessment of these proposals would not only help clarify relationships within the Apocynaceae but would also illuminate the family's ancestry as well. (See also discussion of nectaries, below.)

Walker's (1975a, b, c; 1978) ontogenetic studies on *Catharanthus roseus* have suggested that in this species and perhaps throughout the family, evolution in the nonovuliferous (apical) region of the gynoecium (uppermost part of the ovaries, at least in *C. roseus,* in addition to the style and style-stigma head) has proceeded from a free to a fused condition. Remnants of cuticle and the lack of plasmodesmata between adjacent but independently derived cells in the fused portion of the ovaries, as well as other evidence, apparently indicate that carpel fusion was developmentally superimposed onto an apocarpous condition. Such a conclusion was also supported by experiments in which the surgical destruction of one carpel primordium prior to carpel fusion only slightly affected development of the other. The single carpel differentiated into an ovary, style, and style-stigma head, although the shapes of these structures were slightly unusual, the pubescence of the style-stigma head was irregular, and the umbraculiform structure at the base of the style-stigma head was not formed on the side normally fused with the other carpel. That the normally fused surface of the developed carpel was abnormal indicated genetically based "accommodations" for fusion and, therefore, perhaps a trend from facultative to obligate apical syncarpy in the evolutionary history of this species and possibly the entire family.

The functional significance of the peculiar structure of the gynoecium (basally free but apically united in most Apocynaceae and all Asclepiadaceae) has not been clearly established. The general predominance among angiosperms of gynoecia with variously fused carpels suggests that they are adaptively superior to those in which the carpels are free.

Endress proposed that the suggested superiority of fused carpels results from four general advantages conferred by the condition, at least two of which have to do with the apical, nonovuliferous portion of the gynoecium in particular. In one of these, competition between pollen tubes is intensified in the common growth space resulting from such fusion. That is, fertilizations are effected by the most fit pollen tubes from a single, unified competition rather than from each of a number of separate competitions. The second advantage is the presumed ability of pollen on any part of the stigmatic surface to fertilize ovules in any carpel within the flower—clearly a plus if pollen is limited. In fact, Walker's (1978) experiments on *Catharanthus roseus* demonstrated that pollen tubes are completely uninhibited in growing from one carpel to the other.

According to Endress, one of the other advantages of carpel fusion has to do with resource economy and the entire gynoecium; that is, relatively less wall tissue is produced when the carpels are fused. The fourth advantage results from the fact that a more diverse set of fruit types may be evolved in the case of compound ovaries.

Despite the foregoing, certain advantages are also conferred by gynoecia with free carpels (Endress *et al.*). In such gynoecia ovaries in which few or no ovules have been fertilized need not needlessly consume resources by participating in fruit maturation, and those destroyed by predation need not jeopardize normal development of the others. Thus, since the foregoing suggests that it is at least conceivable that in some instances apocarpy developed from syncarpy, considerations of selective advantage alone cannot resolve the debate concerning the course of gynoecial evolution in the Apocynaceae. In any case, it is reasonable to suggest that in most members of the family the advantages of apically fused gynoecia during anthesis have been combined with those of free ovaries during fruit maturation, and that selection has favored maintenance of this combination in the Asclepiadaceae as well.

Schick (1980) originally recognized two types of style apices (here, style-stigma heads) in the family, a *Plumeria* type and an *Allamanda-Nerium* type, but later (1982) considered those in the series *Plumeria, Catharanthus, Vinca, Thevetia, Allamanda,* and the Apocynoideae to represent a progression from more primitive to more advanced. In all but the putatively primitive "plumerioid" genera, the style-stigma head consists of a stigmatic chamber at the base, a pollen depository at the apex, and an adhesive zone between. The adhesive zone, believed to have been stigmatic originally, was thought by Schick (1982) to effect the attachment of pollen to insects and therefore to be functionally comparable (analogous) to the translator arms (and probably the corpusculum as well) of the Asclepiadaceae. Ultrastructural and biochemical evidence also provided by Schick (1982) suggested that the adhesive zone and the translator arms are homologous as well and that the condition in the Periplocoideae is transitional. Schick's (1982) account of pollination in *Vinca minor* is very similar to but less detailed than that outlined here for *Apocynum,* in the discussion of that genus.

Largely on the basis of anatomical evidence from flowers of *Apocynum androsaemifolium* L. and *A. cannabinum* L., Woodson (1930) interpreted the nectaries in the genus and throughout the family to represent a whorl of vestigial carpels. According to him, the nectaries and carpels are composed of a similar number and type of glandular cells and differentiate from the receptacle simultaneously and in a comparable manner. In addition, three vascular traces of similar origin and orientation were said to serve each. However, while the nectary traces were shown to arise as a single branch from corolla traces, later dividing into three (one central and two lateral, the lateral ones largely disorganized at anthesis), the three traces of each carpel were depicted as having more independent origins. Woodson (1930) mentioned but did not accept an alternate interpretation, at least for the condition in *Apocynum,* whereby the nectaries because of their number (five) and position (alternating with the stamens) would be considered vestigial staminodia. It is notable that Legget (1872b) had suggested earlier that the nectaries of *Apocynum androsaemifolium* probably represented an "inner whorl of stamens."

Woodson & Moore later provided evidence from comparative morphology to support the presumed homology between carpels and nectaries in the Apocynaceae. Among flowers produced by a single plant of *Pleiocarpa mutica* Bentham, they reported gradual transitions from those with four fertile carpels to those with two fertile carpels alternating with two sterile "carpellodes." Indeed, the nectaries of *Catharanthus* and *Vinca* are very similar in appearance to carpels; according to Woodson & Moore they differ from the carpellodes reported in *Pleiocarpa* only to the extent that they are not connected (and, hence, presumably do not contribute) to the style.

Based on acceptance of the proposal that the nectaries, which are common and widespread in the Apocynaceae, do in fact represent vestigial carpels, Woodson & Moore concluded that polycarpy probably represents the ancestral condition in the family. However, they did not comment on the systematic position of the Pleiocarpeae *per se*, a polycarpous tribe of intermediate placement in the schemes of both Woodson (1930) and Schumann that is here considered primitive (see also discussion above).

Various adaxial appendages of the corolla and calyx have long attracted the attention of systematists. Those of the corolla, which are not known to be glandular, include, for example, the petaloid, laciniate structures (the "corona") exserted from the throat in *Nerium*; the deltate, transversely oriented flaps that meet above the anthers, nearly completely sealing the tube at its summit in *Thevetia*; and the pointed projections near the base of the tube in *Apocynum*. Although some (for example, those of *Apocynum, Trachomitum,* and perhaps *Poacynum*) are opposite the lobes of the corolla (i.e., alternating with the stamens) and not vascularized, the majority are marginally inserted (more or less opposite the stamens) and are served by extensions of the lateral veins in each petal. The latter observations led Woodson & Moore to conclude that all appendages of the corolla in the Apocynaceae are homologous to stipules. Among the genera that include plants native to or at least persisting out of cultivation in the southeastern United States, *Thevetia, Nerium,* and *Apocynum* have appendiculate corollas.

Unlike the appendages of the corolla, those of the calyx (the squamellae) are usually glandular and relatively inconspicuous. They arise from the very base of the calyx, toward or at the margin or center of each lobe, or both. Although they usually lack vascular tissue, in some extraregional species they have small traces that extend from the lateral veins of each sepal. Therefore, they too were interpreted as being homologous to stipules by Woodson & Moore, instead of to stamens as Woodson (1930) had earlier proposed. On the basis of such an interpretation, squamellae at or near the margins were considered by Woodson & Moore to be primitive, since such a position is similar to that of true stipules, while those located at or near the center of each sepal, the most common condition in the family, were considered to be advanced; the more or less continuous distribution of squamellae around the base of the calyx was envisioned to have resulted from what they called (p. 148) "developmental laceration" of either type.

Despite the foregoing phylogenetic implications, only the presence or absence of squamellae has been indicated in major floristic and monographic accounts of the Apocynaceae, including Woodson's (1938b) for North America. Although this character has been employed mostly at the generic level, it is perhaps of some importance at higher taxonomic levels as well. Squamellae are rare within the Plumerioideae, with the exception that in the Tabernaemontaninae they are universally—or very nearly so—present (see Schumann). Within the Apocynoideae, on the other hand, they are present in at least some species of perhaps 12 genera of Parsonsieae but are sporadic in the Echiteae (of about 50 genera, 30 have all species squamelliferous, four have some, and perhaps 16 have none) and absent in the Apocyneae, as these groups are circumscribed here. Among genera native to or at least persisting outside of cultivation in the southeastern United States, squamellae are present in representatives of *Carissa* (in which they are otherwise rare), *Tabernaemontana,* and *Thevetia* of the Plumerioideae, and *Echites, Trachelospermum, Angadenia, Pentalinon,* and *Nerium* of the Echiteae.

With respect to vascularization of the calyx, Woodson & Moore recognized four general but taxonomically unimportant types of organization within the Apocynaceae. Although all are unilacunar, there is evidently a fairly gradual transition in the family from a three- to a one-trace condition associated with each sepal. In addition, the four types appear to cross many taxonomic lines, and different combinations of at least two of the types have been reported by Woodson (in Woodson & Moore) from a single inflorescence of *Rauvolfia tetraphylla* L.

Cytological data from the Apocynaceae have been reviewed most recently by Van der Laan & Arends, who provided 520 records (many of them new) for 189 species and 62 genera. The following is based primarily on that account, as well as on a fairly extensive and in part nonoverlapping compilation by Hamel (1984).

In general, the systematic value of chromosome morphology appears to be minimal, with the possible exception that in a group of genera corresponding to the Tabernaemontaninae of Schumann, the chromosomes are sometimes especially long (1–3 μm, vs. 1–2 in the rest of the family) and then occasionally include a single pair in which the centromeres are terminal or subterminal (instead of submetacentric, the usual condition). Although secondary constrictions and satellites have not been detected in a majority of the species investigated, one or two per cell have been indicated for species in six genera in the Plumerioideae, including ones in the Melodininae and Landolphiinae of the Arduineae and the Alstoniinae, Rauvolfiinae, and Tabernaemontaninae of the Plumerieae, as well as in one genus in the Parsonsieae of the Apocynoideae.

Most genera in the Apocynaceae (exceptions include *Alstonia, Apocynum,* and *Ochrosia*), including all investigated genera with discontinuous geographic ranges (such as *Amsonia, Carissa, Catharanthus,* and *Nerium*), are characterized by a single base chromosome number; data for outlying species in a few genera with such ranges (e.g., *Trachelospermum difforme* (Walter) Gray, of southeastern North America, and *Vinca erecta* Regel & Schmalh., of Afghanistan) are not available.

It is evident that infrageneric polyploidy is uncommon in the family, since it has been reported in only eight of the 62 genera investigated, including *Allamanda* ($2n$ = 18, 36), *Alstonia* ($2n$ = 22, 42, 44, 48), *Carissa* ($2n$ = 22, 66), *Tabernaemontana* ($2n$ = 22, 33, 66), and *Rauvolfia* ($2n$ = 22, 44, 66, 88; in addition to 20, 24, 55, 68, according to Hamel, 1984). Cytotypes or chromosomal races (i.e., infraspecific polyploidy) occur even less commonly, having been reported in but one species of *Alstonia* and four of *Rauvolfia*, and probably have arisen exclusively from autopolyploidization.

The base chromosome number x = 11 has been the only one determined in about 60 percent of the 62 genera for which such data are available, including all three of the Pleiocarpeae, all 11 of the Arduineae, and all six of the Tabernaemontaninae; other genera with this number include *Alstonia* (along with x = 20 and 21), *Amsonia, Rauvolfia, Vallesia, Nerium,* and *Apocynum* (along with x = 8). About 12 percent of the 62 genera have x = 10 (e.g., *Ochrosia, Thevetia, Trachelospermum*), eight percent have x = 9 (e.g., *Plumeria, Allamanda*), and five percent have x = 8 (e.g., *Catharanthus, Apocynum* in part); one to three percent have x = 6 (only *Echites* and *Pentalinon*), 12 (from x = 6 in some cases, from x = 11 in others), 16 (from x = 8), 18 (from x = 9), 20 (from x = 10; only *Cerbera* and *Alstonia* in part), 21 (from the unreported x = 22; only *Alstonia* in part), or 23 (also from the hypothetical x = 22; only *Vinca*).

The rather widespread occurrence of the base number x = 11, as well as its apparent universality among genera considered here to be most primitive (i.e., the Pleiocarpeae and Arduineae of Schumann) on the bases of morphological and, according to Leeuwenberg (in Van der Laan & Arends, p. 34), chemical evidence, suggests that it is the primitive or ancestral number within the family. Evidently no correlation exists between derived life forms and derived chromosome numbers within the family.

Only three of 35 investigated genera (of a total of about 40) represented in Africa include base chromosome numbers other than 11. Even so, it would be premature to propose on that basis an origin for the family on that continent primarily because non-African genera are not nearly as well known cytologically. Nevertheless, of 12 investigated genera restricted to America (of about 55), just two have x = 11 only (*Apocynum* has x = 8 and 11); similarly, of six strictly Asian genera (of about 50), only one has this number and no other (one has x = 10 and 11).

Cytological data as reviewed by Van der Laan & Arends also bear on the problem of the systematic position of *Allamanda* (discussed above). According to their scheme, the base number x = 9 was derived from x = 10, which in turn developed from x = 11. All genera with compound ovaries investigated have x = 11 and a primarily African distribution, except *Allamanda,* which has x = 9 and is restricted to the New World. For these reasons, and because x = 10 has been reported only for genera with simple ovaries, an independent origin for compound ovaries in *Allamanda* is suggested.

It is perhaps significant that a base number of x = 9 was reported for only two other genera, *Himatanthus* and *Plumeria*, each naturally distributed in the American tropics and subtropics. The ovaries in these two genera are simple and approach complete inferiority more closely than any others in the family. Although it is unclear whether or how this condition is related to that in *Allamanda*, it is notable that *Allamanda* and *Plumeria* have in common a number of rather rare iridoids (see discussion of *Allamanda*). Nevertheless, Van der Laan & Arends presented an unpublished classification by Leeuwenberg in which *Himatanthus* and *Plumeria* were included in the Plumeriinae, and *Allamanda* was placed alone in the Allamandeae, far removed from other genera with compound ovaries.

Terpenes and various other compounds of terpene origin are well represented and in some cases are systematically important in the Apocynaceae. Iridoid monoterpene glycosides and indole alkaloids characterize the order Gentianales as it is defined here and generally, occurring in all families except the Asclepiadaceae (but see Cronquist, who attributed indole alkaloids to the Asclepiadaceae as well) and perhaps the Buddlejaceae (e.g., they occur in the Menyanthaceae, Loganiaceae *sensu stricto*, Rubiaceae, Gentianaceae, and Apocynaceae; so-called tylophorine alkaloids are reportedly unique to the Asclepiadaceae). Cardiac glycosides occur in the Apocynaceae (see Bisset, 1957, 1961a), Asclepiadaceae, and ten other families of flowering plants (see discussion of suborder). Monoterpenes (noniridoid types), diterpenes, sesquiterpenes, sesquiterpene lactones, and several other terpenoids (perhaps including saponins, see below) have evidently not been found in the Apocynaceae or the Asclepiadaceae (see Dahlgren *et al.* for other compounds absent from these two families). Although present in all groups of land plants (Seigler), triterpenes other than saponins are often taxonomically important and should be investigated in the Apocynaceae. Several were indicated by Gibbs for the family and for the Asclepiadaceae, and one of them (bauerenyl-acetate) may be unique to the Apocynaceae. According to Harborne, Reichstein found triterpenoids to be of value at and below the level of species in the primarily African genus *Acokanthera* G. Don.

Unlike common monoterpenes, which are found in the essential oils of a great diversity of plants exclusive of the Apocynaceae and the Asclepiadaceae, iridoid monoterpenes appear to be restricted to about 40 families of flowering plants, including the Apocynaceae but not the Asclepiadaceae (Seigler). Jensen and colleagues recognized ten major groups, most reported from a variety of families, in their compilation of the literature about these compounds. One group included both primitive and unclassified types, five others comprised those with relatively simple structures ("carbocyclic iridoids"), and the remaining four included more complex types ("seco-iridoids").

Iridoid monoterpenes of the primitive or unclassified group indicated by Jensen and colleagues for the Apocynaceae included loganin (*Catharanthus*, *Rhazya* Dcne., *Vinca*), desoxy-loganin (*Vinca*), ketologanin (*Vinca*), and "iridoid pyridine alkaloids" (*Rauvolfia*). Carbocyclic iridoids reported for the family included aucubin (*Thevetia*), theviridoside (*Cerbera*, *Thevetia*), daphylloside (*Alstonia*), and plumieride (*Allamanda*, *Plumeria*). The seco-iridoids, all ultimately derived from loganin, were divided into a relatively simple group including secologanin (*Catharanthus, Rhazya, Vinca*) and three more groups each derived from secologanin. One of these included sweroside (*Vinca*), while another ("complex iridoid alkaloids") was for the most part composed of compounds biosynthesized by condensations of secologanin and either tryptophane or tryptamine to yield indole (and other types of) alkaloids.

Indole alkaloids have been extensively investigated, primarily because of their considerable economic and medicinal value. Those characterized by relatively simple structures comprise one of two classes recognized by Kisakürek and co-workers (see below) and are quite widespread, having been detected in the Apocynaceae and nine other families including the Loganiaceae and Rubiaceae but not the Asclepiadaceae. Indole alkaloids with more complex structures (i.e., those with either tryptamine or trytophan as the indole unit and either a C_9- or a C_{10}-monoterpene moiety derived from secologanin as the other) make up the second class and have been reported from the Apocynaceae, Loganiaceae, and Rubiaceae almost exclusively. Within the Apocynaceae, the two classes of indole alkaloids have evidently been reported only in the Plumerioideae; steroidal types characterize the Apocynoideae (Kisakürek *et al.*).

A tremendous amount of literature about complex indole alkaloids in the Apocynaceae, Loganiaceae, and Rubiaceae had accumulated by the end of 1978. It was reviewed by Kisakürek and colleagues (754 papers cited), who took into account the absolute configurations and biogenesis of these compounds in attempting to interpret the data for the first time within a systematic context, using the classification of Pichon to assess relationships within the Apocynaceae.[11]

Kisakürek and colleagues recognized eight different skeletal types among the 1200 complex indole alkaloids isolated from the Apocynaceae, Loganiaceae, and Rubiaceae, including those with so-called nonrearranged and rearranged secologanin skeletons. This and other evidence led them to conclude that the Loganiaceae should be considered ancestral to both the Apocynaceae and the Rubiaceae, but more closely related to the former. It was also suggested that of the four tribes of Pichon investigated, the Carisseae (= Arduineae) do not correspond particularly well to any of the groups of genera recognized by Schumann but the Plumerieae, Rauvolfieae, and Tabernaemontaneae (K. Schum.) generally do.

The tribe Arduineae was considered by Kisakürek and co-workers to be closely linked to the Loganiaceae and to be primitive within the Apocynaceae. It is notable in this regard that *Pleiocarpa* was considered most typical of (most primitive within) this primitive tribe. While this would be consistent with the proposal that the ovary of more than two free carpels characterizing the Pleiocarpeae is primitive (see above), it is not consistent with many other classifi-

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[11] Extensive and detailed accounts of the occurrence of alkaloids in general in the Apocynaceae had been previously compiled by, for example, Bisset (1958, 1961b), Willaman & Li, and Willaman & Schubert. Although these treatments considered the taxonomic implications to various extents, each was primarily a listing of compounds by taxa. Less substantial accounts had been provided by Farnsworth, Ganzinger & Hesse, Jensen and co-workers, Raffauf (1970), Raffauf & Flagler, and Taylor & Farnsworth (1973, 1975).

cations, including those of Schumann and of Woodson (1930), in which the Pleiocarpeae were placed in a more intermediate position within the family.

Complex indole alkaloids also suggested to Kisakürek and colleagues that the Plumerieae are more advanced than the Arduineae, and that the tribe may have a profile of skeletal types unique among the four tribes of Pichon that were investigated. Alkaloids of the ibogan skeletal type, evidently characteristic of the Tabernaemontaneae, had been reported for only two genera in the Plumerieae, *Alstonia* and *Catharanthus.* Both ibogan and bisindole alkaloids have been reported for *Catharanthus* but not *Vinca,* thus supporting maintenance of the two as distinct (see also discussion of *Catharanthus*).

The Rauvolfieae were interpreted by Kisakürek and colleagues as being more advanced than the Plumerieae and as lacking ibogan alkaloids (the indication of such compounds for *Vallesia* apparently was a mistake). The characteristic presence of these alkaloids, as well as a unique emphasis on rearranged secologanin skeletons in the Tabernaemontaneae, led them to propose tentative elevation of the group to the rank of subfamily.

On the basis of "evolutionary advancement parameters" calculated (using both degree of skeletal specialization and level of oxidation) for each of the indole alkaloids considered by Kisakürek and co-workers, Bolzani and colleagues later proposed for the Apocynaceae a position closer to the Rubiaceae and farther from the Loganiaceae. Both the calculations of Bolzani and colleagues and other measures based on morphology suggested a relatively low level of advancement for the Rubiaceae, followed in order by the Apocynaceae and the Loganiaceae, also in contrast to the proposals of Kisakürek and co-workers. The calculations of Bolzani and colleagues also suggested that the Arduineae are most primitive within the Apocynaceae, followed in order by the Plumerieae, Rauvolfieae, and Tabernaemontaneae.

Bate-Smith tested leaf material from a large number of species of Apocynaceae, including many represented in the southeastern United States, for phenolic compounds. He found that members of the family produce leucoanthocyanins but lack the trihydroxy constituents leucodelphinidin, myrcetin, and ellagic acid. Other phenolics detected in a majority of the species of Apocynaceae screened include quercetin, kaempferol, and caffeic acid. Cyanidin, an anthocyanin, was reported in only one of nine species of Plumerioideae tested but in five of six in the Apocynoideae. Conversely, whereas *p*-coumaric, sinapic, and ferulic acids were found in a majority of the species of Plumerioideae analyzed, they were mostly absent in the Apocynoideae. In the Apocynaceae *p*-coumaric acid, scopoletin, and possibly luteolin, as well as the anthocyanins delphinidin, hirsutidin, malvidin, and petunidin, have also been detected (Bate-Smith; Carew & Krueger; Gibbs; Farnsworth, in Taylor & Farnsworth, 1973).

Daniel & Sabnis sought phenolics (flavonoids and phenolic acids) in leaf material of 22 species (including a number represented in the Southeast) belonging to 11 genera of Plumerioideae and eight of Apocynoideae. Kaempferol and *p*-coumaric acid appeared to be better represented in the former (they were detected in eight vs. two genera and four vs. one, respectively); glycoflavones, leucoanthocyanins, and three phenolic acids (protocatechuric, gentisic, and sinapic) seemed more common in the latter (one vs. three, three vs. six, two vs. four, one vs. five, and two vs. five genera, respectively). Some compounds were detected only in the Plumerioideae: isorhamnetin in one genus, caffeic acid in another, and α-resorcyclic acid in two others. Several flavonoids were about equally distributed in the Plumerioideae and the Apocynoideae, including quercetin (in eight vs. five genera, respectively), tamarixetin (one vs. one), apigenin (one vs. one), and luteolin (one vs. one), as were the phenolic acids vanillic (ten vs. eight), syringic (11 vs. eight), 2-hydroxy, 6-methoxy (two vs. two), salicylic (two vs. two), melilotic (one vs. one), and *o*-coumaric (two vs. two). Ferulic and *p*-hydroxy benzoic acids were detected in five and seven genera of Plumerioideae and five and two of Apocynoideae, respectively.

According to information compiled by Gibbs, cyanogenesis is relatively rare in the Apocynaceae. Although it had been reported for six genera in the family, including *Alstonia* and *Nerium*, Gibbs's results were positive for only one, an extraregional member of *Alstonia*, and negative or probably negative for nine others, including *Catharanthus*, *Echites*, and *Rauvolfia*.

Gibbs also reported that whereas others had reported saponins from a variety of organs in ten genera of Apocynaceae (including *Alstonia* and *Vinca*) and the probable absence of such compounds in 23 others (including *Allamanda, Alstonia, Amsonia, Apocynum, Carissa, Tabernaemontana, Ochrosia, Rauvolfia,* and *Thevetia*), his own tests using leaf material indicated that they were possibly present in *Allamanda, Nerium,* and *R. verticillata* Baillon but absent or probably so in *Amsonia, Carissa, Catharanthus,* and *R. vomitoria* Afz.

There appears to be some question regarding the occurrence of tannins in the Apocynaceae. According to Gibbs, some reports indicated their absence from species in 14 genera in the family (including *Allamanda, Alstonia, Ochrosia, Rauvolfia, Thevetia, Vallesia,* and *Vinca*), while others indicated their presence in those of six (including *Allamanda, Apocynum, Carissa,* and *Trachelospermum*). His own tests for tannins yielded positive results for species of *Allamanda, Amsonia, Carissa,* and *Nerium* but were equivocal in the cases of *Catharanthus* and *Vinca*. Farnsworth indicated that tannins had been reported in *V. minor*, but he and colleagues failed to detect them in *V. major* (see below). Cronquist stated that the Apocynaceae were not tanniferous.

Other tests conducted by Gibbs indicated that compounds such as syringin, juglone (a naphthaquinone), and aucubin or related substances are probably not produced by members of the Apocynaceae, although he noted that other researchers had reported plumbagin (another naphthaquinone) from an extraregional species of *Rauvolfia* and various aucubin glycosides from genera including *Alstonia* and *Thevetia*.

Farnsworth and colleagues screened leaves and stems of Yugoslavian plants of *Vinca major* for many compounds. Although they confirmed the presence in the species of alkaloids, saponins, unsaturated sterols, organic acids, and phenols, they were unable to detect tannins, flavonols, or cardiac glycosides.

The distribution of polyalcohols, in particular the nonaliphatic types (cyclitols), was considered within a systematic context by Plouvier. One cyclitol, conduritol, had been reported by the time of that review only from the Asclepiadaceae (*Gonolobus* Michx.), while five others, all methyl ethers of inositol, had been detected in the Apocynaceae. Although D-bornesitol had been found only in the Rubiaceae and in both subfamilies of the Apocynaceae (in genera including *Amsonia* and *Vinca*), L-bornesitol had been detected in the Proteaceae, Leguminosae, Rhamnaceae, Boraginaceae, and Apocynaceae (only in *Apocynum*; it has since been reported by Nishibe and co-workers from *Catharanthus* and a Japanese species of *Amsonia*); dambonitol had been reported in the Moraceae and both subfamilies of the Apocynaceae (in genera including *Nerium, Trachelospermum,* and *Vinca*). The two other inositol methyl ethers recorded for the Apocynaceae evidently have wider distributions: L-quebrachitol had been found in 11 families of flowering plants, but within the Apocynaceae only in three (extraregional) genera of the Plumerioideae, and D-pinitol, known from six gymnosperm and 13 angiosperm families, had been detected in the Apocynaceae only in *Landolphia* Beauv.

Information about the fatty acids of seed oils obtained from species of *Catharanthus, Nerium, Rauvolfia* and four other genera of Apocynaceae was provided by Daulatabad & Ankalgi. Although palmitic, oleic, linoleic, and stearic acids, all very widespread among angiosperms in general, were indicated for the nine species involved, lauric, myristic, arachidic, and behenic, each with a more restricted distribution, were reported only for the three (including *C. roseus* and *R. tetraphylla*) they themselves analyzed. Although Gibbs did not claim to list each occurrence of these seed-oil compounds, it is notable that the Apocynaceae escaped mention in his account.

Regarding circumscription and ordering of subfamilies, tribes, and subtribes of Apocynaceae, it is primarily Schumann's system that is adopted here, with a few exceptions. Within the Plumerioideae, the more primitive of the two subfamilies, the extraregional Pleiocarpeae are considered to be most primitive, instead of intermediate. The ordering of two of the four subtribes of Plumerieae has also been changed, due to considerations of plants in the Southeast. Despite the fact that much of the evidence summarized above suggests that the Rauvolfiinae are more advanced than the Alstoniinae, in this treatment the order is reversed because *Vallesia,* the genus of Rauvolfiinae treated here, seems more primitive than *Amsonia, Catharanthus,* and *Vinca,* the genera of Alstoniinae considered. Following Pichon, *Allamanda* has been placed in its own tribe and positioned as the most advanced group within the Plumerioideae.

Three tribes (Echiteae, Parsonsieae, Apocyneae), instead of the two recognized by Schumann, have been recognized in the Apocynoideae. Two of these are represented in the Southeast: the Echiteae, by *Angadenia, Echites, Pentalinon* (*Urechites*), *Rhabdadenia,* and *Trachelospermum,* and the Apocyneae, by *Apocynum.*

In the southeastern United States, the Apocynaceae are represented by indigenous species in the genera *Amsonia, Angadenia, Apocynum, Echites, Pentalinon, Rhabdadenia, Trachelospermum,* and *Vallesia,* and by naturalized plants in *Allamanda, Catharanthus,* and *Vinca.* Whereas several primarily tropical or subtropical genera (*Allamanda, Echites, Pentalinon, Rhabdadenia, Vallesia*) are represented in our area by native or naturalized species solely in Florida, two species of the temperate genus *Vinca* (*V. minor* and *V. major*) that are naturalized throughout much of North America appear not to be so established in Florida or perhaps other of the more southern parts of the Southeast.

In addition to native and naturalized Apocynaceae, an especially large number of species have escaped from or persisted beyond cultivation, particularly in Florida, without having become truly naturalized. At least *Trachelospermum jasminoides* (Lindley) Lem. belongs to a genus represented in the Southeast by native or naturalized plants, while several others (briefly discussed below; included as bracketed entries in the key) do not.

Carissa (subtribe Melodininae), a genus of about 35 species of usually armed shrubs and small trees, is native to warm, dry areas in Africa, Asia, and Australia. I have seen specimens indicating that in southern Florida (e.g., Dade and Lee counties) *C. grandiflora* (E. Meyer) A. DC. (*C. macrocarpa* (Ecklon) A. DC., according to Palmer & Pitman), which is widely grown in this region, sometimes persists beyond cultivation. In addition, according to Judd (pers. comm.) the species fruits abundantly and is a rare escape in this area. Information on the label of an essentially sterile specimen (*Rhoades & West 6/8/28*, FLAS) perhaps assignable to *C. Arduina* Lam. or *C. bispinosa* (L.) Desf. ex Brenan, two species with smaller flowers and fruits than *C. grandiflora*, according to Bailey, indicates that the plant was naturalized somewhere in Florida ("Tropie"). Plants of *C. Carandas* L. (fruits 1.3–2.6 vs. 2.6–5.2 cm long in *C. grandiflora*), are frequently cultivated in Florida but evidently do not escape. The structures usually referred to as spines appear instead to be thorns (that is, they are homologous to stems and not leaves). They develop from accessory buds, according to Jain *et al.*, and are modified inflorescence axes *fide* Palmer & Pitman. They are present on all material I have seen from Florida and are usually bifurcate and axillary.

Alstonia (Alstoniinae), a genus of 30–40 species of large trees, is distributed throughout the tropics of the Old World, especially in the western Pacific region. It is represented in our area by *A. macrophylla* Wall. ex G. Don, a species that, after its intentional introduction to Sri Lanka for its valuable timber, has become one of the most prominent naturalized elements of the secondary rain forest there (Huber). Specimens collected in Florida indicate that it has escaped from cultivation on numerous occasions. Judd (pers. comm.) observed that cultivated plants in Miami grow rapidly and flower and fruit regularly; he believes that they could easily become established from the wind-dispersed seeds in many disturbed habitats in the area.

Considered here in the broad sense to include *Ervatamia*, *Tabernaemontana* (Tabernaemontaninae) is a pantropic genus of about 230 species of small trees and shrubs. (Nowicke recognized both *Tabernaemontana*, with about 140 species in the American and African tropics, and *Ervatamia*, comprising approximately 90 species distributed from Asia to Australia and New Zealand.) I have seen one specimen (*Hansen & Robinson 8473*, FLAS) that was considered by the collectors to be a "legitimate escape" in a "pine flatwoods" in Osceola County, Florida. On the basis of a key provided by Nowicke, it is assignable to *E. coronaria* (Jacq.) Stapf (*Tabernaemontana coronaria* (Jacq.) Willd.; *Nerium coronarium* Jacq.). Huber considered this species to be conspecific with *E. divaricata* (L.) Alston in Trimen (= *Tabernaemontana divaricata* (L.) R. Br.;

Nerium divaricatum L.), a native of the southern Himalayas now cultivated in tropical areas throughout the world. The plants in cultivation may have either single or double flowers. The species is reportedly heterostylous (Huber).

Most species of *Rauvolfia* (Rauvolfiinae), a large, pantropic genus of perhaps 110 species, are shrubs or trees. *Rauvolfia tetraphylla* L., a shrubby plant, is indigenous to an area from Mexico to northern South America and is reportedly naturalized in India and Australia (Nowicke). It has been attributed to our area as a rather uncommon escape, in—for example—Palm Beach County, Florida. Nowicke has remarked that it is variable throughout its natural range, and that it is often difficult to separate from *R. littoralis* Rusby. My observations on material collected in Florida conform with this assessment.

Ochrosia (Cerberinae) includes perhaps 30 species of small to medium-sized trees native to Indonesia and surrounding areas. Because of their nonacuminate leaves and large fruits with relatively narrow wings, variously determined specimens collected in Florida are assignable to *O. elliptica* Labill., according to a key presented by Boiteau. Native to Australia, New Caledonia, and many islands in the Pacific Ocean, the species is cultivated in numerous places, including Hawaii, Puerto Rico, and Florida. The fruits float and remain fertile for long periods in sea water, readily germinating upon contact with land (Boiteau). According to Judd (pers. comm.), the species is probably a very rare escape in Florida, and its naturalization there is doubtful.

A small genus of probably fewer than ten species of trees, shrubs, and rarely vines, *Thevetia* (Cerberinae) occurs naturally from Mexico to Paraguay. *Thevetia peruviana* (Pers.) K. Schum., of this area, is frequently cultivated and is sometimes escaped or naturalized in many tropical and subtropical areas of the world. The species was reported by Small (1913) to be growing naturally in dry soil on Key West, Florida, and Long & Lakela have indicated that in southern Florida, including the Keys, it is naturalized in coastal areas and cultivated more widely. Nevertheless, Judd (pers. comm.) maintains that he has seen no evidence that the species has become established outside of cultivation in the area. It is commonly planted for ornament in Guatemala, where according to Standley & Williams it is not native but sometimes appears to be naturalized along roadsides and in pastures. In contrast, Woodson (1938b) indicated that it was possibly native throughout Central America.

As traditionally considered, *Nerium* (Echiteae) comprises two or three species of shrubs or small trees native to the Mediterranean region, subtropical Asia, and Japan, although Leeuwenberg recently suggested that there is only one, *Nerium Oleander* L. This species is commonly planted as an ornamental throughout the warmer parts of the world and is sometimes escaped and naturalized as well. Occasionally escaped in tropical America, according to Nowicke, it is naturalized throughout the region *fide* Woodson (1938b). It is widely naturalized in the warm parts of North America, including Texas, according to Correll & Johnston. Although Judd (pers. comm.) indicated that it is a rare escape in southern Florida, Long & Lakela did not think that it is established there. Evidently, plants may persist for a long time after cultivation and may even propagate or at least spread to some degree by vegetative means. However, sexual reproduction by plants out of cultivation does not appear to occur anywhere in the Southeast. Many of the plants in our area and elsewhere have double flowers and are sterile. The latex of this plant is lethally poisonous, even in small quantities.

Many other species of Apocynaceae appear to be confined to cultivation in the southeastern United States. Some of these belong to genera not otherwise represented in the area, such as *Acokanthera, Beaumontia* Wall., *Mandevilla* Lindley, and *Plumeria.*

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KEY TO THE GENERA OF APOCYNACEAE IN THE SOUTHEASTERN UNITED STATES

General characters: *trees, shrubs, vines, or herbs with latex; leaves simple, opposite, often with colleters; inflorescences cymose or sometimes flowers solitary; flowers perfect, actinomorphic or nearly so, 5-merous except carpels 2; sepals nearly free, often with squamellae; corollas variously sympetalous, sometimes appendaged adaxially, lobes often overlapping; stamens epipetalous, alternating with corolla lobes, filaments free and short, anthers free (Plumerioideae) or variously agglutinated to each other and to style-stigma head (Apocynoideae), pollen released as tetrads (Apocyneae) or individual grains; nectaries external to ovaries or absent, usually 2 or 5, free to completely connate; carpels free or connate in ovule-bearing region, connate in non-ovule-bearing region into either style and style-stigma head or clavuncle; ovaries generally superior, simple, unilocular, and with marginal placentae or sometimes compound, unilocular* [*or bilocular*] *and with parietal* [*or axile*] *placentae; ovules 1 to many per carpel; fruits follicles, sometimes drupes, capsules,* [*or berries*]; *seeds in follicles glabrous, each with a tuft of trichomes at apex* [*or at both ends*] [*or arillate*], *those in drupes* [*or berries*] *glabrous, those in capsules winged.*

A. Anthers free or only slightly adherent to style-stigma heads; corolla lobes usually overlapping to left, at least in aestivation (but usually to right in *Alstonia macrophylla* and *Ochrosia elliptica*); fruits follicular (seeds then without trichomes, or with trichomes at both ends, or arillate), drupaceous, capsular, or baccate.
  B. Ovary 1, compound, in fruit remaining so; styles not cleft at base.
    C. Ovaries unilocular; fruits capsular, spiny; plants unarmed; leaves usually whorled or subwhorled. .... 5. *Allamanda.*
    C. Ovaries bilocular; fruits baccate, not spiny; plants armed; leaves opposite. .. .. [*Carissa grandiflora.*[12]]
  B. Ovaries 2, simple, in fruit remaining so or fusing; styles cleft at base.
    D. Plants shrubs or trees; fruits follicular (seeds then with trichomes at both ends or arillate) or drupaceous.
      E. Leaves alternate.
        F. Corollas narrower and shorter than leaves, salverform (but tube constricted near middle or widened only subapically); calyces without squamellae; nectaries absent; fruits drupaceous, usually 1-seeded, usually only 1 ovary maturing. .... 1. *Vallesia.*
        F. Corollas wider than and nearly as long as leaves, funnelform; calyces with squamellae; nectaries annular, shallowly 5-lobed; fruits drupaceous, 2- to 4-seeded, both ovaries maturing and fusing together. ... . [*Thevetia peruviana.*[12]]
      E. Leaves opposite or whorled.
        G. Leaves opposite; calyces with squamellae; fruits follicular (seeds arillate, without trichomes). .... [*Tabernaemontana divaricata.*[12]]
        G. Leaves opposite or whorled; calyces without squamellae; fruits follicular (seeds then not arillate, but with trichomes at both ends) or drupaceous (seeds then without trichomes).
          H. Leaves all more or less the same size and shape; ovules/seeds attached at middle; fruits follicular or drupaceous.
            I. Pedicels several times longer than calyces; leaf apices usually acuminate; fruits follicular (ovaries remaining free). .... [*Alstonia macrophylla.*[12]]
            I. Pedicels about as long as calyces; leaf apices usually acute to obtuse; fruits drupaceous (ovaries remaining free during fruit

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[12] Escaped from or persistent beyond cultivation but clearly reproducing neither sexually nor asexually in the southeastern United States. For further consideration see end of family discussion.

development) although each may resemble 2 that are fused, or sometimes becoming fused at base). . . . [*Ochrosia elliptica.*[12]]

H. Leaves clearly of different sizes and shapes; ovules/seeds attached at 1 end; fruits drupaceous (ovaries becoming fused during fruit development). . . . . [*Rauvolfia tetraphylla.*[12]]

D. Plants herbs or subshrubs; fruits follicular (seeds without trichomes).

J. Leaves alternate, sometimes subopposite or subwhorled; nectaries evidently lacking or connate into a shallow ring. . . . . 2. *Amsonia.*

J. Leaves opposite, sometimes subopposite; nectaries 2.

K. Corollas salverform, mouths of tubes constricted or tubes widened subapically; anthers completely fertile. . . . . 3. *Catharanthus.*

K. Corollas funnelform, mouths of tubes not constricted or tubes not widened subapically; anthers incompletely fertile. . . . . 4. *Vinca.*

A. Anthers agglutinated to style-stigma heads or to clavuncles; corolla lobes overlapping to right, at least in aestivation; fruits follicular (each seed with a tuft of trichomes at apex).

L. Plants shrubs or small trees; leaves usually whorled or subwhorled, rarely opposite; nectaries absent; corollas often double; ovaries free but somewhat agglutinated. . . . . [*Nerium Oleander.*[12]]

L. Plants herbs, vines, or scrambling to erect subshrubs; leaves usually opposite, sometimes subopposite, rarely alternate; nectaries 5, free or basally connate; corollas normal (not double); ovaries free and not agglutinated.

M. Plants vines or scrambling to erect subshrubs; corollas funnelform to salverform, unappendaged adaxially; non-ovule-bearing region of gynoecium differentiated into style and style-stigma head; pollen released as individual grains.

N. Plants vines; corollas salverform, about as long as or longer than leaves, tubes usually widened at or near middle; follicle pairs (from single flowers) diverging usually ca. 180° (but ranging from ca. 160 to 200°). . . . . 6. *Echites.*

N. Plants vines or scrambling to erect subshrubs; corollas funnelform, about as long as or longer than leaves (in *Trachelospermum* clearly shorter than leaves, funnelform to sometimes approaching salverform but then tubes widened apically); follicle pairs (from single flowers) diverging ca. 90° or less.

O. Nectaries usually exceeding (and sometimes converging above) ovaries; leaves generally 1–3 cm long, margins revolute and often meeting abaxially. . . . . 7. *Angadenia.*

O. Nectaries not exceeding ovaries; leaves generally 4–9 cm long, margins revolute but not meeting abaxially.

P. Anthers with long, spirally intertwined apical appendages; placentae chaffy (seeds each encased in a subtending, deciduous, boat-shaped scale). . . . . 8. *Pentalinon.*

P. Anthers without apical appendages; placentae not chaffy (seeds not each encased in a scale).

Q. Inflorescences many-flowered; calyx lobes usually aristate and keeled, with squamellae; corollas funnelform or sometimes approaching salverform (but then tubes widened apically), clearly shorter than leaves; leaf apices acute to subcaudate. . . . . 9. *Trachelospermum.*

Q. Inflorescences 1- or 2-, sometimes up to 6-flowered; calyx lobes mucronate, not keeled, without squamellae; corollas funnelform, about as long as or longer than leaves; leaf apices mucronate. . . . . 10. *Rhabdadenia.*

M. Plants herbs; corollas campanulate, short-cylindrical, or urceolate, appendaged within; non-ovule-bearing region of gynoecium a sessile, rhomboid clavuncle; pollen released as tetrads. . . . . 11. *Apocynum.*

Subfam. PLUMERIOIDEAE Schumann, in Engler & Prantl, Nat. Pflanzenfam. IV. 2: 122. 1895, "Plumieroideae."

Tribe PLUMERIEAE Schumann, *ibid.*, "Plumiereae."

Subtribe **Rauvolfiinae** Schumann, *ibid.*

1. **Vallesia** Ruiz & Pavon, Fl. Peruv. Chil. Prodr. 28. 1794.

Terrestrial shrubs or small trees; axes and leaves glabrous. Leaves alternate; blades lanceolate, narrowly ovate, or oblanceolate, apices rarely mucronate, then only slightly so, margins usually revolute, sometimes slightly undulate, bases obtuse to attenuate, often oblique; petioles without lateral appendages, colleters present on bases and adjacent areas of stem. Inflorescences terminal but soon appearing lateral (opposite a leaf) by sympodial growth, pedunculate, few-flowered, bracteate; pedicels much longer than calyces, ebracteolate. Calyx ⅛–⅙ as long as corolla or less, glabrous; lobes triangular, bases usually not imbricate, squamellae lacking. Corolla salverform (but tube widened basally and subapically [or only subapically]), shorter than leaves, with nonglandular pubescence (adaxially, at lobe bases); lobes overlapping to left in aestivation, spreading, elliptic to oblong (apices acute), entire to somewhat undulate and/or revolute, somewhat oblique; tube without adaxial appendages but thickened apically. Stamens inserted at base of subapically widened portion of corolla tube, glabrous; filaments short, slender, terete, straight or slightly curved; anthers not agglutinated to style-stigma head, cordate (apices and basal lobes obtuse), completely fertile, introrsely dehiscent, long axis mostly parallel to that of filament. Nectaries lacking. Carpels completely free in ovule-bearing region, weakly united above; ovaries 2, simple, distinct, unilocular, with marginal placentae and several ovules; style in transverse section bilobed; style-stigma head ellipsoid, not umbraculiform, with 2 obtuse lobes apically, glabrous. Fruits drupaceous, usually only 1 from each flower, oblique, clavate, obpyriform, or ovoid, the surface more or less translucent, whitish. Seeds 1 [or 2] per fruit, usually fusiform, without trichomes. LECTOTYPE SPECIES: *V. glabra* (Cav.) Link (*Rauvolfia glabra* Cav.). Britton & Millspaugh, Bahama Fl. 339. 1920, stated "two known species, the following typical" in reference to *V. glabra*; Woodson, N. Am. Fl. **29:** 138. 1938, also indicated this species. (Named for Francisco Valles, died 1592, physician to Philip II of Spain.)—TEAR-SHRUB.

A small genus of two (Chittenden; Long & Lakela; Schumann) to eight (Bailey *et al.*; Standley & Williams; Woodson, 1938b) or perhaps ten (Airy Shaw, in Willis; Tomlinson) species of shrubs or small trees with alternate leaves, small flowers, and drupaceous fruits. The plants occur from Argentina to Mexico and in the southern parts of California and Florida according to some (e.g., Airy Shaw, in Willis; Schumann; Woodson, 1938b) but are restricted to tropical and subtropical America according to others (e.g., Bailey *et al.*; Chittenden; Long & Lakela; Standley & Williams; Tomlinson). The genus is evidently not represented in Panama (see Nowicke).

Vallesia somewhat resembles and may be most closely related to *Rauvolfia*

L. The latter is a pantropic genus of perhaps as many as 110 species (Nowicke); it is represented in the Southeast by *R. tetraphylla,* a species native to the American tropics and subtropics that has occasionally escaped from cultivation but is evidently not fully naturalized in Florida (see family discussion). Both of these genera are apocarpous and have drupaceous fruits, but in *Vallesia* the leaves are alternate (vs. opposite or whorled), the flowers lack nectaries, and each fruit is the product of a single carpel (vs. both carpels). *Vallesia* has been allied with *Rauvolfia* and eight other genera in the Rauvolfiinae, one of four subtribes comprising the Plumerieae. This tribe also includes eight genera in the Cerberinae. Two of these, *Thevetia* and *Ochrosia,* with bicarpellate and unicarpellate drupes, respectively, have a species each that is cultivated and escaped, but probably not naturalized, in Florida (see family discussion). Plants of *Vallesia* have much smaller flowers than those of *T. peruviana* and can be readily distinguished from those of *O. elliptica* by their alternate (vs. opposite or whorled) leaves.

Vallesia includes one or perhaps two species native to southern Florida and the American tropics. *Vallesia antillana* Woodson, chromosome number evidently unreported, has long been confused with *V. glabra* (Cav.) Link, $2n = 22$, but according to Woodson (1937, 1938b) it differs in its longer (10–12 vs. 5–7 mm), more deeply lobed corollas and wider (1–3 vs. 0.6–2 cm) leaves. Woodson (1938b) indicated only *V. antillana* for the southeastern United States (southern Florida) and reported *V. glabra* from California to Veracruz and Oaxaca, as well as from Pacific coastal South America; Tomlinson agreed that *V. glabra* had been incorrectly attributed to Florida. Nevertheless, Long & Lakela recognized both species in the southern part of the state, using differences in pedicel length (in addition to those outlined above) to distinguish them. However, whereas Long & Lakela indicated that in *V. antillana* and *V. glabra* the pedicels were less than or greater than 5 mm long, respectively, Woodson (1938b) had indicated almost the opposite (4–5 vs. 2–4). According to Long & Lakela, both *Vallesia antillana* and *V. glabra* occur in coastal hammocks in southern Florida and throughout much of tropical America, although in Florida *V. glabra* was indicated only from the Keys.

I do not consider the five specimens I have seen from the Southeast (all from the Florida Keys) to represent more than one species, although the situation remains confused. Four of them have pedicels over 5 mm long (*Vallesia glabra*); two of these have corollas at least 10 mm long (*V. antillana*), while the other two have retained no corollas at all. The fifth specimen has pedicels less than 5 mm long (*V. antillana*) but corollas 6–9.5 mm long (mostly *V. glabra*). According to Tomlinson, the fruits of *V. antillana* develop quickly and are one-seeded; the common name (tear-shrub) refers to their pear shape and whitish, almost translucent quality. At least in southern Florida, flowers and fruits are usually present throughout the year (Tomlinson). It is notable that, although the plants are evergreen, the leaves tend to disappear from herbarium sheets with time.

According to information summarized by Gibbs, leucoanthocyanins and tannins have yet to be detected in the genus, despite specific testing, although alkaloids appear to be numerous.

The fruits of *Vallesia glabra* are sometimes eaten by humans, and a juice from the plants is reportedly used in ophthalmia (Uphof).

REFERENCES:

Under references for the Apocynineae, see AIRY SHAW (in WILLIS); BAILEY *et al.*; CHITTENDEN; GIBBS; LONG & LAKELA; SCHUMANN; STANDLEY & WILLIAMS; and UPHOF.

Under references for the Apocynaceae, see NOWICKE and WOODSON (1938b).

TOMLINSON, P. B. The biology of trees native to tropical Florida. x + 480 pp. Allston, Massachusetts. 1980. [*V. antillana,* 96–98.]

WOODSON, R. E., JR. New or otherwise noteworthy Apocynaceae of tropical America V. Ann. Missouri Bot. Gard. **24:** 11–16. 1937. [Protologue for *V. antillana,* with discussion.]

Subtribe **Alstoniinae** Schumann, in Engler & Prantl, Nat. Pflanzenfam. IV. **2:** 122, 135. 1895.

2. **Amsonia** Walter, Fl. Caroliniana, 98. 1788.

Terrestrial, erect, perennial herbs; axes and leaves glabrous or with nonglandular pubescence. Leaves alternate to sometimes subopposite and/or subwhorled; blades ovate to linear, apices acute to acuminate, margins occasionally revolute, bases obtuse to attenuate, often oblique; petioles without lateral appendages, colleters lacking on bases and adjacent areas of stem. Inflorescences usually terminal, sometimes axillary, pedunculate, several- to many-flowered, minutely bracteate; pedicels usually longer than calyces, rarely bracteolate. Calyx ⅛ as long as corolla or less, glabrous; lobes triangular and sometimes attenuate, bases not imbricate to sometimes slightly so, squamellae lacking. Corolla salverform (but tube usually widened apically), shorter than leaves, with nonglandular pubescence (adaxially, along tube and at lobe bases; abaxially, along tube); lobes overlapping to left in aestivation, usually spreading, sometimes erect, lanceolate to elliptic or narrowly spatulate, entire to undulate, generally not oblique; tube without adaxial appendages. Stamens inserted near top of corolla tube, glabrous; filaments short, terete, slightly curved; anthers not agglutinated to style-stigma head, each sagittate (apex and basal lobes mostly obtuse), completely fertile, introrsely dehiscent, long axis mostly parallel to that of filament. Nectaries evidently lacking or connate into a shallow ring. Carpels completely free in ovule-bearing region, united above; ovaries 2, simple, distinct, unilocular, with marginal placentae and numerous ovules; style terete; style-stigma head short-cylindrical, basally umbraculiform, sometimes with 2 obtuse lobes apically, glabrous. Fruits follicular, usually 2 from each flower (the pair divergent less than 90°), narrowly cylindrical to slightly moniliform; surface striate, glabrous; dehiscence by segmentation and/or disintegration, usually along spiralled lines. Seeds numerous, narrowly cylindrical, without trichomes. LECTOTYPE SPECIES: *A. Tabernaemontana* Walter; see Britton & Brown, Illus. Fl. No. U. S. & Canada, ed. 2. **3:** 20. 1913. (Probably named for Charles Amson, circa 1760, physician of Gloucester Co., Virginia, and friend of John Clayton [see Woodson, 1928b].)—BLUESTAR.

One of the few genera of Apocynaceae in temperate to subtemperate regions, comprising perhaps as few as five highly variable or as many as 20 more narrowly defined species in the southern United States and northern Mexico, and one in Japan (and possibly Korea and China as well; see Ohwi). As originally circumscribed by Walter, the genus comprised only *Amsonia ciliata* Walter and *Amsonia Tabernaemontana* Walter (*Tabernaemontana Amsonia* L.), the latter of which had been included by Linnaeus (Sp. Pl. **2**: 301. 1762) as the sole herbaceous, Temperate Zone member of *Tabernaemontana. Amsonia* was progressively expanded by the addition of both new and transferred taxa (summarized by Woodson, 1928b), perhaps the most interesting of which is the Japanese *A. elliptica* (Thunb.) Roemer & Schultes (*Tabernaemontana elliptica* Thunb.). Members of *Amsonia* are perennial, mostly erect, somewhat woody herbs with alternate leaves, medium-sized flowers with blue corollas (hence the common name bluestar), and continuous or articulated follicles.

Amsonia, with its free, unappendaged anthers, seeds without trichomes, and corolla lobes that overlap to the left in bud, is well placed within the Plumerioideae. It is, furthermore, assignable to the Plumerieae because of its two separate ovaries, and within that to subtribe Alstoniinae on the basis of its many ovules, calyces without squamellae, and dry (follicular) fruits. (The fruits may be follicular in the Tabernaemontaninae, but in such cases the seeds have a fleshy aril.) *Amsonia* is perhaps most closely related to *Haplophyton* A. DC., a monotypic genus with subopposite leaves that is distributed from Arizona and New Mexico southward to Guatemala (reports from southern California and Cuba are evidently unconfirmed; see Woodson, 1928b, 1938b). *Haplophyton cimicidum* A. DC. differs from most Plumerioideae, including *Amsonia,* in its apically comose seeds. Woodson (1928b) considered *Rhazya* (two species, Greece to India) to be another very close relative of *Amsonia,* from which it differs principally in having nectaries.

Two morphologically and geographically distinct sections were recognized in *Amsonia* by Schumann: sect. *Euamsonia* K. Schum. (= sect. AMSONIA) (summits of corolla tubes not constricted, apices of stigmas depressed-capitate or truncate) of southeastern North America and Japan, and sect. SPHINCTOSIPHON K. Schum. (summits of corolla tubes constricted, apices of stigmas with two distinct lobes) of the southwestern United States and northern Mexico. Woodson (1928b) elevated these sections to subgenera, noting that in addition to the differences mentioned by Schumann, the inflorescence bracts were much more conspicuous in subg. SPHINCTOSIPHON (K. Schum.) Woodson. He removed four species from the latter group to subg. ARTICULARIA Woodson (which has articulated instead of continuous follicles, and seeds that are rounded or pointed instead of truncate at the ends) and divided the remainder into sects. MICRANTHAE Woodson and LONGIFLORAE Woodson, the latter with larger flowers, fruits, and seeds. McLaughlin maintained subg. ARTICULARIA but elevated Woodson's two sections to subg. SPHINCTOSIPHON *sensu stricto* and subg. LONGIFLORAE (Woodson) McLaughlin (as subg. "*Longiflora*"), respectively, on the basis of morphological and ecological evidence (see McLaughlin).

There appears to be a hierarchy of relationships within *Amsonia* that is reflected at least partially in the systems of Schumann and Woodson (1928b)

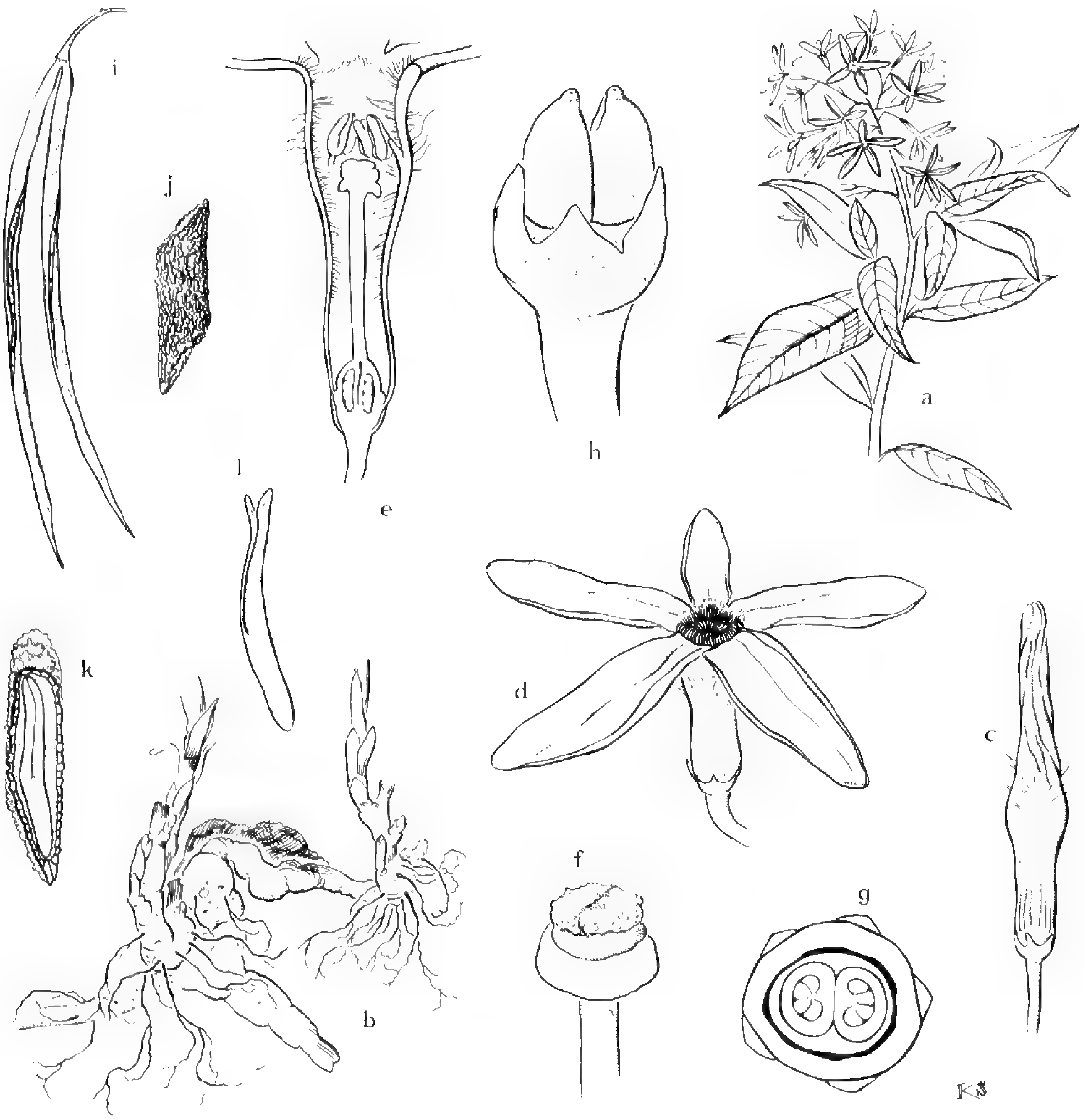

FIGURE 1. **Amsonia.** a–l, *A. Tabernaemontana*: a, distal part of flowering stem, × ½; b, rhizome with bases of 2 vertical, above-ground stems, × ½; c, flower bud, corolla lobes overlapping to left, × 3; d, flower, salverform corolla with apically widened tube, × 3; e, flower cut longitudinally, corolla with nonglandular pubescence, anthers free both from each other and from style-stigma head, gynoecium free in ovule-bearing region, united above into style and style-stigma head, × 5; f, apical part of style (terete) and style-stigma head (umbraculiform basally, slightly bilobed apically), × 12; g, base of flower cut in transverse section through ovaries (5 calyx lobes; corolla tube; shallow, annular nectary; 2 distinct, unilocular ovaries, each with a marginal placenta and numerous ovules), × 12; h, 3 lobes of persistent calyx, annular nectary, 2 immature follicles after fall of style and corolla, × 12; i, mature follicles (both carpels typically developing), × ½; j, seed, × 3; k, mature seed cut longitudinally (seed coat hatched, endosperm stippled, embryo unmarked), × 3; l, embryo, × 3.

but not in that of McLaughlin, who treated the four groups apparent in the genus as subgenera. The most substantial discontinuity among these plants, morphologically and geographically, seems to lie between eastern (in southeastern North America and Japan) and western (in the southwestern United

States and northern Mexico) populations. Thus, although I agree with Schumann that two major groups exist within the genus, I would favor their recognition at the subgeneric level, as subg. AMSONIA and subg. SPHINCTOSIPHON, respectively, in order to accommodate as sections and subsections the additional groups recognized at various levels in the latter by Woodson (1928b) and McLaughlin. Although both recognized subg. ARTICULARIA as a distinct subgenus, Woodson (1928b) indicated that it was more closely related to subg. SPHINCTOSIPHON than to subg. AMSONIA, suggesting that inclusion of the group as sect. ARTICULARIA within subg. SPHINCTOSIPHON would be more indicative of relationships. This proposal would require that the two groups recognized as sections of subg. SPHINCTOSIPHON by Woodson be demoted to subsections.[13]

Possibly two extremely variable, or perhaps as many as seven or even eight species of *Amsonia,* all assignable to subg. AMSONIA, occur in the southeastern United States, although the genus is not represented in southern peninsular Florida. Among those characterized by externally glabrous corollas are *A. rigida* Shuttlew. ex Small (including *A. glaberrima* Woodson, according to Godfrey & Wooten), *A. ciliata,* and *A. Hubrichtii* Woodson, three species for which chromosome numbers have evidently not been reported.

Amsonia rigida is a species of wet or moist, relatively open habitats on the Coastal Plain from southern Georgia and northern Florida to southeastern Texas (but probably only as far west as central Louisiana, if *A. glaberrima* is excluded). *Amsonia ciliata* is a variable species found in relatively dry, open places, often in sandy or limy soil, throughout most of the Southeast and adjacent areas. It differs from *A. rigida* sensu lato in its sessile to subsessile (vs. distinctly petiolate) upper leaves. Many specimens obtained throughout most of the range of *A. ciliata* have linear to nearly filiform leaves (up to 50 times as long as wide by my measurements) and on that basis have been recognized as var. *tenuifolia* (Raf.) Woodson (var. *filifolia* Woodson). Plants in the eastern parts of Oklahoma and Texas are assignable to var. *texana* (Gray) Coulter, which allegedly (Small, 1913) differs from var. *ciliata* in its longer calyx lobes (2 vs. 1 mm) and corolla tubes (9–11 vs. 6–8 mm), as well as in its glabrous (vs. pubescent) stems and branches. Such plants may be transitional to subg. SPHINCTOSIPHON.

Amsonia Hubrichtii is closely related to the so-called Ozark phase of *A. ciliata* var. *filifolia* (= var. *tenuifolia*), according to Woodson (1943), but the plants differ in their larger size, more lustrous foliage, obscurely (vs. distinctly) pedunculate inflorescences held among (vs. well above) the leaves, and smaller, narrower corollas. They reportedly occur in rocky or gravelly creek bottoms in the Ouachita Mountains of western Arkansas and southeastern Oklahoma, although the species was not included by Godfrey & Wooten (coverage includes Arkansas) or Correll & Correll (coverage includes Oklahoma).

Other species of *Amsonia* in the Southeast have externally pubescent corollas. *Amsonia Tabernaemontana,* $2n = 16, 22, 32$, differs from *A. ludoviciana* Vail, $2n = 22$, in its glabrous (vs. pubescent, at least distally) follicles, glabrous

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[13] Such proposals regarding these taxa of the southwestern United States and northern Mexico would require further justification and nomenclatural changes beyond the scope of the present treatment.

calyces, and abaxially glabrous or glabrescent (vs. tomentose) leaves. The former often occurs in sandy soil, in mesic woods and on floodplains, river banks, and lake shores throughout most of southeastern North America with the exception of peninsular Florida and possibly coastal areas. It has reportedly escaped from cultivation in several northeastern states (see Woodson, 1928b). *Amsonia ludoviciana,* on the other hand, is restricted to Mississippi, Louisiana, and Arkansas, where it usually grows in moist, open woods, according to several accounts, although Lemke reported it only from Louisiana, Mississippi, and South Carolina.

Amsonia illustris Woodson, $2n = 22$, occurs in wet sand or gravel in or near streams and ditches as well as in swamps and wet meadows from eastern Kansas and southern Missouri to eastern Texas and western Arkansas. It allegedly differs from *A. Tabernaemontana* in its lustrous (vs. dull) adaxial leaf surfaces, its sparsely pubescent (vs. glabrous) calyces, and its drooping (vs. erect) mature follicles (a condition not seen elsewhere in the genus, according to Woodson, 1929) that are somewhat constricted between the seeds (but by no means articulated as in sect. ARTICULARIA, according to Woodson, 1929).

This group of southeastern species with externally pubescent corollas appears also to include *Amsonia repens* Shinners, chromosome number evidently unreported, which according to Correll & Johnston differs from *A. Tabernaemontana* and *A. illustris* in its usually geniculate (vs. straight) stem bases and more xeric habitats (in prairies and along railroad tracks vs. along streams and near lakes or in wet soil of swamps, meadows, ditches, etc., respectively). Compared to *A. Tabernaemontana, A. repens* also has smaller (less than or equal to 6 by 3 cm vs. 6–15 by 5 cm), thicker, more lustrous leaves, and pilose (vs. glabrous) calyces. That *A. repens* was reported for neither Arkansas (see Smith) nor Louisiana (see MacRoberts) is consistent with its apparent restriction to eastern Texas (Correll & Johnston).

Correll & Johnston remarked that *Amsonia Tabernaemontana, A. illustris,* and *A. repens,* the three species with externally pubescent corollas, along with *A. glaberrima* (and therefore probably *A. rigida*), form an extremely close and possibly conspecific alliance, and that the pubescence characters by which they are largely defined are not entirely reliable. Thus, with the exception of those assignable to *A. ciliata* (or *A. Hubrichtii*) and possibly *A. ludoviciana,* which is also based on pubescence characters, all plants of *Amsonia* (i.e., subg. AMSONIA) that occur or might occur in the Southeast may belong to one extremely variable species, *A. Tabernaemontana.* Nevertheless, after reconsideration of morphological evidence, Mathé & Mathé continued to recognize most of these species.

As McLaughlin pointed out, it is notable that while Woodson's treatments (1928b, 1938b) of the species in subg. AMSONIA are rather consistent, those dealing with species of subg. SPHINCTOSIPHON are not, suggesting that species in the latter subgenus are even less distinct than those in the former. In fact, McLaughlin found that the pubescence characters used by Woodson (1928b), for example, to separate some of the species in sect. ARTICULARIA were not reliable.

Several indole alkaloids have been reported in *Amsonia* (see primarily Kisakürek *et al.*). Tests conducted by Gibbs using leaf material of *A. angustifolia*

(Aiton) Michx. (= *A. ciliata*) were reportedly negative for saponins but gave strong reactions for tannins.

Species of *Amsonia* are grown as ornamentals. The plants are propagated in the spring by division or by seed, and in the summer by cuttings (Bailey *et al.*; Chittenden). At least some species are hardy and have been cultivated in several northeastern states, where *A. Tabernaemontana* has been reported as an escape (Woodson, 1928b).

REFERENCES:

Under references for the Apocynineae, see BAILEY *et al.*; CHITTENDEN; CORRELL & CORRELL; CORRELL & JOHNSTON; GIBBS; GODFREY & WOOTEN; MACROBERTS; OHWI; SCHUMANN; SMALL (1913); and SMITH.

Under references for the Apocynaceae, see KISAKÜREK *et al.* and WOODSON (1928b, 1929, 1938b).

LEMKE, D. E. Recent collections and a redescription of *Amsonia ludoviciana* Vail (Apocynaceae). Sida **12:** 343–346. 1987. [In Louisiana, fewer than 1000 plants known from a number of small populations in the longleaf-pine region, perhaps 200 plants in cultivation.]

MATHÉ, I., & I. MATHÉ, JR. The morphological characteristics of the taxa belonging to the subgenus *Euamsonia.* (In Hungarian; English summary.) Bot. Közlem. **69:** 145–150. 1982. [Includes *A. illustris, A. ludoviciana, A. rigida,* and *A. Tabernaemontana* (vars. *Gattingeri, salicifolia*).]

MCLAUGHLIN, S. P. A revision of the southwestern species of *Amsonia* (Apocynaceae). Ann. Missouri Bot. Gard. **69:** 336–350. 1982.

SMALL, J. K. *Amsonia ludoviciana.* Addisonia **17:** 23, 24. *pl. 556.* 1932. [Color plate.]

———. *Amsonia rigida. Ibid.* **20:** 25, 26. *pl. 653.* 1937. [Color plate.]

WILDEMAN, E. DE. *Amsonia Tabernaemontana* Walt. Ic. Selec. Horti Thenensis **2:** 121. *pl. 69.* 1901. [Helpful illustration; stigma shown to be shallowly bilobed apically.]

WOODSON, R. E., JR. A new *Amsonia* from the Ozarks of Arkansas. Rhodora **45:** 328, 329. 1943. [*A. Hubrichtii* Woodson.]

3. **Catharanthus** G. Don, Gen. Hist. **4:** 71, 95. 1838.[14]

Terrestrial, erect, ascending, or decumbent, annual or perennial herbs, often woody toward the base; axes and leaves glabrous or with nonglandular but

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[14] There has been considerable disagreement regarding the correct name for this genus. Reichenbach (Conspec. Regni Veg. **1:** 134. 1828) was the first to propose that *Vinca rosea* L. is generically distinct from the other species of *Vinca* and published the monotypic *Lochnera* to accommodate it. Unfortunately, the name was not accompanied by a description, although Dwyer argued that by listing *V. rosea* L., and only this species, in a position subordinate to *Lochnera,* an indirect reference to a previously and effectively published description (i.e., the species description of Linnaeus, Syst. Nat. **2:** 944. 1759) was provided. However, Article 41.2, ICBN, 1988, specifies that in order for the name of a genus to be validly published, it must be accompanied either by a description or "by a reference (direct or indirect) to a previously and effectively published description or diagnosis of a genus or subdivision of a genus," the latter referring only to "taxa of a rank between genus and species" (Art. 4, Note 1, ICBN, 1988). In addition, Article 34.1 specifically states that a name is not validly published "by the mere mention of the subordinate taxa included in the taxon concerned." Thus, *Lochnera* Reichenb., a *nomen nudum,* is illegitimate.

Endlicher's description of *Lochnera* in August, 1838 (Gen. Pl. 583. 1838), would have established *Lochnera* Reichenb. ex Endl. as the correct name for the genus, except that current evidence suggests sometimes viscid pubescence. Leaves opposite to rarely subopposite; blades variously ovate to obovate, apices abruptly and narrowly mucronate, margins sometimes slightly revolute, sometimes undulate, bases obtuse to attenuate, often oblique; petioles without lateral appendages, colleters present on bases and adjacent areas of stem. Inflorescences axillary, essentially epedunculate, 1- to less often 4-flowered, ebracteate (but associated leaves often reduced); pedicels usually shorter than calyces, ebracteolate. Calyx ⅛[–⅕] as long as corolla or less, with nonglandular pubescence but sometimes viscid; lobes narrowly triangular and attenuate, bases not imbricate, squamellae lacking. Corolla salverform (but tube widened subapically), as long as or longer than leaves, with nonglandular pubescence but sometimes viscid (adaxially, near juncture of tube and lobes; abaxially, sometimes along tube [and/or lobe margins]); lobes usually overlapping to left in aestivation, spreading, obovate, entire (but mucronate), somewhat oblique; tube without adaxial appendages but thickened apically. Stamens inserted in upper ½ of widened portion of corolla tube, mostly glabrous; filaments very short, narrowly terete, straight or slightly curved; anthers not agglutinated to style-stigma head, each narrowly cordate (apex acute or obtuse, basal lobes mostly obtuse), completely fertile, introrsely and somewhat laterally dehiscent, long axis mostly perpendicular to that of upper part of filament. Nectaries 2, alternating with carpels and widely spaced, elongate and usually exceeding ovaries. Carpels completely free in ovule-bearing region, united above; ovaries 2, simple, distinct, unilocular, with marginal placentae and numerous ovules; style terete; style-stigma head cylindrical, basally umbraculiform, with 2 small or obscure lobes apically, with a tuft of hairs subapically and at base of cylindrical part. Fruits follicular, 1 or 2 from each flower (nearly sessile in leaf axils) (the pair divergent less than 90°), short and usually somewhat moniliform; surface striate, with nonglandular pubescence; dehiscence tardy, primarily by an adaxial (and sometimes also an abaxial) suture. Seeds numerous, ovoid, without trichomes. (*Lochnera* Reichenb., 1828, *nom. illegit.*) LECTOTYPE SPECIES: *C. roseus* (L.) G. Don (*Vinca rosea* L.); Woodson (N. Am. Fl. **29:** 124. 1938) indicated *V. rosea* as the type species of *Lochnera.* (Name from Greek, *katharos,* pure, and *anthos,* flower, according to Don, in reference to the "neatness and beauty" of the flowers.)

A genus of three (Standley & Williams) to six (Nowicke) or seven (Stearn, 1975) species of trailing or erect herbs (often woody at the base) with opposite, deciduous leaves, conspicuous flowers, and follicular fruits. With the exception of *Catharanthus pusillus* (Murray) G. Don of India, all of the species were originally endemic to Madagascar. *Catharanthus roseus* (L.) G. Don (*Lochnera rosea* (L.) Reichenb.; *Vinca rosea* L.), the Madagascar periwinkle, is commonly

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an earlier date for the competing *Catharanthus* G. Don. According to Stearn (1966, 1975), the fourth volume of Don's *General History,* which included on page 95 his description of *Catharanthus,* was listed as being "now first published" in an issue of Bent's *Monthly Literary Advertiser* dated 10 April 1838. In fact, since parts of the fourth volume were issued in advance of its completion, an even earlier date is likely; a reference to page 23 of this 908-page volume was published in the *Botanical Register* in June, 1835. For more detailed accounts of this controversy, see Dwyer, Lawrence, and Stearn (1966, 1975).

and widely cultivated, escaped, and naturalized in tropical and subtropical regions throughout the world, including, in the Southeast, most of peninsular Florida and the Keys (Judd, pers. comm.); it is adventive but is not naturalized in the Florida Panhandle (Anderson), in the Carolinas, and in southern California but has evidently not been reported out of cultivation elsewhere in the continental United States or Canada. The species is completely naturalized throughout most of Central America but is especially abundant in sand under coconut palms along the Atlantic Coast (Standley & Williams). Apparently, no other species of *Catharanthus* has been reported out of cultivation in the Southeast.

Catharanthus conforms to the general characters defining the Plumerioideae and (as *Lochnera*) was assigned by Schumann to the Plumerieae because of its free ovaries of two carpels. Within that tribe it was included with *Amsonia, Vinca,* and 18 other genera in the Alstoniinae, on the basis of its numerous ovules per carpel, calyces lacking squamellae, and dry, follicular fruits. *Catharanthus* is most closely related to *Vinca,* from which it is readily distinguished by its salverform (vs. funnelform) corollas. These two genera differ conspicuously from *Amsonia* in having nectaries and mostly opposite (vs. alternate) leaves.

The segregation of *Catharanthus* from *Vinca* has been widely accepted since Reichenbach first proposed it, some of the notable exceptions being Bailey (but not Bailey *et al.*), Bentham & Hooker, and De Candolle. The genera are clearly distinct morphologically, as is indicated by the numerous differences listed by, for example, Lawrence and Pichon (1949). Although *Catharanthus* appears to be more advanced than *Vinca* in vegetative morphology, it may be less advanced in certain floral characters. It is therefore interesting that within the native ranges and in this hemisphere, species of *Catharanthus* clearly have more tropical as well as more southern distributions than do those of *Vinca.* This is illustrated by the fact that while *C. roseus* is a common, naturalized weed in Florida, especially in the south, *V. minor* and *V. major* are naturalized nowhere in the state (Judd, pers. comm.).

Plants of *Catharanthus* are annual or perennial herbs that do not persist as long as those of *Vinca,* which usually are more woody. In addition, whereas the leaves of the former are in all cases deciduous, those of *Vinca* are more likely to be persistent and evergreen, although those of *V. major* are reportedly deciduous (Woodson, 1938b). The anthers of *Catharanthus* are completely fertile and free from the style-stigma head, as in most Plumerioideae, while those of *Vinca* are only partially fertile and converge above (but are not fused with) it. The latter conditions appear to be transitional to those seen in the Apocynoideae, and for this reason *Vinca* is placed after *Catharanthus* here.

According to Farnsworth, there are few if any anatomical or micromorphological (e.g., pubescence, cuticle) differences between *Catharanthus* and *Vinca,* and those that have been reported are ontogenetic and/or environmental in origin. Nevertheless, Cross & Johnson reported, at least in diploid shoots, tunicas of two and three cell layers in *C. roseus* and *V. minor,* respectively, although in each species derivatives of the three outer layers of the shoot apex form the leaf primordia and cortical tissues. Anatomical and ontogenetic in-

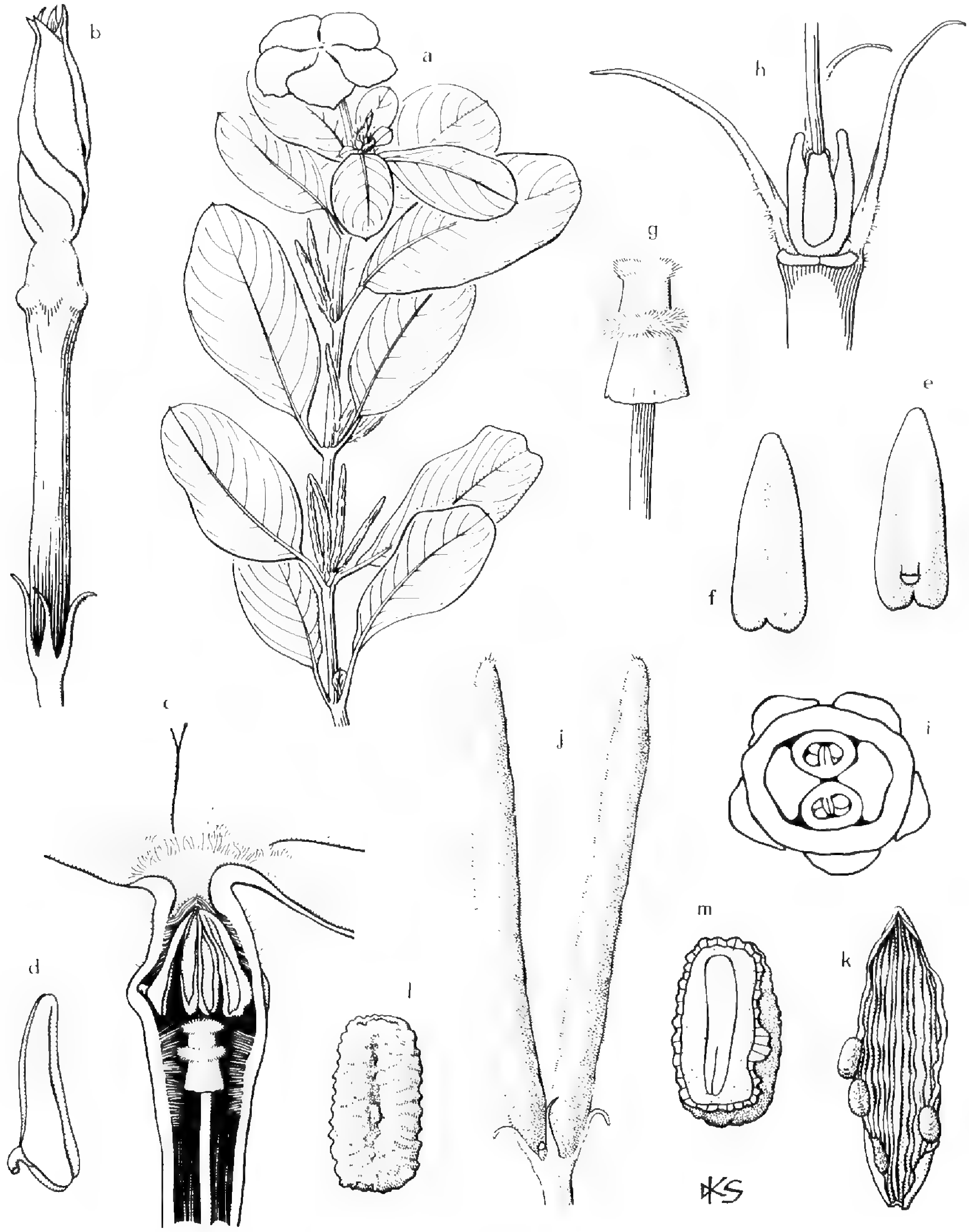

FIGURE 2. **Catharanthus.** a–m, *C. roseus*: a, distal part of stem with axillary flower, buds, and developing fruits (both carpels from each flower developed), × ½; b, flower bud, corolla lobes overlapping to left (the usual condition, but overlapped to the right in "a"), × 3; c, upper part of flower cut longitudinally (salverform corolla with subapically widened tube and nonglandular pubescence, anthers free from each other and from style-stigma head, each completely occupied by 2 locules), × 6; d, anther before dehiscence, side view, with short, curved filament, × 10; e, f, anther before dehiscence, abaxial and adaxial sides, × 10; g, apical part of style (terete) and style-stigma head (umbraculiform basally, tufts of nonglandular trichomes at base of cylindrical part and subapically, concealing 2 small or obscure lobes apically), × 12; h, base of flower, after removal of 2 calyx lobes (foreground) and corolla, 2 nectaries (left and right) exceeding and alternating

vestigations of carpel fusion involving the gynoecium above the ovule-bearing region in flowers of *C. roseus* (Walker, 1975a–c; 1978) are summarized in the family discussion.

Although the literature regarding alkaloid chemistry is enormous (see primarily family discussion), Farnsworth contended that a majority of it is actually of little comparative value because of inaccuracies in plant identification, as well as general failures to provide vouchers and to control variations in plant collecting, in the plant parts used, and in the methods used to isolate the compounds. Nevertheless, Paris & Moyse provided paper chromatographic evidence that distinguished several species of *Catharanthus* (including *C. roseus*) from a number of others belonging to *Vinca* (including *V. major, V. minor*), findings that Farnsworth later substantiated by both one- and two-dimensional thin-layer chromatography. Janot and colleagues reported so-called iboga-type alkaloids (one of the three major classes they recognized) in *Catharanthus* (*C. roseus*) but not *Vinca.* Farnsworth and co-workers reported that of the 21 alkaloids isolated from species of *Catharanthus,* only one, akuammine, had been detected in species of *Vinca* as well; however, Aynilian and colleagues later indicated that this number had grown to eight.

Farnsworth also compiled a long list of nonalkaloid constituents that had been reported for *Catharanthus* and *Vinca.* Among some of the compounds reported in one genus and not the other were formic acid, kaempferol, malvidin, palmitic acid, quercetin, and stearic acid in *Catharanthus* (from *C. roseus*), and caffeic acid, *p*-coumaric acid, fructose, gentisic acid, sucrose, and vanillic acid in *Vinca* (from *V. minor*). Nonalkaloids reported for species in both genera included choline, *o*-protocatechuic acid, tannins, and ursolic acid; saponins had been verified for neither genus (but see below). Daniel & Sabnis later reported from the leaves of *C. roseus* five phenolic acids (2-hydroxy, 6-methoxy benzoic; *p*-coumaric; protocatechuic; syringic; and vanillic) that had not been indicated for the species by Farnsworth and substantiated the presence of two flavonoids (kaempferol and quercetin); three additional phenolic acids (ferulic, α-resorcylic, and salicylic) were also reported for the extraregional *C. pusillus.* According to information compiled by Gibbs, compounds including cyanogenic glycosides and leucoanthocyanins have been confirmed for neither genus, while saponins may be present in *Vinca.* Tests for tannins have evidently been inconclusive.

De Candolle recognized three sections in *Vinca,* two of which included species that are now assigned to *Catharanthus.* Pinchon (1949) recognized these two

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with 2 ovaries (background and foreground), × 6; i, base of flower cut in transverse section through ovaries, showing 5 calyx lobes, corolla tube, 2 distinct nectaries (left and right), and 2 distinct, unilocular ovaries, each with marginal placenta and numerous ovules, × 12; j, 3 lobes of persistent calyx, remnant of 1 nectary (between middle and left calyx lobes), 2 nearly mature follicles, × 2; k, immature follicle, opened along line of carpel fusion, with seeds on marginal placentae, × 2; l, mature seed, showing hilum, × 12; m, mature seed cut longitudinally through hilum on right (seed coat hatched, endosperm stippled, embryo unshaded), × 12.

as well as a third to accommodate an additional species, *C. scitulus* (Pichon) Pichon. Thus, as recognized by Stearn (1975), the genus is divisible into three sections: sect. CATHARANTHUS (stamens inserted near the top of the corolla tube; follicles greater than 20 mm long; corolla tubes greater than 1 cm long; plants perennial), with six species; sect. CUPAVEELA (A. DC.) Pichon[15] (stamens inserted near the top of the corolla tube; follicles greater than 20 mm long; corolla tubes less than 1 cm long; plants annuals), with *C. pusillus*; and sect. ANDROYELLA Pichon (stamens inserted near the middle of the corolla tube; follicles not more than 12 mm long), with *C. scitulus.*

Diploid chromosome numbers have been determined for four species of sect. CATHARANTHUS, including *C. roseus,* as well as for the monotypic sect. CUPAVEELA. In all cases it is $2n = 16$ (Stearn, 1975), except that $2n = 24$ has been reported in *C. roseus* (see Bolkhovskikh *et al.*). In addition, colchicine-induced tetraploids of *C. roseus* have been produced on several occasions, usually in hopes of increasing the levels of economically important alkaloids. Relative to the corresponding diploids, such plants demonstrate overall increased growth rates and have broader leaves, larger stomata, larger, more deeply colored flowers, and larger pollen grains, at least among the viable ones (Janaki Ammal & Bezbaruah). According to data provided by Krishnan and colleagues, alkaloid content does not seem to be appreciably affected by such treatments. Tetraploids obtained by Cross & Johnson had larger cells, shorter, more massive stems, thicker, greener leaves, and larger flowers than the corresponding diploids. The vegetative differences in morphology were attributed to differences in cell shape in the apical meristem.

In addition to its ornamental value, *Catharanthus roseus* has considerable importance as a source of medicinal compounds (see discussion of suborder).

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[15] The original spelling by De Candolle, "Cupa-vleea," is evidently an error of orthography or typography. According to Stearn (1975), the epithet is derived from the Malayan *kapavila,* used for the only species in the section, *Catharanthus pusillus,* and reportedly rendered as *cupa-veela* by Rheede in 1689. The hyphen is here removed in accordance with Article 73.9, ICBN, 1983.

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4. **Vinca** Linnaeus, Sp. Pl. **1:** 209. 1753; Gen. Pl. ed. 5. 98. 1754.

Terrestrial, [erect,] ascending, or decumbent, perennial herbs, often woody toward base, or subshrubs; axes usually glabrous, leaves with nonglandular pubescence. Leaves opposite; blades subdeltoid, ovate, lanceolate, or elliptic, apices obtuse to acute, rarely mucronate, margins flat or revolute, bases truncate to attenuate, often oblique; petioles often with 2 small, lateral, alternate or subopposite appendages, colleters lacking on bases and adjacent areas of stem. **Flowers** solitary, axillary; peduncles usually longer than calyces, ebracteolate. Calyx ½–¼ as long as corolla, with nonglandular pubescence; lobes narrowly triangular to nearly linear, bases not imbricate, squamellae lacking. Corolla funnelform, as long as or longer than leaves, with nonglandular pubescence (adaxially, near juncture of tube and throat); lobes overlapping to left in aestivation, spreading, usually dolabriform, entire, oblique; tube and throat without adaxial appendages but throat thickened and/or with ridges apically (at juncture with lobes). Stamens inserted at summit of corolla tube, with nonglandular pubescence; filaments very short, terete, geniculate;[16] anthers not agglutinated to style-stigma head (but curved over it), each narrowly obovate (apex mucronate to subcaudate, bases attenuate), incompletely fertile (bearing adaxially 2 locules at about middle), introrsely dehiscent, long axis mostly perpendicular to that of filament. Nectaries 2, alternating with carpels and widely spaced, usually not exceeding ovaries. Carpels completely free in ovule-bearing region, united above; ovaries 2, simple, distinct, unilocular, with marginal placentae and numerous ovules; style terete, gradually widened apically; style-stigma head slightly conical, basally umbraculiform, lobes not evident apically, with a tuft of hairs apically and at base of conical part. Fruits follicular, usually 2 from each flower (the pair divergent less than 90°), widened around seeds; surface striate, glabrous; dehiscence tardy, by an adaxial suture. Seeds usually single, ovoid and deeply grooved on funicular side, without trichomes. LECTOTYPE SPECIES: *V. major* L.; see Britton & Brown, Illus. Fl. No. U. S. & Canada, ed. 2. **3:** 20. 1913. *Vinca minor* L. was later selected by M. L. Green (in Hitchcock & Green, Prop. Brit. Bot. 136. 1929) because it was considered to be the better known of the two original species, the other being *V. major,* and because it, and evidently not *V. major,* was included where the generic name was applied in Hortus Cliffortianus and Hortus Upsaliensis. *Vinca minor* was also selected by Woodson (N. Am. Fl. **29:** 125. 1938). (*Vinca* indicated by Linnaeus, Philosophia Botanica, 150. 1751, as a name derived from *Pervinca* of Tournefort, which is evidently also reflected in colloquial Italian (pervinca), French (pervenche), German (Berwinkel, Barwinkel), and English. According to Stearn, the name *vincapervinca,* which was used in reference to these plants by Pliny in the first century A.D., may have been derived from Latin *vincio,* to bind or wind about, in reference to the slender and flexible shoots used in wreath making, and *per,* through, because the leaves of some species remain green throughout the year.)—PERIWINKLE.

A genus of about six or seven species (Stearn) of subshrubs or suffrutescent herbs with opposite leaves, conspicuous flowers, and follicular fruits. All but one of these are native to an area from France, Spain, Portugal, Morocco, and Algeria to the Caucasus region and northern Iran; *Vinca erecta* Regel & Schmalh. is geographically and perhaps taxonomically isolated in Afghanistan and neighboring areas (see below). Two of the species commonly cultivated throughout the world, *V. minor* L. and *V. major* L., are escaped and naturalized in the Western Hemisphere, including parts of the southeastern United States. A third species, *V. herbacea* Waldst. & Kit., is also cultivated in North America and

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[16] An equally likely interpretation is that the filaments are straight and that the stamens distal from the points of geniculation are entirely antherial. Anatomical or other evidence evaluating these alternatives appears to be lacking.

at least has the potential to escape in our area; Fernald reported it out of cultivation in Massachusetts.

Vinca is most closely related to *Catharanthus*, and many aspects of its chemistry, anatomy, morphology, geography, and systematics are considered in the discussion of that genus.

Plants belonging to *Vinca minor*, $2n = 46$ (32 and 92 also reported), are usually smaller in all respects and less erect than those of *V. major*, $2n = 92$ (16 also reported). In addition, the leaves of *V. minor* are coriaceous and evergreen (vs. membranaceous and deciduous or semi-evergreen), tapered (vs. rounded, truncate, or subcordate) at the base, and glabrous (vs. ciliate) at the margin; the calyx lobes are also glabrous instead of ciliate. In *V. herbacea*, $2n = 46$ (92 also reported), and *V. erecta* the secondary veins diverge from the midrib of the leaf at angles of 5–30°, while in all other species this angle is 40–50°. In addition, the leaves of *V. herbacea* are distinguished from those of other species of *Vinca* by their narrowly elliptic to lanceolate (vs. wider) shape and more subtle venation.

The natural distribution of *Vinca minor* and *V. major* (and probably other species as well) has been obscured, perhaps permanently, because of a long history of cultivation in the Old World, where plantings in graveyards and probably other places date back at least to the fourteenth century (see Stearn). Nevertheless, in 1753 Linnaeus indicated a more northern distribution for *V. minor* ("*habitat in Germania, Angliâ, Gallia*") than for *V. major* ("*habitat in Gallia Narbonensi, Hispania*"), a difference that currently persists in Europe and is also reflected in this hemisphere.

The hardiest and most commonly cultivated species in the genus, *Vinca minor* is escaped and naturalized in much of the North Temperate Zone, including an area in North America bounded by Nova Scotia, Minnesota, Georgia, Arkansas, and Kansas (Steyermark). It occurs out of cultivation but rarely fruits in Texas (Correll & Johnston) and has been listed as escaped but evidently not naturalized in Louisiana (MacRoberts) and eastern Tennessee (Sharp *et al.*). According to Radford and colleagues, it occurs in scattered localities in North Carolina (but not South Carolina), where it reportedly spreads from roadsides and waste places to fields and woods. The species was not reported for Guatemala by Standley & Williams, and although Nowicke indicated that it is cultivated in Panama, she only conjectured about its escape there.

Both *Vinca minor* and *V. major* are reportedly naturalized in Georgia (Jones & Coile), although neither is so established in Florida (Judd, pers. comm.). While *V. minor* is a frequent escape in the northeastern United States, *V. major* is only occasionally found outside of cultivation, in the southern part of the country to as far north as Virginia (Gleason & Cronquist). *Vinca major* evidently does not grow in Panama (see Nowicke) but is thoroughly naturalized in Guatemala, where in the western highlands it blooms profusely during the cold dry season when flowers in general are scarce (Standley & Williams).

Vinca herbacea is also grown in North America and is reportedly established outside of cultivation in Massachusetts (Fernald). Nevertheless, I have seen no evidence that it escapes from gardens in the Southeast. The species is native

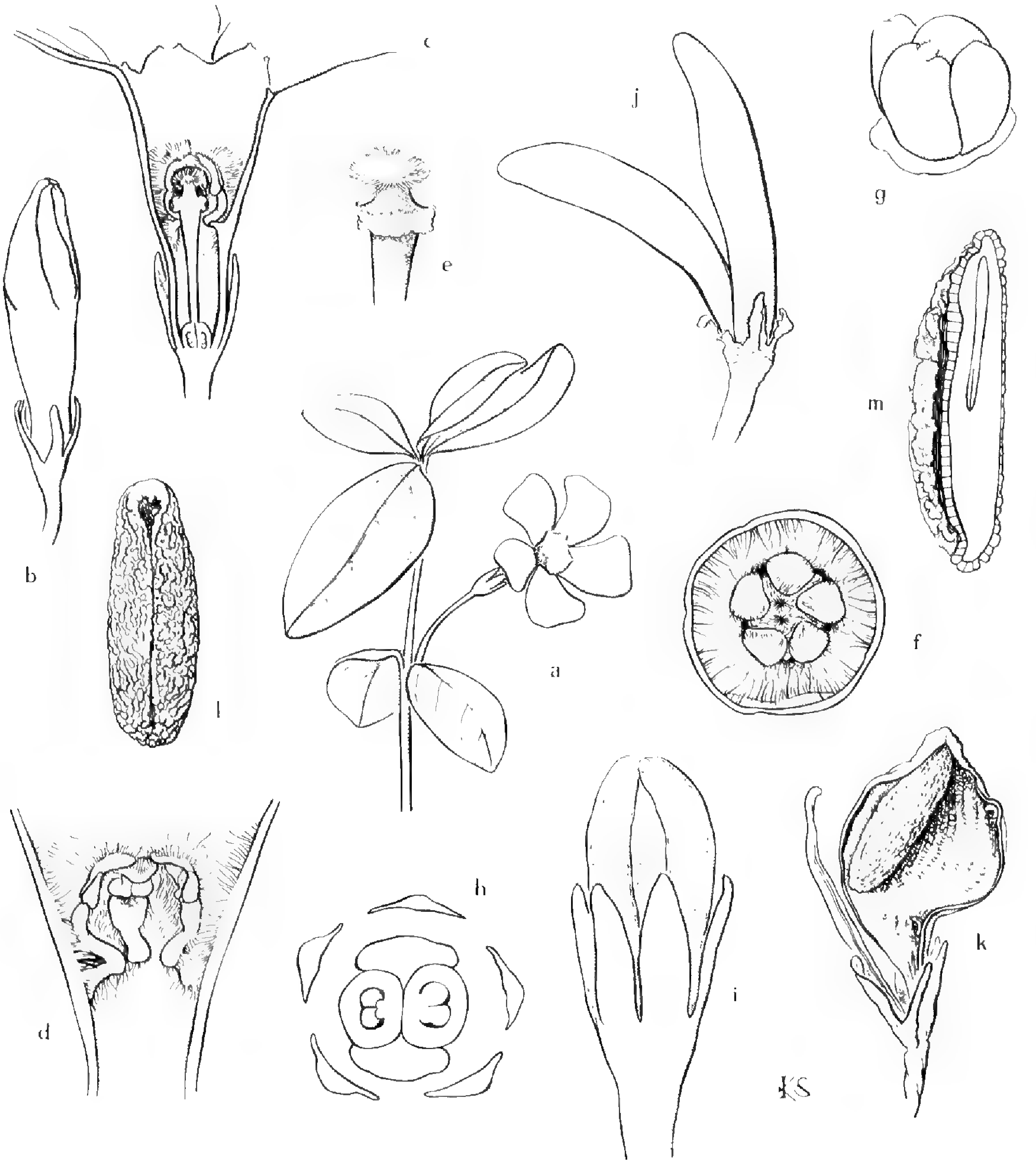

FIGURE 3. **Vinca.** a–m, *V. minor*: a, distal part of stem with axillary flower (corolla lobes dolabriform), × 1; b, flower bud, corolla lobes overlapping to left, × 2; c, flower cut longitudinally, showing funnelform corolla with nonglandular pubescence, adaxial ridge at juncture of throat and lobes (1 overlapping another to left), anthers free from each other and arched over style-stigma head, gynoecium free in ovule-bearing region, united above into style and style-stigma head, × 3; d, corolla throat cut longitudinally, showing anthers free from each other and from style-stigma head, each incompletely occupied by 2 locules, with sterile apical parts curved over space formerly occupied by style-stigma head (not shown) (depending on interpretation, filaments geniculate, or short and straight with the basal part of each anther then sterile), × 6; e, apical part of style (terete but gradually widened apically) and style-stigma head (umbraculiform basally, tufts of nonglandular trichomes at base of conical part and apically), × 6; f, flower cut transversely above stamens, showing sterile apical parts of anthers curved over style-stigma head, × 6; g, 2 distinct, adjacent ovaries with stylar scar, 2 alternating nectaries, × 12; h, base of flower cut in transverse section through ovaries, corolla removed, showing 5 calyx lobes, 2 distinct nectaries (above and below) and 2 distinct, unilocular ovaries

to an area extending from the shores of the Black Sea to Czechoslovakia, Austria, Greece, Israel, northern Iran, and southern European Russia. According to Stearn, it differs from *V. minor,* with which it is often confused, in its nearly cylindrical (vs. obconical) upper corolla tube (i.e., throat).

The adventive occurrences discussed above are consistent with data obtained from plants in their native ranges. Although the six species of *Vinca* recognized by Stearn overlap in the Old World, each occupies an area that reflects its own morphological and ecological peculiarities. These data, in conjunction with cytological evidence, were used by Pannochia-Laj (summarized by Stearn) in the construction of speculative arguments concerning phylogenetic relationships within the genus.

Vinca minor was proposed as being closest to ancestral; it is an evergreen, small-leaved, relatively woody, cold-hardy, diploid species that occurs at higher elevations and more northern latitudes than do most other species. *Vinca major* and *V. difformis* Pourret (*V. media* Hoffmanns. & Link), $2n = 46$ (44 also reported), have larger evergreen leaves and a susceptibility to low temperatures that is consistent with their more southern distributions. The two were presumed to have been independently derived from *V. minor* and to have exhibited a certain degree of gigantism due to chromosomal increases.

Vinca major is a tetraploid with chromosomes about equal in size to those of *V. minor,* while *V. difformis* is a diploid with larger chromosomes (it was thought to be a cryptotetraploid). *Vinca difformis* also differs from *V. major* in being less cold hardy and completely glabrous and in having corollas with narrower, more acutely tipped segments. *Vinca herbacea,* with chromosomes equal in number and size to those of *V. minor,* was envisioned to have evolved smaller leaves and prostrate, completely herbaceous above-ground parts (they die back each year) in connection with its spread to even colder and/or more desiccating conditions. Such adaptations allowed this species, the most variable and widespread in the genus, to occupy the arid scrublands and steppes of southeastern Europe and western Asia.

Although unknown cytologically and somewhat isolated geographically, *Vinca erecta* was nevertheless thought to be closely related to *V. herbacea* (but see below). It, too, is herbaceous and occurs at relatively high elevations (to 1850 m) in Afghanistan. Cytological data would also help clarify the position of *V. balcanica* Pénzes, a species restricted to the Balkan Peninsula that was considered to be closely related to *V. minor* and perhaps more directly ancestral to *V. major.* Morphologically, it is evidently most similar to the latter, from which it differs in its more lax growth form and its smaller leaves.

(left and right), each with marginal placenta and numerous ovules (only 2 in plane of section), × 12; i, persistent calyx and immature follicles, after fall of style and corolla, × 5; j, persistent but deteriorating calyx, nearly mature follicles (both carpels typically developing, but see "k"), × 2; k, aborted follicle on left, dehisced follicle on right (usually widened around a single seed), × 3; l, seed, showing deeply grooved funicular (adaxial) side, × 6; m, mature seed cut longitudinally through funicular groove at left (seed coat hatched, endosperm stippled, embryo unshaded), × 6.

Despite the foregoing, infrageneric classifications and species concepts in *Vinca* sensu stricto have been varied. Four major, primarily classical approaches, including that of Stearn, did not involve generic subdivision above the level of species. De Candolle included seven species in the group, which he recognized as sect. *Pervinca* of *Vinca* sensu lato (the three other species are now included in *Catharanthus*). This number was reduced by Schumann to five, and by Pichon (1951) to three, although some taxa that had previously been accepted as species were treated by him at the level of variety. The classification of Stearn, which included six or seven species, was comparable to that of Schumann, except for the addition of two species unknown to the latter and the consolidation of two others. (Stearn also provided descriptions for numerous cultivars of *V. minor* and *V. major.*)

Pobedimova recognized two sections among the five species she indicated for the Soviet Union. Section *Pervinca* A. DC. (= sect. VINCA) (throats of corollas glabrous; leaves petiolate; stems branched, not erect) comprised *Vinca minor, V. major, V. herbacea,* and *V. pubescens* Urv. (usually treated as conspecific with *V. major,* see below), and sect. VINCOPSIS Pobed. (throats of corollas pubescent; leaves sessile; stems unbranched, erect) evidently included only *V. erecta.*

Three other classifications were based primarily on evidence from alkaloid chemistry (reviewed by Aynilian *et al.*). The earliest of these (Paris & Moyse) contradicted some of the concepts of Pichon (1951), including the latter's treatment of *Vinca difformis* and *V. libanotica* Zucc. as varieties of *V. major* and *V. herbacea,* respectively, instead of as separate species (also, see below). Janot and colleagues confirmed that *V. difformis* and *V. major* differed substantially in alkaloid composition and also established that in this respect *V. minor* is unique within the genus.

According to Aynilian and co-workers, it is the classification of Nováček & Starý (in Trojánek *et al.*) that is most consistent with the alkaloid chemistry of the plants. This scheme, in which *Vinca* is divided into four sections (the names of which are not validly published) and eight species, is in general agreement with the findings of Janot and colleagues but is based on structural data from a considerably greater number of alkaloids. Evidently even more information was available to Aynilian and co-workers in their evaluation of this system, and the following is in part based on that account.

Vinca minor was assigned by Aynilian and co-workers to the monotypic sect. MINOR primarily on the basis of its unique emphasis on aspidospermine-type alkaloids, one of three basic classes often recognized (but see Kisakürek *et al.*). Whereas 32 of the 39 structurally known alkaloids of *V. minor* were classified as this type, a majority of those in each of the other species of *Vinca* qualified as yohimbine types. In addition, many of the aspidospermine-type alkaloids (vincadine, vincaminorine, vincaminoreine, vincaminoridine, minovincine, vincesine, vincaminine, vincinine, vincatine, and others) detected in *V. minor* had not been reported for any other species. It is notable that although the same racemic vincadifformine was reported by Trojánek and colleagues in both *V. minor* and *V. difformis,* the two evidently differed in the stereochemistry of this compound.

Section MAJOR included *Vinca major* (nine of 12 structurally determined alkaloids of the yohimbine type), *V. difformis* (six of nine), and *V. pubescens* (three of three). A close relationship was indicated between *V. major* and *V. difformis* because vincamedine had been reported from both species (and no others). That they should be recognized as distinct species was supported by differences in alkaloid content. While some compounds (elegantine, vincamajoreine, and 10-methoxyvellosimine) had been reported only for *V. major,* others (vellosimine, sarpagine, and vincadaffine) were indicated only for *V. difformis.* (In addition, Paris & Girre reported amino-acid differences between these two species, the latter as *V. media.*) Although only three structurally determined alkaloids were indicated for *V. pubescens,* one of them, carapanaubine, had not been reported for any other species. Majoridine had been reported only for *V. major* and *V. pubescens,* indicating a link between them (see above).

Section HERBACEA included *Vinca herbacea, V. libanotica,* and *V. Haussknechtii* Bornm. & Sint. ex Bornm. While a number of alkaloids (herbaceine, herbaine, isomajdine, herbaline, hervine, lochnerinine, skimmianine, and probably herbavine) were reportedly unique to *V. herbacea,* others (quebrachidine, venalstonine, and vincoline) had been reported only for *V. libanotica,* indicating that the two species are distinct. In addition, the major alkaloid of *V. libanotica* was considered to be vincamajine, reported previously from sect. MAJOR (*V. major* and *V. difformis*) but evidently unknown in *V. herbacea.* Other evidence suggested an affinity between *V. herbacea* and *V. libanotica.* For example, the two species were reported to have at least two alkaloids (herbadine and herbamine) in common that were unknown elsewhere and to be low in vincamine-type alkaloids. Compounds of the latter type, which had not been reported in *V. libanotica* and had been considered minor (only one of 19 characterized alkaloids) in *V. herbacea* had been reported from all other species of *Vinca.* Aynilian and colleagues concluded that *V. libanotica* was perhaps distinct enough to warrant placement in a monotypic section, between sects. MAJOR and HERBACEA (see above). Data from *V. Haussknechtii* evidently were lacking.

The monotypic sect. *Erecta* (= sect. VINCOPSIS) included only *Vinca erecta.* Although also in this species the yohimbine-type alkaloids outnumbered the aspidospermine types, they were not as predominant as they were in sects. MAJOR and HERBACEA. The fact that with few exceptions the alkaloids of *V. erecta* were unique to that species indicated an isolated position for it within the genus.

Further examination of the data obtained from alkaloid chemistry as summarized by, for example, Aynilian and co-workers indicates that in many cases the same reasoning used in favor of the proposed classification could be used just as effectively against it. For example, in view of the discussion above it is probably significant that many of the alkaloids reported for only two species involve more than one of the proposed sections. Alkaloids and species pairs for which this is true include akuammidine in both *Vinca difformis* and *V. erecta* of sects. MAJOR and ERECTA, respectively; reserpine in *V. minor* and *V. herbacea* of sects. MINOR and HERBACEA; vincamidine in *V. minor* and *V.*

libanotica, the latter of sect. HERBACEA; vincarine, vincamine, and akuammicine in *V. erecta* and *V. herbacea,* the former of sect. ERECTA; ervine and picrinine of *V. erecta* and *V. libanotica;* and (+)-quebrachamine, ervamine, ervinceine, (−)-eburnamonine, and eburnamine in *V. minor* and *V. erecta.* This notwithstanding, it is possible that additional data from alkaloid chemistry will lead to systematic interpretations of increased reliability.

Pollination in *Vinca minor* has been described most recently by Schick (1982) and appears in general to conform to that outlined here for *Apocynum* (see discussion of that genus).

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TROJÁNEK, J., M. NOVÁČEK, & F. STARÝ. Chemotaxonomy of *Vinca* species. Pp. 245–278 *in* W. I. TAYLOR & N. R. FARNSWORTH, eds., The *Vinca* alkaloids: botany, chemistry, and pharmacology. New York. 1973.

Vitti, J. D., & R. D. Parker. Seed germination in *Vinca minor* L. (Abstract.) Hortscience **20:** 186. 1985. [Soaking 24 hours in 1000 ppm GA_3 and stratification at 5°C for 90 days optimal (70 percent germination after 30 days); neither treatment effective alone.]

Tribe Allamandeae Pichon, Mém. Mus. Natl. Hist. Nat. **27:** 153–251. 1948.*

5. **Allamanda** Linnaeus, Mantissa Pl. Altera, 146 (214, 215, "*Allemanda*" *cathartica,* often cited as well). 1771.

Terrestrial, woody vines or sometimes shrubs to nearly herbaceous subshrubs; axes and leaves glabrous or with nonglandular pubescence. Leaves whorled or subwhorled, usually in 3's, 4's, or 5's, infrequently opposite, rarely alternate above; blades elliptic to oblanceolate, apices subcuspidate to acuminate, margins flat to slightly revolute, somewhat undulate, bases cuneate to attenuate; petioles without lateral appendages, colleters present on bases but not adjacent areas of stem. Inflorescences terminal or axillary, pedunculate, few- to several-flowered, bracteate; pedicels usually shorter than calyces, sometimes bracteolate. Calyx ⅛[–⅕] as long as corolla or less, glabrous or with sparse, nonglandular pubescence; lobes elliptic [or lanceolate] with acute apices, bases rarely imbricate, then only slightly so [or often clearly imbricate], squamellae essentially lacking. Corolla funnelform, about as long as leaves [or shorter or longer], usually with nonglandular pubescence (adaxially, near juncture of tube and throat); lobes overlapping to left in aestivation, spreading, ovate to obovate, entire, somewhat oblique; tube and throat without adaxial appendages. Stamens inserted near top of corolla tube, with nonglandular pubescence (mostly on filaments); filaments very short, terete, straight; anthers not agglutinated to style-stigma head, each narrowly sagittate (apex and basal lobes acute), incompletely fertile (bearing adaxially 2 locules in upper ⅔), introrsely dehiscent, long axis mostly parallel to that of filament. Nectaries 2, opposite carpels, forming an annulus around base of ovary with 2 shallow notches opposite line of carpel fusion. Carpels united throughout; ovary compound, unilocular, with 2 intrusive, parietal placentae (originating from line of carpel fusion) and numerous ovules; style terete, slightly widened apically; style-stigma head cylindrical, basally umbraculiform [or not], with 2 deltate lobes apically and a tuft of hairs subapically. Fruits capsular, subglobose [to globose]; surface spiny; dehiscence by 2 valves. Seeds numerous, compressed, winged, without trichomes. Type species: *A. cathartica* L. (as "*Allemanda cathartica,*" the only species included in the genus at the time of its original description). (According to Chittenden, named for D. Allamand, a resident of Leyden who sent seeds of the plants to Linnaeus.)

A small genus of about ten (Standley & Williams) to 18 (Long & Lakela; Nowicke) species of woody vines or sometimes woody to nearly herbaceous subshrubs with conspicuous flowers and usually with whorled (in 3's, 4's, or 5's) or opposite leaves. Although all taxa are native to tropical South America, *Allamanda cathartica* L. is cultivated, escaped, and naturalized in the tropics and subtropics of many other parts of the world (Nowicke), including southern Florida.

The systematic position of *Allamanda* has been and remains uncertain despite partially illuminating evidence from gynoecial development, androecial morphology, and chemistry. Because the ovary in *Allamanda* is compound at anthesis, the genus has traditionally been associated with other genera with compound ovaries in putatively primitive alliances, although it has often been somewhat isolated in such groupings because of its unique capsular fruit. Woodson (1930) argued that the compound, unilocular ovary of *Allamanda* was derived from a compound, bilocular condition, which in turn evolved from a gynoecium with two simple (free) ovaries, and proposed an advanced position within the Plumerioideae for the genus. Fallen (1985), on the other hand, presented evidence that it was derived more directly from a gynoecium with two simple ovaries; she therefore favored an isolated but otherwise unspecified position for *Allamanda* within the Plumerioideae. (For a more detailed account of this debate concerning gynoecial evolution within the Apocynaceae, see family discussion.)

Other evidence bearing on the systematic position of *Allamanda,* although no less contradictory and/or inconclusive than the foregoing, nevertheless suggests that retention of *Allamanda* as an advanced, isolated genus within the Plumerioideae is most tenable. Allorge (1975) favored placement of a monotypic Allamandeae in the Apocynoideae because of the presence in the genus of "retinacula," which supposedly are adaxial modifications of the anthers (for their attachment to the style-stigma head) characteristic of the Apocynoideae and thought to be homologous to the translators of the Asclepiadaceae (which, in fact, are actually secretions of the style-stigma head). However, such findings were not confirmed by Fallen (1985), who in addition pointed out that while steroidal alkaloids have been detected in several genera of Apocynoideae (as well as in *Holarrhena* R. Br. of the Plumerioideae; see Hegnauer), they evidently do not occur in *Allamanda.* It is also notable that *Allamanda* and *Plumeria* have in common a number of lactone-containing iridoids, a group of compounds that is otherwise rare, apparently among all plants (Coppen & Cobb). Although the kinds of indole alkaloids that appear to be restricted to and widespread in the Plumerioideae have not been reported in *Allamanda* (see Ganzinger & Hesse; Kisakürek *et al.*; and family discussion), the extent to which the genus has been investigated for such compounds is unclear.

Several phenolic compounds have been confirmed for *Allamanda* since Gibbs's treatment, in which only the probable absence in the genus of aurones and leucoanthocyanins was indicated. Daniel & Sabnis reported two flavonols (kaempferol and quercetin) and two phenolic acids (syringic and 2-hydroxy, 6-methoxy benzoic) from leaf material of *Allamanda cathartica,* as well as four additional compounds of the latter type (*p*-hydroxy benzoic, caffeic, *p*-coumaric, and vanillic) from the extraregional *A. violacea* Gardner.

In contrast to earlier reports that tannins were not present in *Allamanda,* Gibbs obtained definite but weak reactions between leaf material of *A. cathartica* and filter paper dipped in aqueous ferric ammonium citrate.

Allamanda cathartica, $2n = 18$ (20 reported in *A. Schottii* Pohl, which is treated as a variety of *A. cathartica* by Bailey), is most readily distinguished from other native or escaped Apocynaceae in the Southeast by its usually quaternate leaves (Nowicke reported two specimens from Panama with opposite or alternate leaves on terminal branches) and its spiny capsules. In this same group, *Rhabdadenia biflora* (Jacq.) Mueller-Arg. is the only other species in which the calyx lobes are foliaceous, and *Nerium Oleander* L. is the only other in which the leaves are whorled.

Allamanda cathartica is probably native only in northeastern South America (Nowicke; Woodson, 1938b). It is widely cultivated, escaped, and perhaps naturalized along the Atlantic Coast of Central America from Belize to Panama. According to Standley & Williams (p. 337), the species "has every appearance of being native in wet forests" in this area, although in Guatemala, for example, it is commonly planted from the Central Highlands (at ca. 1500 m) down to both the Atlantic and Pacific coasts. In South Florida it often persists at abandoned homesites but may also be found and is evidently naturalized in disturbed areas (Long & Lakela); according to Judd (pers. comm.), it occurs out of cultivation in the state only occasionally. In Venezuela the plants are trees that reportedly attain heights of 40 m and trunk diameters of as much as a meter (Standley & Williams), but in South Florida they are shrubs no taller than about 3 m (Long & Lakela) or vines of comparable size. The fruits are well adapted to dispersal by water because of air trapped within both the locules and the spiny projections.

Nowicke indicated that *Allamanda cathartica* has escaped from cultivation in many tropical areas of the world. Some of the specimens I have seen from Florida (FLAS) evidently belong to other cultivated species.

In Belize the white latex of *Allamanda cathartica* is sometimes used as a substitute for chicle, and in Venezuela it is boiled to produce a caulking for canoes (Standley & Williams). It has also been reported that in Belize a leaf extract is occasionally used by woodsmen to make a beverage (Standley & Williams).

REFERENCES:

Under references for the Apocynineae, see BACKER & VAN DEN BRINK (1965a); BAILEY; CHITTENDEN; GIBBS; HEGNAUER; LONG & LAKELA; and STANDLEY & WILLIAMS.

Under references for the Apocynaceae, see ALLORGE (1975); BOITEAU; DANIEL & SABNIS; FALLEN (1985); GANZINGER & HESSE; KISAKÜREK *et al.*; NOWICKE; and WOODSON (1930, 1938b).

COPPEN, J. J. W., & A. L. COBB. The occurrence of iridoids in *Plumeria* and *Allamanda*. Phytochemistry **22:** 125–128. 1983.

SAKANE, M. Revisão do gênero *Allamanda* L. (Apocinaceae) no Brasil. Dissertação de Mestrado, Universidade Estadual de Campinas. 1983.*

Subfam. APOCYNOIDEAE [Echitoideae Schumann in Engler & Prantl, Nat. Pflanzenfam. IV. 2: 122. 1895.]

Tribe ECHITEAE Schumann (excluding *Apocynoideae* Woodson, Ann. Missouri Bot. Gard. 17: 9. 1930), *ibid.* 122, 160, "Echitidae."

6. **Echites** P. Browne, Civ. Nat. Hist. Jamaica 2: 182. 1756.

Terrestrial, woody vines; axes and leaves glabrous or rarely with sparse [or sometimes dense], nonglandular pubescence. Leaves opposite; blades cordate, rotund, ovate, or lanceolate, often folded in half longitudinally and crescentiform, apices acute, sometimes mucronate, margins somewhat revolute, bases obtuse, often oblique; petioles without lateral appendages, colleters present [or sometimes absent] on bases and adjacent areas of stem. Inflorescences axillary [rarely terminal or subterminal], pedunculate, [1- to] many-flowered, bracteate; pedicels longer than calyces, rarely bracteolate. Calyx 1/16[–⅙] as long as corolla or less, glabrous [or sometimes with sparse, nonglandular pubescence]; lobes triangular [or lanceolate], bases sometimes imbricate, squamellae present. Corolla salverform (but tube widened [or constricted] at or usually below middle), usually longer than leaves, with nonglandular pubescence (adaxially, along tube); lobes overlapping to right in aestivation, spreading, obovate [or lanceolate], undulate, sometimes oblique; tube without adaxial appendages. Stamens inserted at widest point of corolla tube, mostly glabrous; filaments very short, flat, straight; anthers agglutinated to style-stigma head, each narrowly sagittate (apex and basal lobes acute), incompletely fertile (bearing adaxially 2 locules in upper ½[–⅘], introrsely dehiscent, the long axis mostly parallel to that of filament. Nectaries 5, alternating with stamens, free from but adjacent to one another, not exceeding [or exceeding] ovaries, sometimes alternating with 5 smaller, more internal nectaries. Carpels completely free in ovule-bearing region, united above; ovaries 2, simple, distinct, unilocular, with marginal placentae and numerous ovules; style terete, gradually and slightly widened subapically; style-stigma head cylindrical, basally umbraculiform [or not], with 2 obtuse lobes apically, glabrous. Fruits follicular, usually 2 from each flower (the pair divergent 160–200°), cylindrical [or sometimes slightly moniliform]; surface usually striate, glabrous; dehiscence by an adaxial suture. Seeds numerous, rostrate, with a tuft of trichomes at apex. TYPE SPECIES: *Echites scandens foliis ovatis nitidis venosis; floribus herbaceis* = *Tabernaemontana Echites* L. = *E. umbellatus* Jacq. Britton & Millspaugh (Bahama Fl. 336. 1920) gave *Tabernaemontana Echites* L. (1759) as the name of the type species, which they considered to be synonymous with *E. umbellatus*; Woodson (Ann. Missouri Bot. Gard. **20:** 607. 1933) put forth his reasons for selecting *E. umbellatus*. (Name from Greek, *echis*, viper, in reference to the lianous habit and/or poisonous properties of the plants.)

A genus that in the strictest sense, as considered here, includes six (Airy Shaw, in Willis; Woodson, 1936) or seven (Nowicke; Standley & Williams) tropical American species of woody vines with opposite leaves and relatively conspicuous flowers. Although monotypic as first proposed, *Echites* was progressively and for the most part indiscriminately expanded until it became an enormous assemblage of considerable heterogeneity. *Angadenia* Miers, *Rhabdadenia* Mueller-Arg., *Trachelospermum* Lem., and *Pentalinon* Voigt (*Urechites* Mueller-Arg.) among our genera, as well as *Mesechites* Mueller-Arg. (ten species), *Mandevilla* Lindley (100 or more species), *Prestonia* R. Br. (60 to 70 species), and *Odontadenia* Bentham (about 25 species), along with a number of others, have been segregated from *Echites* and generally accepted by authors of contemporary floristic works (e.g., Nowicke; Standley & Williams; Woodson, 1933, 1935a, 1936, 1938b). A list of excluded or uncertain species compiled by Woodson (1936) included over 300 names and indicated transfers to over 20 genera.

De Candolle recognized three sections in *Echites,* but of the species presently included in the genus, only *E. umbellatus* Jacq. was known to him. Woodson (1936) proposed two subgenera and two sections for the six species he included, although the names were not validly published (and, to my knowledge, remain so) because they were not accompanied by Latin descriptions or diagnoses. Subgenus *Pseudoechites* (corollas less than 2.5 cm long, the lobes reflexed at anthesis; inflorescences lax and many-flowered) comprised two species of Mexico, Costa Rica, and Belize, while subg. *Euechites* (= subg. *Echites,* if and when others validated) (corollas greater than 5 cm long, the lobes spreading at anthesis; inflorescences compact and few- to several-flowered) included four species separated into two sections. Section *Yucatanensis* (corolla tube not spirally contorted) included three species of Central America, and sect. *Umbellata* (= sect. *Echites,* if and when others validated) was monotypic.

Echites umbellatus, $2n = 12$ (for var. *crassipes* (A. Rich.) Gómez Maza, see Van der Laan & Arends), the only member of the genus in our area, is easily distinguished from other southeastern Apocynaceae by its salverform corollas in which the tubes are conspicuously widened near or below the middle and by its large follicles that usually diverge about 180°. The plants grow in hammocks and pinelands in southern Florida (including the Keys), the West Indies, the Yucatan Peninsula, Belize, Guatemala, Honduras, and the coast of Colombia, but evidently not in Panama (see Nowicke). Two varieties have been recognized, var. *umbellatus* (leaves 2–7.6 cm wide, pedunculate inflorescences) throughout the range of the species, and var. *crassipes* (leaves 0.2–1.5 cm wide, sessile or subsessile inflorescences of a single flower) in Cuba. However, Woodson (1936) stated that plants assignable to the latter variety appeared to represent nothing more than depauperate individuals; several of the specimens he cited were obtained from barrens and/or serpentine soils.

In general, information about *Echites* in such works as those of Gibbs and Metcalfe & Chalk (1950, 1983) probably refers to species now included in other genera.

According to Chittenden, several species of *Echites,* including *E. umbellatus,* are cultivated.

REFERENCES:

Under references for the Apocynineae, see AIRY SHAW (in WILLIS); DE CANDOLLE; CHITTENDEN; GIBBS; METCALFE & CHALK (1950, 1983); and STANDLEY & WILLIAMS.

Under references for the Apocynaceae, see VAN DER LAAN & ARENDS; NOWICKE; and WOODSON (1933, 1935a, 1936, 1938b).

GENTRY, A. H. A new combination for a problematic Central American Apocynaceae. Ann. Missouri Bot. Gard. **70:** 205, 206. 1983. [*Prestonia Woodsoniana* (Monachino) A. Gentry (*Echites Woodsoniana* Monachino) with characters of both *Echites* and *Prestonia,* and similarities to Asclepiadaceae.]

7. **Angadenia** Miers, Apocynaceae S. Am. 173. 1878, in part; emend. Woodson, Ann. Missouri Bot. Gard. **23:** 191. 1936.

Terrestrial, erect, ascending, or decumbent subshrubs or small woody vines; axes and leaves glabrous or with nonglandular pubescence. Leaves opposite to sometimes subopposite; blades narrowly ovate to lanceolate, sometimes folded in half longitudinally and crescentiform, apices sometimes mucronate, margins markedly revolute, bases truncate to obtuse; petioles short, without lateral appendages, colleters lacking on bases and adjacent areas of stem. Inflorescences usually axillary, pedunculate, few- to several-flowered, bracteate; pedicels much longer than calyces, ebracteolate. Calyx ¼–⅛ as long as corolla, glabrous; lobes triangular and attenuate, bases usually imbricate, with squamellae. Corolla funnelform, about as long as leaves, with nonglandular pubescence (adaxially, along upper part of tube); lobes overlapping slightly to right in aestivation, erect or slightly spreading, obovate, entire, oblique (the overlapped margin with a single, acute lobe); tube and throat without adaxial appendages. Stamens inserted near top of corolla tube, with nonglandular pubescence; filaments short, flat, straight; anthers agglutinated to style-stigma head, each narrowly sagittate (apex and basal lobes acute), incompletely fertile (bearing adaxially 2 locules in upper ½), introrsely dehiscent, long axis mostly parallel to that of filament. Nectaries 5, alternating with stamens, basally connate [sometimes free], converging above and mostly concealing ovaries. Carpels completely free in ovule-bearing region, united above; ovaries 2, simple, distinct, unilocular, with marginal placentae and numerous ovules; style terete; style-stigma head conical, not umbraculiform, with 2 acute lobes apically, with hairs hanging from base. Fruits follicular, usually 2 from each flower (the pair divergent ca. 90° or less), narrowly cylindrical to slightly moniliform; surface striate, glabrous; dehiscence by an adaxial (and sometimes also abaxial) suture. Seeds numerous, rostrate, with a tuft of trichomes at apex. LECTOTYPE SPECIES: *A. Berteroi*[17] (A. DC.) Miers (*Echites Berteroi* A. DC.); see Woodson, Ann. Missouri Bot. Gard. **23:** 192. 1936. (As indicated by Miers, name from Greek, *angeion,* duct or vessel [diminutive of *angos,* jar], and *adin,* gland, in reference to the "urceolated disk" [concealment of the ovaries by the nectaries].)

A genus here considered to include one or two species (Long & Lakela; Woodson, 1936, 1938b) of erect or lianous subshrubs with opposite leaves and rather conspicuous flowers, native to southern Florida (including the Keys) and the West Indies. As originally proposed by Miers, *Angadenia* included a number of species that Mueller-Argoviensis had placed in *Odontadenia* Bentham and *Anisolobus* A. DC. However, Woodson (1936) considered *Angadenia* sensu Miers to be heterogeneous and returned 16 species (of the 21 he removed) to the latter two genera, which he united under *Odontadenia* (a New World genus of about 26 species, one endemic to Hispaniola, some of the others strictly

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[17] According to Article 73.10, ICBN, 1988, incorrect terminations for epithets based on personal names should be treated as orthographic errors to be corrected. Thus, Alphonse de Candolle's original spelling "Berterii" should be corrected to "Berteroi," in accordance with Recommendation 73.C.1(a), since the epithet commemorates Carlo Giuseppe Bertero.

continental). According to Woodson (1936), the two species he retained in *Angadenia* differ from *Odontadenia* in their rostrate (vs. truncate) seeds and from *Rhabdadenia,* in which they were included by Schumann as sect. *Glandulosae* K. Schum., in having (vs. lacking) squamellae. Either the small, narrow, markedly revolute leaves or the five nectaries that equal or exceed the ovaries may be used to distinguish *Angadenia* from all other native or escaped Apocynaceae in the southeastern United States.

Angadenia Berteroi (A. DC.) Miers grows in pinelands throughout the range of the genus. Woodson (1936) indicated that it differs from *A. Lindeniana* (Mueller-Arg.) Miers of eastern Cuba and Jamaica in its simple (vs. dichotomously branched) inflorescences and its shorter corollas (2.5–3.4 vs. 3.7–4.5 cm) with conical to campanulate (vs. tubular) throats. However, deferring taxonomic interpretation until more was known, he also reported that specimens from Santo Domingo are somewhat transitional between the two species in corolla-throat shape but are otherwise assignable to *A. Berteroi.*

According to an annotation by R. E. Schultes, *Robertson 192* (GH), from Long Pine Key, Dade Co., Florida, and assignable to *Angadenia Berteroi,* yielded questionable results when subjected to a simple alkaloid test described by Raffauf (1962).

Evidently very little else has been reported about this genus. It is not mentioned in any of a number of relatively comprehensive works, such as those compiled for the chemistry and embryology of flowering plants, the anatomy and seeds of dicots, and the cytotaxonomy of the Apocynaceae. It also escapes mention in several treatments of cultivated plants.

REFERENCES:

Under references for the Apocynineae, see LONG & LAKELA; RAFFAUF (1962); and SCHUMANN.

Under references for the Apocynaceae, see MIERS; MUELLER-ARGOVIENSIS; and WOODSON (1936, 1938b).

8. **Pentalinon** Voigt, Hort. Suburb. Calcutta, 523. 1845.[18]

Terrestrial to semiaquatic, woody vines to suberect subshrubs; axes and leaves with nonglandular pubescence, but sometimes viscid. Leaves opposite or subopposite; blades ovate, elliptic, or obovate, apices obtuse, acute, or mucronate, sometimes retuse, margins flat or revolute to various degrees, bases obtuse to cuneate; petioles without lateral appendages, colleters occasionally present on bases and adjacent areas of stem. Inflorescences axillary, pedunculate, [few- to] several-flowered, bracteate; pedicels frequently as long as calyces, ebracteolate. Calyx about ¼ as long as corolla, glabrous or with non-

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[18] According to Hansen & Wunderlin, *Pentalinon* is legitimate and should be used instead of the more familiar, but later, *Urechites* Mueller-Arg. Pichon (1950a, p. 36) had recognized this problem earlier, and although he proposed conservation of *Urechites,* no action on the matter appears to have been taken, and *Pentalinon* remains the correct name for the genus. Hansen & Wunderlin (following Woodson, 1936) recognized two species in the genus and provided new combinations, information about types, and many synonyms.

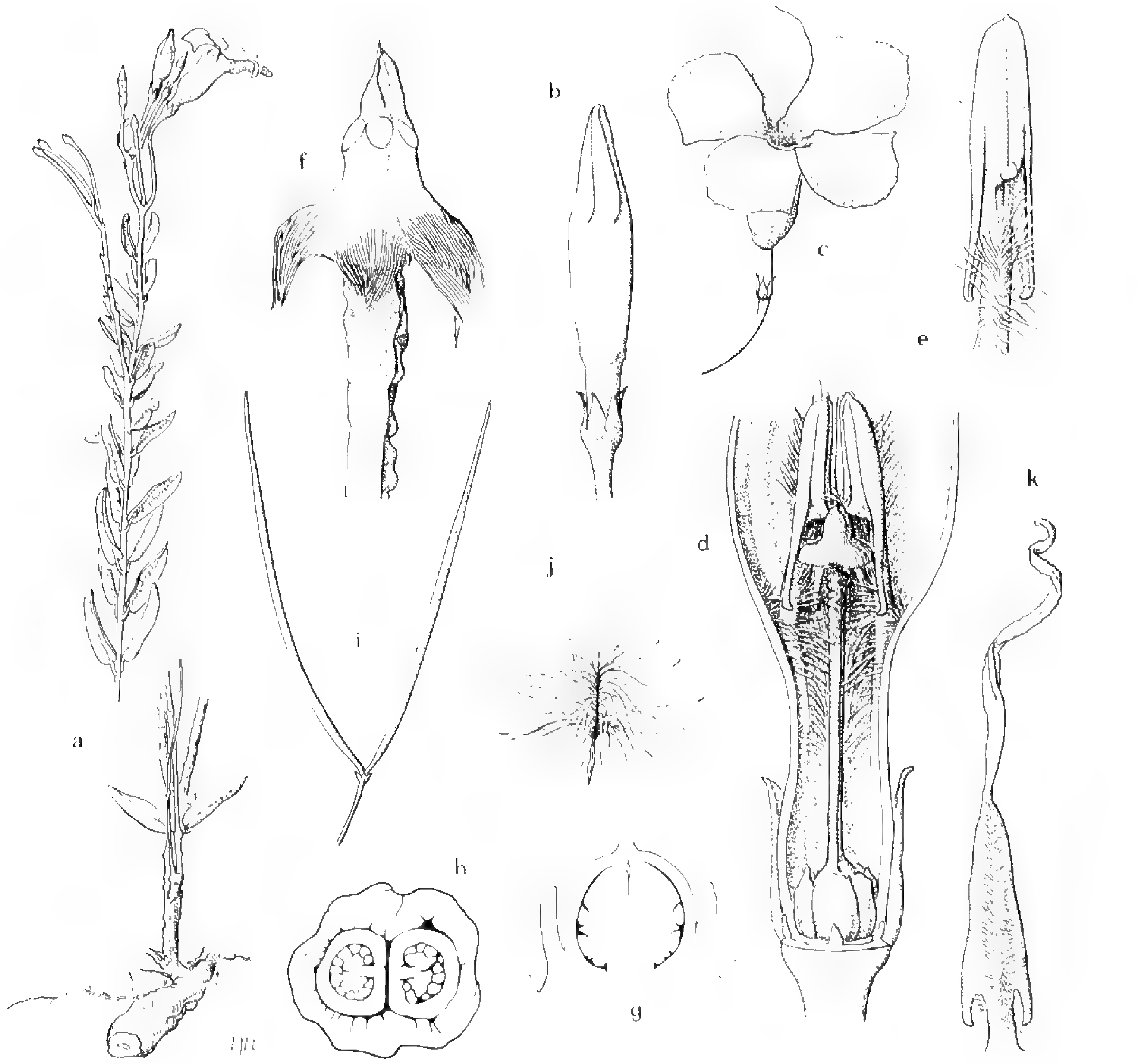

FIGURE 4. **Angadenia** and **Pentalinon** (*Urechites*). a–j. *A. Berteroi*: a, distal part of vertical stem (inflorescences more commonly axillary than terminal) above, and rhizome with base of vertical, above-ground stem below, × ½; b, flower bud, corolla lobes overlapping to right, × 2; c, flower, corolla funnelform, lobes overlapping to right, × 1; d, lower part of flower (2 calyx lobes and half of corolla tube and throat removed), showing 3 of 5 squamellae alternating with calyx lobes, anthers agglutinated to style-stigma head, the 5 nectaries mostly concealing ovaries, × 5; e, stamen, adaxial side, showing short, flat, straight filament with nonglandular pubescence, narrowly sagittate anther (apex often more acute than shown), point of attachment to style-stigma head at base of 2 locules, × 10; f, apical part of style (mostly terete) and style-stigma head (tufts of nonglandular trichomes basally, 3 of 5 points of anther agglutination subapically, 2 acute lobes apically), × 15; g, nectaries and ovaries cut in median longitudinal section, × 15; h, basal, connate portion of nectaries and adjacent ovaries, each with marginal placenta and numerous ovules, cut in transverse section, × 15; i, persistent calyx, 2 mature follicles, × ½; j, seed, with apical tuft of trichomes, × 1. k, *P. luteum*: stamen, abaxial side (filament short, flat, straight; anther narrowly sagittate, with characteristic apical appendage), × 5.

glandular pubescence; lobes narrowly triangular and sometimes keeled and/or attenuate, bases usually imbricate, squamellae present. Corolla funnelform, about as long as leaves, with nonglandular pubescence (adaxially, near juncture of tube and throat; glabrous abaxially or sparsely pubescent throughout); lobes overlapping to right in aestivation, suberect to spreading, obovate, entire, somewhat oblique; tube and throat without adaxial appendages. Stamens inserted near base of throat, with nonglandular pubescence; filaments short, flat, straight or slightly curved; anthers agglutinated to style-stigma head, each narrowly sagittate (apex acute, surmounted by a long appendage intertwining with the others; basal lobes nearly linear [or acute]), incompletely fertile (bearing adaxially 2 locules in upper ½), introrsely dehiscent, long axis mostly parallel to that of filament. Nectaries 5, alternating with stamens, free [or adherent] but adjacent to one another, nearly equaling [or exceeding] ovaries. Carpels completely free in ovule-bearing region, united above; ovaries 2, simple, distinct, unilocular, with marginal placentae and numerous ovules; style bilobed in transverse section; style-stigma head slightly conical, basally umbraculiform, with 2 acute lobes apically, glabrous. Fruits follicular, usually 2 from each flower (the pair divergent less than 90° basally but usually incurved and crossing apically), terete; surface striate, glabrous; dehiscence by an adaxial suture. Seeds numerous (each encased to various degrees by a subtending, deciduous, scaphiform placental scale), rostrate or very narrow throughout, with a tuft of trichomes at apex. (*Urechites* Mueller-Arg., 1860, nom. illegit.) TYPE SPECIES: *P. suberectum* (Jacq.) Voigt (*Echites suberecta* Jacq., the only species included in the genus by Voigt in the protologue) = *P. luteum* (L.) Hansen & Wunderlin (*Vinca lutea* L.).—WILD ALLAMANDA.

A genus probably of only two species (Woodson, 1936; Hansen & Wunderlin) of nearly prostrate subshrubs to woody vines with opposite leaves and large flowers, native to southern Florida, the West Indies, Central America, and perhaps northern South America. Although the plants have been described under several names in other genera, most frequently *Echites* and—of course—*Urechites*, they have two features that are unique among native and escaped Apocynaceae in the southeastern United States. The linear appendage frequently borne at the apex of each anther (but see below) that is spirally intertwined with the others and the scaphiform placental scales encasing each seed to various degrees are perhaps unknown in the rest of the family.

Pentalinon luteum (L.) Hansen & Wunderlin (*Urechites lutea* (L.) Britton), $2n = 12$, is a familiar and typical component of hammocks, thickets, and mangrove swamps in coastal areas of southern Florida and most of the West Indies; it has been reported from, but is probably uncommon in, Belize (see Woodson, 1933) and Colombia (see Woodson, 1936). The species is an especially variable and complex one, as indicated by, for example, individuals in which the anther appendages are extremely short or absent (Woodson, 1936). It differs from *P. Andrieuxii* (Mueller-Arg.) Hansen & Wunderlin (*U. Andrieuxii* Mueller-Arg.), the only other commonly accepted species, in characters including its linear-lanceolate, acute (vs. ovate, obtuse) calyx lobes, which usually are as long as or longer than (vs. shorter than) the cylindrical, basal portion of the corolla tube; its essentially free (vs. concrescent) nectaries; its shorter seed rostrum; and its more delicate, less definitely scaphiform, more readily deciduous placental scales. *Pentalinon Andrieuxii* occurs from Oaxaca to Belize and Guatemala, often in mangrove swamps but also in wet or dry thickets and mixed forests (Standley & Williams).

Gibbs reported for *Urechites lutea* (= *Pentalinon luteum*) the probable absence of leucoanthocyanins, juglone (a naphthoquinone), and syringin (an alcohol glycoside) but detected a number of cardenolides (e.g., oleadrin, urechotoxin).

Very little else seems to have been reported about *Pentalinon*; for example, the plants were mentioned in none of a number of relatively inclusive compilations of information from a variety of fields. *Pentalinon luteum* is used and perhaps grown in Guatemala to treat headaches (Standley & Williams). Primarily because of their cardiac glycosides, plants are also used as a source of arrow poison in tropical America and are employed in several ways medicinally.

REFERENCES:

Under references for the Apocynineae, see GIBBS and STANDLEY & WILLIAMS.

Under references for the Apocynaceae, see PICHON (1950a) and WOODSON (1933, 1936).

HANSEN, B. F., & R. P. WUNDERLIN. *Pentalinon* Voigt, an earlier name for *Urechites* Müll. Arg. (Apocynaceae). Taxon **35**: 166–168. 1986.

9. **Trachelospermum** Lemaire, Jard. Fleur. **1:** *pl. 61.* 1851.

Terrestrial to semiaquatic, woody vines; axes and leaves glabrous or with sparse, nonglandular pubescence. Leaves opposite; blades ovate, lanceolate, elliptic, linear, or rarely obovate (varying greatly in length-to-width ratio; sometimes strongly dimorphic on a single plant), apices acute to subcaudate, margins occasionally revolute and/or undulate, bases obtuse to attenuate, often oblique; petioles without lateral appendages, colleters present on bases and adjacent areas of stem. Inflorescences terminal or axillary, pedunculate [or sessile], many-flowered, bracteate; pedicels usually longer than calyces, sometimes bracteolate. Calyx ½–¼ as long as corolla, glabrous or with sparse, nonglandular pubescence; lobes triangular, usually both aristate and keeled, bases imbricate, squamellae present. Corolla funnelform [or salverform], shorter than leaves, with sparse, nonglandular pubescence (adaxially, near juncture of tube and throat); lobes overlapping to right in aestivation, spreading to usually recurved, triangular to subcordate-ovate, entire or undulate, somewhat oblique; tube and throat without adaxial appendages. Stamens inserted near middle of corolla tube, glabrous; filaments short, subterete, straight or slightly curved; anthers agglutinated to style-stigma head, each narrowly sagittate (apex acute, basal lobes nearly linear), incompletely fertile (bearing adaxially 2 locules in upper ½), introrsely dehiscent, long axis mostly parallel to that of filaments. Nectaries 5, alternating with stamens, free or adherent to one another, nearly equaling ovaries. Carpels completely free in ovule-bearing region, united above; ovaries 2, simple, distinct, unilocular, with marginal placentae and numerous ovules; style obscurely bilobed in transverse section; style-stigma head cylindrical, basally umbraculiform, lobes not evident apically, glabrous. Fruits follicular, usually 2 from each flower (the pair divergent less than 90°), slightly moniliform (very narrow); surface striate, glabrous; dehiscence by an adaxial suture. Seeds numerous, truncate or gradually tapered basally, with a tuft of trichomes at apex. LECTOTYPE SPECIES: *T. jasminoides* Lemaire; see Britton & Brown, Illus. Fl. No. U. S. & Canada, ed. 2. **3:** 23. 1913. (In Index Nominum Genericorum the type species is indicated to be *Echites rhynchosperma* Wall., a substitute name for *Rhynchospermum* A. DC., 1844, non *Rhynchospermum* Reinw., 1825; according to Woodson, Ann. Missouri Bot. Gard. **22:** 233. 1935, the type species is *T. jasminoides* (Lindley) Lem. [*Rhynchospermum jasminoides* Lindley].) (Name from Greek, *trachelos,* neck or throat, and *spermatos,* seed, in reference to the rostrate seeds.)—CLIMBING DOGBANE.

A genus of at least ten (Bailey *et al.*; Ohwi) and possibly as many as 30 (Airy Shaw, in Willis; Correll & Johnston) species native throughout much of southeastern Asia but with one, *Trachelospermum difforme* (Walter) Gray, endemic to the southeastern United States and some adjacent areas. In our area the plants can usually and most readily be distinguished as woody, lianous Apocynaceae with leaves that are opposite and clearly longer than the flowers.

Inclusion of *Trachelospermum difforme* in an otherwise Asian genus has been at least in part justified by considering the case as yet another example of the well-known and extensively documented floristic connection between the eastern parts of Asia and North America (see primarily Li; Woodson, 1928b). One alternative to this arrangement has been to include *T. difforme* in the tropical American *Secondatia* A. DC., as was done, for example, by Schumann. However, whereas all species of *Secondatia* are thought to have fusiform style-stigma heads and calyces with solitary squamellae, *T. difforme* has capitate or subcapitate style-stigma heads and paired squamellae. In part because the latter conditions were not apparent in all Asiatic members of *Trachelospermum,* Woodson (1935a) suspected that the two genera were indistinct. Nevertheless, he prudently avoided uniting them until more was known about the plants, at least in part because such an action would have perhaps unnecessarily replaced *Trachelospermum* with the older and (in North America) less-familiar *Secondatia,* as well as brought about the need for a fairly large number of new combinations. Unfortunately, this issue remains unresolved despite the over 50 years that have elapsed since Woodson addressed it. It is notable that with the exception of $2n = 20$ for two Asian species of *Trachelospermum* (including *T. jasminoides,* see below), these two genera are evidently unknown cytologically.

Two sections were recognized in *Trachelospermum* by Schumann: sect. *Eutrachelospermum* K. Schum. (= sect. *Trachelospermum*), with long-pedunculate inflorescences in the axils of the upper leaves (all of our plants fit this description), and sect. *Axillanthus* K. Schum., with sessile inflorescences in the axils of both upper and lower leaves. However, they appear to have little utility and not to have been accepted by subsequent workers, including Ohwi, who listed three species for Japan, and Tsiang & Li, who treated ten species in the People's Republic of China.

Trachelospermum difforme twines on herbs (including grasses), shrubs, and trees in a variety of dry, moist, and wet habitats, including weedy places. It occurs along both the Coastal Plain and the Piedmont, from southern Delaware to eastern Texas, and in the Mississippi Valley to as far north as the southern parts of Missouri, Illinois, and Indiana. This distribution coincides remarkably with the continental shoreline of the Cretaceous Period and with the present range of *Taxodium distichum* (L.) Rich. (Woodson, 1935a). Although *Taxodium* Rich., with three species, is now restricted to North America, it is usually considered to be closely allied to the monotypic *Glyptostrobus* Endl. of eastern Asia, a relationship that has been considered parallel to that proposed for *Trachelospermum* (Woodson, 1928b).

Woodson (1935a) noted that although the inflorescences and flowers of *Trachelospermum difforme* do not vary much, certain aspects of vegetative morphology do. For example, plants with very narrowly elliptic to almost linear foliage were reported from the southwestern part of the species' range but were considered taxonomically insignificant because of the existence in the same area of both individuals with very broad leaves and others with variable leaf shape. Leaf pubescence was indicated to vary more or less haphazardly.

Trachelospermum jasminoides can be distinguished from *T. difforme* by its larger flowers in which the corolla lobes are longer (vs. shorter) than the tubes, and reportedly by its stouter stems (Woodson, 1938b). In southern Florida the plants rarely escape from cultivation but are not known to be fully naturalized (Judd, pers. comm.). *Brumbach 8326* (FLAS, GH), for example, from Lower Captiva Island, Lee Co., Florida, is indicated on the label to have been obtained from a plant that had escaped to a thicket.

Species of *Trachelospermum* are widely cultivated indoors and, in mild climates, outdoors as well (Bailey *et al.*). Although the plants and flowers have ornamental value, it is the sweet fragrance of the flowers, particularly in *T. jasminoides*, that is best known and appreciated.

REFERENCES:

Under references for the Apocynineae, see AIRY SHAW (in WILLIS); BAILEY *et al.*; CORRELL & JOHNSTON; LI; OHWI; SCHUMANN; and TSIANG & LI.

Under references for the Apocynaceae, see WOODSON (1928b, 1935a, 1938b).

10. **Rhabdadenia** Mueller-Argoviensis in C. F. P. von Martius, Fl. Brasil. **6**(1): 173. 1860.

Terrestrial to aquatic (often in brackish water), woody vines or rarely subshrubs; axes and leaves glabrous. Leaves opposite; blades ovate, elliptic, or linear (varying greatly in length-to-width ratio; sometimes strongly dimorphic on a single plant), apices mucronate [sometimes acute], margins usually revolute, bases obtuse to cuneate, sometimes oblique [sometimes auriculate]; petioles without lateral appendages, colleters lacking on bases and adjacent areas of stem. Inflorescences axillary, pedunculate, usually 1- or 2- but sometimes up to 5- or 6-flowered, bracteate; pedicels longer [sometimes shorter] than calyces, ebracteolate. Calyx $\frac{1}{4}$–$\frac{1}{8}$ as long as corolla, glabrous; lobes elliptic, apices mucronate [or sometimes lanceolate, apices acute], bases imbricate [or sometimes not], squamellae lacking. Corolla funnelform, about as long as leaves, with nonglandular pubescence (adaxially, near juncture of tube and throat); lobes overlapping to right in aestivation, spreading, usually obovate, entire, somewhat oblique; tube and throat without adaxial appendages. Stamens inserted at top of corolla tube, with nonglandular pubescence (mostly on filaments); filaments short, terete, straight; anthers slightly agglutinated to style-stigma head, each slightly and narrowly cordate (apex acute; basal lobes minute, obtuse), incompletely fertile (bearing adaxially 2 locules in the upper 4/5), introrsely dehiscent, long axis mostly parallel to that of filament. Nectaries 5, alternating with stamens, free and/or basally fused, not exceeding ovaries. Carpels completely free in ovule-bearing region, weakly united above; ovaries 2, simple, distinct, unilocular, with marginal placentae and numerous ovules; style bilobed in transverse section; style-stigma head slightly conical, basally umbraculiform, lobes not evident apically, with a tuft of hairs apically. Fruits follicular, usually 2 from each flower (the pair divergent ca. 90° or less), terete; surface striate to mostly smooth, glabrous; dehiscence by an adaxial suture. Seeds numerous, rostrate, with a tuft of trichomes at apex. LECTOTYPE SPECIES: *R. Pohlii* Mueller-Arg.; see Britton & Millspaugh, Bahama Fl. 337. 1920. (Name from Greek, *rhabdos,* rod, and *adenos,* gland, possibly in reference to the long, narrow follicles [the nectaries are not rod shaped].)—RUBBER VINE.

A genus of three (Nowicke) or four (Airy Shaw, in Willis) to perhaps ten (Long & Lakela) species of conspicuously flowered, woody vines or less often erect subshrubs in southern Florida, the West Indies, Mexico, Central America, and South America from Colombia to Paraguay. Although in the past some species have been placed in *Echites, Rhabdadenia* appears to be well defined and widely accepted at present. The plants can be most readily distinguished from other native or escaped Apocynaceae in the Southeast by a combination of characters, including leaves that are opposite, mucronate, and about as long as (but narrower than the greatest widths of) the flowers, and calyx lobes that are foliaceous, half elliptic, and mucronate (those of *Allamanda cathartica* are foliaceous, half elliptic, and acute).

Mueller-Argoviensis distinguished two evidently unnamed groups within *Rhabdadenia,* each treated as a section by Schumann: sect. *Eglandulosae* K. Schum. (= sect. RHABDADENIA) with nonsquamellate calyces, and sect. *Glandulosae* K. Schum. with squamellate ones, treated here as the genus *Angadenia* Miers.

Rhabdadenia is represented in the Southeast by *R. biflora* (Jacq.) Mueller-Arg., a species that is characteristic of shallow water in mangrove swamps (Long & Lakela; Standley & Williams) but also occurs in coastal hammocks and thickets, as well as on canal banks (Godfrey & Wooten). The plants grow on various species of shrubs and trees throughout the range of the genus, except that they appear not to coexist with two other species of *Rhabdadenia* native to the eastern slopes of the Andes from Colombia to Paraguay (Woodson, 1933); in Central America they are reportedly confined to the Atlantic Coast (Standley & Williams).

Data summarized by Young suggested that in some cases the synthesis of flavonoid sulfates by angiosperms might be of systematic importance but in others environmental factors might be more directly responsible; a strong correlation evidently exists between the production of these compounds and growth in such habitats as alkaline deserts, salt marshes, and mangrove swamps. Although flavonoid sulfates were indicated in (unspecified) members of *Rhabdadenia,* the genus was not included in Young's discussion. Therefore, it might be of interest to compare plants of *R. biflora* from mangrove swamps and those from less saline habitats with respect to their production of these compounds.

Surprisingly little else has been reported about this genus. Despite the fact that the plants have large, attractive flowers, they were not included in several standard treatments of cultivated and/or economically important plants. In addition, they escape mention in other relatively inclusive compilations, such as those dealing with chemistry, cytology, anatomy, embryology, and seeds.

REFERENCES:

Under references for the Apocynineae, see AIRY SHAW (in WILLIS); GODFREY & WOOTEN; LONG & LAKELA; SCHUMANN; STANDLEY & WILLIAMS; and YOUNG.

Under references for the Apocynaceae, see MUELLER-ARGOVIENSIS; NOWICKE; and WOODSON (1933).

Tribe APOCYNEAE [subfam. Apocynoideae Woodson, Ann. Missouri Bot. Gard. **17:** 9. 1930.]

11. **Apocynum** Linnaeus, Sp. Pl. **1:** 213. 1753; Gen. Pl. ed. 5. 101. 1754.

Terrestrial, erect or ascending, perennial herbs; axes and leaves glabrous or with nonglandular pubescence. Leaves opposite to sometimes subopposite and/or alternate [rarely whorled]; blades ovate to narrowly lanceolate, apices often mucronate, margins often revolute, bases truncate to attenuate, often oblique; petioles without lateral appendages, colleters present on bases and adjacent areas of stem. Inflorescences terminal or axillary, pedunculate, few- to many-flowered, bracteate; pedicels usually longer than calyces, rarely bracteolate. Calyx ¼ to nearly as long as corolla, glabrous or with nonglandular pubescence; lobes narrowly triangular, bases slightly imbricate, squamellae lacking. Corolla campanulate, short-cylindrical, or urceolate, much shorter than leaves, mostly glabrous; lobes overlapping slightly to right in aestivation, erect, spreading, or reflexed, triangular to subcordate-ovate, entire, not oblique; tube with 5 adaxial appendages opposite lobes and near base. Stamens inserted very near base of corolla tube; filaments short, terete, curved; anthers agglutinated to clavuncle, each sagittate (apex and basal lobes acute), incompletely fertile (bearing adaxially 2 locules in upper ½), introrsely dehiscent, long axis mostly parallel to that of filament. Nectaries 5, alternating with stamens, distinct, not exceeding ovaries. Carpels completely free in ovule-bearing region, united above; ovaries 2, distinct, unilocular, with marginal placentae and numerous ovules; clavuncle rhomboid, with 2 lobes apically. Fruits follicular, usually 2 from each flower (the pair divergent less than 90° basally but sometimes incurved and convergent or even crossing apically), narrowly cylindrical; surface striate, glabrous; dehiscence by an adaxial suture. Seeds numerous, narrowly cylindrical, with a tuft of trichomes at apex. LECTOTYPE SPECIES: *A. androsaemifolium* L.; see Britton & Brown, Illus. Fl. No. U. S. & Canada, ed. 2. **3:** 21. 1913. (*Apocynum* listed by Linnaeus [Philosophia Botanica, 141. 1737] as a name provided by Tournefort, although it had been used by Dioscorides and his contemporaries as early as the fourth century B.C. for nearly any plant with milky sap. Name from Greek, *apo,* away from or separate, and *kynos,* dog, supposedly in reference to the use of some species as a dog repellent.)—DOGBANE, INDIAN HEMP.

A taxonomically controversial genus of herbs for which the number of species is remarkably dependent on generic as well as specific limits. Considered in the strict sense, as it is here, *Apocynum* includes only American plants. Even so defined, the number of described taxa had grown from two species of questionable distinctness late in the nineteenth century to more than 110 species and a number of infraspecific taxa by 1928 (Woodson, 1930). Following Woodson's (1930) treatment, most authors now recognize about seven species in the genus. Naturally distributed from approximately 30°N latitude in northern Mexico and southern Texas to about 55°N in southern Canada, *Apocynum* is probably the only genus in the family that occurs only in temperate climates. While all species, regardless of taxonomic interpretation, are present in the contiguous 48 states, only a few extend into Mexico and Canada, and none is know to occur in peninsular Florida.

Old World members of this assemblage have also been referred to a variable number of species in *Apocynum* and/or two segregate genera. Woodson (1930) recognized two species in *Trachomitum* Woodson and three in *Poacynum* Baillon. However, Correll & Johnston considered *Apocynum* in the broad sense, indicating seven species for North America but 70 for temperate and tropical regions elsewhere. Three or perhaps four species were recognized in Europe by Markgraf (in Heywood), all assigned to *Trachomitum.* One of these, *T. venetum* (L.) Woodson, was indicated for the People's Republic of China by Tsiang & Li, who retained it in *Apocynum* but referred two other species in that country to *Poacynum.* Ohwi treated a single species in Japan. Although he maintained it in *Apocynum,* it is probably closely related to if not conspecific with *T. venetum.* Pobedimova recognized six species of *Trachomitum* and two of *Poacynum* in the Soviet Union. According to Woodson (1930), *Trachomitum* occurs sparingly on the shores of the Adriatic, Aegean, and Black seas in Europe, and more generally from there to the Yellow Sea and the Sea of Japan, while *Poacynum* is found in "Songria and Turkestan."

Apocynum (in both name and generic concept) has had an extraordinarily long and complex history, most of which has been thoroughly recounted by Woodson (1930). Although the name is present in herbals dating back to the fourth century B.C., it probably was not used unequivocally and exclusively for plants now included in the genus until the seventeenth century A.D. It is thought that before that time, and particularly during the lives of, for example, Theophrastus, Pliny, and Dioscorides, the name was used for nearly any plant with milky juice. Many plants once called "Apocynum" are now included in the Asclepiadaceae, while others belong to the Euphorbiaceae.

Tournefort (Inst. Herb. **2:** 91–94. 1700) was apparently the first to propose division of *Apocynum*, once all the euphorbiaceous elements had been removed (see also discussion of suborder). His removal of *Periploca* L. and *Asclepias* L. from the genus appears to have presaged more recent delimitations (including ones adopted here), except that some plants now included in *Asclepias* and related genera were retained as one of two unnamed groups.

In limiting the number of species in *Apocynum* to five, Linnaeus (Sp. Pl. **1:** 213, 214. 1753) conceived a less heterogeneous group than Tournefort's. Nevertheless, only *A. androsaemifolium* and *A. cannabinum* L. have been retained in the genus by modern botanists. According to Woodson (1930), for example, two of the three remaining species actually belong to two closely related genera, *Trachomitum* and *Ichnocarpus* R. Br., and a third is more distantly placed, in *Parsonsia* R. Br. (Apocynoideae: Parsonsieae).

Woodson (1930) considered *Apocynum* and the two segregates, *Trachomitum* and *Poacynum*, to be distinct at the subfamilial level from the remainder of the Echitoideae (= Apocynoideae) as delimited by Schumann. For reasons outlined in the discussion of the family, the group is recognized here as one of three tribes of Apocynoideae, the Apocyneae.

The trichasial inflorescence and the distinct corollar appendages of *Apocynum* were considered by Woodson (1930) to be more primitive than the corresponding conditions in *Trachomitum* and *Poacynum*. In each of these Old World genera, the inflorescence is monochasial and the corollar appendages are fused into a ring. The latter is reduced in *Poacynum*, a condition that could, by extrapolation, be considered even more advanced. In addition, whereas the nectaries are distinct in *Apocynum* and *Trachomitum*, they are fused and therefore presumably more advanced in *Poacynum*. Thus, *Apocynum* might be considered the least specialized of the three genera in this tribe, and *Poacynum* the most advanced. However, of relevance to such a proposal is Woodson's report (1930) that adjacent nectaries in *Apocynum* are sometimes fused early in development.

The revision of *Apocynum* by Woodson (1930) was preceded by a lengthy and detailed account of its taxonomic and nomenclatural history, anatomy and morphology, infrageneric relationships, geography, and economic uses. Some of the more important and/or enlightening aspects of this discussion are summarized below.

Primarily on the basis of anatomical evidence from seed-grown plants, Woodson (1930) was able to provide a relatively clear interpretation of the vegetative life history characterizing the genus. Buds formed on the axis of the hypocotyl or in the axils of the cotyledons develop into more or less vertical rhizomes, from which both the aerial stems and the mostly horizontal, so-called "gemmiferous" roots arise. The latter may attain lengths of several meters and produce buds laterally that develop into new vertical rhizomes that, in turn, give rise to both additional aerial stems and horizontal roots. The rhizomes, which are perennial, bear cataphylls that grade into true leaves on the aerial stems, which are annual. Many species have been proposed to accommodate variations in aerial-stem development that Woodson (1930) thought to be mostly due to environmental and not genetic factors. Absorptive roots are freely produced on both the rhizomes and the horizontal roots, although they are more numerous on the latter. The plumule evidently does not play a significant role in the formation of roots. In the production of rhizomes on the hypocotyl, *Apocynum* and *Trachomitum* appear to be unique within the family.

Woodson's (1930) investigations into the reliability of a diverse set of potential characters have contributed to our understanding of the taxonomic relationships within the genus. While in general the size, shape, and pubescence of leaves are not reliable taxonomic characters, the opposite is true of the angles at which they are held relative to the stem (sometimes unreliable on herbarium specimens) and the degree to which those on primary and other axes are uniform. The interpetiolar appendages (colleters), as in the rest of the family, are superficial (there are no vascular connections) but nevertheless probably represent vestigial stipules. As in many other Apocynaceae, the stomata are anomocytic (there are two or more subsidiary cells parallel to the opening), and they are distributed only on the abaxial surfaces of the leaves. The number of layers of palisade cells in the mesophyll ranges from one in some leaves to several in others and was shown experimentally by Woodson (1930) to be independent of environmental conditions. This character supposedly provides a constant distinction between *Apocynum androsaemifolium*, with only a single layer, and *A. cannabinum*, in which the layers vary from two to several.

Evolution in the flowering portion of the plant body in *Apocynum* was envisioned by Woodson (1930) to have involved foliar reduction, floral aggregation, and a transition from determinate to indeterminate growth. Thus, the condition in *A. pumilum* (Gray) Greene (determinate, terminal, trichasial cymes with scarious bracts and a progressive reduction to individual flowers in the leaf axils below) was considered to be most primitive; those in *A. androsaemifolium* (less-determinate, terminal cymes with scarious bracts and only abortive flowers in the leaf axils below) and *A. sibiricum* Jacq. (indeterminate, terminal cymes with foliaceous bracts and no axillary flowers) representative of intermediate stages; and that in *A. cannabinum* (indeterminate, terminal cymes with scarious bracts and no axillary flowers) most advanced.

Calyx-lobe color is dependent on environmental conditions and therefore of no taxonomic importance. Calyx lobes are entire in all species except *Apocynum medium* Greene var. *lividum* (Greene) Woodson, in which they are minutely toothed. Corolla-lobe shape is not indicative of relationships, although orientation is. The comparative widths of the corolla-tube base and summit are important, as are the relative lengths of the calyx and corolla. With the exception of two varieties of *A. medium*, the corollas in *Apocynum* are glabrous.

Three ridges originating at the base of each petal, in the tubular region, converge to form a pointed tip that projects into the small space between adjacent anthers, at about the summit of their auricles. The possible role of these structures in floral function is discussed below.

The pollen of *Apocynum* is shed as tetrads (see Frye & Blodgett), as is that of *Trachomitum* and *Poacynum*. The individual grains are small, spheroidal, and rather smooth. The pollen of nearly all species is largely abortive, as is

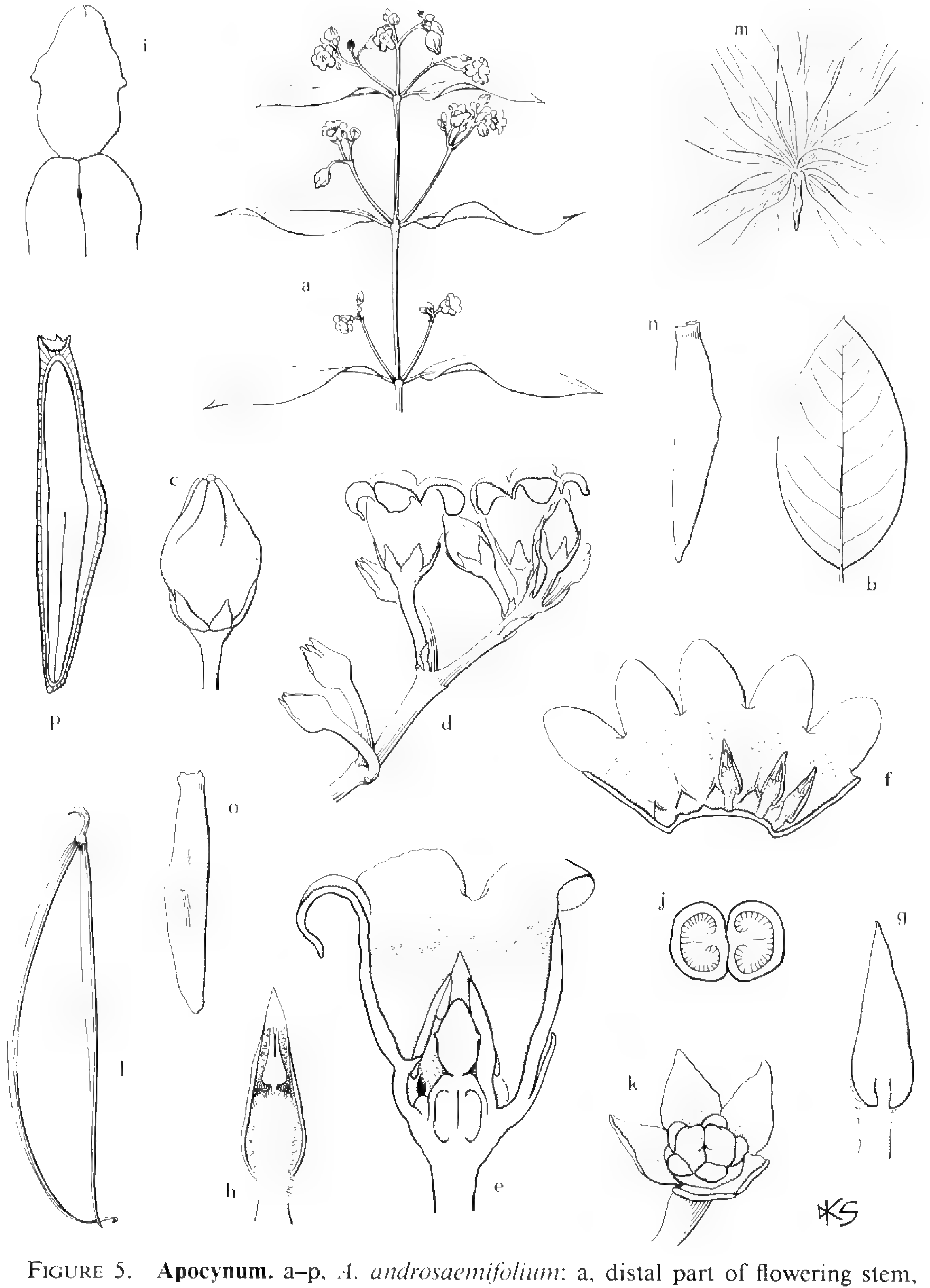

FIGURE 5. **Apocynum.** a–p, *A. androsaemifolium*: a, distal part of flowering stem, with both terminal and axillary inflorescences, × ½; b, leaf, × ½; c, flower bud, corolla lobes overlapping to right, × 3; d, detail of inflorescence with 3 flower buds, 2 open flowers, and 3 post-anthesin flowers, the last with persistent calyces, × 2; e, flower cut longitudinally, showing urceolate corolla with reflexed lobes, anthers agglutinated to clavuncle, 1 nectary, of 5, on left, gynoecium free in ovule-bearing region but united above into clavuncle, × 6; f, corolla cut open between lobes, with 5 adaxial appendages and 3 of 5 stamens, × 3; g, stamen, abaxial side, with basal auricles curved toward each other, × 10; h, stamen, adaxial side, with 2 locules in upper ½ of anther, × 10; i,

indicated by the unequal sizes of members of individual tetrads, and "polysporous" tetrads are frequent, supposedly indicating abnormal meiosis. These observations suggest that hybridization may be frequent within the genus.

The carpels in *Apocynum* are separate in the ovule-bearing region, except that they are partially embedded in the receptacle (hence, semi-inferior ovaries). They are fused in the region that normally corresponds to the style and stigma into a fleshy, rhomboid body known as the clavuncle. Elongate glandular hairs in the upper half of this structure are adjacent to similar outgrowths at the point where the anthers are attached to the filaments. Coherence of the stamens to the clavuncle, a characteristic of the Apocynoideae (as recognized here), is effected by an exudate from these cells. The anthers fit together closely, forming a cone over the top of the clavuncle. Into the space between this cone and the summit of the clavuncle, pollen is shed.

The mechanism of pollination in *Apocynum* is not fully understood, even though the flowers have long been a matter of great curiosity. At least a part of the problem has centered around a debate concerning the location of the stigmatic surface. According to Woodson (1930), Linnaeus and other early workers thought that it is situated at the summit of the clavuncle; indeed, they probably assumed *Apocynum* to be like most other flowering plants in this regard, in spite of the structural peculiarities involved. Many later authors adopted the view that it is located in the basal half of the clavuncle, with the most notable exception that Demeter provided anatomical evidence resurrecting the original idea. Despite Woodson's (1930, p. 66) statement that Demeter's findings were "by no means a help" in the debate, Woodson nevertheless provided an illustration showing that "the upper portion bears typically glandular stigmatic cells" and that the "lower region is scarcely equipped to carry on the function of the stigma." Woodson (1930) also observed that pollen tubes penetrated the clavuncle in the region enclosed by the anther cone. Clearly, resolution of this controversy is essential to understanding pollination in the genus and throughout the family (see also Schick, 1980, 1982).

Woodson (1930) pointed out that, although there was abundant and unequivocal evidence that species of *Apocynum* are self-incompatible, normal insect visits do not effect cross-pollination. Indeed, as stated by a number of observers (e.g., Legget, 1872a–c; 1873a, b; Woodson, 1930), although flowers are abundantly produced by most plants, only a few develop into fruits. Woodson (1930) implied that the reception by a stigma of pollen from another plant

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gynoecium, with 2 distinct ovaries subtending clavuncle, × 12; j, 2 distinct, unilocular ovaries cut in transverse section, each with marginal placenta and numerous ovules, × 12; k, post-anthesin flower, with persistent calyx (tips of 2 lobes removed), 5 nectaries, and 2 ovaries, × 6; l, 2 mature follicles, from a single flower (typically, both carpels developing), × ½; m, seed, with apical tuft of trichomes, × 1; n, seed, tangential side, with trichomes removed and hilum on right, × 6; o, seed, adaxial side, with trichomes removed and hilum in foreground, × 6; p, mature seed cut longitudinally through hilum but otherwise as in "n" (seed coat hatched, endosperm stippled, embryo unmarked), × 10.

is only accomplished after those relatively rare occasions on which trapped insects exert enough energy in attempting to escape that the anther cone is disrupted.

Despite Woodson's (1930) belief that pollination in *Apocynum* is not understood, at least two accounts (Knuth; Legget, 1872a–c, 1873a, b), based primarily on observations of *A. androsaemifolium,* seem to have some merit. The following is based upon a combination of these and my own observations.

Nectar guides in the form of pink stripes extend from the sinuses between corolla lobes to the base of the corolla tube, highlighting five openings to spaces at the base of the flower, between the nectaries. Each opening is defined by the base of one anther and the corolla tube from one of its inwardly projecting appendages to the next. The two auricles at the base of each anther are curved toward each other. They and the appendages of the corolla are shaped and oriented in such a way that while an insect part such as a proboscis or a leg could freely pass through the opening in a downward direction to reach the nectar, it would likely be funneled during withdrawal by one half of one appendage and the nearest auricle into the seam between that anther and the next, which becomes increasingly narrow from its base to its summit. That the insect parts in question thus become tightly wedged between the anthers is indicated by the frequency with which they are left behind by departing insects. A visitor that leaves intact would probably have pulled its inwedged part along the seam between adjacent anthers until the widest part of the clavuncle was reached (the point at which the clavuncle and the stamens are agglutinated). Thus, scraping from three sides ultimately would have been effected during the insect's attempts to free the part and most, if not all, of any pollen that might have been on it would have been deposited on or near the clavuncle immediately beneath the widest part, suggesting that this is the most effective location for the stigmatic surface. The struggle for freedom would usually be sufficient to force apart the anther cone, allowing pollen in the space above the clavuncle to be released, deposited on the visitor, and transferred to another flower. It is perhaps significant that the nectaries are located beneath the corollar appendages, where they are somewhat protected from the activities described above.

Several fruit and seed characters were thought by Woodson (1930) to be taxonomically important. He considered erect follicles to be more primitive than pendulous ones because they occur only in *Apocynum pumilum* (Gray) Greene, in which the inflorescence/infructescence in general was considered primitive. He also used follicle length and shape (straight or curved), as well as seed and coma length, to separate taxa.

Woodson's (1930) key divided the species of *Apocynum* into four groups based on leaf orientation (ascending, spreading, or drooping) and the relative lengths of calyces and corollas. Although the correspondence between these divisions and four sections proposed by Béguinot & Belosersky is close, Woodson (1930, p. 70) contended that recognition of such infrageneric taxa was both unnecessary and artificial because "the species are so confluent as to make sectional lines extremely obscure." It is therefore not entirely clear why he chose to recognize seven species instead of one, except that he was a strong proponent of the idea that hybridization is responsible for most of the intergradation between species.

One of the four species and most of the numerous varieties recognized by Woodson (1930) in eastern North America, as well as 12 of the 21 species and varieties he recognized in the entire genus, were thought by him to have resulted from hybridization. Numerous examples of fruit-bearing, putatively parental populations adjacent to and/or intermingled with sterile, presumably hybrid populations were cited in support of this view. For example, although *Apocynum androsaemifolium, A. cannabinum, A. sibiricum* (cited as *A. hypericifolium* Aiton), and *A. medium* were all abundant in a field near South Bend, Indiana, during the summer of 1928, only plants assignable to the first three species later developed fruits; *A. medium,* then presumed to be a hybrid between *A. androsaemifolium* and *A cannabinum,* was completely sterile in this sense. Woodson (1930) also cited a locality in Colorado at which fruiting clones of *A. androsaemifolium* var. *incanum* A. DC. were intermingled with nonfruiting individuals of *A. medium* var. *floribundum* (Greene) Woodson. One small plant with the leaves of the former and flowers quantitatively intermediate between the two was discovered in 1929. The plant was named *A. androsaemifolium* var. *intermedium* Woodson even though, evidently, no other individuals had been discovered. Whether or not that single plant ever set fruit was not mentioned. Despite the failure of many plants of presumed hybrid origin to set fruit, those of, for example, the common and typical eastern variety of *A. medium* frequently do (although those of the more restricted western varieties evidently do not).

Woodson (1930) was unable to support his presumptions of hybridity with observations of meiosis in pollen mother cells because of the small size of the anthers involved and because of complications posed by the latex. However, meiotic irregularities were often indicated by individual pollen tetrads in which some of the grains were abortive and relatively deficient in nuclear material, while others included more than the usual complement. He reported that, although all taxa have some sterile pollen, percentages were lowest in those not considered to be of hybrid origin.

In what has become one of the truly classic studies in plant biology, Anderson experimentally evaluated what he termed (p. 159) the "rather extreme position" of Woodson concerning the frequency of hybridization in *Apocynum.* Seeds from specimens determined by Woodson to belong to *A. androsaemifolium, A. cannabinum,* and *A. medium* were germinated, and the resulting plants were grown for about a year and a half. Pollen fertility among progeny of the presumed parental species was generally higher than that among offspring propagated from the supposed hybrid: the average percentage among seven seedlings propagated from one individual assigned to *A. cannabinum* was 95.1, with values ranging from 91 to 98; for *A. androsaemifolium* the figures for 11 seedlings from one individual were 80.9 and 42 to 99, respectively; and for *A. medium* the overall figures for 25 seedlings of five individuals were 64.9 and 4 to 99. On the basis of identifications provided by Woodson, who was unaware of the experiment and therefore the origin of the specimens, both of the putatively parental species bred true in the sense that all of the progeny were assigned to the same species as the plants from which they were propagated; however, both glabrous and pubescent varieties were said to have been segregated from each. Of 25 specimens representing the progeny of what he had identified as *A. medium,* Woodson (1930) indicated that only 18 could still be assigned to that taxon (14 definitely, four questionably), five to *A. androsaemifolium* (three definitely), and two to *A. cannabinum* (one definitely). It is also notable that all of the specimens Woodson considered to be of questionable identity had been propagated from *A. medium.*

Anderson concluded that although *Apocynum medium* is a hybrid between *A. androsaemifolium* and *A. cannabinum,* its taxonomic status, at least in an evolutionary context, is not comparable to that of the parental species. Individuals assignable to this entity appear to comprise a spectrum of cases, each one or more generations removed from the original cross (i.e., an original cross) between the species, in which some are sterile, others display high levels of heterozygosity, and still others breed nearly true. He also implied that while hybridization is a frequent occurrence throughout the genus, it is responsible for fewer taxonomic problems in western than in eastern North America. He considered increased variation in species that were originally more distinct to be one of the most significant effects of introgression in the genus.

The conclusions of Woodson (1930) and Anderson regarding hybridization in *Apocynum* appear to be generally accepted at present. However, it is notable that they have remained unsubstantiated by, for example, chemical and cytological evidence, despite considerable advances in and increased taxonomic uses of the techniques involved. Since publication of Anderson's work in 1936, chromosome numbers have been reported for *A. androsaemifolium* ($2n = 16$, 22), *A. cannabinum* ($2n = 16$, 22), and *A. sibiricum* var. *cordigerum* (Greene) Fern. ($2n = 22$) (see Van der Laan & Arends).

Gleason (New Britton & Brown Illus. Fl. No. U. S. & Canada **3:** 72. 1963) and a majority of his contemporaries, according to him, thought that plants assignable to *Apocynum medium* represented hybrids between *A. androsaemifolium* and either of two other species he considered well marked, *A. cannabinum* and *A. sibiricum.* Gleason indicated that a plant should be referred to *A. medium* if it did not agree with at least six of the seven elements he used to distinguish either *A. androsaemifolium* or, collectively, *A. cannabinum* and *A. sibiricum.* Gleason also thought that the extreme variation in *A. cannabinum* was due to hybridization with *A. sibiricum,* and perhaps with another, evidently unnamed, densely pubescent species as well.

While it is clear that *Apocynum androsaemifolium, A. cannabinum,* and various hybrids between them (including those assignable to *A. medium,* as well as to varieties of this and the parental species) are represented in the southeastern United States, the occurrence there of *A. sibiricum* is questionable. The purer forms of *A. androsaemifolium* (corolla pink or striped with pink, the tube at least as long as the calyx, the lobes spreading; leaves drooping) and *A. cannabinum* (corolla whitish or greenish, the tube about as long as the calyx, but sometimes shorter or longer, the lobes erect or nearly so; leaves ascending or only slightly spreading), as well as plants influenced by the genomes of other species, are all widespread in North America and the Southeast.

Plants assignable to *Apocynum androsaemifolium* appear not to occur in Florida (see, for example, Clewell; Correll & Johnston; Small, 1913, 1933) and generally to be scarcer in the more southern parts of our area. According to Hitchcock and colleagues (p. 79), the species occurs throughout much of Canada and the United States, except for "the s.e." Individuals of this species with pubescent abaxial leaf surfaces and perhaps others with glabrous ones may occur in the Southeast, although the latter are more representative of populations in the western United States.[19] *Apocynum cannabinum* is represented in our area by two pubescence-based variants that, perhaps like the foregoing, may be of questionable significance. What has been called var. *pubescens* (Mitch.) A. DC. (many parts of the plants hairy) is mostly restricted to eastern North America, while the typical element (plants glabrous throughout or only sparsely hairy in places) is not. Plants assignable to *A. medium* may be more common in the eastern two-thirds of the continent, although they occur as far west as California (Munz) and the Pacific Northwest (Hitchcock *et al.*).

Apocynum sibiricum (*A. hypericifolium*), at least in its purer forms, differs most conspicuously from other members of the genus that may be found in the Southeast in its sessile or nearly sessile leaves. Variants with deeply cordate leaf blades, the bases of which often clasp the stem, and corollas about as long as broad have been referred to var. *cordigerum* (Greene) Fern., and those with very narrow leaves and corollas longer than broad would qualify as var. *salignum* (Greene) Fern. Evidently, the typical element includes plants that are glabrous and have oblong to narrowly ovate leaves and corollas about as long as broad; pubescent plants otherwise fitting this description have been referred to var. *Farwellii* (Greene) Woodson. While most authors have not indicated *A. sibiricum* for our area in particular, some (e.g., Correll & Correll; Correll & Johnston) have stated that it occurs throughout most of North America. Although Steyermark indicated that in Missouri it occurs as far south as Texas County, the southernmost border of which is within 50 miles of Arkansas, and Harvill and colleagues reported it for Isle of Wight County in Virginia, I have seen no specimens from the Southeast that are assignable to this species.

Species of *Apocynum* occupy a variety of habitats from sea level to the subalpine zone, including saline and fresh-water beaches and shores, cultivated and fallow fields, open woods, roadsides, railsides, prairies, and dunes. In the Carolinas *A. androsaemifolium* appears to be confined to the mountains of North Carolina (Radford *et al.*). At least in Missouri, plants of *A. sibiricum* reportedly occur in moister habitats than do those of other species (Steyermark),

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[19] Determination of the typical element of *Apocynum androsaemifolium* was addressed by Woodson (1932). He considered the variant of eastern North America to be typical, primarily because Linnaeus (Sp. Pl. **1**: 213. 1753) wrote in the protologue "habitat in Virginia, Canada." Although Linnaeus also indicated at that time "foliis ovatis utrinque glabris" and most eastern plants are pubescent, the trichomes are generally evident only with the aid of a hand lens, and according to Woodson (p. 31) "glabrous" at that time "was a relative term of not too great exactitude." Thus, specimens considered by Linnaeus to be glabrous could actually have been pubescent. If Woodson's interpretation is correct, the correct name for the glabrous variety of western North America would be var. *glabrum* Macoun, and most if not all plants in the east would be assignable to var. *androsaemifolium*. Further resolution of this problem appears to be lacking.

although in Ohio individuals assignable to this species were considered to be xerophytic (Schaffner). Other ecological differences among species of *Apocynum* are not obvious.

Apocynum cannabinum is often a serious weed in, for example, crop fields of corn, sorghum, and soybean. According to Schultz & Burnside, yields from irrigated plantings of corn were reduced very little by the presence of this species, but those from unirrigated corn and sorghum were reduced by as much as 15 and 30 percent, respectively.

Apocynum has had a long and varied history of use by humans, most of which has been reviewed by Woodson (1930). The fibrous bark of several species, but most notably that of *A. cannabinum,* Indian hemp, has been and continues to be a source of thread and cord for the construction of such articles as clothing, sails, fishnets, and rope. Studies during the late nineteenth and early twentieth centuries suggested that the fiber could be profitably used to make paper, although nothing much seems to have been accomplished along these lines since then. Dried and usually pulverized roots and rhizomes of *A. cannabinum* have a stimulating effect on heart function (undoubtedly due to the presence of cardiac glycosides; see discussion of the suborder) and were used by early settlers in the treatment of dropsy and as a diurectic (Uphof), while those of most species enhance the movement of a variety of bodily substances in humans. According to Chittenden, the roots of *A. androsaemifolium* and *A. cannabinum* are poisonous and differ in their medicinal effects. Reports published in the early part of this century indicate that latex from species of *Apocynum* (and *Asclepias*) was a better potential source of rubber than was that of any of the many other species investigated and that the production of both latex and fiber was optimal in plants grown on arid land generally unfit for most other crops. Fields in the western United States were, and perhaps still are, allowed to become dominated by species of *Apocynum* because of the nectar they provide for honeybees.

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[Asclepiadaceae to follow]

THE TAMARICACEAE IN THE SOUTHEASTERN UNITED STATES[1]

WILLIAM J. CRINS[2]

TAMARICACEAE Link, Enum. Hort. Berol. **1:** 291. 1821, "Tamariscinae," nom. cons.

(TAMARISK FAMILY)

Small trees or shrubs [subshrubs] of temperate and subtropical deserts, steppes, and shorelines, on sands, clays, and saline soils. Wood ring-porous or semi-ring-porous; sieve-element plastids of the S-type. Branches slender, persistent or deciduous. Root systems variable, ranging from taproots with relatively short lateral roots to extensively branched, horizontally spreading roots (branches when buried often also producing adventitious roots). Leaves scalelike or small, alternate, simple, entire, usually sessile [rarely subpetiolate], exstipulate, subimbricate, [amplexicaul in some species of *Tamarix*], often fleshy or punctate, with salt-secreting glands, usually glaucescent, with sclereids consistently present at or near vein endings; stomata anomocytic, on both surfaces of leaves

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The illustration of *Tamarix* was prepared by Karen Stoutsenberger from dissections by Kenneth R. Robertson and Carroll Wood from material collected by R. E. Umber (*614*, GH; along the Rio Grande west of Mountainair, Socorro Co., New Mexico), R. L. Wilbur (*7173*, GH; Carteret Co., North Carolina), and D. S. Correll and H. B. Correll (*9599*, GH; Cameron Parish, Louisiana).

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[only on abaxial surface in *Myricaria germanica*]. Inflorescences spicate or racemiform, often aggregated in terminal panicles [or flowers solitary in *Hololachna* and *Reaumuria*]. Flowers perfect [2 species of *Tamarix* dioecious], regular, small, hypogynous, 4- or 5- [6-]merous; pedicels subtended by small, scalelike bracts. Sepals 4 or 5 [6], free or slightly connate, persistent, imbricate. Petals 4 or 5 [6], alternating with and larger than sepals, free, sometimes persistent [with a pair of ligular appendages near base in *Reaumuria*], inserted at base of a fleshy or membranaceous disc, imbricate. Stamens 4 or 5 [to 10 in *Tamarix*, to 75 in *Reaumuria*], usually haplostemonous or obdiplostemonous, usually free [monadelphous in *Myricaria*, fasciculate in 5 bundles in *Reaumuria*]; filaments filiform; anthers tetrasporangiate, 2-locular, versatile, extrorse in *Tamarix* [introrse in *Myricaria*], longitudinally dehiscent, slightly longer than wide; pollen (2-) 3- (4-)colpate, simple or in tetrads, binucleate (in *Tamarix*) [trinucleate in *Myricaria*]. Gynoecium of (2) 3 or 4 (5) carpels united in a compound, superior, unilocular ovary; placentation parietal, placentae sometimes intruded, making the ovary appear plurilocular near base and apex, or reduced, making placentation appear basal; styles 3[–5], distinct or connate at base; stigmas apical or decurrent adaxially [sessile in *Myricaria*]; ovules 2 to many on each placenta, with short funiculi, erect, anatropous, bitegmic, crassinucellar. Fruit a loculicidal, pyramidal capsule, the 3[–5] valves placentiferous at base, coriaceous; seeds long-pilose over entire surface [Reaumurieae] or at apex only, with unicellular hairs, which may be prolonged into a conspicuous hygroscopic coma (Tamariceae), micropyle formed by endostome; endosperm with development nuclear [cellular in *Tamarix tetrandra*], degenerating quickly in Tamariceae [persistent in Reaumurieae]; cotyledons 2, oblong, obtuse at apex, flat or plano-convex, the radicle short, conical, inferior; megagametophyte (embryo sac) tetrasporic, but postmeiotic development variable, usually Fritillaria or Adoxa type, embryogenesis of Solanad type, with broad, massive suspensor formed, polyembryony occasional. Base chromosome number 12. (Including Reaumuriaceae Ehrenberg.) TYPE GENUS: *Tamarix* Linnaeus.

A relatively small family of five genera (*Hololachna* Ehrenb., *Myricaria* Desv., *Myrtama* Ovcz. & Kinz., *Reaumuria* L., and *Tamarix* L.) and about 100 species, occurring primarily in central Asia, the Middle East, northern Africa, and the Mediterranean region of Europe. Several species of *Tamarix* have been introduced into North America, and six of these have become naturalized in the Southeast.[3]

The Tamaricaceae are one of numerous families that have been placed in the catchall order Parietales. Other early suggestions of relationship included the Guttiferales (Endlicher; Grisebach; Hallier, 1911), Rutiflorae (Caruel), and

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[3] *Myricaria germanica* (L.) Desv. has been cultivated in the Southeast. The following key will allow its identification in the event that it is discovered as an escape.

Filaments free, inserted on a disc; anthers extrorse; our species with 4 or 5 stamens. . . . *Tamarix*.

Filaments fused into a membranaceous tube (monadelphous); anthers introrse; stamens 10. . . . . . *Myricaria*.

Centrospermae or its segregates (Adanson; Bessey; De Candolle; Hallier, 1903; Jussieu; Saint-Hilaire; Vesque).

In most recent ordinal classifications, the families of the Parietales have been redistributed, and the Tamaricaceae are now generally placed in the small order Tamaricales, along with the Frankeniaceae (Thorne, 1976) and/or Fouquieriaceae (Barkley; Behnke; Bentham & Hooker; Boivin; Hutchinson, 1964; Takhtajan, 1980), or in the larger order Violales (Cronquist, 1981, 1988; Gibbs; Lindley, 1853; Melchior; Thorne, 1983). These hypotheses, based largely on reproductive features, are also supported by the anatomically similar salt glands of the Frankeniaceae and Tamaricaceae (Solereder) and by the production of D-pinitol by members of both families (Plouvier). A recent novel phylogenetic scheme has the Tamaricaceae in the order Primulales (Goldberg), but this placement is virtually unjustified, except on the basis of such ubiquitous character states as simple perforation plates in xylem vessels, lack of stipules, perfect flowers, superior, unilocular ovaries, and the absence of alkaloids. None of the ordinal characters listed by Goldberg would refute the placement of the Tamaricaceae in the Violales or Tamaricales, and in fact, his description of Primulales requires several qualifiers because of the unusual (for Primulales) character states found in the Tamaricaceae. A cladistic analysis utilizing existing data, or the examination of new lines of evidence, may be required to shed further light on the relationships of this family and, indeed, all of the families of the catchall Parietales.

The basis for the uncertainty in ordinal placement of the Tamaricaceae is the inclusion of two groups of genera (comprising the two tribes Reaumurieae Bentham & Hooker (*Hololachna, Reaumuria*) and Tamariceae (*Myricaria, Myrtama, Tamarix*)[4]) within the family, which at times (e.g., Lindley, 1833, 1853; Maout & Decaisne) have been interpreted as being unrelated. This hypothesized polyphyly is probably based on a misunderstanding of certain character states and their ontogeny. The tribes have been differentiated on the basis of inflorescence structure, distribution of pubescence on the seed, and presence or absence of endosperm in the seed. Developmental studies of the seed have shown that members of the tribe Tamariceae produce cellular (or initially nuclear in *Tamarix tetrandra* Pallas) endosperm, which disappears as the embryo grows to occupy all of the space in the embryo sac (Davis; Puri; Sharma). Thus, the Tamariceae merely show reduction in the development of the endosperm, a trend that correlates with other advanced character states exhibited by the tribe, including tendencies toward elaboration of the hygroscopic hairs on the seed, localization of hairs on the seed, reduction in flower size, increasing complexity of inflorescence architecture, elaboration of the disc, and tetramery in some members.

Members of the Tamaricaceae are generally shrubs or small trees of deserts, sandy or saline areas, shores, riverbanks, and dunes, although some taxa also occur along mountain streams. The branches are covered with small, often scalelike leaves that are punctate with salt-secreting glands. The four- or five-

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[4] Several authors (e.g., Bentham & Hooker) have included a third tribe, Fouquierieae, which is generally accorded family status. Its ordinal placement is as unsettled as that of the Tamaricaceae.

[six-]merous, white, pink, or even reddish flowers are quite small but are aggregated into panicles of racemes or spikes that provide spectacular displays. The capsules contain numerous small seeds that may be hairy over the entire surface (tribe Reaumurieae) or have long hairs at the chalazal end forming a conspicuous coma that aids in dispersal (tribe Tamariceae).

Fossils of the Tamaricaceae are very few. *Tamaricoxylon africanum* (Krausel) Boureau, based on fossil wood, is identical in anatomy to modern *Tamarix* (Boureau). The fossils are from northern African Quaternary deposits and thus shed no light on the age of the family. An attribution of Oligocene age to one of these specimens is considered doubtful by Boureau.

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Tamarix Linnaeus, Sp. Pl. **1:** 270. 1753; Gen. Pl. ed. 5. 131. 1754.

Shrubs or small trees of shorelines [deserts, steppes] on sands and clays, often in areas of high salinity, with extensive root systems, often also with adventitious roots from buried branches. Leaves herbaceous, small, scalelike, entire, alternate, exstipulate, glabrous or papillose [or hairy], sessile with narrow base or somewhat amplexicaul [or vaginate], with salt-secreting glands. Inflorescence of simple or compound racemes, often paniculately branched, occurring on branches of previous and/or current year's growth. Flowers small, perfect [imperfect], 4- or 5-merous, actinomorphic. Bracts shorter than, equal to, or longer than their subtended pedicels, single [2 or 3 in *Tamarix rosea* Bunge], scalelike, entire, glabrous or papillose [or hairy], sessile with narrow base or somewhat amplexicaul [vaginate] (not necessarily paralleling leaf morphology). Sepals 4 or 5 (6), connate for a short distance near base, entire to denticulate [incised], glabrous or papillose [or hairy], imbricate. Petals 4 or 5 (6), white, pink, or red, ovate or elliptic to obovate, entire to emarginate, equilateral or not, persistent or deciduous after anthesis, contorted in bud. Androecium diplostemonous, the outer whorl of 4 or 5 antesepalous stamens, the inner whorl abortive and developed into a nectariferous hypogynous disc with antepetalous lobes [or of 4–10 antepetalous stamens]; stamens free, inserted onto the central disc; anthers dithecal, usually cordate, apiculate or not. Pollen usually tricolpate (rarely tetracolpate), prolate to spheroidal, [9.5–]11.5–23.5[–26] μm wide, [12.5–] 14–28.5[–30] μm long, walls with fine [to coarse] reticulate sculpturing, lumina circular, polygonal or irregularly shaped, clearly defined to the edge of colpi or not. Gynoecium pyramidal or bottle shaped, consisting of 3[–5] carpels, each with a parietal placenta; styles and stigmas 3[–5]. Fruit a loculicidal, many-seeded capsule. Seeds 0.5–0.7 mm long, elongate-obovoid, straight, comose at chalazal end, otherwise glabrous [or hairy near apex]; hairs of coma unicellular, hygroscopic, with wavy thickenings near base; endosperm none. Base chromosome number 12. LECTOTYPE SPECIES: *T. gallica* L.; see Britton, North American Trees, 702. 1908. (The etymology of *Tamarix* is uncertain, but the name is probably derived from the Tambre (Tamariz) River in Spain, although the Tamaro River in Nepal and the Hebrew word *tamaruk* have also been suggested as possible sources.)—TAMARISK, SALTCEDAR.

A genus of about 54 species, of the Middle East, the Mediterranean area, central Asia, and southern Africa. Ten species have been introduced into North America, and six of these are naturalized to varying degrees in the Southeast: *Tamarix gallica* L., *T. ramosissima* Ledeb., *T. canariensis* Willd., *T. africana* Poiret, *T. tetragyna* Ehrenb., and *T. parviflora* DC. The first southeastern records of tamarisks as escapes from cultivation appear to date from 1897 (Horton, 1964).

The infrageneric taxonomy of *Tamarix* has undergone many revisions. Bunge divided the genus into sections on the basis of seasonality of flowering and used numbers of floral parts, raceme and vegetative morphology, filament-insertion patterns, petal persistence, and capsule and style morphology as the basis for further subdivisions. However, Baum (1964) and others have shown that seasonality of flowering is unreliable and that many species have both vernal and aestival (or continuous) anthesis. One of the most useful sets of characters derives from disc morphology. The three sections recognized by Baum (1978) are characterized by features of the disc, as well as by raceme width, petal length, and stamen number and position. Section TAMARIX generally has racemes less than 5 mm broad, petals 1–2.25 mm long, and five antesepalous stamens. Series within this section differ in vegetative features such as the presence or absence of papillae and leaf morphology. Species of sect. OLIGADENIA (Ehrenb.) Endl. have broader vernal racemes, some tetrandrous members, and discs with nectariferous lobes. The series within this section differ in bract length relative to pedicel length, petal shape and length, and raceme morphology. Species of sect. POLYADENIA (Ehrenb.) Baum also have broad racemes but have more stamens and discs that lack nectariferous lobes. Its two subdivisions (ser. ARABICAE Baum, ser. PLEIANDRAE Bunge) differ in the number of antepetalous stamens arising from the disc. The taxa in North America belong to sects. TAMARIX and OLIGADENIA.

Collectors should be aware that most tamarisks are virtually unidentifiable in the vegetative state.

Sect. TAMARIX ser. TAMARIX[5] is represented in North America by *T. gallica,* French tamarisk (filaments five, arising directly from the lobes of the disc, raceme rachis glabrous, racemes arising mostly from green (new) wood, sepals entire or subentire, petals oval, caducous), and *T. ramosissima* (*T. pentandra* Pallas, *pro parte,* nom. illegit., *fide* Baum, 1978; *T. odessana* Stev. ex Bunge) (filaments five, inserted under the disc between its lobes, sepals denticulate, petals obovate, persistent). *Tamarix gallica* is the most widely recorded species in North America, including our area (Chapman; Jones & Coile; Long & Lakela; MacRoberts; Radford *et al.*; Small, 1913, 1933). However, most of these records are incorrect; the species is actually quite rare in North America. In the Southeast it is naturalized in Georgia, Louisiana, and North Carolina. Its natural range includes France, Spain, Switzerland, Italy, and Sicily. *Tamarix ramosissima,* a halophyte commonly cultivated in Arizona and California, has become naturalized in the Southwest. Its natural range spans central Eurasia from eastern Turkey, the Ukraine, and eastern Iraq eastward to Mongolia, Tibet, central China, and North Korea. In our area it is known from Arkansas, Georgia, Louisiana, Mississippi, North Carolina, and South Carolina.

Sect. TAMARIX ser. LEPTOSTACHYAE (Bunge) Baum is represented in the naturalized flora of North America by *Tamarix canariensis* Willd. (filaments inserted at tips of lobes of disc, with bases dilated, sepals denticulate, rachis of racemes usually papillose). Although Baum (1967) noted that *T. canariensis* had only recently been introduced into Arizona, an examination of specimens from many southeastern herbaria indicates that it has been naturalized in the Southeast since at least 1903. It has been found in North Carolina, South Carolina, Georgia, and Louisiana. The native range of *T. canariensis* is the

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[5] Series TAMARIX was called ser. *Gallicae* by Baum (1978), but since it contains the type of the genus, it must be called ser. TAMARIX.

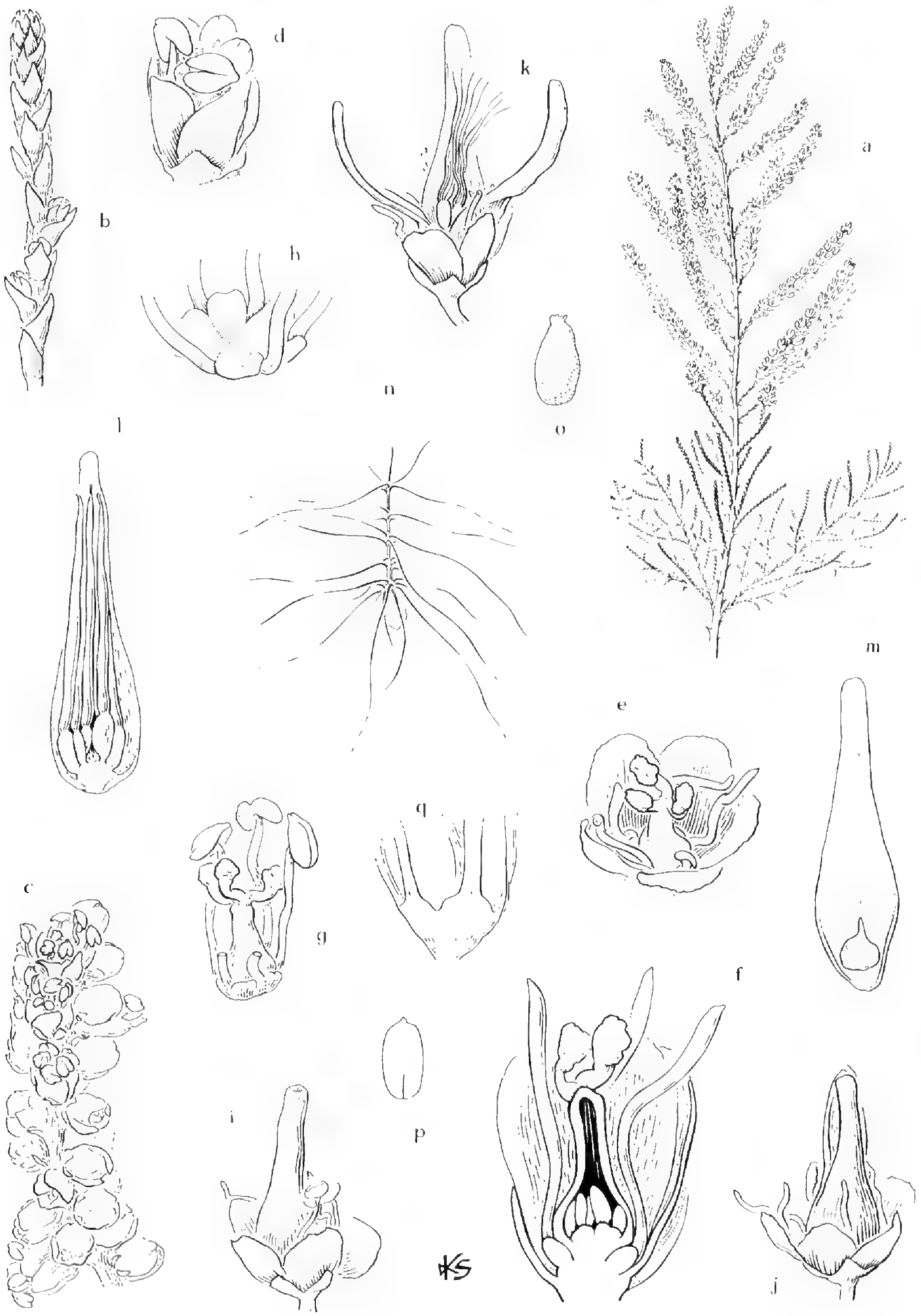

FIGURE 1. **Tamarix.** a–p, *T. ramosissima*: a, tip of branch with inflorescence, × ½; b, detail of vegetative twig with 2 developing lateral buds, × 6; c, detail of inflorescence, × 5; d, young flower with anthers ready to dehisce, × 12; e, flower after anthers have fallen, the stigmas receptive, × 12; f, flower in vertical section, showing attachment of filaments to disc and of ovules to 2 parietal, basal placentae, × 20; g, gynoecium and androecium removed from flower (upper portions of 2 stamens removed), showing attachment of stamens between lobes of disc, × 12; h, detail of disc and bases of filaments,

western Mediterranean Basin (Sicily, extreme southern France, Sardinia, Spain, Morocco, Algeria, Tunisia, and the Canary Islands). Similar to *T. africana* and *T. gallica,* it differs from the former in its smaller flowers (petals less than 2 mm long, racemes not over 5 mm wide) and its obovate (vs. ovate) petals, and from the latter in its denticulate sepals, papillose raceme rachises, and somewhat expanded filament bases. There appears to be considerable morphological overlap between *T. canariensis* and *T. gallica,* however, and the taxonomic and evolutionary relationships of these two taxa require reevaluation.

Section OLIGADENIA ser. ANISANDRAE Bunge is represented in the Southeast by *Tamarix africana* (stamens five, arising directly from disc lobes, petals relatively large, to 3 mm long) and *T. tetragyna* (antesepalous stamens 4 or 5, arising from lobes of disc, one to several smaller antepetalous stamens also present along edge of disc; sepals denticulate; raceme rachis densely papillose; leaves tending to be amplexicaul; vernal racemes more than 5 cm long, loosely flowered). *Tamarix africana* is naturalized in Louisiana and South Carolina. Its indigenous range includes southern Europe (France and Spain to Italy and Yugoslavia) and northern Africa (Canary Islands and Morocco to Tunisia). Similar to *T. gallica* in disc morphology, it has dilated filament bases. *Tamarix tetragyna,* native to the Middle East (Egypt, Israel, Jordan, Lebanon, Syria, and Cyprus), is reported here for the first time as a naturalized member of the North American flora. It is established on Cumberland Island in Camden Co., Georgia (*W. H. Duncan 29934,* 9 April 1982; DAO). This species differs from all the others that have become naturalized in North America in having antepetalous stamens in addition to the antesepalous ones. It has been the subject of physiological investigations on salt tolerance (see below).

Section OLIGADENIA ser. ARBUSCULAE Baum contains *Tamarix parviflora* (*T. tetrandra* of American authors, not Pallas), small-flowered tamarisk, the only naturalized North American species that is consistently tetramerous and tetrandrous. Its sepals are denticulate and ridged, and its filaments arise directly from the lobes of the disc. Naturalized in Florida, Louisiana, Mississippi, and North Carolina, as well as throughout the Southwest, its natural range includes southern Europe from Corsica to Turkey, and perhaps also Spain and northern Algeria.

In addition, Baum (1967) recorded *Tamarix aphylla* (L.) Karsten (sect. TAMARIX ser. VAGINANTES (Bunge) Bunge), *T. aralensis* Bunge (sect. TAMARIX ser. LEPTOSTACHYAE), and *T. chinensis* (sect. TAMARIX ser. LAXAE Gorshk.) as being naturalized or cultivated in North America. *Tamarix aphylla* is known to be naturalized only in the southwestern United States; it is native to North

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gynoecium removed, × 20; i, mature, unopened fruit, with persistent calyx lobes, petals, and filaments, × 10; j, capsule with the 3 valves beginning to separate apically, × 10; k, fully open capsule, 2 seeds still inside, × 10; l, nearly mature capsule with 1 valve removed to show seeds attached to parietal, basal placenta, × 12; m, valve of capsule after shedding of seeds, placenta visible below, × 12; n, wind-dispersed seed with coma, × 12; o, seed body, × 25; p, embryo, oriented as in seed body in "o," × 25. q, *T. canariensis*: detail of disc, showing insertion of filaments on lobes of disc, × 20.

and East Africa, the Middle East, and western Asia eastward to central India. *Tamarix aralensis* has not yet been found as an escape in the Southeast, but it has been grown as an ornamental shrub in Orange Co., North Carolina (*W. C. Coker s.n.,* 2 June 1942; NCU). It is indigenous to the southern Soviet republics of Kazakhstan, Turkmenistan, Tadzhikistan, and Uzbekistan, as well as to Iran and northern Afghanistan. It differs from its close relative, *T. canariensis,* in having filaments that arise from between the lobes of the disc rather than directly from the lobes. *Tamarix chinensis* (*T. pentandra* of American authors, in part, not Pallas; *T. juniperina* Bunge) is widely cultivated in North America. It has been grown in North Carolina (*N. Henry s.n.,* 5 July 1932; NCU), but contrary to Baum's (1967) findings, I have located no authentic record of escape from cultivation in the Southeast. The natural range of *T. chinensis* includes Mongolia, The People's Republic of China, and Japan. It is not a halophyte, unlike most other species of the genus, although it is a xerophyte. Although very similar to *T. ramosissima, T. chinensis* has subentire sepals, and in the vernal flowers some of the filaments are inserted between the lobes of the disc on its margin rather than below it. However, in aestival flowers the filament-insertion pattern breaks down. It is difficult to see how these taxa can be recognized as different species, let alone members of different sections of the genus! Both *T. chinensis* and *T. ramosissima* have gone under the name *T. pentandra* in North America, where they are considered to be serious pests along water courses in the deserts of the Southwest. An extensive body of literature on their spread, physiological ecology, and control has developed (see below). One additional species, *T. mascatensis* Bunge (sect. TAMARIX ser. TAMARIX) has been cultivated in Florida and Texas but is not yet known to have escaped.

There are two centers of diversity for the genus. One of these, the Indo-Turanian region, is also said to be its center of origin, with several of the species there exhibiting primitive character states (poorly developed nectariferous disc, large flowers, both as in *Tamarix ericoides* Rottler). A secondary center of diversity exists in the Middle East. Although most species of *Tamarix* are desert or shoreline plants, Vasilchenko & Vasileva argued that the genus may have originated in mesic habitats along mountain streams on what were probably islands in the Tethys Sea during the Paleogene. Their argument is based on the current distribution of *T. arceuthoides* Bunge, which, however, is not one of the more primitive taxa, at least according to Baum (1978). More detailed analyses of the biogeography of the region, and of that time period, will be needed to test their hypothesis.

Brotherson & Winkel have outlined several aspects of the life history of *Tamarix ramosissima* that contribute to its success as a colonizer. These include the ability to produce seeds throughout the growing season and under a wide range of conditions, cross-pollination by wind, self-compatibility when cross-pollination is not effected, high seed output, long- and short-range dispersal capabilities, vigorous vegetative reproduction, allelochemical potential (presumably by way of salt secretion), and wide environmental tolerances. Seed germination can take place at any time during the growing season as long as sufficient moisture is available. The primary root elongates very quickly after germination.

There is contradictory evidence regarding the mode of pollination in *Tamarix*. Although Brotherson & Winkel suggested that pollination is mediated by wind, floral morphology indicates that entomophily must also occur in some species. The staminal disc secretes nectar, a nutritional reward for potential pollinators. However, within *Tamarix* there has been a trend toward the production of smaller grains of pollen in smaller flowers, which has been interpreted as a tendency toward anemophily (Baum *et al.*, 1971). No experimental investigations of incompatibility systems have been undertaken, and self-compatibility may vary from species to species. It has been reported for *T. ramosissima* and for *Myricaria germanica*, but cultivated material of *T. chinensis* in New York has failed to set seed (R. G. Means, New York State Museum, pers. comm., 1988).

Vegetative modes of reproduction are also important in the spread and persistence of *Tamarix* species. Several species are known to produce adventitious roots and vigorous new shoots from stem tissue that becomes buried. Periodic burning, clearing, or flooding may lead to the development of impenetrable thickets of *Tamarix* (Everitt). Thus, although reproduction from seed may be important, the significance of layering and reproduction from vegetative fragments that have been dispersed along water courses should not be underestimated in the rapid spread and colonization of extensive areas in the Southwest by *T. ramosissima* and other species.

Horton (1964) reviewed the history of the introduction and spread of tamarisks in the United States, and several authors have dealt with the problem of the "weedy" species since then. *Tamarix "gallica"* had become naturalized along the Gulf Coast of Texas by 1877. Its migration into Kansas is well documented. It moved east from Colorado during the 1920's on floods of the Arkansas River and had spread halfway across Kansas by 1939 (Gates). *Tamarix "pentandra"* had become naturalized in North Carolina by 1897 and was first recorded as an escape in Arizona in 1901. Not present in Utah before 1925, it spread rapidly along the major river systems and lake shores between 1935 and 1955. More recently, it has begun to invade mountain streams and reservoirs (Christensen, 1962). It is now a common riparian tree in Utah, Nevada, Arizona, New Mexico, Colorado, and Texas (in Texas, 450,000 acres had been colonized by 1965) and is also known from southern Montana, Idaho, Nebraska, and South Dakota. *Tamarix "tetrandra"* (*T. parviflora*), introduced into the Southwest largely to prevent erosion resulting from overgrazing by livestock, became established in Texas by 1888 and in North Carolina by 1897 (Horton, 1964). This species has also been reported as an escape in Portugal. Numerous other studies document the spread and effects of tamarisks along river systems and in irrigable land in the Southwest.

The weediness of tamarisks, especially in dry areas, stems from their ability to become established by rapid seed germination and quick growth of very extensive root systems where water resources are limited. Once established, the plants may cause reductions in the width of stream channels, which leads to flooding, as well as to excessive use of limited water supplies (although varying opinions exist on this point; see, for example, Waisel, 1960b).

Tamarix chinensis has the capacity for stomatal closure under conditions of high wind or temperature, thereby diminishing its evapotranspiration rate. In *T. aphylla* diurnal stomatal closure may be mediated by an endogenous circadian rhythm (Hagemeyer & Waisel). Other xeromorphic features of the leaves probably also minimize water loss. In *T. chinensis* stomata appear to respond directly to changes in the leaf-to-air absolute humidity gradient, leading to more efficient water use during the hottest part of the day, when the evaporative demand is greatest.

Tamarisks replace native vegetation and are less attractive to most species in the southwestern avifauna. Only the mourning dove (*Zenaida macroura* (L.)) and the white-winged dove (*Z. asiatica* (L.)) find tamarisk stands to be suitable nesting sites, according to a 1977 report by B. W. Anderson and colleagues, although ladder-backed woodpeckers (*Picoides scalaris* (Wagler)) have since been recorded as nesting in *Tamarix chinensis* in the Southwest.

The salt glands of several species of *Tamarix* have been studied extensively, with the aim of determining mechanisms by which these xerophytes survive in soils with high salt concentrations. Located on both leaf surfaces and young branches, the glands consist of two highly vacuolated and six less vacuolated cells, surrounded by epidermal cells with thickened walls. Numerous plasmodesmata connect the collecting cells with adjacent mesophyll cells. Although Mace believed that there was no association between the salt glands and vascular bundles, later studies of apoplastic transport (e.g., C. J. Campbell & Thomson) indicate that solutes can be shunted from the xylem to the salt gland under conditions of high salinity. The types of salts secreted by these glands vary, depending on the root environment. Both monovalent and divalent cations, including Na^+, K^+, Ca^{++}, and Mg^{++}, are present in the solutions. There is no apparent selectivity between cations of the same valence, but divalent cations are prevalent. Anion constitution also varies, with Cl^-, NO_3^-, HCO_3^-, and SO_4^{--} being the major ones. In one investigation HCO_3^- comprised 60 percent of the anion pool (Berry, 1970), and in another SO_4 was predominant (Hem). Salt secretions are sometimes so extensive that columns or cuboidal crystals of salts develop above the gland pores, and concentrations of salts in the secretions may be 20 times greater than those in the local ground water. *Tamarix tetragyna* (and probably other species) has additional physiological adaptations to soil salinity. Tolerance to salinity stress is at least partially mediated by very large amounts of free proline in the roots.

The only investigations of organic natural products in the Tamaricaceae have involved *Tamarix* species. Long-chain alkanes and esters have been partially characterized in *T. gallica*. The alkanes generally contain 18–35 carbons, and the esters have 40–52. Various hydroxylation substitutions occur along these chains, but the level of hydroxylation is very low. The pool of waxy constituents generally contains mixtures of isomers. In *T.* "*pentandra*" the epicuticular waxes are variable in constitution, with the variability apparently unrelated to ecological factors (Wilkinson, 1980). Several complex or unusual phenolics, including tannins, a furanofuran, a phenolic glyceride (niloticol), a 3,4-benzocoumarin (a rare class of natural products), a new 4-methylcoumarin, a new digalloylglucose (nilocitin), and several aldehydes, have been isolated from *Tamarix* species. Various flavonoids, including unmethylated, mono-, and dimethyl ethers of the flavonols quercetin (rhamnetin, isorhamnetin, tamarixetin, tamarixin) and kaempferol (kaempferide, rhamnocitrin), as aglycones, glycosides (glucosides, rhamnosides, and glucuronides), and sulfates, have also been found in such tissues as leaves, flowers, and roots. The leaves of all five species of *Tamarix* analyzed contain D-pinitol (Plouvier). In various species the organic acids trans-2-hydroxy-4-methoxycinnamic acid, ellagic acid and its 3,3′-dimethyl ether, gallic acid, and isoferulic acid have been isolated. The systematic significance of most of these compounds has yet to be determined.

There is some evidence of host-specificity among certain gall-forming insects associated with tamarisks. For example, most species of *Psectrosema* (Diptera: Cedidomyiidae) utilize only a single species of *Tamarix*. One species is known to use two hosts; two other species use three. Host specificity is maintained in mixed stands of tamarisks. When more than one species of *Psectrosema* utilizes the same host species, the insects attack different parts of the tree, minimizing competition (Habib; Harris; Kieffer). There is also some suggestion that other insects, such as mirids (Heteroptera) and aphids (Homoptera), are monophagous or oligophagous with regard to *Tamarix* species (Habib *et al.*; Zocchi). Girdling of branches by cicadas (Homoptera) has been noted in Arizona, but vigorous regrowth from below the girdled areas indicates that no measure of biological control is achieved by these insects.

Despite the detrimental effects *Tamarix* species have had on natural ecosystems in North America, some of the same species, as well as others, are economically important in a positive sense. *Tamarix aphylla* and other species are sources of tannins, which are produced in healthy branch, bark, fruit, and leaf tissue, as well as in galls induced by various insects, including moths, scale insects, and gall midges. Tamarisks have also been used for afforestation of dunes and other "unproductive" sandy areas (Decaux; Trabut, 1926; Vilbouchevitch). The wood serves as a source of fuel, charcoal, and construction material, and its ash yields various inorganic salts. Decaux noted that a fine powder of *Tamarix* ash acted as a successful contact insecticide against caterpillars. In Manchuria and Tibet young branch tips of tamarisk have been used to make tea, and in northern Europe tamarisk has served as a substitute for hops in the making of beer. *Tamarix "pentandra"* has been shown to accumulate trace elements such as boron, cadmium, copper, lead, lithium, manganese, molybdenum, nickel, and zinc (Dreesen & Wangen; Shiber), both as surface deposits on leaves and internally, which may mean that the plants could serve as indicators of environmental contamination. Medicinally, species of *Tamarix* have been used in the treatment of infections, hemorrhages, enteritis, rickets, gout, and rheumatism, and as astringents, antiseptics, and diuretics (Vilbouchevitch). Some tamarisks are also prized for the honey produced from their nectar. The biblical "manna" is a gummy exudate composed mainly of carbohydrates secreted by coccids (scale insects) that feed on the branches of *T. mannifera* (Ehrenb.) Bunge (Maleki & Djazayeri). Several species, including those naturalized in North America, are also grown as ornamentals (Bailey *et al.*).

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NEW OR NOTEWORTHY DRABA (BRASSICACEAE) FROM SOUTH AMERICA

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Four Colombian species, *Draba boyacana, D. cocuyana, D. pseudocheiranthoides*, and *D. ritacuvana*, are described as new. Two new names, *D. argentifolia* and *D. ecuadoriana*, are proposed to replace the later homonyms *D. argentea* O. E. Schulz and *D. affinis* J. D. Hooker, respectively.

Draba L. is the largest genus of the Brassicaceae, with about 350 species distributed primarily in the Northern Hemisphere (Al-Shehbaz, 1987). There are at least 75 species in South America that grow at high elevations from Colombia and Venezuela southward along the Andes to Patagonia.

During the past several years, I have been working on a revision of the South American species of *Draba*. In this continent the genus is more highly diversified in habit and morphology of its species than elsewhere in the world. There are many undescribed drabas in South America, and the nomenclature of several species is problematic. In the present paper, four new species are described and two new names are proposed.

Draba argentifolia Al-Shehbaz, nom. nov.

Based on *Draba argentea* O. E. Schulz, Pflanzenr. IV. **105**(Heft 89): 134. 1927, non *D. argentea* (All.) Lam. Encycl. **2:** 329. 1786.

A close examination of *Draba argentifolia* and *D. pickeringii* A. Gray supports Schulz's (1927) view that the two species are indeed very closely related. However, the latter species has slender styles ca. 1 mm long, fruiting pedicels 4–6 mm long, petals 4–5 mm long, fruits 4–6 mm long, and valves primarily covered with simple trichomes. In *D. argentifolia* all these structures are clearly shorter than those of *D. pickeringii*, and the fruit valves are covered with furcate and stellate trichomes.

Draba boyacana Al-Shehbaz, sp. nov. FIGURE 1.

Herba perenna pusilla. Caulis erectis vel ascendens, 2.5–9 cm longa, pilis crispis simplicibus vel stipitato-furcatis. Folia basalia rosulata, obovata vel spathulata, acuta, 2-dentata, ciliata, sessilia, superne hispida, pilis rigidibus subappressis simplicibus usque ad 1.4 mm longis et brevioribus stipitato-fur-

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FIGURE 1. Holotype of *Draba boyacana.* Scale bar = 1 cm.

catis, inferne glabrescentia, 7–23 mm longa, 4–8 mm lata; folia caulina 2–5, sessilia, oblonga vel ovata, 5–8 mm longa, 1.5–3.5 mm lata. Inflorescentia corymbosa, ebracteata; pedicelli fructiferi divaricati, 3–5 mm longi. Sepala ovata, erecta, nonsaccata, 3–3.5 mm longa, 2–2.5 mm lata. Petala alba, obovata, cuneata, 5–6 mm longa, 2–2.5 mm lata. Siliqua elliptica vel sublanceolata, compressa, glabra, 7.5–8.5 mm longa, 3–3.5 mm lata; stylus 0.6–0.9 mm longus. Semina matura ignota.

Small perennial herbs. Stems erect to ascending, 1 or few from base, unbranched, 2.5–9 cm long, crisped pubescent with mixture of simple trichomes and shorter, stalked, furcate or substellate ones. Basal leaves forming rosettes, sessile, obovate to spatulate, 7–23 mm long, 4–8 mm wide, acute at apex, cuneate at base, 2-toothed, ciliate, the upper surface hispid with mixture of long, simple, subappressed trichomes to 1.4 mm long and fewer much shorter, stalked furcate ones, the lower surface glabrescent. Cauline leaves 2 to 5, sessile, oblong to ovate, 5–8 mm long, 1.5–3.5 mm wide, entire, pubescent on both surfaces (or only on the upper) with mixture of simple and stalked furcate or substellate trichomes. Inflorescences ebracteate, corymbose racemes, slightly elongated in fruit; fruiting pedicels divaricate, 3–5 mm long, pubescent. Sepals erect, ovate, nonsaccate, 3–3.5 mm long, 2–2.5 mm wide, membranaceous at margin, pubescent. Petals obovate, cuneate, not clawed, 5–6 mm long, 2–2.5 mm wide, white. Filaments erect, dilated at base, 2.2–2.5 mm long, white; anthers ovate, ca. 0.6 mm long. Nectar glands confluent, low, subtending bases of all filaments. Fruits elliptic to sublanceolate, flattened parallel to septum, 7.5–8.5 mm long, 3–3.5 mm wide, glabrous; styles slender, 0.6–0.9 mm long. Mature seeds not seen.

TYPE. Colombia, Depto. Boyacá, Sierra Nevada del Cocuy, in paramo below Ritacuva glacier, 4300 m alt., 5 Aug. 1957, *P. J. Grubb, B. A. B. Curry, & A. Fernández-Pérez 303* (holotype, US!).

ADDITIONAL SPECIMEN EXAMINED. **Colombia.** DEPTO. BOYACÁ: Sierra Nevada del Cocuy, Alto Ritacuva, *Barclay & Juajibioy 7485* (MO).

Draba boyacana, which grows on peat at the base of *Espeletia* Mutis plants or on moraines above the *Espeletia* stands (4300–4500 m alt.), has no close relatives among the northern South American drabas. Of the 11 Mexican and Guatemalan species (Rollins, 1984), only *D. helleriana* Greene bears some superficial resemblance to *D. boyacana.* However, the latter has white instead of yellow flowers and is quite different in leaf morphology and pubescence, as well as in habit and inflorescence. Perhaps the nearest relative of *D. boyacana* is *D. magellanica* Lam., a species widely distributed in Patagonia (Boelcke, 1984). From that, *D. boyacana* is easily distinguished in having glabrous rather than pubescent fruits, few- instead of many-flowered inflorescences, confluent instead of no median nectaries, and primarily simple or furcate as opposed to stellate leaf pubescence.

Draba cocuyana Al-Shehbaz, sp. nov. FIGURE 2.

Herba perenna suffruticosa caudicibus simplicibus vel ramosis. Caules lignosi, 4–8(–20) cm longi, inferne petiolis bruneis, foliorum emortuorum adpressis imbricatis indurati, superne dense foliati. Folia caulina integra, oblonga vel ovata, imbricata, glabrescentia, ciliata, 3–8(–10) mm longa, 2–3 mm lata. Racemi corymbosi ebracteati; pedicelli fructiferi divaricati, 4–9(–11) mm longi. Sepala oblonga, subsaccata, 4–5 mm longa. Petala obovata, flava, 6–7 mm longa, ca. 3.5 mm lata. Siliqua elliptica vel subovata, compressa, glabra, (6–)8–12 mm longa, (3.5–)4.5–5.5 mm lata; stylus 1.5–2.7 mm longus; semina brunnea, compressa, ovata, reticulata, 1.6–1.8 mm longa, 1.2–1.4 mm lata.

Suffrutescent perennial herbs; caudex short, simple or branched. Stems several from caudex, unbranched, 4–8(–20) cm long, leafless below and covered with persistent, imbricate, appressed, brown, petiolar remains of previous years, leafy above. Leaves oblong to ovate, 3–8(–10) mm long, 2–3 mm wide, obtuse to subacute at apex, abruptly ending in a thick, brown, persistent petiolar base, entire, ciliate, the upper surface glabrous, the lower sparsely pubescent with dendritic trichomes but soon glabrescent. Inflorescences ebracteate corymbose racemes, slightly elongated in fruit; rachis sparsely to densely pubescent with furcate to dendritic trichomes; fruiting pedicels divaricate, usually straight, 4–9(–11) mm long, pubescent. Sepals erect, oblong, subsaccate, 4–5 mm long, ca.

FIGURE 2. Holotype of *Draba cocuyana*. Scale bar = 1 cm.

2.5 mm wide, yellow, sparsely pubescent. Petals broadly obovate, 6–7 mm long, ca. 3.5 mm wide, bright yellow. Filaments erect, ca. 4.5 mm long; anthers oblong, ca. 1 mm long. Nectar glands confluent, subtending bases of all filaments. Fruits elliptic to subovate, flattened parallel to septum, (6–)8–12 mm long, (3.5–)4.5–5.5 mm wide, glabrous; septum complete, membranaceous; styles slender, 1.5–2.7 mm long. Seeds 4 to 7 per locule, broadly ovate, compressed, 1.6–1.8 mm long, 1.2–1.4 mm wide, brown, reticulate.

TYPE. Colombia, Depto. Boyacá, Sierra Nevada del Cocuy, Valle de los Corallitos, in peaty rock crevices, ca. 4000 m alt., 31 July 1957, *P. J. Grubb, B. A. B. Curry, & A. Fernández-Pérez 188* (holotype, US!; isotype, MSC!).

ADDITIONAL SPECIMENS EXAMINED. **Colombia.** DEPTO. BOYACÁ: Sierra Nevada del Cocuy, W face of Boquerón de Cusiri, *Grubb, Curry, & Fernández-Pérez 831* (US); Sierra Nevada del Cocuy, Quebrada Bocatoma, *Cleef & Florschütz 5644* (US).

Draba cocuyana is most closely related to *D. litamo* L. Uribe, resembling it in many features of habit, leaves, flowers, and fruits. Both species are known in Colombia as "litamo real" and are extensively collected for alleged medicinal purposes. A note on the holotype reads: "a potion made of whole plant in boiling water used to relieve pain and prolong life." García-Barriga (1974) stated that *D. litamo* is greatly demanded in Colombia for medicinal properties and is used even against cancer. The differences between the two species can hardly be recognized by those who collect them for such use. Therefore, both species may well be endangered.

Draba cocuyana is easily distinguished from *D. litamo* in having ebracteate inflorescences, glabrous fruits, and usually dendritic trichomes on the inflorescence rachis, pedicels, and lower leaf surfaces (see FIGURE 3a). *Draba litamo* has bracteate inflorescences, scabrous fruits with simple trichomes, and usually simple or furcate trichomes on the rachis, pedicels, and lower leaf surfaces (see FIGURE 3b).

Both *Draba cocuyana* and *D. litamo* belong to a group of four species that Schulz (1927, 1929, 1936) recognized as sect. *Dolichostylis* (Turcz.) O. E. Schulz. This section includes the Colombian *D. schultzei* O. E. Schulz and the Venezuelan *D. empetroides* Brandt, Gilg, & O. E. Schulz, *D. lindenii* (W. J. Hooker) Linden ex Sprague, and *D. arbuscula* J. D. Hooker. The last species also grows in the Sierra Nevada de Santa Marta, Colombia. Unlike most of Schulz's (1936) other sections of *Draba*, sect. *Dolichostylis* is well defined and evidently monophyletic. Its six species can be distinguished as follows.

KEY TO THE SPECIES OF SECTION DOLICHOSTYLIS

A. Styles (5–)8–12(–17) mm long; pedicels (1–)1.5–2.5(–3.5) cm long; leaves glabrous. . . . . *D. lindenii.*

A. Styles 0.75–3 mm long; pedicels 0.3–1(–1.4) cm long; leaves variously pubescent.

  B. Leaves narrowly linear, conspicuously ciliate; styles 2–3 mm long. . . . . *D. schultzei.*

  B. Leaves ovate to narrowly oblong, nonciliate to ciliate; styles usually less than 2 mm long.

    C. Fruits with long-stalked stellate trichomes. . . . . *D. empetroides.*

    C. Fruits glabrous or scabrous with simple or furcate trichomes.

      D. Leaves canescent, tomentose, almost exclusively with dendritic trichomes. . . . . *D. arbuscula.*

      D. Leaves neither canescent nor tomentose, with simple, furcate, or dendritic trichomes.

        E. Inflorescences ebracteate; fruits glabrous; leaves and pedicels with dendritic trichomes. . . . . *D. cocuyana.*

        E. Inflorescences bracteate; fruits scabrous; leaves and pedicels with both simple and furcate trichomes. . . . . *D. litamo.*

Draba ecuadoriana Al-Shehbaz, nom. nov.

Based on *Draba affinis* J. D. Hooker, Fl. Antarct. **2:** 235. 1845; non *D. affinis* Host, Fl. Austr. **2:** 238. 1831; non *D. affinis* Hoppe *in* Sturm, Deutschl. Fl. I, Abt. **14**(Heft 60). 1833; non *D. affinis* Ledeb. Fl. Ross. **1:** 148. 1842.

As shown above, the Ecuadorian *Draba affinis* J. D. Hooker is a later homonym of three binomials that represent minor variants of the highly polymorphic European *D. aizoides* L. and *D. alpina* L.

Draba pseudocheiranthoides Al-Shehbaz, sp. nov. FIGURE 4.

Planta perennis, caudicibus crassis, petiolis foliorum emortuorum persistentibus; caulis erectis, 15–46 cm longis. Folia basalia rosulata, anguste oblanceolata, remote serrulata, ciliata, 3–8 cm longa, 4–6 mm lata, pilis simplicibus et furcatibus. Inflorescentia bracteata, multiflora; pedicelli fructiferi divaricati, (5–)8–12(–17) mm longi. Sepala oblonga, 2–3 mm longa. Petala flava, obovata, subemarginata, 5.5–7 mm longa, 2–2.5(–3) mm lata; filamenta 2–2.5 mm longa;

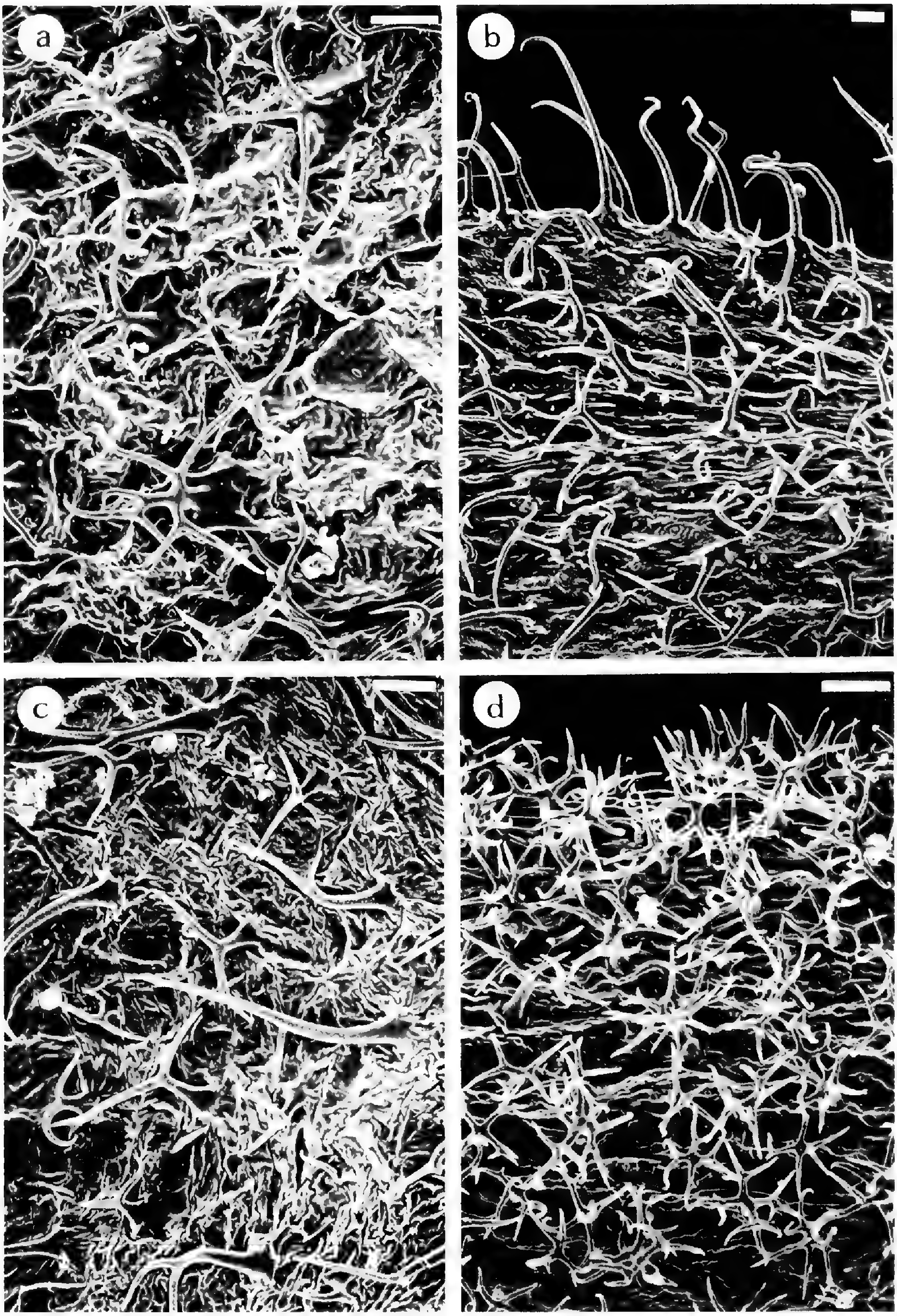

FIGURE 3. Leaf surfaces of *Draba*: a, *D. cocuyana* (holotype), lower surface; b, *D. litamo* (*Grubb et al. 834*, US), lower surface; c, *D. pseudocheiranthoides* (isotype), upper surface; d, *D. cheiranthoides* (*Cuatrecasas & Castañeda 24610*, US), upper surface. Scale bars = 100 μm.

anthera oblonga, 0.6–0.7 mm longa. Siliqua ovata, glabra, valde compressa, 5–8 mm longa, (2–)3–4(–5) mm lata; locula 1 vel 2 sperma; stylus 0.6–1 mm longus. Semina valde compressa, brunnea, suborbiculata, pendula, ca. 2 mm in diametro.

Perennial cespitose herbs; caudex thick, unbranched, covered with petioles of previous years. Stems erect, simple or branched above, 15–46 cm long, softly pubescent with simple and short-stalked, submalpighiaceous, furcate trichomes. Basal leaves rosulate, narrowly oblanceolate, 3–8 cm long, 4–6 mm wide, subacute at apex, attenuate at base, ciliate, serrulate, glabrescent below, moderately pubescent above with simple and furcate, stalked trichomes. Cauline leaves similar to basal, progressively reduced in size upward. Inflorescences corymbose racemes, elongated in fruit, bracteate throughout; fruiting pedicels straight, divaricate, (5–)8–12(–17) mm long. Sepals erect, oblong, 2–3 mm long, scarious at margin, green to yellow, sparsely pubescent. Petals obovate, attenuate to short clawlike base, 5.5–7 mm long, 2–2.5(–3) mm wide, subemarginate, bright yellow. Filaments erect, 2–2.5 mm long, yellow; anthers oblong, 0.6–0.7 mm long. Fruits ovate, strongly compressed parallel to septum, 5–8 mm long, (2–)3–4(–5) mm wide; valves glabrous, obscurely nerved; septum complete, membranaceous; styles 0.6–1 mm long. Seeds 1 or 2 per locule, pendulous, suborbicular, strongly compressed, ca. 2 mm in diameter, brown.

TYPE. Colombia, Depto. Magdalena, Sierra Nevada de Santa Marta, Río Sevilla, 3570–3840 m alt., 28 Jan. 1959, *H. G. Barclay & P. Juajibioy 6733* (holotype, GH!; isotype, MO!).

ADDITIONAL SPECIMENS EXAMINED. **Colombia.** DEPTO. MAGDALENA: Sierra Nevada de Santa Marta, S of Laguna Río Frío, *Kirkbride & Forero 1793* (GH, NY, US); Río Sevilla, *Barclay & Juajibioy 6544* (GH, MO), *6667* (GH, MO).

Draba pseudocheiranthoides is a very close relative of—and can be easily confused with—*D. cheiranthoides* J. D. Hooker. Both species grow in the same mountain range, the Sierra Nevada de Santa Marta, but it is not known if they are sympatric. The new species is easily distinguished from *D. cheiranthoides* in having ciliate, noncanescent leaves that are glabrescent on the lower surface and pubescent on the upper with a mixture of simple and furcate trichomes (see FIGURE 3c), as well as in having glabrous fruits, bracteate inflorescences, and pubescent stems with a mixture of simple and submalpighiaceous furcate trichomes. On the other hand, *D. cheiranthoides* has nonciliate, canescent leaves that are densely pubescent on both surfaces with dendritic trichomes (FIGURE 3d), scabrous fruits with minute simple or rarely furcate trichomes, ebracteate to rarely bracteate inflorescences, and pubescent stems with dendritic trichomes. The two species are somewhat similar in their overall leaf, flower, and fruit morphology, but the differences above strongly support their recognition at the specific level.

Draba pseudocheiranthoides belongs to a small group of species that Schulz (1927, 1936) placed in sect. *Chamaegongyle* O. E. Schulz. As shown by Al-Shehbaz (1987), however, Schulz's sectional classification of *Draba* is controversial, and a thorough reevaluation of his sectional boundaries is needed. Two

FIGURE 4. Isotype of *Draba pseudocheiranthoides*. Scale bar = 1 cm.

FIGURE 5. Holotype of *Draba ritacuvana*. Scale bar = 1 cm.

recently described Colombian species, *D. cryophila* Cuatr. (Cuatrecasas, 1972) and *D. hammenii* Cuatr. & Cleef (Cuatrecasas & Cleef, 1978), should also be assigned to this group.

Draba ritacuvana Al-Shehbaz, sp. nov. FIGURE 5.

Herba perenna caespitosa, caudicibus crassis brevibus, ramis lateralibus tenuibus basibus foliorum emortuorum instructis. Caules simplices, 1.2–4 cm longi, foliis paucis. Folia basalia rosulata, numerosa, late obovata vel suborbiculata, rotundata, crenato-dentata, ciliata, sessilis, 7–15 mm longa, 4–12 mm lata, sparse pubescentia vel glabrescentia, pilis simplicibus vel stipitato-furcatis. Inflorescentia bracteata; pedicelli fructiferi divaricati, recti, 4–5 mm longi. Sepala viridia, late ovata, 4–4.5 mm longa, 2–3 mm lata. Petala flava. Siliqua elliptica, compressa, 8–10 mm longa, 4–4.5 mm lata, subhirsuta, pilis simplicibus vel furcatis usque ad 0.4 mm longis; stylus 0.7–0.8 mm longus. Semina ovata, compressa, numerosa, biseriata, atrobrunnea, 1–1.1 mm longa, 0.7–0.8 mm lata.

Cespitose perennial herbs; caudex short, thick, with the slender, spreading lateral branches covered with leaf bases of previous years, each terminating in a rosette. Flowering stems simple, 1.2–4 cm long. Basal leaves numerous, forming rosettes, sessile, broadly obovate to suborbicular, 7–15 mm long, 4–12 mm wide, rounded at apex, crenate-dentate, ciliate, glabrescent to sparsely pubescent with mixture of simple and furcate-stalked trichomes; cauline leaves few, sessile, much smaller. Inflorescences bracteate racemes, slightly elongated in fruit; fruiting pedicels straight, divaricate, 4–5 mm long, pubescent. Sepals broadly ovate, nonsaccate at base, 4–4.5 mm long, 2–3 mm wide, green, sparsely pubescent. Petals broadly obovate, 4.5–5 mm long, 3–3.5 mm wide, yellow. Filaments 1.6–2 mm long; anthers ovate, ca. 0.5 mm long. Fruits elliptic, flattened parallel to septum, 8–10 mm long, 4–4.5 mm wide, subhirsute with simple and furcate trichomes to 0.4 mm long; septum complete; styles 0.7–0.8 mm long. Seeds many in each locule, biseriately arranged, ovate, compressed, 1–1.1 mm long, 0.7–0.8 mm wide, dark brown to blackish.

TYPE. Colombia, Depto. Boyacá, Cordillera Oriental, Sierra Nevada del Cocuy, Alto Ritacuva, 11 April 1959, *H. G. Barclay & P. Juajibioy 7323-A* (holotype, GH!; isotype, MO!).

ADDITIONAL SPECIMENS EXAMINED. **Colombia.** ARAUCA: Sierra Nevada del Cocuy, Cabeceras de la Quebrada El Playón, Patio Bolos, 2.5 km S of Alto La Plaza, *Cleef 8883, 8991* (both GH). BOYACÁ: Sierra Nevada del Cocuy, below Ritacuva glacier, *Grubb, Curry, & Fernández-Pérez 291* (K).

Draba ritacuvana grows on morainal rocky slopes. It occupies an area between the dense stands of *Espeletia* and the permanent snow at an altitude of 4500–4550 m. Its nearest relative, *D. funkiana* Linden & Planchon ex Sprague, grows primarily in Venezuela and is apparently represented in Colombia by an undescribed subspecies that grows in the Sierra Nevada del Cocuy.

Draba ritacuvana is easily distinguished from *D. funkiana* in having broadly obovate to suborbicular leaves with softly pubescent surfaces and margins, subhirsute fruits 4–4.5 mm broad, and small (1–1.1 mm long) seeds that are many per locule. On the other hand, *D. funkiana* has linear-lanceolate leaves with glabrous surfaces and subsetose margins, glabrous fruits ca. 3 mm wide, and larger seeds that are usually one or two per locule.

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G. C. K. DUNSTERVILLE, 1905–1988
AN APPRECIATION

Gustavo A. Romero[1]

The Orchid Herbarium of Oakes Ames and the field of orchidology suffered a great loss when Galfrid Clement Keyworth Dunsterville died on November 26, 1988, in Caracas, Venezuela, at the age of 83. He is survived by his wife, Ellinor, and two daughters. Dunsterville had been a Research Associate at the Ames Orchid Herbarium since 1958.

Dunsterville was born on February 18, 1905, in Devon, England. He started work as a petroleum engineer with Shell Oil Company in 1925. After his marriage to Ellinor "Nora" Freeman in 1929 in Egypt, his career took them to Holland, Romania, the United States, Trinidad, England, Colombia, and finally to Venezuela in 1947. He then settled in Venezuela for the remainder of his life. He served as president of Shell Oil in Venezuela from 1957 to 1959; upon retiring he worked full time in orchidology.

His interest in orchids was first expressed in oil paintings in the early 1950's. Photographs of these paintings were sent to L. A. Garay, then in Toronto, for identification. On Garay's encouragement, Dunsterville took up pen-and-ink line drawings to attain greater botanical precision. He went on to produce over 1100 orchid drawings from live material, executed in remarkable detail. Collaboration between Dunsterville and Garay gained strength when Garay was appointed Curator of the Orchid Herbarium of Oakes Ames in 1957. Their combined work resulted in the publication of the outstanding six-volume *Venezuelan Orchids Illustrated* (1959–1976). This series presented 1000 orchids, many new to science or new to Venezuela; 55 additional species appeared in the *Field Guide to the Orchids of Venezuela* published in 1979. Over the years Dunsterville sent the flower material upon which his drawings were based to Garay for identification. These pickled flowers are now part of the Oakes Ames Orchid Herbarium, which holds the copyright to Dunsterville's drawings. Dunsterville donated the remaining collection of pickled flowers and his original drawings to the American Orchid Society in 1985. A smaller amount of duplicate pickled material is at the Venezuelan National Herbarium.

Dunsterville wrote extensively on orchids and on his numerous orchid-collecting expeditions, publishing over 250 articles in the *American Orchid Society Bulletin,* the *Orchid Review,* the *Orchid Digest,* and several other orchid journals and books of Brazil, Germany, the United States, and Venezuela. As

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[1] Orchid Herbarium of Oakes Ames, Harvard University Herbaria, 22 Divinity Avenue, Cambridge, Massachusetts 02138.

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G. C. K. Dunsterville in his study in Caracas, Venezuela, ca. 1965.

a tribute to him, an anthology of 64 of his articles, *Orchid Hunting in the Lost World (and Elsewhere in Venezuela),* was published by the American Orchid Society in late 1988. He was also a skilled photographer. His black and white and color photographs illustrated his *World of Orchids,* published in simultaneous editions in English, Spanish, and German in 1962, and *Orchids of Venezuela* published in 1987 in English and Spanish.

The Venezuelan government awarded Dunsterville the order of "Francisco de Miranda," third class, in recognition for his work on the taxonomy and conservation of Venezuelan orchids, and the order of "Henri Pittier" for his many efforts toward orchid conservation and other endeavors in natural history. In addition, Dunsterville received the Veitch Memorial Gold Medal from the Royal Horticultural Society, London, in 1984, and both he and his wife were awarded the American Orchid Society Silver Medal of Merit in 1987 for their contributions to the orchid world. He was also a member of the American Orchid Society Conservation Committee from its creation 1965 until 1983, as well as its first chairman.

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CONTENTS OF VOLUME 70, NUMBER 3

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VOLUME 70 OCTOBER 1989 NUMBER 4

THE GENERA OF SUBORDER APOCYNINEAE (APOCYNACEAE AND ASCLEPIADACEAE) IN THE SOUTHEASTERN UNITED STATES[20]

THOMAS J. ROSATTI

ASCLEPIADACEAE R. Brown, Mem. Wernerian Soc. **1:** 19. 1811,[21] "Asclepiadeae," nom. cons.

(MILKWEED FAMILY)

Terrestrial (sometimes in xeric habitats) to aquatic (sometimes in or near fresh, brackish, or salt water), erect to prostrate or scandent and/or twining, perennial or rarely annual herbs (often becoming woody toward base) or sometimes suberect or prostrate subshrubs [or infrequently erect shrubs, trees, or succulents] with usually white latex; axes and leaves glabrous or with various degrees of nonglandular and sometimes glandular pubescence. Leaves simple, opposite or sometimes whorled, subwhorled, subopposite, or alternate, sometimes caducous [and/or, on succulents, often reduced]; blades broad to filiform, apices acute, acuminate, subcuspidate, or mucronate, sometimes obtuse, rarely emarginate, margins often revolute [rarely toothed or lobed], bases attenuate, truncate, hastate, cordate, obtusely sagittate, or auriculate (and clasping stem); petioles distinct, sometimes very short and/or indistinct (especially when leaves linear or filiform), without or very rarely with lateral appendages, bases and/or adjacent areas of stems without or sometimes with usually a few small colleters. Inflorescences terminal but usually appearing lateral and often interpetiolar by sympodial growth, pedunculate to sessile, many- [to rarely 1-]flow-

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[20] Continued from page 401.

[21] According to the title page, this paper was read to the Society on 4 November 1809; according to Stafleu and Cowan (Taxonomic Lit. **1:** 366. 1976), preprints were available in 1810. The entry for the Asclepiadaceae in "Nomina Familiarum Bryophytorum et Spermatophytorum Conservanda" (ICBN, 1988) cites pp. 12 and 17, but the family is actually proposed by name on p. 13 (the formal, Latin description begins on p. 19).

Journal of the Arnold Arboretum **70:** 443–514. October, 1989.

ered, cymose but usually appearing umbellate or sometimes racemose, corymbose, or paniculate, bracteate; pedicels longer or rarely shorter than calyces, ebracteolate. Flowers perfect [or rarely carpellate or staminate functionally], sometimes conspicuous, actinomorphic; sepals, petals, and stamens 5, carpels 2. Calyx synsepalous but usually divided nearly to the receptacle, persistent in fruit; lobes usually with squamellae (small, usually scalelike, glandular or nonglandular projections in axils and/or between bases), commonly imbricate to various degrees basally or sometimes valvate, usually acute. Corolla sympetalous, divided nearly to receptacle to sometimes as much as basal ⅔ united, rotate to sometimes variously campanulate, salverform, urceolate [or funnelform]; tube [or throat] sometimes with corona (see filaments); lobes alternating with those of calyx, sometimes all overlapping either to right or left in aestivation, but valvate or sometimes imbricate (then all usually not overlapping in a single direction) at anthesis, erect, ascending, spreading, or reflexed. Stamens alternating with the corolla lobes. Filaments connate, forming a column (i.e., tube) surrounding but free from ovaries and styles [or, in the Periplocoideae, distinct from one another but sometimes basally united by an annular or discoid corona], basally adnate to corolla tube [and sometimes throat], short to long, more or less straight, coronas (i.e., abaxial appendages) 1, 2 [or rarely, as in *Eustegia,* 3], often elaborate [or sometimes absent]. Outer (i.e., lower) corona, when present, exceeded by anthers, discoid, entire to variously 5-lobed, basally adnate to but often distinguishable from corolla and apically free, forming a spreading, ascending, or erect annulus at summit of corolla tube. Inner (i.e., upper) corona, when present, exceeding to exceeded by the anthers; segments 5, distinct or less often connate (e.g., in *Matelea, Cynanchum scoparium*), each laminate (e.g., in *Cynanchum, Matelea*), conduplicate (i.e., hood- or tubelike, as in *Asclepias*), vesicular (e.g., in *Sarcostemma*), or rarely digitate (e.g., in *Cynanchum Northropiae*), sometimes with an adnate appendage adaxially (e.g., horns in *Asclepias,* ligules in *Matelea*) and/or lateral lobes apically (e.g., auricles in *Asclepias,* lateral projections in *Matelea*), stipitate to sessile (i.e., column between corolla and bases of segments visible to not visible, respectively), free from corolla but rarely (e.g., in *Cynanchum clausum*) partially adnate to outer corona. [Coronas in extraregional members as above, or otherwise complex and variable; e.g., in the Periplocoideae, often discoid, adnate to corolla, and bearing anther stalks (i.e., the corona itself is an elaboration of the filament) and/or long, narrow, simple or apically once- or twice-bifurcate and/or coiled lobes]. Anthers each with an apical (and more or less adaxial), hyaline flap inflexed over style-stigma head, unappendaged or (as in *Gonolobus*) appendaged abaxially; united into anther head (i.e., more or less a cylinder or inverted cone) around, adnate to (except along vertical furrows, see below), and mostly concealing lateral surfaces of style-stigma head, immediately subtended by inner corona, or outer corona, or corolla, or (in *Asclepias pedicellata* and *Morrenia odorata*) held well above and separated from inner corona; anther wings from each adjacent pair meeting to form an outwardly projecting slot at plane of contact, enclosing (except for slot) a stigmatic chamber (i.e., enclosed part of vertical furrow including stigmatic and other secretory surfaces); dithecal and bisporangiate [tetrasporangiate in the Secamonoideae], the contents of each sporangium comprising a single pollinium (i.e., linear pollen tetrads tightly coherent and completely encased by tapetal secretions), 2 of which (1 from each of 2 adjacent anthers) comprising (with translator arms and corpusculum; i.e., hardened secretions of the style-stigma head) 1 pollinarium [or, in the Secamonoideae, 4 of which (2 from each of 2 adjacent anthers) comprising (with relatively undifferentiated secretions of the style-stigma head) 1 pollinarium]. [Anthers in the Periplocoideae mostly without adaxial flaps, unappendaged abaxially; not united into anther head (but sometimes adherent to one another as well as appressed against, often forming a cone above, and concealing style-stigma head), immediately subtended by or held somewhat above corona or corolla; mostly without anther wings; dithecal and tetrasporangiate, the contents of each sporangium (tetrahedral, isobilateral, or sometimes linear pollen tetrads) released at dehiscence into and onto hardened secretions of the style-stigma head (see structures involved in pollen transfer, under style-stigma head of the Periplocoideae, below).] Nectaries near ovaries lacking (but see style-stigma head, below). Carpels completely free in ovule-bearing and stylar regions, united apically into style-stigma head. Ovaries 2, superior to subinferior, simple, distinct, unilocular, each with a marginal placenta; styles short, mostly terete; style-stigma head cylindrical or short-obconic, with convex (and sometimes conical and/or bilobed), flat, or concave (i.e., depressed) apex. Lateral surface of style-stigma head with 5 vertical furrows alternating with the anthers, each with secretions forming: 1 central corpusculum (not concealed by but exceeding to exceeded by the anthers) with 2 attached, pendulous, horizontal [or sometimes erect] translator arms (mostly concealed by anthers), these unbranched and each attached after anther dehiscence to 1 pendulous, horizontal [or erect] pollinium [or, in the Secamonoideae, each apically bifurcate and attached after anther dehiscence to 2 erect pollinia] from each of 2 adjacent anthers to form 1 pollinarium with 2 [or, in the Secamonoideae, 4] pollinia; stigmatic surface within stigmatic chamber (enclosed by anther wings); and nectar. [Style-stigma head in the Periplocoideae short-cylindroid to discoid, with convex (and sometimes conical) or flat apex; lateral surface with 5 approximately vertical areas alternating with the anthers, each with secretions forming structure involved in pollen transfer (adhesive disc attached to base of internally adhesive, inverted, usually elongate cone or partial cone into which individual pollen tetrads fall and are held after anther dehiscence).] Ovules 1 to usually many per locule, often pendulous, anatropous, pseudocrassinucellar, and with a single, massive integument; megagametophyte of the Polygonum type. Fruits follicular, 1 or rarely both carpels developing (the pair, when present, from single flower divergent about 90° or less [or sometimes ca. 160–200°]), lance-ovoid, narrowly fusiform to fusiform-ovoid, acute to attenuate apically, dehiscent along adaxial suture, erect on erect pedicels to pendulous on pendulous ones, sometimes (usually in *Asclepias*) erect on deflexed pedicels; surface tuberculate, winged longitudinally, or smooth, sometimes with short nonglandular and rarely glandular pubescence. Seeds usually many per developed carpel, ovate-lenticular, each usually with a tuft of trichomes at apex;

seed-coat surface papillate or smooth, lateral wings crenate-undulate, variously serrate, or entire; endosperm nuclear, oily and commonly starchy; embryo usually straight, its development of the Solanad type (but see discussion of suborder).[22] (Including Periplocaceae Schlechter, 1905.) TYPE GENUS: *Asclepias* L.

Recognized here as distinct from the Apocynaceae (see the discussion of the suborder), the family Asclepiadaceae includes 250 or more genera by most accounts, but with as few as perhaps 50 if the taxonomic concepts developed by Woodson (1941; see below) are applied throughout. Estimates of the number of species have ranged from about 2000 (most authors) to as high as 3000 (Huber). The plants are widespread in tropical and subtropical regions throughout the world but seem to be especially abundant in southern Africa (Huber) and South America (Lawrence). They are both less numerous and less diverse, but still well represented, in the Temperate Zones; nearly 100 genera in the New World north of South America were reduced by Woodson (1941) to nine, five of which are represented in the native flora of the southeastern United States.

Many and perhaps most Asclepiadaceae occur in environments that are from one cause or another water stressful. Several genera in the Old World, most notably *Stapelia* L. (see White & Sloane) and *Sarcostemma* R. Br. (treated here), include succulent-stemmed species with caducous and/or reduced leaves. Most of the species in the Southeast occur in relatively dry, terrestrial habitats; some are found in or near salt or brackish water. A few of our species are adapted to more mesic conditions, and others grow near or in fresh water.

Plants of the Asclepiadaceae are nearly always perennial. They are most commonly herbaceous or variously woody vines, sometimes erect to prostrate herbs, and rarely erect shrubs or small trees. Native representatives in the

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[22] An excessive and inconsistently applied terminology, especially regarding the flowers, has accumulated over many years. Bookman attempted to standardize the terms used for floral structures in *Asclepias*, and her proposals are generally adopted here. However, because her efforts were based on a single species, her choices are sometimes unacceptable for a genus and/or the family as a whole. For example, she stated that the "culculus" is composed of the "hood" and the "horn," when in fact horns are absent in many species of *Asclepias* and other genera; she also used "bifid fleshy pad" instead of the "alternating lobule" of Woodson (1954), even though in some species of *Asclepias* the structure is not bifid.

In contrast to most others who have studied the Asclepiadaceae, I have chosen not to use "gynostegium" for these plants. I have found the term to be both unnecessary and unclear. For example, Bookman (p. 675) defined the gynostegium as "the union of the stamens with the fleshy stigma head at the flower's center," more or less in accord with Woodson (1941) and others. However, since the various coronas present in the family are considered to be abaxial appendages of the filaments, they would by this definition also have to be considered part of the gynostegium. Bramwell (p. 226) wrote that the "anthers are usually fused to the gynoecium to form a gynostegium," implying that the ovaries are included, while according to Stevens (p. 37) "the gynostegium can be loosely referred to as the androecium plus the style apex but the corolla, below the insertion of the stamens, forms at least the base of the structure."

Other structures for which the terminology has been confused include those here called "style-stigma heads" (see footnote 4) and "colleters" (see footnote 6). The various kinds of coronas present among the Asclepiadaceae in the Southeast are defined in the discussion of *Matelea*.

Southeast include about 17 species in *Cynanchum* L., *Gonolobus* Michx., *Matelea* Aublet, and *Sarcostemma,* all but perhaps three of which (the usually prostrate *M. cynanchoides* (Engelm.) Woodson and *M. pubiflora* (Dcne.) Woodson; the sometimes prostrate *S. cynanchoides* Dcne.) are scandent and/or twining herbs or subshrubs, and perhaps 30 or more species of *Asclepias,* all of which are erect herbs.

The family is also represented in the Southeast by three introduced species of more or less woody vines. *Morrenia odorata* (Hooker & Arnott) Lindley, a native of South America, has become naturalized in Florida, mostly in citrus groves, whereas *Cryptostegia grandiflora* R. Br. and *Periploca graeca* L., natives of Africa and Europe, respectively, seem rarely to have escaped from and/or to have persisted beyond cultivation in Florida but have not become truly naturalized.[23] *Araujia sericofera* Brot., another vine, is grown as an ornamental in both Florida and California but has escaped from cultivation and become naturalized only in California (Spellman & Gunn).

The putatively more primitive Apocynaceae are the closest living relatives of the Asclepiadaceae. In fact, an increasing number of botanists favor uniting the families because there is no sharp distinction between them (see discussion of the suborder). Nevertheless, as represented by plants native to or naturalized in the Southeast, the families are easily distinguished by the presence in the Asclepiadaceae of a number of floral modifications related to pollination. These include, among others, the coronas, anther wings, and pollinia of the androecium, and the hardened secretions of the style-stigma head (i.e., the corpusculum and translator arms) that function in the transport of pollinia. Outside of an indirect connection through the Apocynaceae, the Asclepiadaceae appear to be unlinked to other flowering plants.

Genera of the Asclepiadaceae have been classified on a worldwide basis in a number of systems differing to various degrees in character emphasis, group sequence, and hierarchical arrangement. At the time he initially separated it from the Apocynaceae, Brown subdivided the Asclepiadaceae into three groups. Within each flower the so-called "Asclepiadeae verae" were described as having ten pollen masses, in pairs (the members of each pair from two adjacent anthers), attached to a two-parted, longitudinally furrowed corpusculum on the stigma, as well as connate, abaxially appendaged filaments. The second group, including only *Secamone* R. Br., was unnamed and was said to have 20 pollen

[23] *Calotropis procera* (Aiton) Aiton f., a species of erect herbs or subshrubs native to Asia, has been naturalized in the West Indies, as well as along the east coast of South America, for some time (Spellman, 1975b). According to Spellman & Gunn, plants have escaped from cultivation but are evidently not naturalized in the Miami area, although they did not cite, and I have been unable to locate, specimens that would confirm the former.

The flowers of *Calotropis procera* have a corona structure that is unique yet comparable to that of *Asclepias,* particularly members of subg. ASCLEPIODORA (Gray) Woodson (see discussion of *Asclepias*). In *C. procera* each hood appears to be joined to the column for most of its length and is free only at its very short, coiled apex, which is adjacent to the base of the column and much exceeded by the anther head. In *Asclepias* subg. ASCLEPIODORA, on the other hand, each hood appears to be joined to the column for much less than half its length and is otherwise spreading or ascending, with an apex that is uncoiled and only slightly exceeded by the anther head.

masses, in fours (from two adjacent anthers), attached to an unfurrowed corpusculum on the stigma, as well as connate, abaxially appendaged filaments. The third group, the "Periploceae," was described as having five to 20 granular pollen masses (the units or tetrads of each comprising four spheres), with one to four affixed to a single, apically widened corpusculum on the stigma. It is notable that even without completely understanding the structures involved, Brown proposed a classification more in line with current thinking than the majority of those that were subsequently formulated.

Bartling essentially ignored the importance Brown had placed on pollinium number in isolating *Secamone* and thus recognized only two groups in the Asclepiadaceae, the "Asclepiadea genuina," including *Secamone,* with pollinia, and the "Periplocea," without. Lindley, who was probably the first to use the family name in its present form, explicitly adopted Bartling's classification; in fact, most botanists have favored division of the family into two main groups along these lines, although evidence now suggests that the recognition of three may be more appropriate.

Endlicher proposed a system that now appears to reflect suprageneric relationships within the Asclepiadaceae more accurately than does any other. He recognized the three groups proposed by Brown, each as a "subordo," but improved on the latter's scheme by placing the "Periploceae" first, the "Secamoneae" second, and the "Asclepiadeae verae" third.[24] The last was divided into three tribes differing in orientation of the pollinia, the "Cynancheae" (pendulous), the "Gonolobeae" (horizontal), and the "Pergularieae" (erect). The "Pergularieae" were separated into two subtribes, the "Hoyeae" and the "Stapelieae," with and without terminal, membranaceous anther appendages, respectively. Divided into groups of unspecified rank and differing in characters of the corolla and corona now thought not to be of value above the generic level were the "Cynancheae" (six groups) and the two subtribes of the "Pergularieae" (two groups each).

Classifications subsequent to Endlicher's included one or more features that now appear to have been regressive, although some included improvements and/or clarifications of the characters used. Decaisne recognized as tribes the three groups proposed by Brown and agreed with Endlicher in placing the "Periploceae" first, the "Secamoneae" second, and the "Asclepiadeae verae" third. However, Decaisne segregated from and placed after the last tribe two additional ones (in order, the "Gonolobae" and the "Stapeliae"), essentially because of differences in the orientation of pollinia, thus obscuring the hierarchy of relationships established by Endlicher. Other characters now thought to be of questionable importance were used to separate the tribes and to divide both the "Asclepiadeae verae" and the "Stapeliae" into a number of named "divisios."

Bentham (in Bentham & Hooker) resurrected Bartling's division of the family

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[24] Article 18.2 (ICBN, 1988) states that names intended for families but published with rank designations such as "ordo" are to be treated as having been published as names of families. This implies that these names of Endlicher should be treated as names of subfamilies.

into two main groups, each a "subordo." The "Periploceae" were followed by the "Euasclepiadeae," which were divided into six tribes. Although differences were indicated between the "Secamoneae," which were placed immediately after the "Periploceae," and the others (e.g., four vs. two pollinia per anther, respectively), they were not reflected in the taxonomy. Some of the remaining tribes differed from one another in orientation of the pollinia: the "Cynancheae" (pendant), followed in order by the "Gonolobeae" (horizontal), and the "Marsdenieae," "Ceropegieae," and "Stapelieae" (all erect). The last three were distinguished on the basis of what are now generally thought to be less substantial characters. Perhaps the most significant of these involved terminal, membranaceous anther appendages, said to be inflexed over the stigmatic disc in the "Marsdenieae," but lacking in the other two. From the "Ceropegieae" the "Stapelieae" were distinguished by their succulent, nearly always leafless stems.

Baillon's system was regressive in two important respects but in some ways contributed to an understanding of the family. Not only was the sequence of suprageneric taxa that had been gaining acceptance essentially reversed, but the hierarchy of relationships was again obscured, in this case by recognition within the family of six "séries." Although it was not reflected in the classification, the first five were said to differ from the last, the "Périplocées," in having pollinia instead of unpackaged pollen. Although this character had been used in previous classifications, Baillon seems to have been among the first to recognize the importance of the fact that the pollen of the "Périplocées" was more or less adherent to an appendage of a corpusculum. Baillon indicated but did not emphasize taxonomically that anthers in the first four "séries" each contained two pollinia, whereas those in the "Sécamonées" produced four. In addition, Baillon implied that corpuscula in the first four "séries" were much larger than those in the "Sécamonées," again affixing a level of importance to this character more in line with current thinking. His reference to apically enlarged anthers in the "Gonolobées" indicates an appreciation of the abaxial appendages now used to distinguish genera within the group (see discussions under *Matelea* and *Gonolobus*).

Schumann recognized as subfamilies two groups within the Asclepiadaceae, the "Periplocoideae" and the "Cynanchoideae," emphasizing not only pollinia but associated structures that contribute to more effective transfer of male gametes in the latter group. A seemingly unnatural distinction was drawn between the "Asclepiadeae" and the other three tribes included in the "Cynanchoideae," based primarily on placement of the pollinia in the basal or the apical part of the anthers, respectively. In addition, the "Asclepiadeae" were divided into five subtribes differing mainly in characters of the corona now thought not to be of value above the level of genus. Perhaps one of the most significant features of Schumann's classification was its unification into a single taxon of all plants with essentially erect pollinia (i.e., the inclusion in the "Tylophoreae" of the "Ceropegiinae" and the "Marsdeniinae"), an arrangement proposed much earlier by Endlicher but mostly ignored otherwise (in fact, the "Tylophoreae" of Schumann is superfluous since Endlicher's "Pergularieae" is available for use as the group's name).

Wagenitz's recent treatment of the Asclepiadaceae was patterned closely after Schumann's. Improvements included more explicit descriptions of the subfamilies and tribes and rejection of the subtribes Schumann had included in the "Asclepiadeae." Indeed, Schumann had included *Philibertia* HBK. and *Oxystelma* R. Br. in the "Glossonematinae," *Funastrum* Fourn. in the "Asclepiadinae," and *Sarcostemma* R. Br. in the "Cynanchinae," whereas Woodson (1941) had included all four in the same genus (i.e., *Sarcostemma* sensu lato, as recognized here). In contrast, Wagenitz's decision to recognize as tribes (i.e., the "Marsdenieae" and "Ceropegieae") the subtribes that Schumann had included in the "Tylophoreae" seems less tenable.

Woodson's (1941) extensive contributions notwithstanding, it is often difficult to assess the applicability of his ideas above the level of genus because of the extent to which his studies were limited to North American plants. Nevertheless, it is worthwhile to note his reservations concerning the importance of pollinial orientation in the suprageneric classification of the Asclepiadaceae (see FIGURES 6j; 8d, e, g). Although his concern about the distortion of this feature after removal of the pollinia from the anthers seems irrelevant, it is perhaps significant that he (p. 197) was "willing to be convinced that the normal position of the Gonoloboid pollinium may be truly horizontal," even though his "interpretation of the tribe includes forms with pollinia that range in position from pendulous to ascending."

Woodson (1941) considered the structure of the pollinia to be much more important than their orientation, and primarily on this basis he recognized three tribes of "Asclepiadoideae" in North America: the "Asclepiadeae" and the "Tylophoreae," with pollinia entirely fertile and uniformly rounded or flattened adaxially and abaxially (and pendulous or erect, respectively), and the "Gonolobeae," with pollinia sterile near attachment to the translator arms and either rounded or furrowed on one side and flattened or furrowed on the other (and usually more or less horizontal; occasionally ascending or descending). (See also El-Gazzar & Hamza.)

For reasons elaborated below, it is essentially Endlicher's system that is adopted here, except that the sequence of tribes within his "Asclepiadeae verae" has been reversed and the lower suprageneric groups have been ignored. Thus, recognized here are the Periplocoideae R. Br. ex Endl., the Secamonoideae Endl., and the Asclepiadoideae, and within the last the Pergularieae Endl., the Gonolobeae G. Don, and the Asclepiadeae. Recognition of additional suprageneric taxa is less certain. For example, whereas the subtribes of the Asclepiadeae that Schumann based on characters of the corona are now generally considered to be unnatural (see above), recognition of those that Endlicher included in the Pergularieae on the basis of the presence or absence of the terminal, membranaceous, inflexed anther appendages—that is, the "Hoyeae" (in which he included *Tylophora* R. Br., *Hoya* R. Br., *Marsdenia* R. Br., *Pergularia* L., and 12 other genera) and the "Stapelieae" (in which he included *Ceropegia* L., *Stapelia,* and 13 other genera), respectively—might be justified. Segregation within the latter of a succulent group, corresponding, for example, to the "Stapelieae" of Bentham (in Bentham & Hooker) (in which he included

Stapelia and ten other genera, and from which he excluded *Ceropegia* and ten others), is also worthy of consideration.[25]

Only the Asclepiadoideae are represented by plants native in the Southeast. *Matelea* and *Gonolobus* (recognized separately for reasons outlined in the discussions of each) belong to the Gonolobeae, while *Cynanchum, Sarcostemma,* and *Asclepias* are included in the Asclepiadeae. The latter group is also represented by *Morrenia odorata,* naturalized in Florida, and possibly by *Calotropis procera* (see footnote 23). The Periplocoideae are represented by *Cryptostegia grandiflora* and *Periploca graeca,* each sometimes escaped from cultivation in Florida.

Despite its frequent and perhaps usual inclusion in the Asclepiadoideae, *Secamone* is similar in a number of characters to putatively more primitive taxa within the suborder, justifying placement of the genus in its own subfamily (Safwat). Anthers are four-locular in the Apocynaceae, Periplocoideae, and *Secamone,* but two-locular in the remainder of the Asclepiadoideae. However, Safwat showed that the condition in *Secamone* is not due to the formation of a false partition in each of two essentially two-locular anthers, as Demeter had reported for *Thevetia neriifolia* Juss. ex Steudel (= *T. peruviana* (Pers.) K. Schum.) (Apocynaceae; Plumerioideae), but rather that four groups of arche-

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[25] Sundell provided an annotated list of available and rejected names for taxa between the levels of family and genus in the Asclepiadaceae. According to him, the correct names and author citations for Endlicher's subtribes "Hoyeae" and "Stapelieae" would be Hoyinae G. Don and Stapeliinae G. Don, respectively. Although Sundell did not include them, Endlicher's names should evidently be rejected in favor of Don's because of priority. According to Stafleu and Cowan (Taxonomic Literature, ed. 2, 1976), the pages in Endlicher's *Genera Plantarum* on which his subtribal names appeared were published in August 1838, whereas those in the fourth volume of Don's *A General History of the Dichlamydeous Plants* on which his subtribes "Hoyaceae" and "Stapelieae" appear (according to Sundell) were published no later than April 1838, and possibly as early as 1837. It is essentially for this same reason that Don is cited instead of Endlicher as the author of the Gonolobeae. Not surprisingly, there appear to be no available names between the levels of subtribe and genus for the possible nonsucculent and succulent groups within the Stapeliinae.

According to Sundell, the correct author citation for the Asclepiadoideae as a subfamily of the Apocynaceae (i.e., the Asclepiadaceae as here defined) is Meisner, Pl. Vasc. Gen. **1:** 257, 266; **2:** 174. 1838. However, according to Stafleu and Cowan (Taxonomic Literature, ed. 2, 1976), these pages were all published in April 1840. In any case, the "Asclepiadoideae" would have been established within the Asclepiadaceae as an autonym with the publication in August 1838 of the Periplocoideae R. Br. ex Endl. and the Secamonoideae Endl. (See also footnote 23.)

It should be noted that Swarupanandan presented a very complex case against some of the names Sundell listed as available. According to this argument, all of the names Sundell indicated as being based on *Pergularia* L. were illegitimate because they were actually based on *Pergularia* R. Br., considered a later homonym and itself therefore illegitimate. For example, although Endlicher cited Linnaeus as the author of *Pergularia* and excluded the species listed under the genus by Brown, he referred only to material from India and China that is excluded from the genus by the selection of material from "Arabia" as typical. Thus, whereas Sundell rejected as superfluous Céropégiées Dcne. (1842), Marsdenieae Bentham (1868), and Stapeliae Dcne. (1844) in favor of Ceropegieae Bentham (1873), Marsdenieae N. E. Br. (1907), and Stapelieae Bentham (1868), respectively, because they all included *Pergularia* and therefore competed with the earlier Pergularieae Endl. (1838), Swarupanandan considered them legitimate because the Pergularieae Endl. is not. If Swarupanandan were to be considered correct, the tribe with erect pollinia recognized here (i.e., the Pergularieae Endl.) would be in need of a legitimate name.

sporial cells are evident in the hypodermis during the earliest stages of internal differentiation.

Demeter had also noted that in the Plumerioideae (Apocynaceae) the four locules are essentially equal in pollen production, but that in the Apocynoideae the abaxial two are partially sterile and perhaps otherwise less developed. He therefore proposed that the bilocular condition in the Asclepiadoideae represented the culmination of a trend involving progressive suppression of the abaxial locules; that is, that the two adaxial locules in the Apocynaceae, Periplocoideae, and Secamonoideae are homologous to the two locules in the Asclepiadoideae. Evidence cited by Safwat supports this (however, see Frye, 1901; Richharia). According to Safwat (p. 110), the two adaxial groups of archesporial cells in the four-locular anther appear "in exactly the same position" as the two in the two-locular condition. In addition, he showed that although the staminal vascular bundle is between the adaxial and abaxial locules in the four-locular anther, it is adjacent to the abaxial epidermis in the two-locular condition.

According to Safwat, the two meiotic divisions of pollen mother cells are simultaneous in most Apocynaceae, most Periplocoideae, and *Secamone*, but successive in all cases investigated in the Asclepiadoideae (e.g., *Asclepias, Cynanchum, Gonolobus, Matelea,* and *Sarcostemma*). The resulting tetrads are usually tetrahedral or isobilateral in the Apocynaceae; generally tetrahedral or isobilateral but sometimes linear (or T-shaped; see Maheswari Devi) in the Periplocoideae; rhomboid and T-shaped in *Secamone* (within pollinia) but perhaps linear as well; and linear (or rarely T-shaped; see Maheswari Devi) in the Asclepiadoideae (within pollinia).

The style-stigma head in *Secamone* also appears to retain certain putatively primitive features according to Safwat, although in my view the supporting generalizations he cited need information from additional taxa. According to Safwat, its entire surface is secretory in the Apocynaceae, although in *Apocynum,* an advanced genus, the secretions in areas alternating with the stamens are loosely organized into five amorphous bodies. At the extreme opposite, in most Apocynaceae—that is, in all Asclepiadoideae investigated but not in *Secamone*—secretions comprising both nectar and complex elements of the pollinaria (i.e., the corpuscula and the translator arms) are limited to well-defined areas within the stigmatic furrows that alternate with the stamens.

The style-stigma heads in the Periplocoideae and in *Secamone* appear to be intermediate between the extremes described above, but in different ways. In the Periplocoideae, as in the Asclepiadoideae, secretions in each of five relatively well-defined areas form structures involved in pollen transfer. In the Periplocoideae these include an adhesive disc that is attached to the base of an internally adhesive, inverted, usually elongate cone or partial cone into which individual pollen tetrads fall and are held after anther dehiscence. On the other hand, in *Secamone,* as in the Apocynaceae, the entire surface of the style-stigma head is secretory, but unlike the condition in *Apocynum,* the secretions in areas alternating with the stamens are tightly organized into structures thought to be homologous with but reduced from those described for the Periplocoideae. Pollen tetrads in *Secamone* are held within pollinia, as in the

Asclepiadoideae, and the inverted or partial cones present in the Periplocoideae do not develop (presumably because they would serve no purpose); instead the hardened secretions in *Secamone* become attached to the pollinia after anther dehiscence in much the same way that the translator arms become attached to the pollinia in the Asclepiadoideae.

Safwat also presented evidence suggesting that the hardened secretions in *Secamone* are homologous only to the corpuscula in the Asclepiadoideae, and that the translator arms of the latter were separately (and perhaps subsequently) evolved. Indeed, I have observed (see illustrations in Schumann) that the structures in *Secamone* are similar in appearance and orientation to corpuscula (i.e., they resemble inverted V's or U's), and that they and the pollinia to which they are attached are very similar to the pollinaria with erect pollinia characterizing the Pergularieae.

In view of the foregoing, I suggest that intercalation of translator arms between the bases of the hardened secretions of the style-stigma head and the bases of the pollinia in *Secamone* (and reduction in the number of pollinia involved from four to two) could have resulted in the condition in the Pergularieae and that within the Asclepiadoideae the erect pollinia of the Pergularieae are most primitive. By similar reasoning, the horizontal pollinia of the Gonolobeae are more primitive than the pendulous ones in the Asclepiadeae. The tribal sequence employed here is intended to reflect these possibilities.

Safwat concluded that his investigations suggested recognition of the Apocynaceae in the broad sense, and within that group the subfamilies Plumerioideae, Apocynoideae, Periplocoideae, Secamonoideae, and Asclepiadoideae. Among recent workers, some (e.g., Stevens) have adopted this arrangement, while others (e.g., Pichon, 1948b) have chosen to recognize an additional subfamily, the Cerberoideae Pichon, near the Plumerioideae and the Apocynoideae (see discussion of the Apocynaceae). However, the case for recognizing the Secamonoideae at the subfamilial level seems more compelling than that for the Cerberoideae. Therefore, while only the Plumerioideae and Apocynoideae are recognized in my treatment of the Apocynaceae, the Periplocoideae, Secamonoideae, and Asclepiadoideae are all accepted here in the Asclepiadaceae, although only the first and third are represented by plants that in the southeastern United States are native, naturalized, or escaped from or persistent beyond cultivation.

As indicated above, the Periplocoideae are generally considered to be more primitive than the Asclepiadoideae, especially with regard to the structures involved in the transfer of male gametes from one flower to another. As mentioned above, secretions from each of five areas on the style-stigma head in the Periplocoideae solidify to form an adhesive disc connected to the base of an internally adhesive, inverted cone or partial cone, into which individual pollen tetrads fall from adjacent anthers and are held after anther dehiscence; this entire unit often becomes attached by the adhesive disc to an insect visitor. In the Asclepiadoideae, secretions from each of five areas on the style-stigma head harden to form a corpusculum and, in addition, two connected translator arms that each become attached after anther dehiscence to one pollinium (the tetrads of one anther locule encased in tapetal secretions) from each of two adjacent anthers; this entire structure (i.e., pollinarium) frequently becomes attached by the corpusculum to an insect visitor. (See description of pollination in discussion of *Asclepias*.)

The mechanism of pollen transfer in the Periplocoideae is less effective than that in the Asclepiadoideae, due in part to the greater effectiveness in the latter of the corpusculum. Whereas insect parts become attached to the disc just by adhesion, they become wedged—often irreversibly—in an abaxial groove in the corpusculum. In addition, although pollen tetrads are merely adherent to the structures described for the Periplocoideae, in the Asclepiadoideae they are completely enclosed in the pollinia, which are firmly attached to the corpusculum by the translator arms.

The Periplocoideae also differ from the Asclepiadoideae in the extent to which the anthers are associated with one another and with the style-stigma head. Although sometimes adherent to one another, they are not connate into an anther head. In addition, they are appressed against, but not agglutinated to, the style-stigma head. Anthers in the Periplocoideae also lack the wings that characterize the Asclepiadoideae, the adaxial, hyaline flaps present in some Pergularieae and in the Asclepiadeae, and the abaxial appendages of *Gonolobus* (and the extraregional *Fischeria* DC.).

Many aspects of the chemistry, anatomy, embryology, and morphology of the Asclepiadaceae are summarized in the discussion of the suborder. Of taxonomic relevance within the family is Huber's observation that a wide distribution of cardiac glycosides in the Asclepiadeae indicates a "primary position" of the tribe, as well as a close affinity with the Periplocoideae (and the Apocynaceae, especially the Apocynoideae). In other tribes of Asclepiadaceae, these compounds are "gradually" replaced by more specialized types of picric substances. Clearly, a primitive position for the Asclepiadeae within the family is contrary to what has been suggested by morphological evidence (discussed above).

Cytological data regarding the Asclepiadaceae (and Apocynaceae) that had accumulated up to about 1976 were evaluated and summarized to the level of tribe by Stevens. As in the Apocynaceae, the most common and presumably ancestral base chromosome number in the family is $x = 11$; in fact, about 90 percent of the genera and 78 percent of the species for which chromosome counts are available include the sporophytic number $2n = 22$, and only sporophytic numbers based on $x = 11$ have been reported for the Secamonoideae (*Secamone*; $2n = 22$), Pergularieae (20 genera; $2n = 22$, 33, 44, and 66), and Gonolobeae (*Matelea*; $2n = 22$). Other base numbers include $x = 8$, 9, 10, and possibly 12 and 23, each of which could have been derived from $x = 11$. Although polyploidy in the Periplocoideae, Secamonoideae, and Gonolobeae may be only apparently absent (i.e., due to insufficient sampling), it may be less common throughout the family than in the Apocynaceae (see also Albers).

In general, the Asclepiadaceae are not well known cytologically. For example, of about 300 species thought by Stevens to comprise the Gonolobeae, only a single, extraregional member of *Matelea* is known in this regard (see above). According to data compiled by Bolkhovskikh and colleagues, sporophytic numbers have been reported for, among genera represented in one way or another in the Southeast, *Asclepias* ($2n = 22$; also 20 and 24), *Calotropis* ($2n = 22$, 44, and 48), *Cryptostegia* ($2n = 24$), *Cynanchum* ($2n = 22$; also 18 and possibly 44), *Periploca* ($2n = 22$ and 24), and *Sarcostemma* ($2n = 22$ and possibly 20).

The Asclepiadaceae are usually considered to be of relatively little economic importance. The seed trichomes are silky but too brittle to be of much use as a textile (Standley & Williams). However, in the southern United States they have been used as a substitute for down, especially in making pillows and cushions (Bramwell). Several uses for these plants have been proposed and to some extent investigated. Particularly during World War II, species of *Asclepias* were evaluated as potential crop plants and sources of alkaloids for oral contraceptives, of latex for the production of rubber, and of stem fibers as substitutes for hemp in rope and paper making (see primarily Whiting; Woodson, 1954). In the year following its construction in 1943, a United States Government "milkweed floss- and seed-extracting plant" in Petoskey, Michigan, using material of (evidently) several species obtained from uncultivated plants in 26 states, provided the military with two million pounds of seed trichomes for use instead of kapok as a stuffing in life-saving equipment (Berkman). Upon restoration of peace, interest in the cultivation of these plants waned, primarily because of their toxicity to livestock (however, see Van Emon & Seiber). Recently there have been evaluations of *Asclepias* for these and related purposes (e.g., Buchanan *et al.*; Campbell; Van Emon & Seiber), as well as a historical account of the many uses of *A. syriaca* (Gaertner).

Many species of Asclepiadaceae, especially those belonging to *Asclepias, Cryptostegia, Hoya,* and *Stapelia* (among the genera discussed above), are used in horticulture. *Cryptostegia grandiflora* has reportedly been grown as a potential source of natural rubber (Lawrence), although the expenditure of substantial amounts of time and energy on this species during World War II in the Dominican Republic resulted in only one small sheet of rubber (C. E. Wood, Jr., pers. comm.). Many species are toxic to livestock and humans, and the latex of some (especially of *Matelea,* according to Lawrence) is used as arrow poison in Central and South America. Nevertheless, young, tender follicles of several viny species of *Matelea* and other Asclepiadaceae are eaten either fresh or cooked in this same area (Spellman, 1975b; Standley & Williams).

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KEY TO THE GENERA OF ASCLEPIADACEAE IN THE SOUTHEASTERN UNITED STATES

General characters: *subshrubs, vines, or herbs with latex; leaves simple, opposite, sometimes with colleters; inflorescences terminal but often appearing interpetiolar, cymose but often appearing umbellate; flowers perfect, actinomorphic or nearly so, 5-merous except carpels 2; sepals nearly free, often with squamellae; corollas variously sympetalous, often appendaged adaxially (see filaments), lobes often overlapping; stamens epipetalous, alternating with corolla lobes; filaments connate, forming a column around ovaries and styles, bearing abaxially 1 or 2 coronas; outer corona (when present) usually discoid, basally adnate to corolla, often apically free; inner corona (when present) comprising 5 free or connate, laminate, conduplicate, vesicular, or rarely digitate segments, each sometimes appendaged adaxially; anthers connate into anther head around style-stigma head, subtended by inner corona, outer corona, or corolla; pollen released in pollinia, 2 from adjacent anthers united by 2 translator arms and 1 corpusculum into 1 pollinarium; nectaries within stigmatic chambers, alternating with anthers on style-stigma head; carpels free in ovule-bearing and stylar regions, united apically into style-stigma head; ovaries superior to subinferior, simple, unilocular, with marginal placentae; ovules usually numerous in each carpel; fruits follicles; seeds each with a tuft of trichomes at apex.*

A. Pollen released as tetrads; corpuscula absent.

B. Inflorescences several- to many-flowered; corolla rotate, diameter at apex 2–3 cm; follicles long, narrow, subterete, divergent less than 45° at base, usually erect. .... [*Periploca graeca.*[26]]

B. Inflorescences few-flowered; corolla funnelform, diameter at apex 5–8 cm; follicles short, stout, angled, divergent ca. 180° at base, usually horizontal. .... [*Cryptostegia grandiflora.*[26]]

A. Pollen released in pollinia; corpuscula present.

C. Corpuscula exceeding style-stigma head, translator arms more or less horizontal, pollinia horizontal.

D. Anthers lacking abaxial appendages; outer corona absent; inner corona laminate to fleshy, mostly erect, free from corolla, with 15 lobes (usually 5 shallow, obtuse, single, and alternating with 5 longer or sometimes shorter, acute pairs), often with 5 adaxial, adnate, ligulate appendages (opposite each single lobe), exceeding corpuscula (corona in *M. alabamensis* intermediate between inner and outer in position, orientation, fusion to corolla, and morphology). .... 1. *Matelea.*

D. Each anther with an abaxial, fleshy to laminate appendage; outer corona fleshy, mostly spreading, adnate to corolla but free apically (forming a mostly spreading annulus), entire or with 10 lobes (each very shallow and obtuse), unappendaged adaxially, not exceeding corpuscula; inner corona absent. .... 2. *Gonolobus.*

C. Corpuscula not exceeding or (in *Morrenia*) exceeding style-stigma head, translator arms more or less pendulous, pollinia pendulous.

E. Inner corona of 5 distinct, vesicular segments; outer corona laminate, spreading, adnate to corolla but free apically (forming an erect or ascending annulus), entire. .... 5. *Sarcostemma.*

E. Inner corona of 5 distinct or basally connate, often conduplicate (and sometimes apically enclosed) but not vesicular segments; outer corona absent.

F. Segments of inner corona either digitate and distinct (in *C. Northropiae*) or laminate, flat, and distinct (but basally adnate to corolla in *C. Blodgettii*) or basally connate (in *C. scoparium* and *Morrenia*), without adaxial, adnate appendages; stems twining.

G. Segments of inner corona distinct or (in *C. scoparium*) connate to level well beneath that of style-stigma head apex (then corolla lobes less than 2 mm long, leaves linear), glabrous adaxially; anther head immediately subtended by base of inner corona (although segments adnate to corolla in *C. Blodgettii*); bases of leaf blades attenuate, truncate, or cordate. .... 4. *Cynanchum.*

G. Segments of inner corona connate to or above level of style-stigma head apex (and corolla lobes greater than 8 mm long, leaves broad), with nonglandular pubescence adaxially; anther head held well above base of inner corona; bases of leaf blades hastate or less often cordate. .... 3. *Morrenia.*

F. Segments of inner corona fleshy, conduplicate, and distinct, usually with adaxial, adnate appendages (exserted horns) if apically opened; stems prostrate to erect, not twining. .... 6. *Asclepias.*

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[26] Escaped from or persistent beyond cultivation but clearly not reproducing either sexually or asexually in the southeastern United States. For further discussion, see family discussion.

Subfam. ASCLEPIADOIDEAE [R. Brown ex Endlicher, Gen. Pl. 589. 1838, "Asclepiadeae verae."]

Tribe GONOLOBEAE G. Don, Gen. Hist. Dichlamydeous Pl. 4: 107, 136. [1837?] 1838.

1. **Matelea** Aublet, Hist. Pl. Guiane **1:** 277; **3:** *pl. 109, fig. 1.* 1775.

Terrestrial, scandent and/or twining or (in *M. cynanchoides, M. pubiflora*) prostrate to suberect, perennial herbs (usually woody toward base) or subshrubs with white latex; axes and leaves with often dense nonglandular and (usually much shorter) glandular pubescence. Leaves opposite; blades ovate, elliptic, lanceolate, or sometimes orbiculate, especially near base of stem, apices acute, acuminate, or sometimes obtuse, rarely emarginate, margins sometimes revolute, bases cordate or obtusely sagittate; petioles distinct, without lateral appendages, bases and/or adjacent areas of stems usually without colleters. Inflorescences pedunculate or (in *M. cynanchoides* and *M. pubiflora*) sessile, 2- (often in *M. cynanchoides* and *M. pubiflora*) to several-flowered, cymose but appearing umbellate, racemose, corymbose, or paniculate, sometimes with both flowers and pedicel scars present simultaneously, bracteate; pedicels longer or (often in *M. cynanchoides* and *M. pubiflora*) shorter than calyces, ebracteolate. Calyx about ⅔ as long as corolla or less, free nearly to base, usually with both nonglandular and glandular pubescence abaxially, glabrous adaxially; lobes acute, bases imbricate or sometimes valvate, usually with minute squamellae (usually 1 near each sinus). Corolla much shorter than leaves, free nearly to base to united throughout the basal ⅔, rotate to campanulate, often glabrous or (in *M. pubiflora*) with nonglandular pubescence adaxially, with nonglandular and sometimes glandular pubescence or sometimes nearly glabrous abaxially; lobes valvate or sometimes imbricate, erect, ascending, spreading, or reflexed. Outer corona absent [or, reportedly, sometimes present]. Inner corona exceeding or (in *M. alabamensis*) exceeded by anther head, sessile, cyathiform (segments connate about to level of style-stigma head) and more or less erect (mostly concealing anther head and style-stigma head) and free from corolla or (in *M. alabamensis*) discoid and spreading, free from but in contact with corolla [and/or outer corona]; lobes 5, laminate, each with (or, in *M. cynanchoides,* often without) 2 lateral, shorter to longer projections, and with or without a single, adaxial, adnate, shorter or sometimes equally long appendage (especially the latter giving the appearance of a lobe apex tangentially split into adaxial and abaxial flaps or tongues). Anther head short-obconic, immediately subtended by base of inner corona; anther wing slots directed outward but mostly downward. Anthers each with an apical, adaxial, hyaline flap inflexed over style-stigma head, unappendaged abaxially. Style-stigma head short-obconic, with flat or depressed, distinctly 5-sided apex. Corpuscula clearly exserted from anther head; translator arms mostly horizontal; pollinia horizontal, each with sterile, hyaline tissue adjacent to attached end. Fruits follicular [unknown for many species], 1 (or, reportedly, rarely 2) from each flower, lance-ovoid, narrowly fusiform to fusiform-ovoid, acute to attenuate apically, dehiscent along

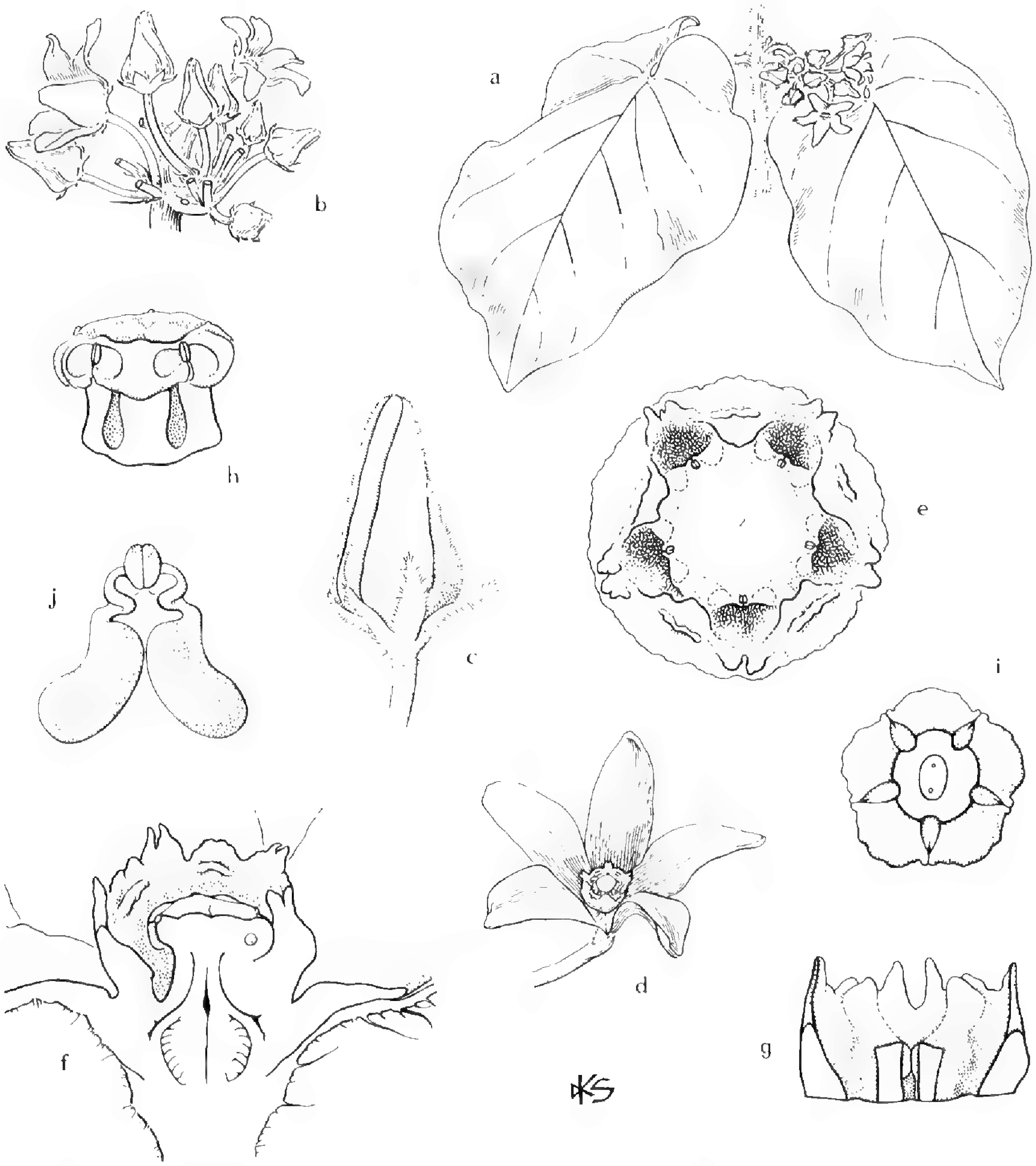

FIGURE 6. **Matelea.** a–j, *M. carolinensis*: a, node, with leaves and terminal inflorescence appearing interpetiolar by sympodial growth, × ½; b, inflorescence, with pedicel scars and corolla lobes all overlapping to left (clearly seen in only 2 buds, uppermost and rightmost), × 1; c, flower bud, with corolla lobes all overlapping to right, × 3; d, flower at anthesis, with corolla lobes all overlapping to right, × 2; e, flower, from above, without calyx and corolla (5 principal lobes of corona [erect, i.e., perpendicular to page] opposite 5 adaxial ligules [arching over style-stigma head; solid outline, 2 clearly 2-lobed] and 5 apical, adaxial, hyaline anther flaps [inflexed over style-stigma head; dotted outline], alternating with 5 pairs of lateral projections [more or less erect] and 5 corpuscula [between bases of hyaline anther flaps]), × 12; f, flower, cut longitudinally through calyx (1 lobe, of 5, in section, at right), corolla (2 lobes, of 5, in section), androecium (including corona: 2 principal lobes, of 5, and 2 adaxial ligules, of 5, entire, 1 of each in section, at right, immediately subtending anther head; 2 pairs of lateral projections, of 5, entire, each exceeding principal lobes), and gynoecium (both carpels free in ovule-bearing and all but most apical part of stylar regions, united apically into style-stigma head), × 10; g, 2 segments, of 5, of corona, removed from flower (2 adaxial ligules in foreground, about equaling 2 principal lobes in background; 1 pair [at center] and 2 single [at left and right] lateral projections exceeding principal lobes), areas of fusion between segments (i.e., between paired lateral projections; leftmost and rightmost) and between segments

adaxial suture, erect on erect pedicels to pendulous on pendulous ones, sometimes erect on deflexed pedicels(?); surface with many or, rarely, a few tubercles [or shallowly winged lontigudinally], usually with short nonglandular and glandular pubescence. Seeds many, ovate-lenticular, each with a tuft of trichomes at apex; seed-coat surface papillate or smooth, lateral wings crenate-undulate or entire. (Including *Cyclodon* Small, 1933; *Edisonia* Small, 1933; and *Odontostephana* E. J. Alex. in Small, 1933. Excluding, among others, *Gonolobus* Michx., 1803.) TYPE SPECIES: *M. palustris* Aublet; although Aublet originally included more than one species in *Matelea, pl. 109, fig. 1,* an illustration of *M. palustris,* was cited after the name of the genus. (Name of unknown etymology.)—CLIMBING MILKWEED, SPINY-POD.

Recognized here as distinct from *Gonolobus* Michx. (for reasons summarized in the discussion of that genus, and below), *Matelea* includes a total of 180 to 200 species distributed from the central and southern parts of the United States into South America, according to Spellman (1975b), who treated nine species in Panama. *Matelea* had been considered by most botanists (e.g., Schumann) to comprise less than ten species in tropical South America until Woodson expanded it to encompass North and South American plants to which many other generic names had been applied. In his revision of subg. DICTYANTHUS (Dcne.) Woodson, Stevens indicated that even after the recognition of a few genera of Gonolobeae in addition to those favored by Woodson, nearly 200 species of *Matelea* would remain.

Standley & Williams adopted Woodson's circumscription of *Matelea,* but not without certain misgivings. They thought that species in Mexico and Central America that had been placed in the genus in fact represent several genera, and that (p. 450) some of them are "less closely related . . . than certain other" species of *Matelea* are to members of *Gonolobus* and *Fischeria.* Woodson recognized both *Matelea* and *Fischeria* but considered them to be closely related. Murphy also maintained them as distinct, stating that *Matelea* is probably paraphyletic and that uniquely derived character states within *Fischeria* suggest it is monophyletic.

Woodson retained formal taxonomic status for some of the genera he placed in *Matelea* merely because the names were familiar. Mostly on the basis of corollas, coronas, and pollinia, he defined a total of 16 subgenera and six sections, at least some of which were "not entirely satisfactory," according to Stevens (p. 71).

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and column (i.e., opposite ligules; at left and right near center, partly defining area opposite stigmatic chambers) not stippled, × 12; h, androecium without corona and gynoecium without ovule-bearing region (2 corpuscula, partly exceeding anther head, opposite and at summit of 2 outwardly projecting slots between anthers and 2 stigmatic chambers [column unmarked; openings in column to stigmatic chambers stippled evenly]), × 12; i, structures shown in "h," seen from below (corpuscula not visible; 5 outwardly projecting slots between anthers external to and opposite 5 stigmatic chambers; apical, connate portion of stylar region at center), × 12; j, pollinarium, abaxial side (1 pollinium from each of 2 adjacent anthers [sterile area near attachment of translator arms unmarked], 2 translator arms, and corpusculum with surface grooved for attachment to insects; pollinia and translator arms more or less horizontal before removal from anthers]), × 50.

Despite recognition of a large number of infrageneric taxa, Woodson included all but one of our species, in addition to a number of others, in subg. CHTHAMALIA (Dcne.) Woodson, which he did not further divide and which he considered to be characteristic of the genus in the southern United States and northern Mexico; *Matelea alabamensis* (Vail) Woodson was placed in subg. *Eumatelea* (= subg. MATELEA), in the "Reticulatae" (name not validly published). These subgenera are distinguished in Woodson's key (pp. 220–222) primarily by characters of the pollinia ("subquadrate- or oblong-reniform, with a narrow hyaline margin" in subg. CHTHAMALIA; "subtriangular-pyriform, with a conspicuous hyaline indentation or margin" in subg. MATELEA and three others).

In a biosystematic study of *Matelea* in an area comparable to and perhaps equaling ours, Drapalik recognized nine species, one of which, *M. gonocarpa* (Walter) Shinners, was included by Woodson—and is included here—in *Gonolobus* (as *G. gonocarpus* (Walter) Perry). Drapalik agreed more closely with Small's treatment (1933) of these plants, in the sense that among them he recognized four groups of species instead of the three favored by Woodson, although he did not think, as Small did, that they should be recognized at the generic level. Thus, he considered *M. gonocarpa, M. alabamensis* (*Cyclodon alabamense* (Vail) Small), and *M. pubiflora* (Dcne.) Woodson (*Edisonia pubiflora* (Dcne.) Small) to be, at least morphologically, unrelated to one another or to a group of six closely related species Small (1933) had included in *Odontostephana* E. J. Alex. Comprising what Drapalik called the "Odontostephana group" were *M. Baldwyniana* (Sweet) Woodson, *M. carolinensis* (Jacq.) Woodson, *M. decipiens* (E. J. Alex.) Woodson, *M. flavidula* (Chapman) Woodson, *M. floridana* (Vail) Woodson, and *M. obliqua* (Jacq.) Woodson (in which Drapalik included *M. Shortii* (Gray) Woodson). The species concepts of Drapalik appear to be sound and are adopted here.

I recognize *Matelea* as distinct from and less specialized than *Gonolobus* because of the absence in the former and presence in the latter of abaxial anther appendages. Despite this fact and Drapalik's contention that there are four morphologically unrelated groups involved (even though he included them all in the same genus), plants in our area suggest to me a close link between *Matelea* and *Gonolobus*.

There appear to be four principal types of androecial appendages in the Asclepiadaceae, at least as the family is represented in the Southeast: an outer, discoid, spreading corona that is adnate to the corolla and sometimes shallowly lobed (i.e., the "faucal corona" or "faucal annulus" of many authors, characteristic of, for example, *Gonolobus gonocarpus*); an inner, erect or ascending corona with five principal, distinct or, less often, connate segments (e.g., the hoods of *Asclepias*, the vesicular segments of *Sarcostemma*, the five-lobed, cuplike structures characterizing the "Odontostephana group" in *Matelea*); a whorl of five structures adnate to the adaxial surfaces of the inner corona (e.g., the horns of *Asclepias*, the ligules of *Matelea*); and abaxial anther appendages (as seen in *Gonolobus*). There are, in addition, structures in *M. alabamensis* and *M. pubiflora* that do not entirely fit into any of the foregoing categories and are therefore of particular interest.

That the anther appendages characterizing *Gonolobus* represent abaxial adnations to the stamens of structures homologous to the adaxial ligules of *Matelea* (also considered in the discussion of *Gonolobus*) was rejected by Woodson because of the widespread occurrence in *Gonolobus* of both. Nevertheless, in *G. gonocarpus* the anther appendages are accompanied only by an outer corona; there is evidence neither of an inner corona nor of ligules.

With regard to androecial appendages in general, *Matelea alabamensis* appears to be intermediate in three major respects between *Gonolobus gonocarpus* and members of the "Odontostephana group," which have an inner, cuplike corona with ligules but lack an outer corona. *Matelea alabamensis* approaches *G. gonocarpus* in having a corona that is discoid, instead of cuplike; that is, more like an outer and less like an inner corona. Furthermore, to the extent to which it is adnate to the corolla, the corona of *M. alabamensis* is intermediate between that of *G. gonocarpus*, which is adnate above the point of filament insertion and is therefore a true outer corona, and those of species in the "Odontostephana group," which are not adnate above this point and are therefore true inner coronas. Moreover, the corona of *M. alabamensis* bears ligules that are, relative to those of the "Odontostephana group," less extensively adnate to the corona and more closely associated with the androecium, a disposition that has implications regarding the possibly homologous relationship between the ligules of *Matelea* and the anther appendages of *Gonolobus* (but see below).

Other morphological evidence also suggests a relationship between *Matelea alabamensis* and *Gonolobus gonocarpus*. As indicated in photomicrographs provided by Perry (*pl. 494*) and drawings included by Drapalik (*fig. 7*), the pollinaria of these two species are similar in size and morphology, yet they are much larger and of considerably different shape than those of *M. Baldwyniana, M. carolinensis, M. decipiens, M. obliqua,* and *M. pubiflora*, which are among themselves also fairly uniform in these features. In addition, the apex of the style-stigma head tends to be larger and more clearly pentagonal in *M. alabamensis* and *G. gonocarpus* than in our other species of *Matelea*.

It is notable that *Matelea alabamensis* is reportedly quite rare and has not been much collected. Outside of his own specimens, only those obtained by Harbison (on which Vail based the protologue) and by Thorne were known to Drapalik, who indicated after intensive searching that the plants are probably restricted to a few populations near the Apalachicola River in Florida, where the species is considered endangered (Drapalik in Ward), and along the same river in southeastern Alabama and southwestern Georgia (in these places called the Chattahoochee).

Matelea pubiflora is another species Drapalik considered to be isolated from the others he treated, primarily because of its prostrate habit, sessile inflorescences, and campanulate corollas; however, it too suggests a link between *Matelea* and *Gonolobus*. The corona in *M. pubiflora* is similar to that of species in the "Odontostephana group" in being more or less erect, connate around the anther head, not subtended by an outer corona, and not adnate to the corolla. However, it differs in having small, inconspicuous lateral projections on each of the five principal lobes instead of very prominent ones, thus approaching the condition of the discoid, essentially entire outer corona of *G.*

gonocarpus (and *M. alabamensis*). The corona of *M. pubiflora* is also similar to that of *G. gonocarpus* (and *M. alabamensis*) in that it is not entirely erect and is in contact with the corolla. However, the contact in *M. pubiflora* is at least as much due to the campanulate shape of the corolla as to the suberect orientation of the corona; the two structures clearly are not adnate.

Other similarities between *Matelea pubiflora* and *Gonolobus gonocarpus* are evident. Whereas ligules are associated with the inner corona in several species of *Matelea* (including *M. alabamensis*), such structures evidently occur neither on the inner corona of *M. pubiflora* nor on the outer one of *G. gonocarpus*. Thus, it is perhaps significant that according to illustrations provided by Drapalik (*fig. 6*), the lateral seed-coat wings of *M. pubiflora* and *G. gonocarpus* are crenate and undulate, while those of the other two species depicted, *M. alabamensis* and *M. Baldwyniana*, are nearly entire and flat.

According to Drapalik, *Matelea pubiflora* is most closely allied to species comprising prostrate plants that occur farther west than the area covered in his investigations. In fact, one of these, *M. cynanchoides* (Engelm.) Woodson, has been reported since Drapalik's work from the southeastern United States as we define the region, from Miller County in southwestern Arkansas (Smith), and indeed appears to be related to *M. pubiflora*. Both species are characterized by a prostrate habit, sessile inflorescences, and campanulate corollas, in addition to very small or sometimes nonexistent lateral projections on each of the five principal lobes of a suberect inner corona. That the inner corona bears very prominent ligules in *M. cynanchoides* but is without such structures in *M. pubiflora* (see also above) suggests either that the resemblance between these two species is only superficial or that the taxonomic significance of this character lies at or below the level of species and has been overestimated (see also below).

Matelea pubiflora and *M. cynanchoides* also have smaller leaves than our other species, probably reflecting the drier habitats in which they occur. Drapalik noted that the former is found in more xeric conditions than the other species he treated, and *M. cynanchoides* is known from sandy areas mostly in open woodlands (Correll & Johnston). Whereas *M. pubiflora* is rare and endemic to the Coastal Plain in Georgia and Florida (Drapalik; see also Anderson), *M. cynanchoides* is frequent in northern and central Texas (Shinners, 1964) and is also known from Oklahoma (Correll & Johnston) and, as indicated above, southwestern Arkansas.

Our six remaining species of *Matelea*, the "Odontostephana group" of Drapalik, are indeed closely related. This is an assemblage of scandent and twining vines with large, cordate leaves; essentially rotate corollas; no outer coronas; cyathiform, mostly erect inner coronas with five principal lobes, each with lateral projections and sometimes adaxial (or possibly abaxial, see below) ligules as well; relatively small, cylindrical style-stigma heads; and tuberculate follicles.

Efforts to reveal the true nature of the ligule sometimes present on the inner corona of members of the "Odontostephana group" probably would considerably enhance our understanding of the relationships within *Matelea* and perhaps between this genus and *Gonolobus* as well. According to Drapalik (p. 19), in the six species of this group (and in *M. pubiflora*) "the corona lobes may also have additional small adaxial and abaxial lips, protrusions, or indentations." Clearly, if these structures were in some cases truly abaxial, it would be more difficult to argue that they are homologous to the anther appendages in *Gonolobus* than if they were in all cases truly adaxial. In fact, my own observations suggest that the latter interpretation is more tenable.

In most cases in the "Odontostephana group," the ligules clearly arise from the adaxial surfaces of the inner corona and are exceeded by its principal lobes. However, in many instances the principal lobes instead appear to be apically split into equal adaxial and abaxial halves (see FIGURE 6g); in such cases the former could easily be interpreted as an adaxial ligule that equals the principal lobe. In some instances, and especially frequently in *Matelea floridana,* the smaller, shorter structure (i.e., the apparent ligule) is the outermost, suggesting an abaxial adnation on the principal lobe. In fact, in *M. floridana* (and perhaps other species) the outer structure appears to be the appendage (i.e., ligule) when the corona is viewed from the adaxial side but is just as easily seen as the principal lobe when the corona is observed from the abaxial side. In view of the foregoing, it seems most reasonable to interpret this as yet another adaxial ligule, but one longer than the principal lobe.

Even if the ligules were in all cases truly adaxial, their taxonomic importance (and the likelihood that they are homologous to the anther appendages of *Gonolobus*) is greatly diminished by the degree to which their presence, absence, and size relative to the principal lobes are variable both among and within our six species of the "Odontostephana group." For example, each species and in some cases individual flowers have both ligulate and nonligulate principal lobes. In addition, whereas the ligules were shown to exceed the principal lobes in perhaps 13 of 17 illustrations of *Matelea floridana* provided by Drapalik (*fig. 2*), my own examination of three herbarium specimens evidently belonging to this species (as determined by Drapalik and by me, using his key, but see below) revealed this condition on only one. Although in 12 of 13 drawings of *M. carolinensis* (Drapalik's *fig. 2*) the ligules were exceeded by the principal lobes, among four herbarium specimens I saw they much exceeded them (i.e., the principal lobes appeared as abaxial ridges) on one and were about equal to them (i.e., as in FIGURE 6g) on two others. It seems likely that with enough observations each of the conditions described above would be represented in each of the six species.

The foregoing examples involving closely related species (i.e., *Matelea cynanchoides* and *M. pubiflora* on one hand, and those in the "Odontostephana group" on the other) suggest that the ligule is of limited or no taxonomic value in *Matelea.* Indeed, although Drapalik documented with illustrations much of the variation he observed, the character was used in neither the key nor the formal descriptions he provided. In contrast, the abaxial anther appendages invariably absent in *Matelea* and present in *Gonolobus* appear to represent a much more stable character, one by which these genera can consistently be distinguished. The differences in stability between the ligules of *Matelea* and the abaxial anther appendages in *Gonolobus* imply genetic differences, which in turn suggest that the structures are not strictly homologous.

The closely related species in the "Odontostephana group" differ mainly in aspects of the corolla and corona that are often difficult to discern on living plants and are nearly impossible to observe in herbarium material. These include, among others, color of corolla and corona, size and shape of corolla lobes, and shape and size of the lateral projections relative to the principal lobes of the inner corona. As Drapalik documented extensively, the shapes and relative sizes of these structures, particularly the lateral projections, are frequently and irreversibly distorted by drying. He therefore stated that the correct assignment to species of herbarium specimens is frequently impossible and that liquid-preserved flowers should be included by collectors when possible. I have frequently observed in herbarium material both color distortion and the loss of significant portions of the lateral projections, the latter evidently due to shriveling in life and/or upon drying.

Matelea floridana supposedly differs from the other species in the "Odontostephana group" in that the principal lobes of the inner corona usually exceed the lateral projections. According to Drapalik, the species is rare and endemic to the Coastal Plain in northern Florida, although the possibility that it may occur in southeastern Georgia should be investigated because of the presence there of open or dense oak-hickory (*Quercus-Carya*) mixed hardwood forests. Wunderlin and colleagues have recently reported the species from central Florida. Drapalik reported that *M. floridana* occurs in shadier conditions than do other members of this group, and the later flowering observed among plants of this species in nature was maintained in common-garden experiments.

The lateral projections usually equal or exceed the principal lobes in the remaining five species in the "Odontostephana group." Two of these supposedly differ from the rest in having rotate-reflexed or rotate instead of rotate-ascending corollas; *Matelea carolinensis* and *M. flavidula* are very similar but can be distinguished on the basis of corolla-lobe color (usually dark maroon vs. some shade of green or rarely light maroon, respectively) and the relative lengths of the principal corona lobes and the lateral projections (the lateral projections always longer in *M. carolinensis,* see FIGURE 6f, g; the structures usually about equally long in *M. flavidula*). Both species are evidently infrequent and occur in open or second-growth oak-hickory forests, but *M. carolinensis* appears to have a wider geographic range (see, however, Wunderlin *et al.*). Whereas this species occurs in various floristic provinces from Delaware to Texas, *M. flavidula* is restricted to the Coastal Plain in South Carolina, Georgia, Florida, and Alabama.

Matelea Baldwyniana[27] usually differs from the other two species with rotate-ascending coronas (*M. obliqua* and *M. decipiens*) in its white corollas; flowers with cream-colored corollas also occur in *M. Baldwyniana* and, rarely, *M. obliqua,* but the lateral projections of the corona lobes are usually much longer in *M. Baldwyniana.* The corollas of *M. obliqua* are otherwise normally rose colored, light maroon, or infrequently dark maroon or green, while those of *M. decipiens* are always dark maroon; in addition, the corolla lobes of *M. obliqua* are usually four to six times as long as wide, whereas those of *M. decipiens* are nearly always stouter.

[27] According to Drapalik, application of this name is based on common, modern usage; type material has not been found, and the species is not now known from the type locality, near Savannah, Georgia.

Matelea Baldwyniana is rather common in northwestern Arkansas and adjacent parts of Missouri, particularly in places close to springs, but it is rare east of the Mississippi River; in addition to Arkansas, the species is known in our area only from Alabama and Florida. *Matelea obliqua* and *M. decipiens* are infrequent over large areas in the eastern United States: *M. obliqua* approximately from Georgia north to Missouri and Pennsylvania; *M. decipiens* from Georgia north to Maryland and west to Texas.

Drapalik reported that for most species of *Matelea* included in his investigation, vegetative growth in nature was greatest in either exposed or partially shaded conditions, but that in garden experiments partial shade was optimal for *M. carolinensis, M. decipiens,* and *M. obliqua.* Flowering was not observed among the few individuals (species not indicated, probably indeterminable) found in places with northern exposures. It is thought to occur under dense shade only in *M. alabamensis* and *M. floridana* (as well as *G. gonocarpus*), which flower under very exposed conditions as well.

All species of *Matelea* that Drapalik studied are evidently best adapted to well-drained soils, and none is found in areas subject to inundation. *Matelea pubiflora* and *M. cynanchoides* occur in drier conditions than the other species; according to Drapalik, *M. pubiflora* (he did not study *M. cynanchoides*) has especially large taproots and is restricted to communities dominated by turkey oak (*Quercus laevis* Walter) and long-leaf pine (*Pinus palustris* Miller). With the exception of *M. cynanchoides,* our species of *Matelea* are usually found in or at the edges of forests dominated by oaks, hickories, and other hardwoods.

Drapalik also reported the pH of soil samples obtained within 15 cm of the surface at each of his study sites. All of the samples associated with *Matelea Baldwyniana* and *M. obliqua* and most of those collected with *M. carolinensis* and *M. decipiens* were basic to circumneutral. In contrast, a majority of those obtained for *M. alabamensis, M. flavidula, M. floridana,* and *M. pubiflora* were acidic, although Drapalik reported growing plants of all four species from seed to flowering in pH-neutral substrates.

Drapalik reported natural pollination involving plants both in and out of cultivation for each of the species included in his study except *Matelea pubiflora*; observation during daylight hours revealed no insect visitors to flowers of this species, although numerous fruits were produced by plants in cultivation. Visitors with attached pollinaria were in all cases small flies belonging to the Anthomyiidae, Chloropidae, Milichiidae, and Phoridae. Indeed, the flowers were said to emit the kinds of odors (i.e., unpleasant, at least to most humans) and in many cases to have the colors (i.e., reds, maroons) to which such insects are attracted. The flies have been observed to effect pollination while feeding on nectar produced by the flowers.

The details of pollination as described by Drapalik are very much like those presented here for *Asclepias,* with a few notable exceptions. Although nectar is produced in the stigmatic chambers in both genera, in *Matelea* it accumulates at the base of the inner corona immediately outside the base of the outwardly projecting slot, instead of in the hoods at either side. In many but not all cases involving species of *Matelea,* pollinator parts appear not to be wedged into the corpusculum, as they evidently always are in *Asclepias,* but instead to adhere to it even though corpuscular secretions have not been noted. In *Matelea*, in contrast to *Asclepias*, the anther wings are much smaller and more rigid and the pollinia are larger than the slot opening, so that pollinia are not and need not be inserted completely but merely placed against the slot. Nevertheless, as in *Asclepias*, the convex side must be adjacent to the opening for successful pollen-tube growth.

In nature all of our species of *Matelea* appear to be reproductively isolated, with the exception of *M. carolinensis* and *M. decipiens* of the "Odontostephana group." Drapalik reported populations of these two species and various intermediates between them throughout Georgia and the Carolinas. He specifically mentioned genetically unmixed populations of *M. carolinensis* in Tennessee, Maryland, and Virginia, and of *M. decipiens* in Louisiana and Missouri, but did not address the issue for the remaining geographic areas in which these species occur. Drapalik attributed the infrequency of interspecific hybridization to various factors, including temporal, geographic, ecological, and mechanical isolation. Evidence suggested that pollinator specificity was of limited importance in this regard.

Breeding experiments conducted by Drapalik in cultivation using the six species belonging to the "Odontostephana group" indicated that each is self-incompatible (a gametophytic system was assumed) but revealed little about the relationships among them. Artificial cross pollinations involving six of the 15 possible species pairs were successful in the sense that mature fruits and viable seeds were produced. Although fruit set among plants in cultivation was greater than that observed in nature (6.10 vs. 0.22 fruits per plant), the overall percentage of successful interspecific pollinations among them was low (6.84 percent). This observation, together with the fact that successful artificial crosses between *Matelea carolinensis* and *M. decipiens* were no more frequent than those between species not known to hybridize in nature, diminishes the reliability of these results. Nevertheless, it is tempting and perhaps reasonable to suggest that additional attempts might eventually result in successful crosses between all pairs of species in this group. This is especially so because the percentage of successful pollinations between species was equal to that observed between individuals from different populations of the same species, indicating that interfertility between and within species might be approximately equal. A lower rate of success resulted from pollinations within single populations of a given species, presumably due to self-incompatibility and a greater genetic similarity among the individuals. As expected, an even lower success rate was obtained from self-pollinations.

Compared to the parents, the F_1 hybrid plants resulting from artificial pollinations were intermediate in flower color and morphology (Drapalik). In addition, the hybrids were as fertile as the parents, as determined by pollen stainability, the number of seeds per fruit, and seed viability. Drapalik provided helpful illustrations of coronas representing the parents and progeny involved in several of the interspecific crosses. Unfortunately, this documentation does not elucidate the genetic basis of ligule variation.

Matelea carolinensis is cultivated in North America with sufficient frequency to have been treated by Bailey and colleagues. Drapalik provided instructions for growing all species found in the southeastern United States, both from seed and by transplanting mature plants.

REFERENCES:

Under references for the Apocynineae, see ANDERSON; BAILEY *et al.*; CORRELL & JOHNSTON; SCHUMANN; SMALL (1933); SMITH; and STANDLEY & WILLIAMS.

Under references for the Asclepiadaceae, see DRAPALIK; MURPHY; PERRY; SHINNERS (1964); SPELLMAN (1975b); STEVENS; WARD; and WOODSON.

VAIL, A. M. Studies in the Asclepiadaceae.—VII. A new species of *Vincetoxicum* from Alabama. Bull. Torrey Bot. Club **30:** 178, 179. *pls. 9, 10.* 1903. [= *M. alabamensis.*]

WUNDERLIN, R. P., B. F. HANSEN, & D. W. HALL. The vascular flora of central Florida: taxonomic and nomenclatural changes, additional taxa, II. Sida **13:** 83–91. 1988. [According to annotations by DRAPALIK, *M. floridana,* but not the previously reported *M. carolinensis,* present.]

2. **Gonolobus** Michaux, Fl. Bor. Am. **1:** 119. 1803.

Terrestrial, scandent and/or twining [or sometimes prostrate], perennial herbs (usually woody toward base) or subshrubs with white latex; axes and leaves nearly glabrous or with usually sparse nonglandular and sometimes (usually much shorter) glandular pubescence. Leaves opposite; blades ovate, elliptic, or sometimes suborbiculate especially near base of stem, apices acute, acuminate, or subcuspidate, sometimes obtuse, rarely emarginate, margins not revolute, bases cordate or obtusely sagittate [sometimes obtuse or cuneate]; petioles distinct, without lateral appendages, bases and/or adjacent areas of stems usually without colleters. Inflorescences pedunculate [or subsessile], few- to several-flowered, cymose but appearing umbellate, racemose, or corymbose, bracteate; pedicels longer than calyces, ebracteolate. Calyx about ½ as long as corolla or less, free nearly to base, sometimes with nonglandular pubescence abaxially, glabrous adaxially; lobes acute, bases valvate, with minute squamellae (usually 1 near each sinus). Corolla much shorter than leaves, free nearly to base to united throughout the basal ⅓, rotate [to subcampanulate], usually with at least some degree of nonglandular pubescence adaxially, glabrous abaxially; lobes valvate, spreading to reflexed [or sometimes erect to ascending]. Outer corona discoid, fleshy, crenate-undulate, basally adnate to the corolla tube but apically free, forming a mostly spreading [or erect] annulus. Inner corona absent [or reportedly exceeded by anther head, substipitate, essentially discoid and spreading, free from but in contact with outer corona and/or corolla; lobes 5, laminate but sometimes revolute, unappendaged]. Anther head short-obconic, immediately subtended by base of outer [or inner] corona; anther wing slots directed outward but mostly downward. Anthers each with an apical, adaxial, hyaline flap inflexed over style-stigma head, and an apical, abaxial, fleshy, appendage projecting outward. Style-stigma head short-obconic, with flat or depressed, distinctly 5-sided apex. Corpuscula clearly exserted from anther head; translator arms mostly horizontal; pollinia horizontal, each with sterile, hyaline tissue adjacent to attached end. Fruits follicular [unknown for many species], 1 from each flower, lance-ovoid, narrowly fusiform to fusiform-ovoid, acute to attenuate apically, dehiscent along adaxial suture, erect on erect pedicels to pendulous on pendulous ones, sometimes erect on deflexed pedicels; surface winged longitudinally [or sometimes reportedly with tubercles], usually with sparse, nonglandular pubescence. Seeds many, ovate-lenticular, each with a tuft of trichomes at apex; seed-coat surface papillate or smooth, lateral wings crenate-undulate. (*Vincetoxicum* Walter, 1788, nom. illeg., not Von Wolf, 1776, not Moench, 1794.) LECTOTYPE SPECIES: *G. gonocarpus* (Walter) Perry[28] (*Vincetoxicum gonocarpum* Walter); Perry (Rhodora **40:** 283. 1938) selected *G. macrophyllus* Michx. as the "standard-species," a name, as she correctly recognized, invalidated by Michaux's citation in synonymy of the earlier *V. gonocarpum.* (Name from Greek, *gonia,* angle, and *lobos,* pod, evidently in reference to the longitudinally winged (i.e., angled in transverse section) follicles of the first (and the type) but not the other two species originally included by Michaux.)—ANGLE-POD.

Recognized here as distinct from *Matelea* (for reasons put forth in the discussion of that genus, and below), *Gonolobus* includes perhaps 100 species (Spellman, 1975b). Although most of these occur in Mexico and Guatemala, *Gonolobus* is distributed from the southeastern United States and nearby areas, where it is represented by a single species, *G. gonocarpus* (Walter) Perry, to Panama, where fewer than ten species are known.

The correct name and appropriate circumscription of this genus have been unclear as well as controversial. As proposed by Michaux in 1803, *Gonolobus* included three species. *Vincetoxicum gonocarpum* Walter (as *V. gonocarpos* Walter) and *V. acanthocarpum* Walter (as *V. acanthocarpos* Walter), comprising the totality of *Vincetoxicum* Walter (Fl. Caroliniana, 104. 1788) as originally delimited, were listed as synonyms of the first two, *G. macrophyllus* Michx. and *G. hirsutus* Michx., respectively (thus invalidating these two names of Michaux), while the third, *G. laevis* Michx., was newly described.

Although it is generally conceded that the material on which *Gonolobus laevis* was based actually represents more than one species, interpretations regarding it are confusing and/or in some cases contradictory. Gray (p. 75) partially described *G. laevis* with the phrase "folliculis laevibus 5-angulatis," suggesting that he chose portions agreeing with Michaux's description of *Gonolobus* ("folliculi plerumque costati seu angulosi") but contradicting the latter's concept of *G. laevis.* Although Michaux had explicitly indicated that the fruits of *G. macrophyllus* and *G. hirsutus* are angled and muricate, respectively, he had described (p. 75) those of *G. laevis* merely with the phrase "folliculis laevibus," implying that they are smooth and not angled. According to Woodson, the material selected by Gray is probably conspecific with *G. gonocarpus.*

Unlike Gray, Vail chose material contradicting Michaux's generic concept but agreeing with his description of *Gonolobus laevis.* She maintained that such

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[28] Because *Gonolobus* is masculine, the correct epithet is *gonocarpus,* even though *gonocarpos* was used initially in this combination by Perry and has been employed by nearly everyone since. Similarly, *Vincetoxicum* is neuter, so the epithet in this case should be *gonocarpum,* even though *gonocarpos* had been proposed initially by Walter and, again, widely used thereafter.

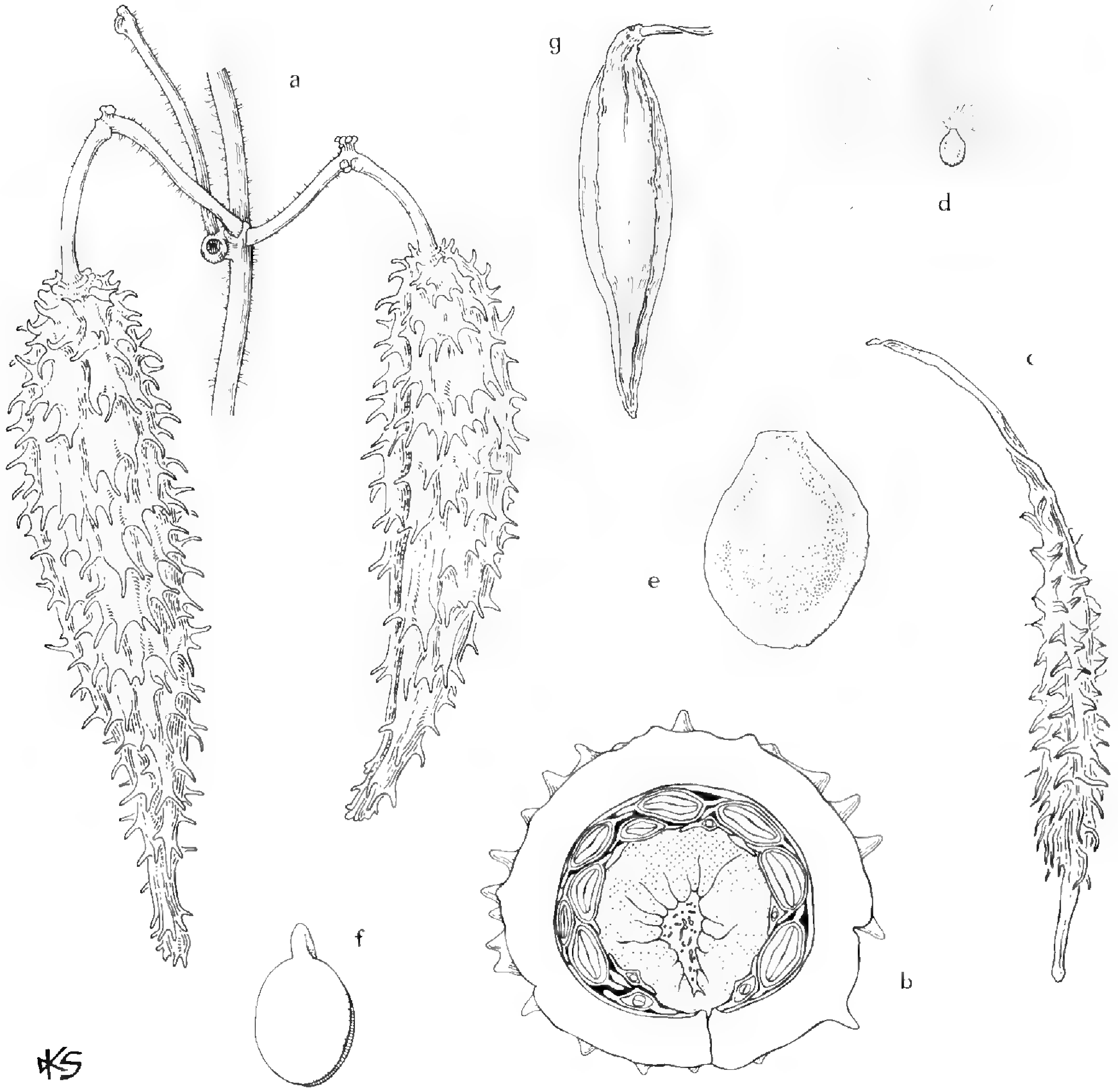

FIGURE 7. **Matelea** and **Gonolobus.** a–f, *M. carolinensis* (from flowering material collected earlier): a, 2 mature follicles, from 2 flowers of 1 inflorescence, surfaces tuberculate, × ¾; b, mature follicle, cut transversely (pericarp and laterally winged seeds unmarked; area of compacted, apical tufts of trichomes stippled evenly; marginal placenta near center), × 2; c, placenta, after release of seeds, × 1; d, seed, with apical tuft of trichomes, × ½; e, seed, apical tuft of trichomes removed, seed coat winged laterally, × 3; f, embryo, somewhat expanded from soaking in water (oriented as in "e"), × 3. g, *G. gonocarpus*: mature follicle, surface winged longitudinally, × 2.

material was much more abundant than that selected by Gray but nevertheless assignable to *Enslenia albida* Nutt. (= *Cynanchum laeve* (Michx.) Pers.). Her assessment accords better with "The guide for the determination of types" (ICBN, 1983; element T.4.e) and is now generally accepted, although it is difficult to determine "current usage" in this case.

Vail logically returned to *Vincetoxicum* Walter the first two species included in *Gonolobus* by Michaux (see above), leaving in the latter only *G. laevis*. Vail's interpretation of this species was adopted by, for example, Small (1933), but not by Perry, who accepted Gray's interpretation but nevertheless reestablished the original concept of *Gonolobus* by selecting Michaux's first species, *G. mac-*

rophyllus (= *G. gonocarpus*), as the type of the genus. This designation is especially significant because of nomenclatural problems with Walter's *Vincetoxicum.*

Both the name and the description of *Gonolobus* provided by Michaux suggest that he envisioned a group of plants with angled (i.e., longitudinally winged) follicles, so it seems inconsistent for him to have indicated such a condition in only the first of the three species descriptions he included. In doing this he might have been simply following Walter, who had done essentially the same both in naming and in describing the two species comprising his *Vincetoxicum* (*viz., V. gonocarpos* and *V. acanthocarpos,* the epithets meaning angled and thorny fruit, respectively) but did not address the issue in his generic description.

The second species included in *Gonolobus* by Michaux, *G. hirsutus* (*Vincetoxicum acanthocarpos*), was placed by Alexander (in Small, 1933), together with six other species of the southeastern United States in *Odontostephana* E. J. Alex., in synonymy under *O. carolinensis* (Jacq.) E. J. Alex. Although the descriptions (p. 1076) indicated that the follicles in *Vincetoxicum* (here *Gonolobus,* for reasons given below) and *Odontostephana* were "unarmed, wing-ridged toward the apex" and "armed with fleshy spines," respectively, the genera were separated in the key (p. 1065) on the basis of corona structure, primarily "disk-like or saucer-shaped" in the former and "cup-shaped or incurved at the tip" in the latter (Small, 1933). *Odontostephana* was included in an expanded *Matelea* Aublet by Woodson, and Michaux's second species is now generally known as *M. carolinensis* (Jacq.) Woodson (see discussion of *Matelea*).

The correct generic name for the first species listed by Michaux (i.e., the one with longitudinally winged follicles) remained in doubt for several reasons. Although *Vincetoxicum* Walter (1788) preceded *Gonolobus* Michx. (1803), it would have been eliminated as a *nomen rejiciendum* if a proposal to conserve *Vincetoxicum* Moench (1794) had been adopted (see Perry). Although the latter did not occur, *Vincetoxicum* Walter is to be considered a later homonym and therefore illegitimate on the basis of Ross's argument that *Vincetoxicum* Von Wolf (1776) had in fact been validly published, so *Gonolobus* now appears to be correct.

As indicated above, there has been in addition to the nomenclatural confusion a considerable amount of taxonomic disagreement regarding *Matelea* and *Gonolobus.* It is perhaps surprising that the genera usually have been combined by botanists dealing with the relatively few species in North America (e.g., Clewell; Correll & Johnston; Duncan & Kartesz; Jones & Coile; Radford *et al.*; Shinners, 1950, 1964; Smith; Steyermark) but retained as separate by those treating plants in Central America (e.g., Spellman, 1975b; Standley & Williams), where the two genera are better represented and evidently less distinct.

Woodson chose to maintain both *Gonolobus* and *Matelea* despite drastically reducing (from 97 to nine) the number of asclepiadaceous genera represented in the New World outside of South America. Although he stated that differences between the two in corona structure did not exist, he maintained that the fleshy, abaxial appendages of the anthers universally present in *Gonolobus* do not occur in *Matelea* and thus based his separation primarily on this character. He considered the possibility that the anther appendages of *Gonolobus* represented adnations to the stamens of structures corresponding to the ligules often adnate to or at least associated with the adaxial side of the corona in *Matelea,* but he rejected the idea because such structures "almost invariably" occur in *Gonolobus* in addition to the anther appendages. It is notable that ligules nevertheless do not occur in *G. gonocarpus* (see also discussion of *Matelea*).

Woodson cited fruit and pubescence characters as further support for his generic separation. For the relatively few species of each genus for which fruits were known, he stated that those of *Gonolobus* are usually winged, while those of *Matelea* are usually muricate (i.e., angled and thorny, respectively, in the sense of Walter). He also pointed out that a mixture of long, nonglandular and short, glandular trichomes is unique to most members of *Matelea* (and possibly the closely related if not congeneric *Fischeria* DC.) and never found in *Gonolobus.*

Shinners (1950), who believed that *Matelea* and *Gonolobus* are not sufficiently distinct for separation at the generic level, provided a rebuttal to Woodson's position. He reported that the follicles of *M. producta* (Torrey) Woodson (western Texas to southern Arizona and northern Mexico) are not at all muricate (they are smooth but evidently not angled or winged, according to Correll & Johnston), and that those of *M. reticulata* (Gray) Woodson (central, southern, and western Texas; northeastern Mexico) are only sparingly so. Indeed, I have seen a specimen of *Matelea* obtained in Florida (*Curtiss 5948*; GH), probably belonging to *M. flavidula* (Chapman) Woodson (based on the key provided by Drapalik) that bears a single follicle with only a few short projections; although it does not appear to have been angled before pressing, an intermediacy between the genera in fruit is nevertheless suggested.

My observations of both glandular and nonglandular trichomes on specimens of *Gonolobus gonocarpus* are consistent with those reported by Shinners (1950) for this species and for the probably conspecific *G. suberosus* (L.) R. Br. as well (see below), except that it seems to me that pubescence in general is not as substantial in this species as it is in our representatives of *Matelea.* Shinners (1950) also cited other evidence suggesting that *Gonolobus* and *Matelea* are not distinct, at least in Texas.

Shinners (1950) regarded the presence of anther appendages in *Gonolobus* and their absence in *Matelea* to be insufficient grounds for separating the two genera, citing Woodson's (p. 239) observation that the structures in the former were "rather poorly developed as a rule in the temperate representatives." However, although those of *G. gonocarpus* evidently are not as elaborate as those of some more tropical species, they are nevertheless quite apparent and unlike any structures present in *Matelea.*

Drapalik studied nine of these species in the southeastern United States, including *Gonolobus gonocarpus* (as *Matelea gonocarpa* (Walter) Shinners) and eight other species here included in *Matelea.* He believed (p. 80) that all nine should be included in the same genus because of "many similarities" among them, despite the fact that the follicles of *G. gonocarpus* and the others are "quite different." His concession that glandular trichomes are relatively scarce on plants of *G. gonocarpus* is consistent with my observations (as indicated above), and I agree that trichome density should not be used as a generic distinction. However, I do not agree with his implication (p. 80) that the anther appendage present throughout *Gonolobus* and completely lacking in *Matelea* also fails in this regard merely because it is "simply a sterile enlargement . . . that protrudes outward." Characters of the androecium, primarily a variety of sterile enlargements of the filaments (i.e., coronas), have served as the morphological bases for many and perhaps most genera of Asclepiadaceae, including all those in the Southeast.

Despite the taxonomic decision to recognize a single genus, Drapalik stated that *Gonolobus gonocarpus* was not morphologically related to the eight species of *Matelea*. He also reported several other differences between them, involving aspects of physiology, phenology, and ecology. He found greater susceptibility to infections by fungi and rusts in *G. gonocarpus* than in the six species of the "Odontostephana group" (see discussion of *Matelea*), among cultivated (but not wild) plants, and reported a fragrance (presumably floral) in *G. gonocarpus* unlike any in the other eight.

Drapalik also determined that in garden plots individuals of *Gonolobus gonocarpus* were always the first to resume growth in the spring, yet they flowered later than adjacent plants belonging to the "Odontostephana group" of *Matelea*. Although he reported some overlap in flowering between *G. gonocarpus* and members of the "Odontostephana group," he found that of six possible hybrids (among 99 flowering individuals grown from seeds resulting from natural pollinations of the cultivated plants), none showed evidence of parentage by *G. gonocarpus*. According to Drapalik, when plants of *G. gonocarpus* and species of *Matelea* occur together in nature, those of the former usually are found in the moister conditions and flower a bit later (except that *M. floridana* evidently flowers at about the same time or earlier). At least in the Southeast, plants of *G. gonocarpus* occur in a wider range of substrate moisture and pH than do individual species of *Matelea* and, as in the case of only two of our species of *Matelea* (*M. alabamensis* and *M. floridana*), flower under conditions ranging from densely shaded to sunny. This wider ecological amplitude would account, at least in part, for the fact that *G. gonocarpus* appears to be more abundant in the Southeast than any of the species of *Matelea*.

While Drapalik's position in combining *Matelea* and *Gonocarpus* is certainly not without merit or support from other botanists, it resulted from study of only nine of the perhaps 300 species in question. Despite the existence of southeastern species of *Matelea* (*M. alabamensis* and *M. pubiflora*) that I believe are in several ways intermediate between the genera (see discussion of *Matelea*), my studies support the decisions of those familiar with all of the plants involved (e.g., Spellman, 1975b; Standley & Williams; Stevens, pers. comm.; Woodson) to recognize both *Matelea* and *Gonolobus*.

Gonolobus gonocarpus (as *Vincetoxicum gonocarpos* Walter) and *G. suberosus* (L.) R. Br. (as *V. suberosum* (L.) Britton) were both recognized in the southeastern United States by Small (1933), but according to Drapalik, the Linnaean epithet has been misapplied and the plants are certainly conspecific. The species have been separated on the basis of corolla-lobe size and pubescence, those in *G. gonocarpus* being more than twice as long as the calyx lobes (vs. twice as long or less) and glabrous (vs. pubescent) adaxially. However, on the basis of these characters, Drapalik found both species and "every conceivable intermediate" in several populations and grew both from seeds of a single fruit obtained from a plant in Tennessee. Drapalik emphasized that any endeavors to interpret the considerable morphological variation in this species taxonomically should be preceded by adequate field (and, presumably, other biosystematic) study.

Woodson recognized three subgenera[29] in *Gonolobus,* one of which, the extraregional subg. "Pseudolachnostoma," has erect or ascending (vs. spreading or reflexed) corolla lobes and lacks the outer, discoid, annular corona present in the other two. Anthers in the extraregional subg. "Pterolobus" are supposedly partially exserted from the style-stigma head, while those in subg. "Eugonolobus" are not.

Gonolobus gonocarpus occurs throughout the southeastern United States with the exception of southern Florida, in all states bordering our area, and in Illinois and Indiana. The plants often occur in low, moist, rich but well-drained areas with hardwood trees in swamps and on floodplains.

Gonolobus gonocarpus is of sufficient horticultural interest in North America to have been treated by Bailey and colleagues, and Drapalik provided instructions for growing the plants both from seed and by transplantation. According to Standley & Williams, the tender young fruits of Central American species of *Gonolobus* (and related genera) are commonly eaten as vegetables and are sold for this purpose in markets in Guatemala City.

REFERENCES:

Under references for the Apocynineae, see BAILEY *et al.*; CLEWELL; CORRELL & JOHNSTON; DUNCAN & KARTESZ; JONES & COILE; RADFORD *et al.*; SMALL (1933); SMITH; STANDLEY & WILLIAMS; and STEYERMARK.

Under references for the Asclepiadaceae, see DRAPALIK; PERRY; SHINNERS (1950, 1964); SPELLMAN (1975b); and WOODSON.

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ROSS, R. The generic names published by N. M. von Wolf. Acta Bot. Neerl. **15:** 147–161. 1966.

VAIL, A. M. Studies in the Asclepiadaceae.—IV. II. The types of *Gonolobus* Michaux and descriptions of new species in *Vincetoxicum* Walter. Bull. Torrey Bot. Club **26:** 425–431. 1899.

Tribe ASCLEPIADEAE [R. Brown ex A. P. de Candolle, Bot. Gallicum **1:** 323. 1828.*]

3. **Morrenia** Lindley, Bot. Regist. **24**(Misc.): 71. 1838.

Terrestrial, scandent and/or twining subshrubs with white latex; axes and leaves with often dense nonglandular pubescence. Leaves opposite; blades ovate, elliptic, or lanceolate, apices acute or acuminate, margins sometimes undulate,

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[29] The names of these subgenera were not validly published by Woodson, since they were accompanied in 1941 neither by a Latin description or diagnosis nor by a reference to a previously and effectively published Latin description or diagnosis (i.e., they were not published in accordance with Art. 36.1 [ICBN, 1988], the effective date of which is 1 January 1935). Therefore, they are enclosed in quotation marks here.

rarely revolute, bases hastate or less often cordate; petioles distinct, without lateral appendages, bases and/or adjacent areas of stems usually with a few colleters. Inflorescences short-pedunculate, few-flowered, cymose but appearing racemose or sometimes subumbellate, bracteate; pedicels longer to shorter than calyces, ebracteolate. Calyx ca. ½–⅔ as long as corolla, free nearly to base, glabrous or with nonglandular pubescence abaxially, glabrous adaxially; lobes acute, bases valvate, usually with 2 or 3 squamellae near each sinus. Corolla much shorter than leaves, free nearly to base, salverform (but with lobes much longer than tube, and therefore appearing nearly rotate), glabrous adaxially and abaxially; lobes valvate, spreading to reflexed, the margins revolute. Outer corona absent. Inner corona exceeding anther head, stipitate, cyathiform (segments connate about to level of or above style-stigma head), erect (concealing anther head and style-stigma head), free from corolla; lobes 5, each with 2 lateral, shorter projections near sinuses between segments, and either emarginate, with (as viewed from the adaxial side) a mucronate convexity at base of emargination, or entire, with acute, marginally incurved apices. Anther head cylindrical, held well above [or sometimes immediately subtended by] base of inner corona; anther wing slots directed outward. Anthers each with an apical, adaxial, hyaline flap inflexed over style-stigma head, unappendaged abaxially. Style-stigma head short-obconic, with conical, bilobed apex. Corpuscula clearly exserted from anther head; translator arms mostly pendulous; pollinia pendulous, each completely fertile. Fruits follicular, 1 from each flower, lance-ovoid to ovoid, obtuse or truncate and often mucronate apically, dehiscent along adaxial suture, mostly pendulous on pendulous pedicels; surface smooth or sometimes shallowly winged longitudinally [or rugose], usually with short nonglandular and glandular pubescence. Seeds many, elliptical-lenticular, each with a tuft of trichomes at apex; seed-coat surface rugose, lateral wings crenate-undulate or entire. TYPE SPECIES: *M. odorata* (Hooker & Arnott) Lindley (*Cynanchum odoratum* Hooker & Arnott), the only species initially included in the genus by Lindley. (Named for Charles Morren, 1833–1886, professor of botany and director of the botanical garden at Liège, Belgium.)—MILKWEED VINE, STRANGLER VINE.

A genus of probably two species. *Morrenia odorata* (Hooker & Arnott) Lindley is native to Paraguay, southern Brazil, and northern and central Argentina but has escaped from cultivation and become naturalized in Florida and perhaps elsewhere (see below), whereas *M. brachystephana* Griseb. is evidently restricted to northern and central Argentina. Compared to the latter, *M. odorata* has larger flowers (e.g., corollas 10–15 vs. 5–6 mm long), stipitate (vs. sessile) anther heads, and smooth (vs. rugose) follicles (see, for example, Fabris; Schumann).

Details are uncertain regarding the introduction to Florida of *Morrenia odorata* (see primarily Tucker *et al.*), a species favored by horticulturists for the vanillalike fragrance of its flowers (Ryan & Knorr). An individual was reportedly cultivated in Pasco County in 1939, and plants were first reported from citrus groves, clearly the preferred habitat in the adventive range of the species, in Orlando in 1957. The species is now widespread in central peninsular Florida but is most abundant in Lake, Orange, and Seminole counties. In addition to citrus groves, where they are both numerous and problematic, the plants have been infrequently observed in other man-made and/or disturbed habitats. They have been found in natural habitats as well, albeit rarely.

Morrenia odorata is a perennial, vigorously growing vine that in Florida often kills support plants, particularly citrus trees, through both shading and girdling (hence, "strangler vine"); parasitism evidently does not occur (Ryan & Knorr), although individuals compete for water and nutrients (Spellman & Gunn). Infestations by *M. odorata* also reduce the efficiency of irrigation, spraying, and harvesting in citrus groves.

Control of *Morrenia odorata* has been difficult, and further spread of the weed seems likely for several reasons (see primarily Tucker *et al.*). The plants produce an abundance of viable, wind-dispersed seeds (about 1000 per fruit) at a young age (two years or less) and also propagate vegetatively from root fragments resulting from tillage. They have been known to survive freezing temperatures and have demonstrated high degrees of tolerance to the chemical herbicides registered for use in citrus groves.

Biological control of *Morrenia odorata* is complicated by the presence of latex, which renders the plants (and most members of the suborder) toxic or at least unpalatable to most animals. Woodhead and co-workers reported that populations were reduced by more than 90 percent within one or two years after citrus plants were somehow "treated" in 1978, 1979, and 1980 with a fungus, *Phytophthora palmivora* (E. J. Butler) E. J. Butler. Mitchell & Kannwischer-Mitchell determined that applications under citrus trees of 1.5 chlamydospores per square centimeter of soil resulted in the death of over 95 percent of the plants of *M. odorata.* Nevertheless, the species evidently continues to be a serious problem.

Singh & Achhireddy studied germination and seedling growth to gain a better understanding of the biology and therefore the possibilities for control of *Morrenia odorata.* They found that germination rates were markedly reduced above and below pH 7—to zero percent after seven days at pH 8.0 and pH 5.5; on either side of a 20/25°C (12-hour) thermoperiod, although seedling growth was highest at about 30°C; and at soil depths greater than 2.5 and less than 0.5 cm. Both germination rates and seedling growth decreased with decreasing water potential.

Allelopathic effects on *Morrenia odorata* have been suspected of *Lantana Camara* L. (Verbenaceae), native to tropical America and the Coastal Plain in the Southeast, but also a serious weed in citrus groves in Florida. In fact, Achhireddy & Singh found that incorporation into the soil of dried material of *L. Camara* significantly inhibited vegetative growth in *M. odorata* (e.g., 50 percent seedling mortality within 15 days of germination in soil containing, in terms of dry weight, one percent root material of *L. Camara*), although it had no apparent effect on final germination percentages.

Morrenia odorata is one of several species of Asclepiadaceae reported to be used in South America to stimulate lactation in cattle and humans. The latex is used in the manufacture of cheese, while people in the Chaco region of Argentina eat the follicles either raw or cooked (see Spellman & Gunn).

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Under references for the Apocynineae, see SCHUMANN.

Under references for the Asclepiadaceae, see FABRIS; SPELLMAN & GUNN; and SUNDELL.

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WOODHEAD, S. H., W. H. RIDINGS, C. L. SCHOULTIES, R. K. CLARK, & N. E. EL-GHOLL. Field efficacy of *Phytophthora palmivora* for control of milkweed vine. Phytopathology **71:** 913. 1981.

4. **Cynanchum** Linnaeus, Sp. Pl. **1:** 212. 1753; Gen. Pl. ed. 5. 101. 1754.

Terrestrial to semiaquatic (sometimes at edges of salt marshes), scandent, perennial herbs (usually woody toward base) [or erect to prostrate subshrubs] with white latex; axes and leaves glabrous or with various degrees of nonglandular pubescence. Leaves opposite, sometimes caducous and the plants leafless or nearly so; blades ovate, elliptic, lanceolate, linear, or filiform, apices acute, acuminate, or mucronate, margins often revolute, bases attenuate, truncate, or cordate; petioles distinct, sometimes very short and/or indistinct (especially with linear or filiform leaves), without lateral appendages, bases and/or adjacent areas of stems sometimes with a few small colleters. Inflorescences pedunculate or sessile, few- to many-flowered, cymose but appearing umbellate and/or racemose, bracteate; pedicels longer than calyces, ebracteolate. Calyx about ½ as long as corolla or less, free nearly to base, usually with nonglandular pubescence abaxially, glabrous adaxially; lobes acute or sometimes subotuse, bases variously imbricate, with minute squamellae. Corolla much shorter than leaves, free nearly to base to united throughout the basal ⅓ (in *C. Blodgettii, C. Northropiae*), campanulate (but lobes mostly free), campanulate-salverform (in *C. Northropiae*), or campanulate-urceolate (in *C. Blodgettii*), glabrous or with dense, nonglandular pubescence adaxially (in *C. Blodgettii* and *C. Northropiae*), glabrous abaxially; lobes valvate or variously imbricate, erect proximally but ascending, spreading, or reflexed distally. Outer corona absent. Inner corona exceeding or (in *C. scoparium*) exceeded by anther head, stipitate to substipitate or sessile, comprising distinct or (in *C. scoparium*) basally connate, erect to ascending segments, each basally free from or (in *C. Blodgettii*) adnate to corolla [or rarely absent]; segments 5, laminate or (in *C. Northropiae*) fleshy and subterete (solid, not conduplicate), apically acute, subobtuse, or (sometimes in *C. angustifolium*) emarginate, or (in *C. laeve*) with 2 linear, erect lateral appendages. Anther head cylindrical, immediately subtended by or (in *C. Blodgettii*) seemingly (by adnation) separated from base of inner corona; anther wing slots directed outward. Anthers each with an apical, hyaline flap erect to arching over style-stigma head, unappendaged abaxially. Style-stigma head short-cylindric, with flat, conical, or bilobed apex. Corpuscula exceeded by anther head; translator arms subhorizontal; pollinia pendulous, completely fertile. Fruits follicular, 1 or sometimes 2 from each flower (the pair, when present, from single flower usually divergent less than 90°), narrowly fusiform to fusiform-ovoid, acute to attenuate-caudate apically, dehiscent along adaxial suture, erect on erect pedicels or pendulous on pendulous ones; surface smooth (or reportedly sometimes in *C. laeve*) winged longitudinally, with various degrees of non-glandular pubescence. Seeds many, ovate-lenticular, each with a tuft of trichomes at apex; seed-coat surface usually smooth, lateral wings entire or remotely crenate. (Including, among others, *Ampelamus* Raf., 1819; *Amphistelma* Griseb., 1861, at least in part; *Epicion* Small, 1933; *Enslenia* Nutt., 1818, at least in part; *Enslinia* Reichenb., 1828, at least in part; *Gonolobus* Michx., 1803, in part; *Lyonia* Ell. non Nutt., of the Ericaceae, 1821; *Mellichampia* Gray, 1887; *Metalepis* Griseb., 1866; *Metastelma* R. Br., [preprinted 1810] 1811, at least in part; *Roulinia* Dcne., 1844; *Rouliniella* Vail, 1902; and *Tylodontia* Griseb., 1866.) LECTOTYPE SPECIES: *C. acutum* L.; see Meyer, Comment. Pl. Afr. Austral. 216. 1837 [1838]. (Name from Greek, *kynos,* dog, and *ancho,* to strangle or lace up, perhaps in reference to the similarity of the plants in morphology and in use to those of *Apocynum,* and possibly to their usually lianous habits, as well.)—VINE MILKWEED, SAND VINE.

Considered here in the broad sense, *Cynanchum* comprises 200 or more species (Spellman, 1975b) in tropical and to lesser extents temperate regions throughout the world. As with some of our other genera of Asclepiadaceae, *Cynanchum* owes its large size mainly to the taxonomic reorganization of the family by Woodson. Small (1933) had placed our five species, all indigenous in the Southeast, in five separate genera, the names of which comprise only a minority of those now generally considered to be synonymous with *Cynanchum.*

As originally proposed by Linnaeus, *Cynanchum* included five species. Only one or, depending on taxonomic interpretation, two of these were retained in the genus by Brown, who nevertheless included a total of 15 species in six unnamed "sections" that he thought would eventually be accepted as genera. Indeed, genera were subsequently proposed for many of Brown's "sections," as well as for other plants now generally thought to be congeneric. The consolidation of these genera appears to have begun with Schumann, who in reverting to a system more in line with Brown's, included under *Cynanchum* 11 generic synonyms (and over 100 species) that had been in use for plants throughout the world. Woodson listed two of these genera plus 21 other generic synonyms for plants in North and Central America and stated that several more eventually would be added for species in South America.

It is difficult to know how Schumann's concept of *Cynanchum,* which he assigned to subtribe Cynanchinae of tribe Asclepiadeae, compares to the one employed here. Only one of our species, *C. laeve* (Michx.) Pers., was actually mentioned in his treatment of the family, and it was included (as *Enslenia albida* Nutt.) in a different subtribe of the Asclepiadeae, the Asclepiadinae. (For this reason and others, these subtribes are not recognized here; see family discussion.) Some of our other species were included, for example, by Small (1933), in genera also separated from *Cynanchum* by Schumann: *C. Blodgettii* (Gray) Shinners was placed in *Metastelma* R. Br., and *C. scoparium* Nutt. was included in *Amphistelma* Griseb.; Schumann included *Amphistelma* in *Metastelma,* which he placed with *Enslenia* in the Asclepiadinae. Small (1933) included *C. angustifolium* Pers. (as *C. palustre* (Pursh) Heller) in *Lyonia* Ell. (non Nutt.), which was ignored by Schumann, and *C. Northropiae* (Schlechter) Alain in the newly proposed *Epicion* Small. Schumann recognized two sections in *Cynanchum*: *Cynoctonum* (E. Meyer) K. Schum. (= sect. *Cynanchum*), with completely to nearly completely fused corona segments, and *Vincetoxicum* (Moench) K. Schum., with basally fused to almost entirely free corona segments.

Woodson based six subgenera on characters of the inflorescence, corolla, and corona. However, the subgenera are difficult to interpret because of the existence of specimens assignable to the genus that are not accommodated by the key (see below), and because only a few representative species were listed for each. The inflorescences were said to be umbelliform in subg. *Metastelma* (R. Br.) Woodson (corolla lobes ascending or spreading) and subg. "Cleistolobus"[30] (corolla lobes inflexed and hoodlike) but racemiform to corymbiform in the other four. The corollas were reported to be urceolate in one of these, subg. *Tylodontia* (Griseb.) Woodson, and campanulate to rotate-subcampanulate in the other three. The segments of the corona were said to be broad, mostly connate, and emarginate in subg. *Metalepis* (Griseb.) Woodson, but elongate and free or only basally united in the other two. They were indicated as being acuminate and entire or with some very obscure lateral lobes in subg. *Mellichampia* (Gray) Woodson, but deeply bifid (i.e., with two long, linear lobes apically) in subg. *Ampelamus* (Raf.) Woodson.

As defined by Sundell (p. 11), subg. *Mellichampia* comprised 11 New World species and included as three (of four) sections "elements from three of Woodson's (1941) subgenera," subg. *Ampelamus,* subg. *Mellichampia,* and subg. *Metalepis.*[31] Sundell described the subgenus as having an inner corona of five segments united basally into a short tube. However, it is difficult to evaluate the group because of the inclusion of plants that do not fit this description and the exclusion of others that do (see below).

Five species of *Cynanchum,* some of which appear not to be accommodated by any of the relevant treatments outlined above, occur in the southeastern United States. *Cynanchum laeve* (*Gonolobus laevis* Michx., *Enslenia albida* Nutt., *Ampelamus albidus* (Nutt.) Britton) is readily (and, among our species,

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[30] The name of this subgenus was not validly published by Woodson, since it was accompanied in 1941 neither by a Latin description or diagnosis nor by a reference to a previously and effectively published Latin description or diagnosis (i.e., it was not published in accordance with Art. 36.1 [ICBN, 1988], the effective date of which is January 1935). Therefore, it is enclosed in quotation marks here.

[31] Sundell was evidently the first to unite these three subgenera of Woodson (the names of which were published simultaneously), so the name he chose has priority.

uniquely) placed in Woodson's subg. *Ampelamus* by virtue of its racemiform inflorescences and deeply bifid corona segments. It was included in Sundell's subg. *Mellichampia* despite its entirely free corona segments, although because of this fact it was isolated in the monotypic sect. *Ampelamus* (Raf.) Sundell. (None of our other species was mentioned by Sundell.) *Cynanchum laeve* is unique among our representatives of the genus in having cordate leaves. (*Sarcostemma cynanchoides* Dcne., which enters our area in Arkansas and which is sometimes confused with *C. laeve,* has narrower cordate leaves.) It is found in alluvial thickets and old fields, as well as along stream banks and roadsides, from Pennsylvania to Kansas and generally southward to the Florida Panhandle and central Texas.

Cynanchum scoparium (*Amphistelma scoparia* (Nutt.) Small) has shallowly lobed coronas and would appear to belong to subg. *Metalepis* sensu Woodson. However, the lobes are not emarginate and the inflorescences are sometimes umbellate, so it is unclear to which subgenus in Woodson's system it belongs. On the basis of its basally connate corona segments, the species might also appear to belong to subg. *Mellichampia* sensu Sundell, and presumably to sect. *Metalepis* (Griseb.) Sundell. However, *C. scoparium* lacks the stipitate anther heads (they are sessile) that in part characterize this section, and the species was not treated by Sundell. In addition to its sometimes umbellate inflorescences and basally connate corona segments, *C. scoparium* is unique among our species of *Cynanchum* in several ways: the leaves (which are linear-lanceolate to linear but nevertheless petiolate) are deciduous relatively early, so the plants are often leafless or nearly so; the calyx lobes are obtuse (vs. acute); and the lobes of the corona do not exceed the anther head. *Cynanchum scoparium* is known from hammocks and pinelands in Beaufort County, South Carolina, and in central and southern Florida.

Cynanchum Northropiae (*Metastelma Northropiae* Schlechter; *Epicion Northropiae* (Schlechter) Small) is the only one of our species that can be placed in subg. *Mellichampia* sensu Woodson—an assignment primarily due to its racemose inflorescences. Its corona structure, however, suggests that it is more closely related to species in Texas and Mexico that, on the basis of umbellate inflorescences and ascending or spreading corolla lobes, are assignable in Woodson's system to subg. *Metastelma* (see Henrickson). In addition, the species has ovate to elliptic leaves with mucronate or acuminate (rarely emarginate) apices; corollas united in the basal third, with lobes that are densely pubescent adaxially; and clearly stipitate coronas, with segments that are distinct (and free from the corolla), narrowly lanceolate, radially (i.e., laterally) compressed, and adaxially grooved. The species is known from hammocks, pinelands, and cut-over lands in southern Florida, including the Keys, and in the West Indies.

Two of our species are assignable to subg. *Metastelma,* although on the basis of corona structure they appear to be related neither to *Cynanchum Northropiae* nor to the species in Texas and Mexico discussed above. *Cynanchum Blodgettii* (*Metastelma Blodgettii* Gray) has linear-lanceolate to linear leaves with acute and/or sometimes mucronate apices; corollas united in the basal third (or less) and urceolate (a condition partially characterizing subg. *Tylodontia*), with lobes densely pubescent adaxially (sometimes only near the apex); and sessile coronas with lanceolate segments distinct from one another but basally adnate to the corolla and tangentially (i.e., dorsiventrally) compressed. The plants grow in hammocks and in rocky or sandy soil in pine and pine-palm woods in southern Florida, including the Keys. Although the species was reported from southern Texas by Small (1933), it was not treated by Correll & Johnston, and I have seen no specimens from the state.

Cynanchum angustifolium (*C. palustre* (Pursh) Heller; *Lyonia palustris* (Pursh) Small) is also assignable to subg. *Metastelma*. The leaves are linear with acute apices, but they are sessile and usually reflexed as well, two conditions not evident in our other species. In addition, *C. angustifolium* has glabrous, rotate-campanulate corollas divided nearly to the base, and stipitate to substipitate coronas with ovate to elliptic, distinct segments that are obtuse, retuse, or emarginate. The plants occur in coastal marshes with saline or brackish water and in sandy (probably moist) or marly soil of adjacent hammocks and dunes from North Carolina to southern Florida, including the Keys, and from there to Texas.

Several species of *Cynanchum*, including *C. laeve* (Bailey *et al.*), are cultivated in North America.

Standley & Williams's comment that *Cynanchum* in North America would be a good subject for dissertation research appears still to be true.

REFERENCES:

Under references for the Apocynineae, see BAILEY *et al.*; BROWN; CORRELL & JOHNSTON; SCHUMANN; SMALL, 1933; and STANDLEY & WILLIAMS.

Under references for the Asclepiadaceae, see SPELLMAN, 1975b; and WOODSON.

HENRICKSON, J. Notes on *Cynanchum* (Asclepiadaceae). Sida **12:** 91–99. 1987. [Three species in Texas and northern Mexico evidently do not enter the Southeast but appear to be related to *C. Northropiae*; very helpful illustrations.]

SUNDELL, E. The New World species of *Cynanchum* L. subgenus *Mellichampia* (A. Gray ex Wats.) Woods. (Asclepiadaceae). Evol. Monogr. **5:** 1–63. 1981.

5. **Sarcostemma** R. Brown, Mem. Wernerian Soc. **1:** 50. 1811.

Terrestrial (often in xeric habitats) to aquatic (sometimes rooted in standing fresh, brackish, or salt water), scandent and/or twining, perennial herbs (usually woody toward base) or suberect to prostrate subshrubs [or erect succulents] with white latex; axes and leaves glabrous or with various degrees of nonglandular pubescence [or sometimes glaucous]. Leaves opposite, sometimes caducous and the plants leafless or nearly so; blades ovate, elliptic, lanceolate, linear, or filiform [or scalelike], apices acute, acuminate, or mucronate, margins often revolute, bases attenuate, truncate, obtuse, or cordate [or hastate]; petioles distinct, without lateral appendages, bases and/or adjacent areas of stems usually with colleters. Inflorescences pedunculate [or sessile], few- to many-flowered, cymose but appearing umbellate [or racemose or corymbose], rarely with both flowers and pedicel scars present, bracteate; pedicels longer than calyces, ebracteolate. Calyx about ⅓ as long as corolla or less, free nearly to base, usually with nonglandular pubescence abaxially, glabrous adaxially; lobes acute, bases variously imbricate, with (or, reportedly, sometimes without) minute squamellae. Corolla much shorter than leaves, free nearly to base to united throughout the basal ⅓, subrotate or subcampanulate [or sometimes campanulate or salverform], glabrous or with nonglandular pubescence abaxially, mostly glabrous adaxially; lobes valvate or variously imbricate, spreading [to nearly erect] basally, ascending, spreading, or reflexed apically. Outer corona [rarely absent] discoid, membranaceous or fleshy, mostly entire, basally adnate to corolla tube but apically free, forming an erect or ascending annulus. Inner corona exceeding to sometimes exceeded by anther head, substipitate or sessile, composed of distinct, mostly erect segments, each basally free from or (at least in *S. clausum*) adnate to annulus; segments 5, fleshy, vesicular, ovoid [or nearly spheroid]. Anther head cylindrical, immediately subtended by base of inner corona; anther wing slots directed outward. Anthers each with an apical, hyaline flap inflexed over style-stigma head, unappendaged abaxially. Style-stigma head short-cylindric, with flat, bilobed, or umbonate apex. Corpuscula partially exserted from anther head; translator arms arching downward; pollinia pendulous, completely fertile. Fruits follicular, 1 or sometimes [in some species, usually] 2 from each flower (the pair, when present, from single flower usually divergent less than 90° [to about 180°]), lance-ovoid, narrowly fusiform to fusiform-ovoid [or obclavate], acute to attenuate apically, dehiscent along adaxial suture, erect on erect pedicels to pendulous on pendulous ones; surface shallowly striate longitudinally, with various degrees of nonglandular pubescence. Seeds many, ovate-lenticular, each with a tuft of trichomes at apex; seed-coat surface rugose and/or papillate, lateral wings (at least in *S. clausum*) coarsely serrate. (Including *Ceramanthus* (Kunze) Malme, 1905; *Funastrum* Fourn., 1882; *Oxystelma* R. Br., 1809; *Philibertella* Vail, 1897; and *Philibertia* HBK., 1819.) LECTOTYPE SPECIES: *S. viminale* (L.) R. Br. (*Euphorbia viminalis* L.); see Holm, Ann. Missouri Bot. Gard. **37**: 506. 1950. (Name from Greek, *sarkos,* flesh, and *stemmatos,* crown or wreath, probably in reference to the fleshy (and inflated) segments of the corona.)—MILK WITHE.

Considered here in the broadest sense, *Sarcostemma* is a genus of approximately 34 species, 22 in the New World (Holm) and about 12 in an area from Africa to Australia (Huber). There has been a great deal of confusion regarding *Sarcostemma* and several other genera with which it is here combined. Much of this has had to do with imprecise and/or inadequate treatment of the plants involved, shortcomings that are best appreciated by a brief consideration of their taxonomic history.

According to Holm, the most recent monographer of the genus, *Sarcostemma* originally included only succulent-stemmed, scale-leaved lianas of Asia and Africa with rotate corollas and both outer and inner coronas, the outer annular and the inner with five separate, inflated segments. In fact, however, in the protologue of *Sarcostemma,* Brown said nothing about succulence; indicated that the stems were without leaves (although he was probably referring to plants with scale-leaves) or that the leaves were far apart ("foliis . . . distantibus"); reported the genus from eastern India, Africa, and Australia, as well as New Caledonia; and did not address the issue of inflation of the inner corona segments (he and many authors have referred merely to the fleshiness of the segments). Evidently, the summary provided by Holm was based on consideration of the species mentioned by Brown as they are now understood and/or on information that has come to light subsequently; generally, the same approach seems to have been taken in the remainder of his account. In addition to *Sarcostemma,* Brown also established *Oxystelma* R. Br. for plants of eastern India and possibly Australia with laminate foliage, rotate corollas, and single (i.e., only inner) coronas, without addressing the subject of corona-segment inflation.

From populations in the New World, Kunth (in Humboldt *et al.*) included in *Sarcostemma* some with lanceolate—albeit membranaceous—leaves and rotate corollas, and he erected *Philibertia* HBK. for others with cordate leaves and partly described with the phrase "corolla urceolato- (campanulato-?) rotata," without addressing corona-segment inflation for either. Decaisne later described the corollas of *Sarcostemma solanoides* (HBK.) Dcne. (*Philibertia solanoides* HBK.), the only species included in *Philibertia* by Kunth, with the word "pelviformi" (i.e., basin or saucer shaped), which would seem to lie somewhere between rotate and campanulate.

Decaisne adopted a broad view of *Sarcostemma,* in which he recognized two sections. Section *Eusarcostemma* (= sect. *Sarcostemma*) included plants with rotate corollas and was divided into three unnamed groups, one comprising Old World species with scale-leaves ("aphylla" presumably in the sense that the foliage is not laminate), another of New World plants with linear to linear-lanceolate leaves (including *S. clausum* (Jacq.) Schultes, one of our two species), and a third of New World species with cordate leaves and deeply divided (but nevertheless rotate) corollas (including *S. cynanchoides* Dcne., the other of our two species). Section PHILIBERTIA (HBK.) Dcne. included New World species with cordate leaves and urceolate-rotate (possibly campanulate in the sense of others) corollas.

Despite employing a broad concept of *Sarcostemma,* Decaisne continued to recognize *Oxystelma* R. Br., in which he included Old World species with rotate corollas, as distinct. His description of *Oxystelma* differed significantly from Brown's account of the genus in at least two respects. Decaisne referred to an annulus on the corolla tube ("fauce annulo . . ."), that is, an outer, annular corona as now interpreted, and described the segments of the (inner) corona, possibly for the first time, as being at least partially inflated. Even so, Decaisne did not mention this character state for *Sarcostemma,* even though he included in the latter our two species, each of which has inner corona segments that are clearly inflated.

Bentham (in Bentham & Hooker) included in *Sarcostemma* plants from Africa, Asia, and Australia with succulent stems, scalelike leaves (again, stems were said to be leafless), subrotate corollas, and at least sometimes subsaccate (i.e., somewhat inflated) inner-corona segments. For reasons that are not entirely clear, he referred all of the New World species in question to *Philibertia,* which he described as having very widely campanulate to subrotate corollas and, at least occasionally, saccate segments of the inner corona. Significantly, he also noted an affinity between *Sarcostemma* and *Oxystelma,* and between *Oxystelma* and *Philibertia*; in fact, his descriptions of the last two genera were very similar. However, although no such terms were applied to *Oxystelma,* he indicated that the inner corona segments were at least sometimes saccate in *Philibertia.* (He also noted other differences in the segments.)

Fournier adopted very narrow generic concepts in establishing the New World genus *Funastrum* Fourn., which was described in part as having fleshy, vesicular corona segments; neither corolla shape nor the presence or absence of an outer corona was specified. Of the two species included, one actually belongs in *Cynanchum* L. according to Holm, while the other, *F. angustissimum* (Andersson) Fourn. (*Asclepias angustissima* Andersson, = *Sarcostemma angustissimum* (Andersson) R. Holm), of the Galapagos Islands, was indicated as having axillary umbels. Nevertheless, Holm (p. 535) reported that it is the only species of *Sarcostemma* with a "truly terminal inflorescence" (i.e., one that is not overtopped by sympodial growth; he actually considered the inflorescence to be terminal throughout the family), and on this basis he assigned it to the monotypic ser. ANGUSTISSIMA R. Holm.

Schumann also employed rather narrow generic concepts, maintaining in *Sarcostemma* only Old World species with prostrate or twining, succulent stems, scale-leaves (his "blattlose Sträucher"), and rotate corollas. He divided the genus into a sect. *Eusarcostemma* (= sect. *Sarcostemma*), with both outer and inner coronas (the former annular and, surprisingly, five- to ten-lobed; the latter sometimes partially vesicular), and a monotypic sect. *Sarcocyphula* (Harvey) K. Schum., with only an outer one.

Oxystelma and *Philibertia* were two other genera recognized by Schumann. The former included species in both Eastern and Western hemispheres, while the latter was used only for plants in the New World. Although the descriptions of the two genera were essentially identical (e.g., each was described as having twining, presumably nonsucculent stems; laminate foliage; rotate or campanulate corollas; and both outer and inner coronas, the former annular and the latter with vesicular segments), the key indicated that corollas were campanulate in *Oxystelma* and rotate in *Philibertia.* Schumann accepted *Funastrum* in exactly the same sense as Fournier had proposed it; that is, as including the same two South American species. According to Schumann, these are twining subshrubs with (presumably) nonsucculent stems, linear basal and scalelike upper leaves, rotate corollas, no outer coronas, and inner coronas with vesicular segments. It is surprising and often regarded as one of many unsatisfactory aspects of Schumann's classification that, within the Asclepiadeae, *Sarcostemma* and *Funastrum* were placed in two separate subtribes, while *Oxystelma* and *Philibertia* were included in a third.

Vail proposed *Philibertella* for the same American plants that had constituted *Philibertia* in Schumann's system, evidently because she felt the plants did not adequately match Kunth's (in Humboldt *et al.*) description of *Philibertia* and because the only species Kunth had included in the genus was generally placed by that time in *Oxystelma.* Nevertheless, she indicated that corollas in *Philibertella* were either campanulate or rotate, so the distinction she attempted to make remains unclear.

Kunze established subg. CERAMANTHUS Kunze for New World members of *Sarcostemma* with urceolate corollas. Malme used the same name in elevating the group to generic status, even though it is at that rank a later homonym for a genus of Euphorbiaceae (i.e., *Ceramanthus* Hassk.) and several other generic names were available for the taxon that he envisioned (i.e., he included *Funastrum, Philibertella, Philibertia,* and others as synonyms).

Schlechter concluded that the New World species in question should be separated at the generic level and therefore resurrected *Funastrum* and *Philibertia.* Among other differences, *Funastrum* was indicated to have (compared to *Philibertia*) more rotate (vs. more campanulate) corollas, stipitate (vs. sessile or substipitate) anther heads (i.e., anther heads held above vs. immediately or nearly immediately subtended by inner coronas), and entire (vs. two-cleft) style-stigma head apices.

Following Decaisne in taking a broad view of *Sarcostemma,* Woodson united within it *Funastrum, Philibertia,* and others; *Oxystelma* was ignored because he was treating only New World plants. Although Holm formally treated only New World taxa in his revision, he adopted an even broader generic concept in adding *Oxystelma* to the taxa that had been included in *Sarcostemma* by both Decaisne and Woodson. Unlike Woodson, who did not subdivide the genus, Holm recognized three subgenera, one with three sections and another with five series. In view of the discussion above, his treatment seems most tenable and therefore is followed here.

Subgenus *Eusarcostemma* (Dcne.) R. Holm (= subg. SARCOSTEMMA), although based on sect. *Eusarcostemma* Dcne. (26 species, in both Eastern and Western hemispheres), was restricted to those species from Africa to Australia with succulent stems and scalelike leaves (i.e., the genus as originally delimited). Although the species included in this subgenus were not listed by Holm, the key indicated that the group was also characterized by rotate-subcampanulate corollas; an annular outer corona adnate to the filaments; and ovoid, vesicular (i.e., inflated) inner-corona segments.

The two other subgenera recognized by Holm included plants with nonsucculent stems and laminate foliage. Subgenus OXYSTELMA (R. Br.) R. Holm was characterized by campanulate corollas; an annular outer corona either adnate to the corolla or more or less obsolete; and variously ovoid or spheroid, vesicular inner-corona segments. It included sect. EUOXYSTELMA R. Holm (*Oxystelma* sensu Brown), with a single species in Africa and Asia, as well as sect. PENTACYPHUS (Schlechter) R. Holm (*Pentacyphus* sensu Schlechter) and sect. PHILIBERTIA (HBK.) Dcne. (*Philibertia* sensu Kunth), with two and six species, respectively, in South America.

Subgenus CERAMANTHUS Kunze (*Ceramanthus* (Kunze) Malme), comprising 14 New World species, corresponded to *Philibertia* as conceived by Bentham (i.e., the plants were said to have rotate-subcampanulate or salverform [rotate, as interpreted earlier] corollas), *Funastrum* of Fournier, and *Philibertella* of

Vail. It was otherwise indicated to have an annular outer corona (absent in one species) free from the corolla, and variously ovoid or spheroid, vesicular inner-corona segments. My observations of *Sarcostemma clausum* (Jacq.) Schultes and *S. cynanchoides* (discussed more fully below) indicate that in each the outer corona is adnate to the summit of the corolla tube. Near the apex it is sufficiently free from the corolla to form an annulus, which is fused with the bases of the inner-corona segments in *S. clausum* but free from them in *S. cynanchoides.* Subgenus CERAMANTHUS was divided into five series. One of these, ser. FLAVA R. Holm, included only a single, South American species with flowers lacking an outer corona. The other four differed primarily in characters of the inflorescence.

Two series of subg. CERAMANTHUS are represented in the southeastern United States, each by a single species. Series CLAUSA R. Holm (peduncles usually as thick as or thicker than subtending internodes, or lacking; when lacking, and sometimes otherwise, leaf bases obtuse to cuneate) included *Sarcostemma clausum* (leaves often caducous, elliptic to ovate). An extremely variable species (Holm listed nearly 60 synonyms, in six genera), *S. clausum* is found mostly in savannas or sandy areas in Mexico and northwestern South America but sometimes on wooded slopes, on floodplains, or rooted in standing water in Florida, the Greater Antilles, Central America, and eastern South America (Holm). The only other species in the series, *S. glaucum* HBK. of Panama, Colombia, and Venezuela, has salverform corollas with constricted tubes (vs. rotate-subcampanulate corollas with unconstricted tubes), and the plants are glaucous (vs. at least somewhat pubescent) throughout.

Series CYNANCHOIDES R. Holm (peduncles not as thick as subtending internodes, or lacking; when lacking, and sometimes otherwise, leaf bases cordate) included *Sarcostemma cynanchoides,* represented in our area, and eight other species distributed from the southwestern United States to central Argentina. Although in material I have seen from the Southeast the peduncle is often thinner than the subtending internode in *S. clausum* (in contrast to the usual condition in ser. CLAUSA), it is relatively even narrower in *S. cynanchoides.* Among specimens I have examined, the outer corona annulus is fused to the bases of the inner-corona segments in *S. clausum,* while these structures are free in *S. cynanchoides.*

Two subspecies were recognized in *Sarcostemma cynanchoides* by Holm. Subspecies *cynanchoides* was said to differ from subsp. *Hartwegii* (Vail) R. Holm in its broadly (vs. narrowly) lanceolate leaves with cordate or rarely truncate (vs. hastate or rarely truncate or obtuse) bases. Subspecies *cynanchoides* was indicated by Holm to grow in sandy soils of rivers and ditches and in rocky canyons from southern Arizona to the central parts of Oklahoma and Texas, as well as in adjacent parts of Mexico, and it has since been observed to enter our area in Arkansas. Smith indicated it for Franklin, Izard, and perhaps Pope counties, and I have seen a specimen (*Thomas & Reid 20640,* GH) from cliffs near the White River in Izard County that is assignable to this subspecies but misidentified as *Cynanchum laeve.* Subspecies *Hartwegii* occurs in more xeric habitats (e.g., dry, sandy, or rocky soils of arroyos and plains) and is distributed farther south and west, to central Mexico and southern California.

Sarcostemma cynanchoides subsp. *cynanchoides* begins to flower nearly two months later than subsp. *Hartwegii* (Holm). Nevertheless, putative hybrids have been found in the area of geographic overlap between the two, mostly along the border between the United States and Mexico, from Arizona to western Texas. The low number of such hybrids might be related to the fact that the species is poorly collected in that area.

As defined here, *Sarcostemma* is most closely related to *Cynanchum* and *Blepharodon* Dcne. The latter includes about nine species and, according to Woodson, is perhaps divisible into a North American group of twining plants and a South American assemblage of erect, herbaceous ones. *Blepharodon* was considered to be in part intermediate in corona structure between *Cynanchum* and *Sarcostemma* by Holm (p. 504), who stated, without mentioning the groups proposed by Woodson, that the genus is divisible into one group with corona segments consisting of "two radially arranged, laminate lobes partially fused by their margins" and another in which such segments are "semi-vesicular." The flowers of *Blepharodon* and *Cynanchum* lack the outer (annular) corona characterizing *Sarcostemma,* although according to Holm they sometimes have structures that might be mistaken for one.

Despite the foregoing, the annular outer corona and the five inflated segments of the inner corona of the African and Asian genus *Pergularia* L. were considered by Holm to represent only superficial resemblances to *Sarcostemma.* Among other differences, *Pergularia* supposedly has a five-lobed, denticulate (vs. entire; however, see Schumann) outer corona and spurred (vs. not spurred) inner-corona segments.

The strong, flexible stems of *Sarcostemma clausum* (subg. CERAMANTHUS) are used in Guatemala for stringing fish and as a substitute for twine (Standley & Williams). Holm remarked that species of sect. PHILIBERTIA *sensu* Holm were often grown in English greenhouses during the nineteenth century and that those belonging to subg. SARCOSTEMMA *sensu* Holm are still commonly cultivated; in the latter group is *S. viminale,* which is sometimes sold as "*Euphorbia pendula*" (Bailey *et al.*).

REFERENCES:

Under references for the Apocynineae, see BAILEY *et al.*; BENTHAM & HOOKER; BROWN; DECAISNE; HUBER; HUMBOLDT *et al.*; SCHUMANN; SMITH; and STANDLEY & WILLIAMS.

Under references for the Asclepiadaceae, see FOURNIER and WOODSON.

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6. **Asclepias** Linnaeus, Sp. Pl. **1**: 214. 1753; Gen. Pl. ed. 5. 102. 1754.

Terrestrial to semiaquatic (sometimes in brackish water), erect, perennial (or the introduced *A. curassavica*[32] [and perhaps 2 other species] annual) herbs [or small shrubs] with white latex (only *A. longifolia* and *A. tuberosa* without latex); axes and leaves glabrous or with various degrees of nonglandular pubescence. Leaves usually decussate, less often irregularly alternate and/or subwhorled (whorled, usually in 4's, at node subtending inflorescence in *A. quadrifolia*); blades ovate, elliptic, lanceolate, linear, or filiform, apices acute, sometimes rounded, infrequently emarginate, sometimes mucronate, margins often revolute, bases attenuate, truncate, hastate, cordate, or auriculate; petioles sometimes very short and/or indistinct (especially when leaves linear or filiform), without lateral appendages, bases and/or adjacent areas of stems sometimes with a few small colleters. Inflorescences pedunculate, few- to many- [rarely single-]flowered, cymose but usually appearing umbellate, bracteate or rarely ebracteate; pedicels longer than calyces, ebracteolate. Calyx about ½ as long as corolla but usually much less, free nearly to base, glabrous or with various degrees of nonglandular pubescence abaxially, glabrous adaxially; lobes usually acute, bases sometimes slightly imbricate, usually with minute squamellae. Corolla much shorter than leaves, free nearly to base, essentially rotate (but see below), mostly glabrous abaxially and adaxially; lobes variously imbricate or sometimes valvate, reflexed or spreading proximally but reflexed or sometimes spreading or ascending (erect only in *A. pedicellata*) distally (when reflexed or spreading distally, often ascending apically). Outer corona absent. Inner corona exceeding to exceeded by anther head, stipitate to substipitate or sometimes sessile, composed of distinct, essentially erect or ascending (then sometimes basally deflexed) hoods (i.e., segments), each basally free from (but sometimes in contact with) corolla; lobules (i.e., small, erect, bifid or less often entire appendages) alternating with hood bases; hoods 5, fleshy, conduplicate (and therefore vessel- or tubelike), each open apically (openings not appressed against anther head) and exceeding to usually exceeded by horns (i.e., exserted, elongate, terete or laterally flattened, adaxially adnate appendages originating within hoods), or sometimes (in subg. ASCLEPIAS, subg. ASCLEPIODELLA) exceeding crests (i.e., nonexserted, ridgelike, rounded, adaxially adnate appendages originating within hoods), or less often (in subg. POLYOTUS) apparently unappendaged within, or (in *A. pedicellata*) each apically opened (openings not

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[32] This and epithets for many other species in the genus customarily have been given the feminine form, even though *Asclepias* would appear to be masculine and, in fact, was indicated as such by Stearn (Bot. Latin, 306. 1966). Nevertheless, as indicated by nearly all of the epithets appearing in *Species Plantarum* (1753), Linnaeus treated it as feminine. According to Art. 76.1 (ICBN, 1988), "a generic name retains the gender assigned by its author, unless this is contrary to botanical tradition," which, according to Note 1, "usually maintains the classical gender of a Greek or Latin word, when this was well established." The first example under this recommendation included names (other than *Asclepias*) "for which botanical usage has reestablished the classical gender despite another choice by Linnaeus." Therefore, it appears that if *Asclepias* is masculine according to "botanical tradition," Linnaeus should probably be overruled and the name should be treated as masculine.

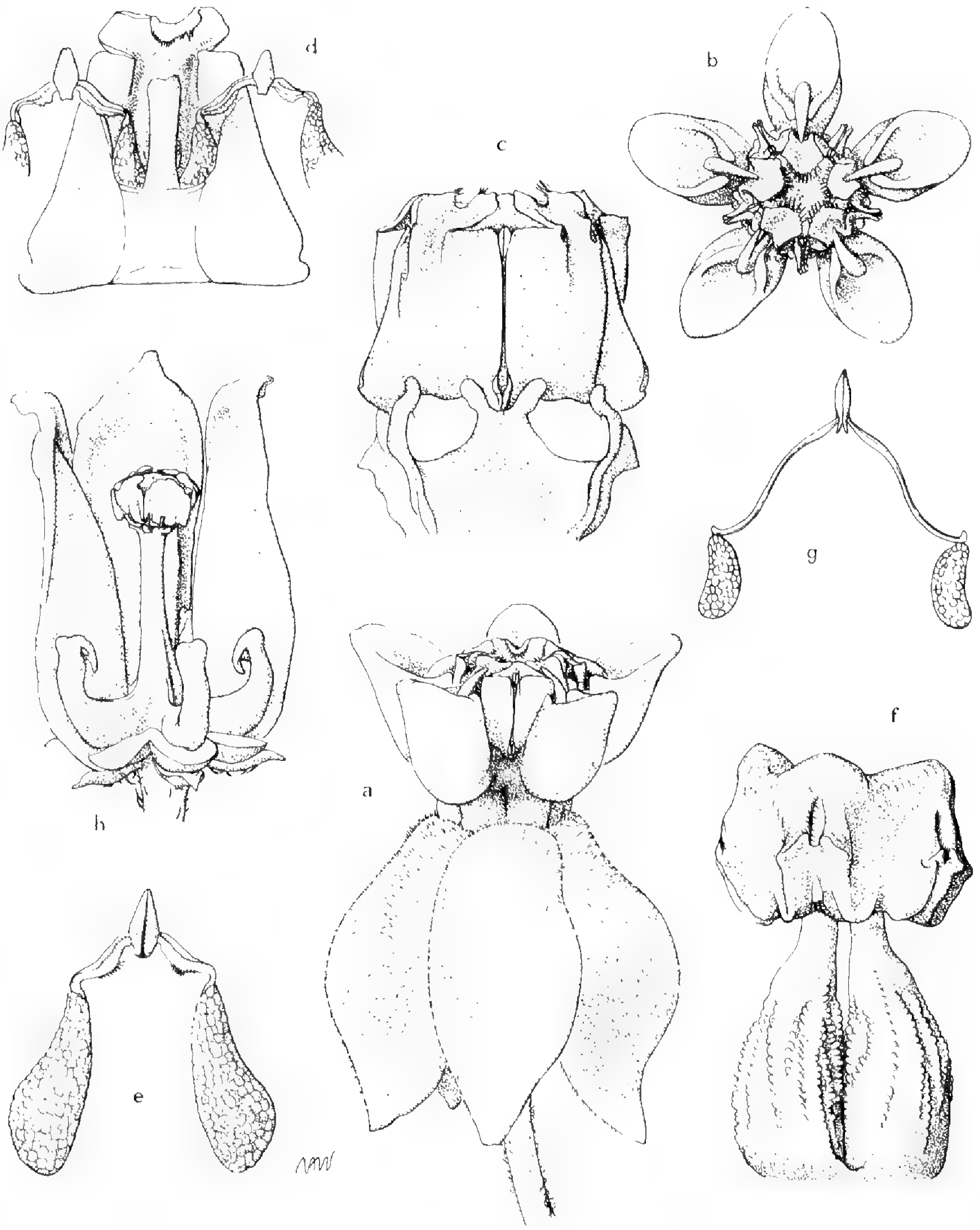

FIGURE 8. **Asclepias.** a–f, *A. syriaca*: a, flower (corolla lobes reflexed; corona stipitate [but saccate hoods partly concealing column]; hoods open at apex [openings not appressed against anther head] and here slightly exceeding exserted horns and anther head, abaxial surfaces exceeding those adjacent to anther head and not recurved apically, margins auriculate; anther head [excluding wings and terminal flaps] shorter than broad, immediately subtended by hoods; corpusculum at summit of outwardly projecting slot between wings of adjacent anthers), × 5; b, flower, from above (hoods, with horns, opposite terminal, hyaline anther flaps over style-stigma head, alternating with corpuscula and outwardly projecting slots of adjacent anthers), × 5; c, androecium (and, within, gynoecium) distal to level of adnation to corolla, with hoods removed (1 bifid lobule of corona flanked by 2 others; 1 outwardly projecting slot flanked by 2 others; 1 corpusculum; 1 hyaline flap terminating each of 2 anthers), × 12; d, anther, adaxial side, with 2 pollinia (partly concealed) each connected by a translator arm, a corpusculum (surface not grooved),

appressed against anther head) but inwardly geniculate (and the openings therefore concealed) and apparently unappendaged within, or (in subg. ACERATES) each apically opened (openings appressed against anther head) and exceeding crests or apparently unappendaged within, or (in subg. ANANTHERIX, subg. ASCLEPIODORA) each apically enclosed (by conduplication) and apparently unappendaged within. Anther head cylindrical, immediately subtended by or (in *A. pedicellata*) held well above and separated by a long stipe from base of inner corona; anther wing slots directed outward. Anthers each with an apical, hyaline flap inflexed over style-stigma head, unappendaged abaxially. Style-stigma head cylindrical, with flat or depressed apex. Corpuscula partially exserted from anther head; translator arms arching downward; pollinia pendulous, completely fertile. Fruits follicular, 1 or very rarely 2 from each flower (the pair, when present, from single flower usually divergent less than 90°), narrowly fusiform to infrequently fusiform-ovoid or broadly ovoid, acute to attenuate-caudate apically, dehiscent along adaxial suture, erect on deflexed pedicels (the latter therefore S-shaped) or less frequently erect on erect ones (pendulous on pendulous pedicels in *A. perennis*); surface smooth or with elongate tubercles [or spines], nearly glabrous to rarely with dense nonglandular pubescence. Seeds many, ovate-lenticular, each with (or without, in *A. perennis*) a tuft of trichomes at apex; seed-coat surface usually smooth, lateral wings usually entire and more or less flat, sometimes crenate and/or undulate. (Including *Acerates* Ell., 1817; *Anantherix* Nutt., 1818; *Asclepiodella* Small, 1933; *Asclepiodora* Gray, 1877; *Biventraria* Small, 1933; *Oxypterix* Greene, 1897; *Podostemma* Greene, 1897; and *Podostigma* Ell., 1817. Excluding *Gomphocarpus* R. Br., [preprinted 1810] 1811; *Schizoglossum* E. Meyer, 1838; and *Xysmalobium* R. Br., [preprinted 1810] 1811.) LECTOTYPE SPECIES: *A. syriaca* L.; see Hitchcock & Greene, Prop. Brit. Bot. 136. 1929. (According to Linnaeus [Critica Botanica, p. 76, 1737; p. 60 in A. Hort, English translation, 1938], named for the physician Aesculapius; *Asclepias* listed by Linnaeus [Critica Botanica, p. 102, 1737; p. 83 in A. Hort, English translation, 1938] as an ancient Greek name, but later [Philosophia Botanica, p. 141, 1751] as a name provided by Tournefort; according to Morse, 1985b, named for Asclepios, the Greek god of healing.)—MILKWEED.

Considered here in neither the broadest nor the narrowest of senses, *Asclepias* includes more than 100 North and Central American as well as "less than a dozen poorly differentiated" southeastern South American species (Woodson, 1954, p. 28).

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and another translator arm to 1 pollinium (partly drawn) from adjacent anther, × 12; e, pollinarium, abaxial side (1 pollinium from each of 2 adjacent anthers, 2 translator arms, and 1 corpusculum with surface grooved for attachment to insects; pollinia and translator arms oriented as in intact anther, × 16; f, gynoecium, with androecium removed (the 2 carpels mostly free in ovule-bearing and stylar regions, united apically into style-stigma head; 1 vertical furrow, of 5, of style-stigma head [center], with stigmatic surface [below] and position of corpusculum at summit of gynoecial walls of stigmatic chamber), × 12. g, *A. connivens*: pollinarium (cf. "e"), with characteristically long translator arms, × 12. h, *A. pedicellata*: side view of flower with 2 corolla lobes removed (sepals spreading; corolla lobes erect; corona sessile, hoods ascending, open but geniculate apically; anther head held well above hoods), × 5.

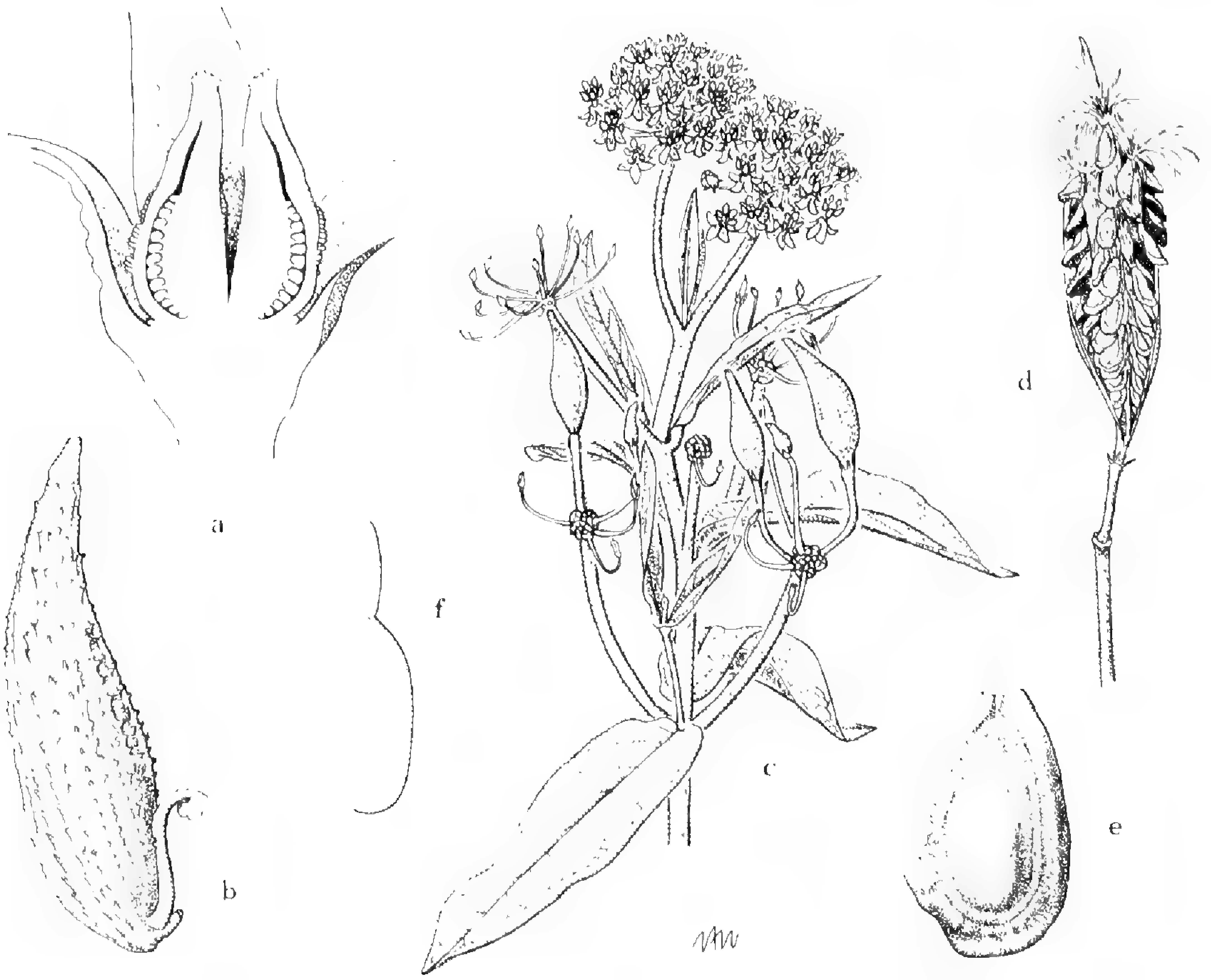

FIGURE 9. **Asclepias.** a, b, *A. syriaca*: a, flower with very young fruit, cut longitudinally, after fall of corolla, androecium, and style-stigma head but before disappearance of calyx and probable abortion of 1 follicle, showing 3 calyx lobes, 2 with squamellae at base, 2 very young follicles, mostly free, with axile placentation and numerous developing seeds, × 8; b, nearly mature follicle, erect on deflexed pedicel, with aborted carpel at lower right, × ½. c–f, *A. incarnata* subsp. *pulchra*: c, distal part of stem with some inflorescences and infructescences paired at nodes, young follicles erect on erect pedicels, × ½; d, mature, dehisced follicle, releasing seeds with apical tufts of trichomes, × ½; e, seed, apical tuft of trichomes removed, seed coat winged laterally, × 3; f, embryo, somewhat expanded from soaking in water (oriented as in "e"), × 4.

Here excluded from *Asclepias* is *Gomphocarpus* R. Br., which was tentatively included by Woodson (1954). According to Pobedimova, the latter includes about 100 species in central and northern Africa, about ten in Central and South America, and one in Arabia. Although in both genera the segments of the inner corona are conduplicate (hood shaped), those in *Gomphocarpus* lack the adaxial appendages (horns or crests) characteristic of but not universally present in *Asclepias* (some of our species at least appear to lack them; see below). *Asclepias* may also be related closely to two genera of tropical and southern Africa with laminate (i.e., flat, not conduplicate) inner-corona segments. These structures have and do not have adaxial appendages in *Schizoglossum* E. Meyer (about 25 species) and *Xysmalobium* R. Br. (about ten species), respectively (see Schumann). Good informally recognized four assemblages of Asclepiadaceae with representatives in both the Old and New worlds; one of them was composed entirely of these four genera.

Here included in *Asclepias* are a number of segregate genera that were recognized, for example by Small, as being monotypic and confined to the Southeast (*Anantherix* Nutt., *Asclepiodella* Small, *Oxypterix* Greene, and *Podostigma* Ell.), monotypic and geographically centered in but not limited to the Southeast (*Biventraria* Small), or composed of several species and relatively widespread in North and Central America (*Acerates* Ell. and *Asclepiodora* Gray).

According to Woodson (1954), the natural distributions of 27 species of *Asclepias* include at least part of the southeastern United States, while those of five others (*A. asperula* (Dcne.) Woodson, *A. Engelmanniana* Woodson, *A. linearis* Scheele, *A. oenotherioides* Cham. & Schlecht., and *A. Sullivantii* Engelm.) were shown to approach this area closely from the west; *A. Sullivantii* has since been recorded from Arkansas (Smith). The showy-flowered *A. curassavica* L., native to Central America and/or the Antilles and/or South America, has been widely introduced in the tropics and subtropics of both the Old and New worlds, including, in North America, parts of the Coastal Plain, from Florida to Texas, and southern California.[33] In most cases, these 33 species can be readily distinguished using relatively few vegetative and floral characters (see below).

Woodson (1954) recognized nine subgenera (one of which included nine series), 108 species, and 14 subspecies in his treatment of North and Central American plants. Of these, seven or possibly eight subgenera and seven series are represented in the southeastern United States. Although Woodson (1954) considered these species groups to be mostly unnatural, they are nevertheless used here for purposes of presentation and species identification. They are presented in a different order for logistical purposes, and in some cases the characteristics defining them have been modified to reflect my studies of the 33 species that occur or possibly occur without cultivation in the Southeast. Lynch & Martin have suggested that cardenolide profiles obtained from thin-layer chromatography would be of value to the infrageneric classification of *Asclepias*.

Nearly all of the herbarium specimens I have seen are readily identified using criteria presented below. A much longer discussion, and in some cases liquid-preserved or fresh material as well, would be needed to identify the remainder. Vegetative and floral characters have been used instead of ones involving the fruits, at least in part because the latter are not nearly as variable within the genus, are unknown for some species, and are not present on most specimens. Because the following is limited to features discernible on herbarium specimens,

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[33] Whether or not *Asclepias curassavica* is truly naturalized anywhere in North America is not entirely clear. Long & Lakela stated that it is a pantropical weed that has become naturalized on the Coastal Plain from Florida to Texas and in California, and Wunderlin included it among plants "native or naturalized" in central Florida. However, it was listed neither among native and naturalized species of the Florida Panhandle (Clewell) or Georgia (Jones & Coile), nor among "some exotic ornamental species that persist after the abandonment of land" (Clewell, p. 1) included with the former. MacRoberts listed the species among those growing without cultivation in Louisiana but did not indicate whether or not the plants were reproducing. Correll & Johnston (p. 1233) referred to it in their treatment of plants in Texas simply as an "almost ubiquitous waif" of the tropics and subtropics in the New World, and Munz (p. 457) indicated that in California it is occasionally cultivated and escaped, "as at Mandeville Canyon, Santa Monica Mts."

several characters often used in identification (e.g., color of flowers; shape of abaxial surfaces of hoods) have been avoided.

Asclepias pedicellata Walter (*Podostigma pedicellata* (Walter) Vail), of the Coastal Plain from Florida to North Carolina, is our only representative of subg. PODOSTIGMA (Ell.) Woodson. The species appears to be unique within the genus in its erect or nearly erect corolla lobes (vs. reflexed or less often spreading and/or ascending). Furthermore, whereas the anther head is held above and separated from the hoods by a long section of the column in *A. pedicellata* (see FIGURE 8h), it is immediately subtended by them in all other species in the genus, including the other three included in subg. PODOSTIGMA by Woodson (1954). In fact, although Woodson (1954, p. 48) stated that the anther head is "borne on a stipe . . . high above the hoods" in subg. PODOSTIGMA, it is only slightly elevated in these other three species, which in this respect grade into subg. ASCLEPIODORA (Gray) Woodson.

The hoods are closed at the apex in species of two of our subgenera. In the monotypic subg. ANANTHERIX (Nutt.) Woodson they are spreading or erect at the base and converge above the anther head, and the coronas are stipitate to substipitate (i.e., the column is visible between the bases of the hoods and the corolla). The single representative of subg. ANANTHERIX, *Asclepias connivens* Baldwin (*Anantherix connivens* (Baldwin) Feay), occurs on the Coastal Plain in the northern half of Florida and in the southern parts of Georgia, Alabama, and Mississippi. (For the pollinarium of *A. connivens,* see FIGURE 8g.)

In subg. ASCLEPIODORA (Gray) Woodson (seven species, two in the Southeast) the hoods are deflexed at the base but otherwise ascending, although not convergent above the anther head, and the coronas are sessile (i.e., the column is not visible between the bases of the hoods and the corolla). *Asclepias viridis* Walter (*Asclepiodora viridis* (Walter) Gray), with hoods that are about one-half or less as long as the spreading or ascending corolla lobes, is known from all of the Southeastern States except the Carolinas, although it appears to be most common from Nebraska and Missouri south to eastern Texas and Louisiana and is sporadic east of the Mississippi River. The distribution of *A. asperula,* with hoods that are nearly as long as the spreading or ascending corolla lobes, is centered even farther west, in the southwestern United States, and very closely approaches but evidently does not include Arkansas.

The hoods are open at the apex (see FIGURE 8a, b) in species of the other five subgenera under discussion, although the openings are appressed against the anther head and/or column in subg. ACERATES (Ell.) Woodson (five species, three in the Southeast). The coronas are sessile in *Asclepias viridiflora* Raf. but clearly stipitate in *A. hirtella* Woodson and *A. longifolia* Michx. (*Acerates longifolia* (Michx.) Ell., *Acerates floridana* (Lam.) Hitchc., *Acerates delticola* Small).

Asclepias viridiflora is widespread in the eastern two-thirds of the United States as well as in some adjacent parts of Canada, and it occurs throughout the Southeast; however, its distribution appears to be centered in the lower Midwest and adjacent parts of the Central Plains, and it has only recently been reported from Florida (Anderson). *Asclepias hirtella* (inflorescences lateral, hemispheric to nearly spherical; hoods with small crest at base within) is geographically centered in the lower Midwest but is known from all of our states except Florida and the Carolinas, whereas *A. longifolia* (inflorescences mostly terminal, less than hemispheric; hoods unappendaged within) is distributed along the Coastal Plain from Louisiana to Maryland.

The hoods are open at the apex and the opening is not appressed against the anther head in the remainder of the 33 species of the Southeast. The hoods at least appear to lack internal appendages in subg. POLYOTUS (Nutt.) Woodson (three species, one or possibly two in the Southeast). The hoods are apically trilobed in *Asclepias stenophylla* Gray, with the shorter middle lobe evidently representing an otherwise completely adnate horn, whereas they are apically unlobed and truly unappendaged in *A. Engelmanniana. Asclepias stenophylla* is geographically centered in eastern Nebraska, western Missouri, and Oklahoma east of the panhandle and is probably fairly common in northwestern Arkansas. *Asclepias Engelmanniana* is distributed more to the west, from which it approaches but apparently does not enter the Southeast.

Each hood has an internal appendage in the remainder of the 33 Southeastern species. In most the appendage is an exserted horn (exceeded by to exceeding the hoods), while in some it is a nonexserted crest that probably represents a reduced horn. The coronas are sessile or very nearly so in two of the subgenera involved, subg. ASCLEPIODELLA (Small) Woodson and subg. PODOSTEMMA (Green) Woodson. The hoods do not exceed the anther head in subg. ASCLEPIODELLA, a group of seven species, two of which are represented in the Southeast by plants with linear to filiform leaves. The hoods of *Asclepias cinerea* Walter (southern South Carolina to northwestern and central Florida) have horns, while those of *A. Feayi* Chapman (*Asclepiodella Feayi* (Chapman) Small) (restricted to peninsular Florida) have crests.

The hoods exceed the anther head by between about one- and two-thirds their lengths in the six species of subg. PODOSTEMMA, one of which, *Asclepias oenotherioides* Cham. & Schlecht., with broader than linear leaves, is distributed from eastern Texas (near to but evidently not in Louisiana) to northwestern Mexico, southward to Costa Rica.

The coronas are not always completely sessile in *Asclepias cinerea* (subg. ASCLEPIODELLA) and *A. oenotherioides* (subg. PODOSTEMMA). The plants involved therefore might be confused with members of the last subgenus to be considered, subg. ASCLEPIAS, except that the hoods in *A. cinerea* have very prominent, erect, marginal auricles that clearly exceed the rest of the hood and those of *A. oenotherioides* are much narrowed toward the base.

The coronas are stipitate or sometimes substipitate in subg. ASCLEPIAS, although in some cases the column is hidden by deeply saccate and/or deflexed hoods. Woodson (1954) recognized nine series[34] in the subgenus, seven of which are represented in the southeastern United States. In three of these (sers. "Incarnatae," "Tuberosae," and "Exaltatae") the anther heads, excluding wings and terminal flaps of the anthers, are usually about as long as to longer than

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[34] The names of these series were not validly published by Woodson (1954), since they were accompanied neither by a Latin description or diagnosis nor by a reference to a previously and effectively published Latin description or diagnosis (i.e., they were not published in accordance with Art. 36.1 [ICBN, 1988], the effective date of which is January 1935). Therefore, they are enclosed in quotation marks here.

broad, while in four (sers. "Roseae," "Syriacae," "Macrotides," and "Purpurascentes") they are usually shorter than broad.

Subgenus ASCLEPIAS ser. "Incarnatae" includes about 16 species, four or perhaps five of which occur in the Southeast. The hood margins are without auricles and the leaves are opposite in all of these except *Asclepias verticillata* L. (throughout our area and the eastern United States in general, also in adjacent parts of Canada, and sporadically to as far west as Arizona), in which the hood margins are usually auriculate and the leaves on individual plants are whorled (in 3's, 4's, or sometimes 5's) or, infrequently, usually whorled and otherwise opposite. The hoods clearly exceed the anther head in *A. curassavica* (see above) but range from slightly exceeding to clearly being exceeded by it in three other species. The inflorescences are usually paired at the upper nodes and solitary below in *A. incarnata* L., while in *A. perennis* Walter (leaves broader than linear) and *A. linearis* Scheele (leaves linear to filiform) they are nearly always solitary. *Asclepias incarnata* is widespread in the eastern three-fourths of the United States and adjacent parts of Canada but is most concentrated in the area north of ours. It seems to be fairly common in Florida, eastern Tennessee, and the Carolinas but is poorly known if not absent in other parts of the Southeast. *Asclepias perennis* has a curious and possibly artifactual distribution, involving the Coastal Plain from Texas to South Carolina and the lower Ohio River valley. *Asclepias linearis* is endemic to southeastern Texas, according to Woodson (1954) and Correll & Johnston. Although Small indicated that it extends into our area to as far east as Alabama, the species was listed for neither Louisiana (MacRoberts) nor Arkansas (Smith).

In subg. ASCLEPIAS sers. "Tuberosae" and "Exaltatae" the hood margins have auricles and the leaves are opposite or irregularly alternate. The auricles are closer to the hood bases and the hoods clearly exceed the anther head in ser. "Tuberosae." This series is represented in our area by three species, one, *A. tuberosa* L. (with irregularly alternate leaves), widely distributed (to as far west as Arizona) but primarily eastern North American (including southern parts of Canada), and two (with opposite leaves) of the Coastal Plain (from eastern Texas to southern New York). *Asclepias rubra* L. (absent in peninsular Florida) has acute hood apices and broadly ovate to lanceolate leaves, while *A. lanceolata* Walter (common throughout Florida) has rounded hood apices and linear-lanceolate leaves.

The auricles are closer to the hood apex (but usually do not exceed the rest of the hood by as much as they do in *Asclepias cinerea* of subg. ASCLEPIODELLA), and the hoods never exceed the anther head by much (they range from slightly exceeding it to being slightly exceeded by it) in ser. "Exaltatae." Two of the nine species in this group are represented in the southeastern United States. *Asclepias exaltata* L. (leaf-blade bases not clasping stem, peduncles usually lateral and much shorter than subtending leaves), of the northeastern United States and adjacent Canada, enters our range along the Appalachian Mountains to about as far south as northern parts of Georgia and perhaps Alabama. *Asclepias amplexicaulis* Small (leaf-blade bases clasping stem, peduncles usually terminal and much longer than the subtending leaves) is widespread in the eastern two-thirds of the United States (and probably occurs in southern Canada), including our area, although it is not known to occur in peninsular Florida.

The basis for Woodson's (1954) inclusion of two of our species and 11 others in ser. "Roseae" is not altogether clear. Among our representatives of this series, the abaxial surface of each hood is exceeded by the surfaces adjacent to the anther head and is not recurved apically in *Asclepias tomentosa* Ell. (hoods slightly to clearly exceeded by anther head) but clearly exceeds the surfaces adjacent to the anther head and is recurved apically in *A. obovata* Ell. (hoods clearly exceeding anther head). Both species are known from scattered localities along the Coastal Plain from eastern Texas to the Carolinas, except that *A. obovata* (*Acerates obovata* (Ell.) Eaton) has been reported from neither North Carolina nor peninsular Florida; Clewell (p. 251) indicated that it is a ruderal in the Florida Panhandle in "Jackson and Gadsden to Bay Cos."

The abaxial surface of each hood exceeds the surfaces adjacent to the anther head but is not recurved apically in sers. "Syriacae," "Macrotides," and "Purpurascentes." The marginal auricles of the hood generally are sharply incised and acute at the apex in ser. "Syriacae" but shallow and broad in sers. "Macrotides" and "Purpurascentes."

Four of the 11 species belonging to ser. "Syriacae" occur in the southeastern United States. *Asclepias viridula* Chapman has linear to filiform, opposite leaves and appears to be endemic to northern Florida and perhaps adjacent parts of Georgia, while our other three species have wider, nearly always opposite leaves and are more widespread. *Asclepias humistrata* Walter (leaf-blade bases clasping stem, leaves opposite) occurs on the Coastal Plain from Louisiana to North Carolina, while *A. quadrifolia* Jacq. (leaf-blade bases not clasping stem, leaves whorled or subwhorled at or near first node beneath inflorescence but otherwise opposite) and *A. syriaca* L. (leaf-blade bases not clasping stem, leaves opposite) mostly grow in the northeastern quarter of the United States and adjacent parts of Canada, including in our area northern Arkansas and the Appalachian Mountains to about as far south as Georgia and Alabama. *Asclepias syriaca* is widespread in the northeastern quarter of the United States and adjacent parts of Canada; it may be native to the northern parts of our range but naturalized farther south (see Woodson, 1954; Broyles & Wyatt).

One of the eight species included in ser. "Macrotides," *Asclepias Michauxii* Dcne. (*A. angustifolia* Ell.), occurs in the Southeast. It is endemic to the Coastal Plain from Louisiana to South Carolina, including peninsular Florida, and can be distinguished from our species of ser. "Purpurascentes" by its irregularly alternate, filiform to linear (vs. opposite, broader than linear) leaves.

Three or four of a total of eight species comprising ser. "Purpurascentes" occur in the Southeast. The hoods are acute to narrowly rounded apically and exceed the anther head by more than half their length in *Asclepias purpurascens* L. and *A. Curtissii* Gray (*Oxypterix Curtissii* (Gray) Small). *Asclepias purpurascens* (plants erect) occurs primarily in the northeastern quarter of the United States and in adjacent parts of Canada but enters our range in parts of Louisiana, Arkansas, Tennessee, and North Carolina, whereas *A. Curtissii* (plants decumbent) is endemic to peninsular Florida. The hoods are broadly rounded to truncate apically and exceed the anther head by less than half their length in *A. variegata* L. (*Biventraria variegata* (L.) Small) and *A. Sullivantii. Asclepias variegata* (leaf-blade bases not clasping stem) is widespread in the area southeast of a curve from about southern New England to Arkansas and eastern Texas but has not been reported from peninsular Florida. *Asclepias Sullivantii* (leaf-blade bases clasping stem) is mainly distributed in the southern half of the Midwest (reported also from southern Canada) and enters our area only in Jackson County, Arkansas (Smith).

Woodson (1954) recognized infraspecific taxa in only three of the 33 species mentioned above. On the basis of morphological, ecological, and geographic evidence, two subspecies, both of which occur in the Southeast, were recognized in *Asclepias incarnata.* Subspecies *pulchra* (Ehrh.) Woodson (plants conspicuously pubescent instead of essentially glabrous, leaves broader than in the typical element, and other minor differences) occurs along the Atlantic Coast (as well as in adjacent, inland areas) in Florida and from Maine and Nova Scotia to North Carolina, where it frequently grows in brackish tidal marshes, while subsp. *incarnata* has a more inland distribution (essentially throughout the Midwest, but with widely scattered stations elsewhere) and is only associated with fresh water. The possibility that the morphological characteristics of subsp. *pulchra* are induced by saline environments apparently has not been investigated.

Woodson (1954) recognized four subspecies in *Asclepias tuberosa* based on leaf shape and to some extent geography; three of them are known from the Southeast. However, he had earlier demonstrated "extremely active" introgression among them (Woodson, 1953), and I have observed them to be morphologically indistinct. Two subspecies were treated in *A. asperula,* the more eastern of which, subsp. *capricornu* (Woodson) Woodson (sessile to subsessile instead of clearly pedunculate inflorescences, in addition to other differences) was reported from a locality in McCurtain County, Oklahoma, within about 40 miles of Arkansas and was said sometimes to spread to pastures from more natural habitats.

According to Woodson (1954), few North American species of *Asclepias* occur at elevations above 2000 meters, and a minority (perhaps as many as 12 of ours) are distributed as far north as Canada. Most of the species discussed above appear to be optimally adapted to relatively open, dry habitats such as pine barrens, flatwoods, prairies, glades, thickets, and sand dunes. In addition to *A. incarnata* (see above), other species at least sometimes occurring in moister habitats than these include *A. asperula* (desert swales), *A. connivens* (marshes, low areas in woods), *A. curassavica* (moist places), *A. Engelmanniana* (washes, bottoms, swales), *A. exaltata* (moist woods and meadows), *A. longifolia* (swamps, low pine lands), *A. perennis* (low swampy ground), *A. rubra* (bogs, marshes, wet meadows, low pine barrens), and *A. syriaca* (alluvial bottoms); *A. lanceolata* is found in wet pine barrens and low glades, as well as in both fresh water and brackish marshes. Although Woodson (1954) stated that, among the 33 species in our area, only *A. curassavica, A. syriaca,* and possibly *A. incarnata* are to any extent weedy, he indicated that *A. amplexicaulis, A. Feayi, A. hirtella, A.*

obovata, A. oenotherioides, A. purpurascens, A. Sullivantii, and *A. viridiflora* often spread to roadsides, old fields, and/or railways from more natural habitats.

Natural hybrids between species of *Asclepias* appear to be very rare, presumably because of mechanical isolation effected by sets of rather exact pollination requirements. Natural and fertile artificial hybrids have been reported in subg. ASCLEPIAS between *A. exaltata,* of ser. "Exaltatae," and *A. syriaca,* of ser. "Syriacae" (see Kephart & Heiser; Kephart *et al.*). Included by Woodson (1954) in a list of nine apparent but untested hybrids are some specimens combining the characteristics of *A. amplexicaulis* (ser. "Exaltatae") and *A. humistrata* (ser. "Syriacae"), from Florida; *A. amplexicaulis* and *A. syriaca,* from New York; and *A. syriaca* and *A. viridiflora* (subg. ACERATES), from Indiana. Other specimens intermediate between one of the 33 species in the Southeast and another species were also reported. These involve *A. verticillata* and the extraregional *A. pumila* (Gray) Vail (both of ser. "Incarnatae"); *A. syriaca* and the extraregional *A. speciosa* Torrey (ser. "Purpurascentes"), between which hybrids were obtained experimentally (see also Thomson & Wagner); and *A. oenotherioides* and the extraregional *A. Emoryi* (Greene) Vail (both of subg. PODOSTEMMA), between which intermediates are frequent in nature. Plants grown by Moore (1946b) from seeds probably resulting from natural pollinations and produced by plants of *A. speciosa* growing in experimental plots with *A. syriaca* were intermediate in flower, stem, and leaf character states at least in part defining these two species.

Moore (1946b) attempted to produce artificial hybrids involving several of the species discussed here, for the most part unsuccessfully. Although ovary enlargement, presumably resulting from successful fertilization, was observed for crosses of *Asclepias tuberosa* (ser. "Tuberosae") with *A. Sullivantii* (ser. "Purpurascentes"), *A. curassavica* (ser. "Incarnatae") with *A. syriaca* (ser. "Syriacae"), and *A. curassavica* with *A. speciosa* (ser. "Purpurascentes"), the fruits and seeds did not mature. Moore's list of even-less-successful artificial crosses (i.e., those after which no ovary enlargement was observed) included various other combinations involving these species and *A. incarnata, A. Sullivantii,* and *A. tuberosa,* to which Woodson (1954) added *A. curassavica* crossed with *A. quadrifolia* (ser. "Syriacae") and *A. purpurascens* (ser. "Purpurascentes"), *A. verticillata* crossed with *A. incarnata* (both of ser. "Incarnatae"), and others involving these and two extraregional species.

Cytological evidence has not been useful in the evaluation of putative hybrids, primarily because all of the species involved are of the $2n = 22$ cytotype. Otherwise it has been of interest in the sense that the chromosomes of *Asclepias curassavica* are significantly smaller than those of the other species investigated by Moore (1946b), all native to North America, consistent with the idea that this species is a more distantly related introduction to the continent.

Even though fruits are not especially variable within the genus, the spatial relationships between the follicle and pedicel appear to be of phylogenetic importance (Woodson, 1954). During fruit maturation in most species, the pedicel becomes deflexed while the follicle remains erect. Despite being common within the genus and (supposedly) in the rest of the Asclepiadeae (but see generic descriptions here), this condition was thought to be relatively advanced because it is unknown in the rest of the Asclepiadaceae. The production of erect follicles on erect pedicels or pendulous follicles on pendulous ones is more characteristic of the family as a whole, and although less common in *Asclepias,* was therefore considered to be more primitive than erect follicles on deflexed pedicels. Erect or pendulous pedicels are most frequent in subg. ASCLEPIAS, while erect follicles on deflexed pedicels are unknown in ser. "Incarnatae" (cf. FIGURE 9c); these taxa were considered on the basis of floral morphology to be the most primitive within their genus and their subgenus, respectively.

Despite the foregoing, erect follicles on erect pedicels or pendulous follicles on pendulous ones occur as well in other subgenera of *Asclepias* and in other series of subg. ASCLEPIAS. Among the Southeastern species, erect follicles and pedicels are known in *A. incarnata, A. linearis, A. curassavica,* and *A. verticillata* of ser. "Incarnatae," as well as in *A. quadrifolia* and *A. viridula* of ser. "Syriacae," *A. Michauxii* of ser. "Macrotides," *A. cinerea* and *A. Feayi* of subg. ASCLEPIODELLA, and *A. stenophylla* of subg. POLYOTUS. Among this same group, pendulous follicles and pedicels (and, incidentally, noncomose seeds) occur only in *A. perennis* of ser. "Incarnatae"; the fruits of *A. Curtissii* and *A. pedicellata* are evidently unknown. Pendulous follicles and pedicels also occur in extraregional species of ser. "Roseae" and subg. PODOSTEMMA. Woodson (1954) considered most of these species to be primitive within their respective series and subgenera on the basis of floral morphology.

The precise location of nectar production in flowers of *Asclepias* has been controversial. The hoods were generally accepted as the site, probably because of the conspicuous accumulation of nectar there, until, according to Galil & Zeroni (1965), Stadler concluded in 1886 that it was produced in the stigmatic chambers as well. More recent workers reverted to the original idea, and some even regarded the horn as its ultimate source. Working with *A. curassavica* in Israel, Galil & Zeroni (1965) showed that nectar accumulates both in the hoods and in the stigmatic chambers, although histochemical and other tests demonstrated that it is produced only in the latter (see also Schnepf & Christ). Using very small pipettes and a solution of ten percent sucrose with a few drops of india ink, they also established that liquid passes from the base of each stigmatic chamber into the two nearest hoods through passageways largely defined by the lobules of the corona and the bases of the two adjacent anthers; that is, each lobule causes the nectar to flow from the base of the stigmatic chamber laterally into the bases of the two nearest hoods, instead of down the column between them.

The hoods evidently allow for accumulation of the massive amounts of nectar required by insect visitors large enough both to fly the great distances often separating individual plants and effectively to engage the pollination mechanism involved, which in various ways favors outcrossing. In many cases during nectar-feeding visits, one (or more) of an insect's appendages (usually a leg or a head part) becomes wedged in the abaxial groove of the corpusculum, to which it is sometimes guided from below by the outwardly projecting, apically narrowing slot (and associated, upwardly oriented bristles) between the anther wings. Visitors of sufficient strength depart for another flower intact, carrying away the corpusculum with attached translator arms and pollinia, while others remain trapped or leave behind the wedged part because the pollinia are too heavy and/or too tightly held within the anthers.

According to most accounts, the translators begin to rotate within a few minutes after removal from the flower, continuing until the wide axes of the pollinia are perpendicular to their original orientation and their more sharply convex sides are adaxial. This action orients pollinia such that the same pollinator behavior that effected their removal from the anthers of one flower can result in their insertion, one at a time, into the outwardly projecting anther wing slots of another, with their more sharply convex sides inward, adjacent to the receptive surfaces within the stigmatic chambers. Because such effective insertion of pollinia into the slots is substantially more likely after translator rotation, delay of the latter until after the pollinator is likely to have departed for another individual is generally thought to promote outcrossing. However, my observations of *Asclepias syriaca* indicate that the translator arms are under tension while the pollinarium is in place, and that they begin to rotate immediately upon removal.

Pollinator activity at a flower visited after translator rotation in the pollinarium being transported sometimes results in the insertion of one pollinium of the pair into a stigmatic chamber, usually from somewhat below. As the insect moves its trapped appendage toward the apex of the flower in attempting to free itself, the inserted pollinium may become detached by pressure exerted against the anther wings forming the anther slot, so that the inserted pollinium remains in the stigmatic chamber. At other times the translator arm or the insect's appendage to which it is attached becomes wedged in the abaxial groove of the resident corpusculum, forcing detachment of the inserted pollinium, perhaps along with the translator arm and sometimes the insect's appendage as well. Continued pollinator movement may also result in removal of the resident pollinarium in the manner described above. If an inserted pollinium remains attached to its translator arm and to the insect's appendage and if either of the latter is wedged in the resident corpusculum upon its removal, the inserted pollinium will be removed along with the resident pollinarium. Successive repetitions of such occurrences often result in chains of pollinaria.

Wyatt (1976) advanced the idea that inserted pollinia are more likely to remain so when the associated resident pollinarium (especially the corpusculum) is still intact and in place. (For extraregional species, see also Lynch.) That removal of resident pollinaria is possible without upsetting a previous insertion was offered to explain unexpected observations that the numbers of insertions into chambers associated and not associated with intact resident pollinaria are frequently about equal. However, Wyatt (1978) later provided experimental evidence from manipulated flowers in natural populations of *Asclepias tuberosa* in North Carolina that insertions were in fact more numerous in chambers associated with intact resident pollinaria. He believed that these findings confirmed his original hypothesis that the corpusculum helps to ensure that the translator arm will be broken and the inserted pollinium will remain behind. Such a mechanism presumably favors outcrossing, and it perhaps simultaneously decreases the wasteful placement of pollinia, to the extent that insertion of pollinia would be less likely into the stigmatic chambers of flowers that have already been pollinated (because one or more of the five corpuscula would have been removed).

Most evidence suggests that Hymenoptera generally are more frequent pollinators of *Asclepias* flowers than are Lepidoptera, and that the latter in turn are more frequent than Coleoptera, Diptera, and Hemiptera. Such was indicated in Robertson's (1928) compilation in Illinois, in which visitors with pollinaria, among others, were listed for each of eight species represented in the Southeast (*A. incarnata, A. purpurascens, A. Sullivantii, A. tuberosa, A. longifolia, A. syriaca, A. verticillata,* and *A. viridiflora*); ruby-throated hummingbirds (*Archilochus colubris*) were reported to visit the flowers of the first four of these, although none was observed with pollinaria.

More detailed and recent studies also have indicated that, in general, Hymenoptera are more important than Lepidoptera in the pollination of *Asclepias* flowers (for exceptions, see Bierzychudek; Wyatt, 1980a). Wyatt (1976) found that, in comparison with localities farther east, many pollinaria were removed but few inserted among 15 populations of *A. tuberosa* in eastern Kansas and western Missouri that were visited by relatively small numbers of Hymenoptera (mostly bumblebees, honeybees, and wasps) and large numbers of Lepidoptera (primarily monarch, swallowtail, and sulfur butterflies). Although butterflies (especially monarchs) were frequent visitors to flowers of *A. syriaca* in a coastal area in Maine, bumblebees were usually ten to 20 times more numerous and carried pollinaria four times as often (Morse, 1985b).

Morse (1985b) also noted that, although at night flowers of *Asclepias syriaca* were quite fragrant, produced considerably more nectar than during the day, and were visited by large numbers of moths, Lepidoptera were responsible for only five to 25 percent of the total number of pollinial insertions (day and night) (but see Willson & Bertin). Nevertheless, Bertin & Willson demonstrated with *A. syriaca* and *A. verticillata* that, although insect visitors and pollinial insertions were less frequent at night, seed-set and "pod-set" were equal or greater, suggesting that nocturnal pollinators may be superior to diurnal ones. Bertin & Willson also suggested that the predominance of diurnal visitors may be due largely to the introduction of the honeybee (*Apis mellifera*).

Data provided by Willson, Bertin, & Price indicated that for *Asclepias verticillata* Hymenoptera were more frequent carriers of pollinaria than were Lepidoptera at three of four study sites in Illinois, and that whereas the former were more important than the latter at the least disturbed site (70 percent vs. 0 percent of all vectors, respectively), the opposite was true at the most disturbed site (15 percent vs. 51 percent).

Pollinaria of three species of *Asclepias* represented in the Southeast were found by Kephart (1983) on a wide variety of insects collected from experimental plantings in Indiana. Although close associations between individual plant and pollinator species were not evident, *A. syriaca* was associated with a narrower range (Hymenoptera, including bees in *Apis* and *Bombus* and wasps in *Polistes* and *Sphex*; Lepidoptera in *Cisseps, Danaus,* and *Speyeria*; Coleoptera in *Chauliognathus*; and Diptera and Hemiptera in unspecified genera) than either *A. incarnata* (bees in *Apis, Bombus,* and *Xylocopa*; wasps in *Cerceris,* *Myzinum, Polistes,* and *Sphex*; Lepidoptera in *Battus, Cisseps, Danaus,* and *Speyeria*; Coleoptera in *Chauliognathus*; and Diptera and Hemiptera in unspecified genera) or *A. verticillata* (all taxa mentioned above for *A. syriaca* and *A. incarnata* except *Speyeria*; also wasps in *Entypus*).

Beare & Perkins's field observations of two populations of *Asclepias tuberosa* in south-central Oklahoma revealed the existence of fruiting and nonfruiting individuals. The slots over the stigmatic chambers were significantly wider than the pollinia were thick in plants that developed fruits, while the reverse was true of those that did not (pollinial thickness was constant). Fruiting individuals clearly had greater numbers of pollinial insertions and greater percentages of intact pollinaria as well, supporting Wyatt's (1976) hypothesis that the likelihood of pollinial insertion is enhanced by the presence of intact pollinaria. Dimorphism in slot width would favor outcrossing to the extent that flowers with narrow slots are much less likely to be pollinated in general (3.45 percent vs. 96.55 percent insertion) and therefore to be self pollinated in particular. Evidently, nonfruiting plants act primarily as pollinial donors.

A variety of explanations, including infrequent, ineffective, or disruptive insect visitation, resource limitations for developing ovules and fruits, and/or various levels of physiological incompatibility, have been offered to account for the low percentage (ca. 1 percent according to Woodson, 1954) of flowers that develop into mature fruits in species of *Asclepias*.

That pollination does not limit fruit-set has been suggested by various studies of *Asclepias syriaca* in North America in which the percentage of flowers with inserted pollinia has ranged from about 65 among natural populations in southeastern lower Michigan (Sparrow & Pearson) to about 95 among experimental plants in southeastern Ontario (R. J. Moore, 1947). However, much lower (but unspecified) values were obtained for *A. tuberosa* in natural populations throughout much of the eastern half of the United States, perhaps at least in part because pollinia of this species are thought to be removed but not inserted by some species of butterflies (Wyatt, 1976).

Low insertion rates in *Asclepias tuberosa* might also be due to nectar-robbing ants, on which pollinaria of this species have been observed in large numbers (Wyatt, 1976). Indeed, insertions were more frequent among inflorescences of *A. curassavica* in Costa Rica from which ants were excluded (Wyatt, 1980a). Thus, nectar-robbing can reduce both the number of pollinaria and the amount of nectar available to legitimate pollinators, some of which, especially in *A. curassavica* (Galil & Zeroni, 1965), have been observed to remove nectar directly from the stigmatic chambers of flowers in which the hoods were emptied, resulting in the relatively ineffective placement of pollinaria on head parts (see also Fritz & Morse). Wyatt (1980a) suggested that the opposite, sessile, amplexicaulous leaves of several species (e.g., *A. amplexicaulis, A. humistrata, A. Sullivantii*) might reduce the number of ants reaching inflorescences and thereby enhance sexual reproduction.

Fruit-set among species of *Asclepias* may also be limited by physiological incompatibility systems and resource limitation. Sparrow & Pearson found that only flowers pollinated with pollinia from distant plants or from clones producing fruits of a different type (see Sparrow) developed mature fruits. All other pollen was either completely ineffective or resulted in fruit abortion at various stages early in development. Willson & Price (1980) demonstrated that various aspects of seed and fruit production by uncultivated plants of *A. incarnata, A. syriaca,* and *A. verticillata* in Illinois were generally increased by the addition of nitrogen, phosphorus, and potassium and were decreased by defoliation and perhaps by shading.

Not only is fruit-set in *Asclepias* infrequent overall, but almost invariably only one of the two carpels per flower develops into a mature fruit. Sparrow & Pearson reported that in artificially pollinated flowers of *A. syriaca,* pollen tubes from a single stigmatic cavity enter only a single style, suggesting that in general the ovules of one carpel may be fertilized only by pollen in two adjacent chambers, and that those in the other might receive pollen tubes only from the other three. If this is indeed true, fertilization of both carpels would require pollinial insertion in both groups of stigmatic chambers.

The rarity of natural hybrids between species of *Asclepias,* despite the close geographic and/or ecological proximity of many, has usually been attributed to mechanical isolation effected by a specific fit between stigmatic chambers and pollinia (i.e., the "lock and key" of many authors, the "tongue-in-groove" of Beare & Perkins) of individual species (see especially Holm). Vector specificity has not been invoked because pollinaria of several diverse species have often been observed on individual insects.

Kephart & Heiser studied pollination in natural and experimental populations of three sympatric, mostly self-incompatible species of *Asclepias* in Indiana, *A. incarnata, A. syriaca,* and *A. verticillata.* Despite statistically significant differences among the species in the sizes of both stigmatic chambers and pollinia, effective pollinations were observed for all combinations except those involving the relatively large pollinia of *A. syriaca* and their insertion into the comparatively small stigmatic chambers of *A. incarnata* and *A. verticillata*; pollinaria of *A. tuberosa* (and other species) were also occasionally found in the stigmatic chambers of all three species. Thus, Kephart & Heiser concluded that, while such mechanical barriers to hybridization are neither as effective nor as significant as was previously thought, they and other pre-pollination barriers may nevertheless sometimes contribute to decreased interspecific pollination.

Indeed, Macior's field observations of *Asclepias incarnata, A. syriaca,* and *A. verticillata* in southeastern Wisconsin suggested that other floral characteristics affect the positioning of pollinaria on pollinators. Poor footing on flowers and wide spaces between hoods (as in *A. syriaca*) were positively correlated with pollinarial placement on insect pulvilli, while good footing and narrow spaces (as in *A. incarnata* and *A. verticillata*) seem to favor placement on the tarsal claws subtending them, at least in part because the tarsus in such cases is less likely to be drawn through the stigmatic chambers directly from below. Macior also implied that behavioral diversity among insects might in some cases decrease the likelihood of cross-pollination. That the foregoing may be, nevertheless, ineffective in preventing the misplacement of pollinia is indicated by his observations of chains composed of pollinaria belonging to two or more of these and other species.

The failure of all of 279 attempted artificial crosses involving *Asclepias incarnata, A. syriaca,* and *A. verticillata* as reported by Kephart (1981) indicates that post-pollination barriers are considerably more important than those discussed above. Pollen-tube penetration into the styles and, in some crosses between *A. incarnata* and *A. verticillata,* into the ovules as well suggests late pre- or early post-fertilization, physiological incompatibility. The evidently weaker barrier between *A. incarnata* and *A. verticillata* may imply greater genetic similarity between them, consistent with their separation from *A. syriaca* at the level of series by Woodson (1954).

Many insects are rendered unpalatable by ingestion of plants in several species of *Asclepias* (as well as other Apocynineae), due primarily to the presence of cardiac glycosides in the latex (e.g., see Brower *et al.*; Duffey & Scudder; Erickson; Euw *et al.*; Isman *et al.*; Rothschild; Seiber *et al.*). The resemblance of the palatable viceroy butterfly to the unpalatable monarch is perhaps the best-known and most frequently taught example of Batesian mimicry.

Bailey and colleagues listed about 20 of our species of *Asclepias* as being cultivated in North America. Some are grown as ornamentals, while others have been evaluated as potential crop plants for a variety of purposes (see family discussion). Several species in the southeastern United States were used by "Indians" in various ways: latex for chewing gum; bark fiber to make rope and string; buds, young shoots, leaves, and fruits for food; and dried roots for medicine (Uphof). *Asclepias curassavica* is one of the most common weeds in the lowlands of Central America, where the latex is placed in the nostrils to treat head colds and in cavities to relieve toothache; it is also sometimes used internally as an emetic and purgative and is believed to be useful in the treatment of poisonous bites (Standley & Williams). The many uses of *A. incarnata, A. syriaca, and A. tuberosa* have been discussed by M. I. Moore.

In addition to the literature discussed above, see annotations of the references below for information about overall biology (Bhowmik & Bandeen), general ecology (Blakley & Dingle; Price & Willson, 1976, 1979; Wilbur, 1976), pollination biology and breeding systems (Boyden; Chaplin & Walker; Corry, 1883a, 1883b; Dailey *et al.*; Frost; Galil & Zeroni, 1969; Kephart, 1979; Morse, 1981, 1982; Morse & Fritz, 1983, 1985; Pleasants & Chapin; A. K. Southwick & Southwick; E. E. Southwick; Willson & Price, 1977), fruit and seed production (Bell; Bookman, 1983a, 1983b, 1984; R. J. Moore, 1946a; Morse, 1987; Queller, 1983, 1985; Wilbur, 1977), seed germination (Baskin & Baskin; Farmer *et al.*; Jeffery & Robison; Kis; Morse & Schmitt; Oegema & Fletcher), and the taxonomic significance of latex (Moyer).

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Under references for the Apocynineae, see BAILEY *et al.*; CLEWELL; CORRELL & JOHNSTON; JONES & COILE; LONG & LAKELA; MACROBERTS; MUNZ; POBEDIMOVA; ROBERTSON (1928); SCHUMANN; SMALL (1933); SMITH; STANDLEY & WILLIAMS; UPHOF; and WUNDERLIN.

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Under references for *Sarcostemma,* see HOLM.

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DACTYLOCARDAMUM (BRASSICACEAE), A REMARKABLE NEW GENUS FROM PERU

Ihsan A. Al-Shehbaz[1]

Dactylocardamum imbricatifolium, a new genus and species, is described from the Sierra Blanca of Peru. Its relationships to *Eudema* and *Xerodraba* are discussed. Scanning electron micrographs of leaves, fruits, and seeds of *Dactylocardamum* and leaves of *Xerodraba* are presented.

During the past several years I have been studying the systematics and evolution of various South American genera of the Brassicaceae (Cruciferae). Almost every genus that I have examined critically (see, for example, Al-Shehbaz, 1986, 1989a, 1989b, 1989c, 1990) included one or more novelties. However, the discovery of a new genus with unique morphology and evident relationships to well-defined, monophyletic genera was rather surprising.

The new monotypic genus (hereafter called *Dactylocardamum,* which literally means a digitate crucifer—in reference to the fingerlike branches) was collected from Cordillera Blanca, Peru, and was misidentified as *Xerodraba* Skottsb. A close examination of the plant immediately revealed that it belongs to an undescribed genus, not only because it has several unique features that separate it readily from its nearest relatives, *Eudema* Humb. & Bonpl. and *Xerodraba,* as well as from all other genera of the Brassicaceae, but also because its type locality is separated from the nearest known range of *Xerodraba* by at least 3200 air kilometers.

The overall growth habit and certain aspects of the leaves of *Dactylocardamum* are fairly similar to those of *Xerodraba.* However, the two genera are readily distinguished from each other by the nature of their fruits, the length of the style and the fruiting pedicels, and the texture of the leaves (see FIGURE 1 and TABLE). On the other hand, *Dactylocardamum* resembles *Eudema* in the texture of the leaves and in a few characters of the fruits. However, it differs markedly in habit, leaf persistence, number of flowers per branch, pedicel length, and fruit position (see TABLE). The flowers in *Eudema* are few to several on each branch, and they mature in a racemose fashion (Al-Shehbaz, 1990), while those of *Dactylocardamum* are solitary. The three genera are easily separated from each other by the following key:

A. Leaves appressed, densely imbricate, persistent as a whole; branches fragile, fingerlike; flowers 1 at tip of each branch.
    B. Leaves thin, papery; fruits subterete, indehiscent, completely included and sandwiched between leaf bases; septum absent; style 2.5–3 mm long; valves membranaceous; fruiting pedicels to 0.4 mm long. . . . . *Dactylocardamum.*
    B. Leaves thick, fleshy; fruits flattened parallel to septum, dehiscent, exserted above

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Phenetic comparison of Dactylocardamum, Eudema, and Xerodraba.

	GENUS		
CHARACTER	*Dactylocardamum*	*Eudema*	*Xerodraba*
Fruits			
Flattening	Not flattened, subterete	Latiseptate or subterete	Latiseptate
Dehiscence	Indehiscent	Dehiscent (rarely indehiscent)	Dehiscent
Valve texture	Membranaceous	Somewhat leathery	Somewhat leathery
Septum	Absent	Complete or perforated	Complete or rarely perforated
Position	Sandwiched between leaf bases	Exserted above leaves	Exserted above leaves
Style length (in mm)	2.5–3	0.4–3.5	0.4–1
Fruiting-pedicel length (in mm)	≤ 0.4	2–20	1.6–6
Flowers per branch	1	Few to several	1
Leaves			
Length (in mm)	2.5–3.5	3–22	1.6–9
Arrangement	Densely imbricate	Loose, not imbricate	Densely imbricate
Blade orientation	Appressed	Divaricate to ascending	Appressed
Texture	Thin, papery	Thin, not papery	Thick, rather fleshy
Persistent portion	Entire leaf	Petiole	Entire leaf
Branch shape	Fingerlike	Various, but never fingerlike	± Fingerlike

leaf rosette; septum complete or rarely perforate; style 0.4–1 mm long; valves somewhat leathery; fruiting pedicels 1.6–6 mm long. . . . . *Xerodraba.*

A. Leaves neither appressed nor imbricate, almost always with only petioles persistent; branches neither fragile nor fingerlike; flowers few to several at tip of each branch. . . . . *Eudema.*

The evolutionary relationships among the three genera is rather interesting. Although *Dactylocardamum* resembles *Xerodraba* in several aspects of habit and foliage, the bizarre vegetative morphology probably evolved independently in the two genera. On the other hand, *Dactylocardamum* does show certain affinities to *Eudema,* particularly in some aspects of the fruits and in leaf pubescence, and they may be more closely related to each other than either is to *Xerodraba.* However, *Dactylocardamum* is unique in the Brassicaceae in having axillary fruits that are completely concealed and sandwiched between the appressed, densely imbricate leaf bases (see FIGURE 2a–c). These hidden fruits can be seen only after the removal of the subtending leaves. Although the solitary flower of *D. imbricatifolium* is terminal in the bud stage and during anthesis, the developing fruit is gradually pushed to an axillary position due to the production of new leaves by the terminal leaf bud. The fruits of a given

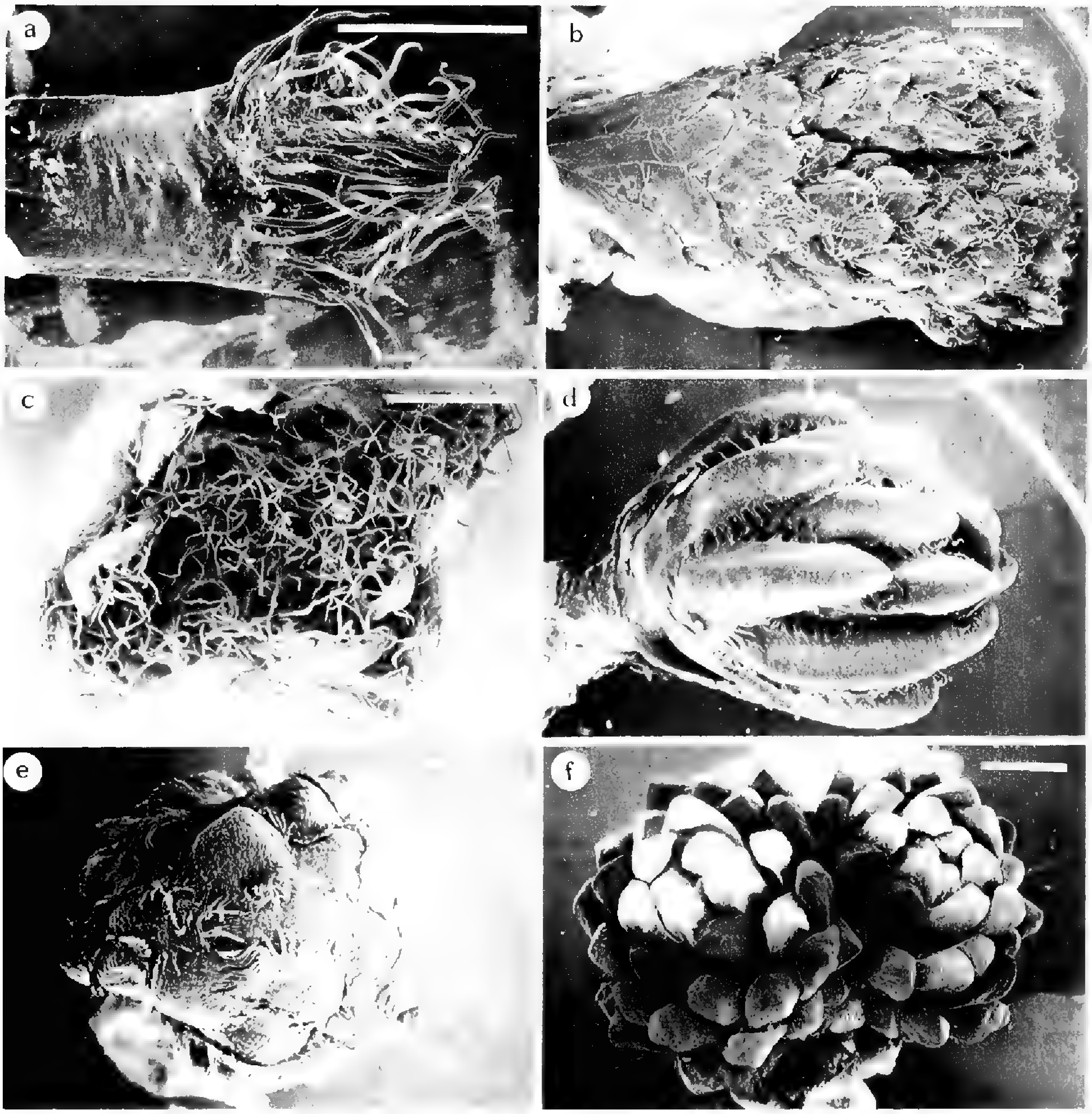

FIGURE 1. Scanning electron micrographs of *Dactylocardamum* and *Xerodraba.* a–c, *D. imbricatifolium* (holotype): a, leaf; b, portion of branched stem; c, top view of branch tip. d, *X. pectinata* (*Pisano & Cárdenas 4749,* HIP), leaves; e, *X. glebaria* (*Koslowsky 19,* z), leaves; f, *X. patagonica* (*Donat 181,* GH), leaves. Scale bars = 1 mm.

branch can therefore be separated by several to many obsolete to very short nodes.

Dactylocardamum is easily distinguished from all other genera of the Brassicaceae by a unique combination of characters: the septum is completely lacking, the inflorescence is reduced to a terminal subsessile flower, the axillary fruits are sandwiched and completely hidden between the densely imbricate, wholly persistent leaves, the fruiting pedicel is reduced to only 0.4 mm long, the internodes are obsolete or reduced to only 0.05–0.2 mm long, and the branches are subdichotomous and fingerlike (see FIGURES 1a–c, 3).

Two other South American genera of the Brassicaceae, *Delpinophytum* Speg. and *Lithodraba* Boelcke (Boelcke, 1952; Boelcke & Romanczuk, 1984), produce dense cushions and have growth habits fairly similar to those of *Dactylocar-*

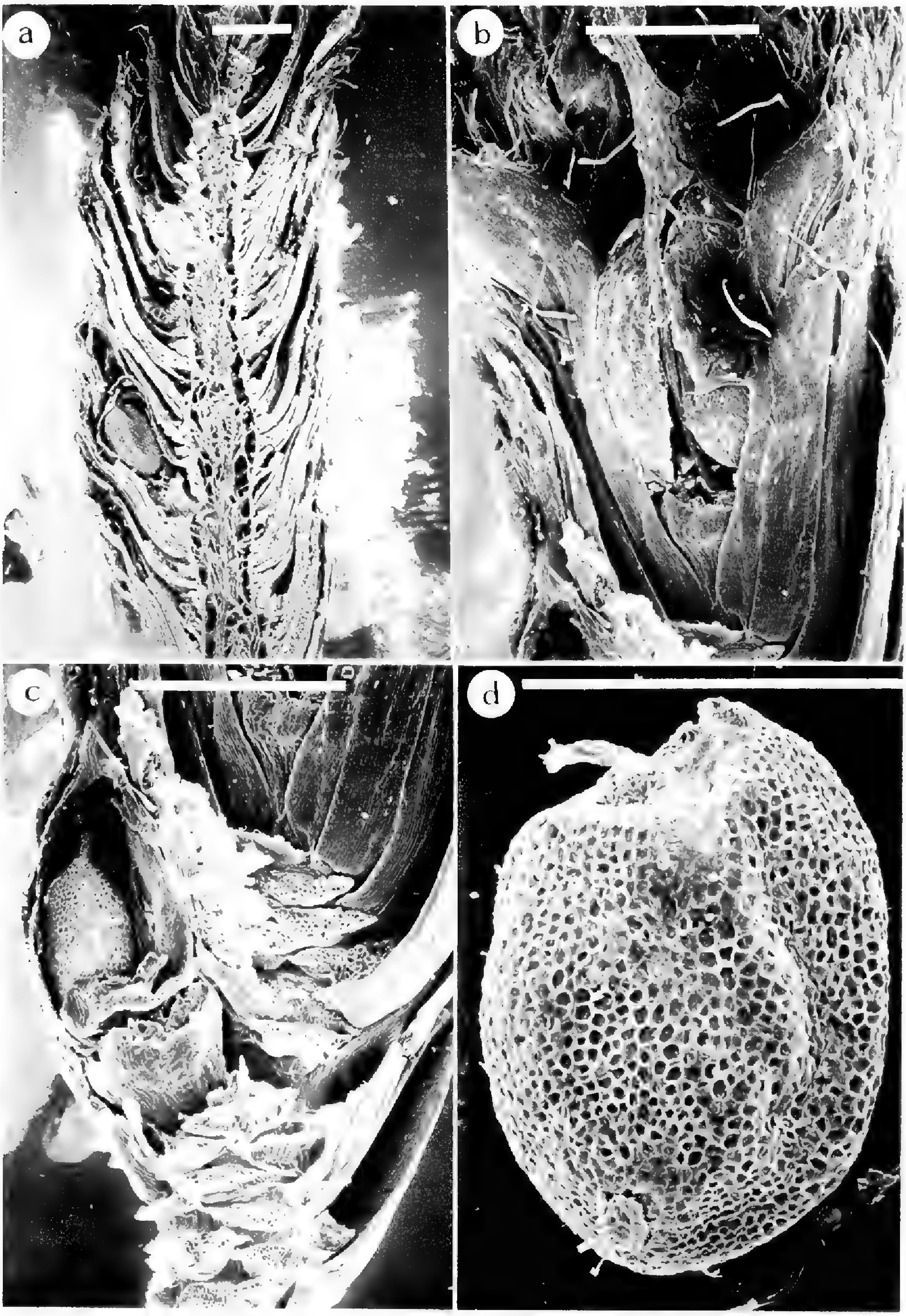

FIGURE 2. *Dactylocardamum imbricatifolium*: a, longitudinal section of branch showing fruit with 1 seed and densely imbricate leaves; b, fruit surrounded by several leaves; c, portion of branch showing fruit on short peduncle and scars of removed leaves; d, seed. Scale bars = 1 mm.

damum and *Xerodraba*. *Lithodraba* is somewhat related and is perhaps a sister group of *Englerocharis* Muschler. It is easily distinguished from the new genus in having racemose inflorescences, four stamens, long nonimbricate leaves, septate fruits, and ringlike nectar glands. *Delpinophytum* is indistinguishable from *Xerodraba* in almost every aspect except the type of fruit flattening: the former has angustiseptate fruits, while the latter has latiseptate ones. Although Schulz (1936) placed *Delpinophytum* in the tribe Lepidieae DC. and *Xerodraba* in the Sisymbrieae DC., I believe that they are sister genera and may even be congeneric.

Dactylocardamum imbricatifolium Al-Shehbaz, gen. et sp. nov.

Plantae perennantes pulviniforme; ramis subdichotomis dactyliformibus dense imbricati-foliosis, usque ad 3 cm longis, 3–4.5 mm latis. Folia minuta oblongo-obovata, imbricata, persistens, subappressa, papyracea, superne pilosi-ciliata, 2.5–3.5 mm longa, 1.1–1.6 mm lata. Flores solitares apicales subsessiles. Sepala erecta oblonga, membranacea, 2.5–3 mm longa. Petala lineari-spathulata, 4–4.5 mm longa, ca. 1 mm lata. Pedicelli fructiferi crassi, axillari, usque ad 0.4 mm longi. Siliqua ovoidea, membranacea, aseptata, glabra, brevissime pedunculata; stylo filiforme 2.5–3 mm longo. Semina 1 vel 2, oblonga vel ovata, pendula; cotyledones incumbentes.

Perennial herb forming dense cushions, woody and much branched at base, the ultimate branches fingerlike, thick, 1–3 cm long, 3–4.5 mm in diameter. Leaves persistent, papery, densely imbricate, separated by internodes 0.05–0.2 mm long, subappressed, oblong-obovate, 2.5–3.5 mm long, 1.1–1.6 mm wide, obtuse at apex, ciliate and sparsely pubescent on the upper surface of the green, distal, bladelike half, the petiolelike lower half conspicuously flattened, straw colored, 1.4–1.9 mm long, 0.8–1 mm wide; trichomes unbranched, 0.5–1.2 mm long. Flowers solitary, subsessile, each terminating a branch, soon becoming lateral as young fruit develops. Sepals erect, membranaceous, oblong, 2.5–3 mm long, 1–1.2 mm wide, sparsely pubescent below rounded apex, nonsaccate at base. Petals spatulate-linear, 4–4.5 mm long, ca. 1 mm wide, attenuate at base, obtuse at apex, somewhat crisped distally. Stamens 6, somewhat tetradynamous; filaments erect, filiform, 2.5–3 mm long; anthers oblong, 0.7–0.8 mm long. Nectar glands 4, 1 on each side of each lateral stamen. Fruiting peduncles thick, axillary, to 0.4 mm long. Fruits ovoid, sessile, sandwiched and completely hidden between leaves, indehiscent except when subjected to force, somewhat inflated, 1.2–1.8 mm long, 1–1.4 mm wide; valves membranaceous, glabrous; septum lacking; style filiform, 2.5–3 mm long in flowering or fruiting material; stigma entire. Seeds 1 or 2 per fruit, oblong to ovate, plump, 1–1.2 mm long, 0.8–0.9 mm wide, dark brown, reticulate, wingless, pendulous from short, subapical funicles; cotyledons incumbent or obliquely so.

TYPE. Peru, Cordillera Blanca, Llanganuco Valley, Pisco Creek, 15,500 ft [ca. 5085 m] alt., August 1959, *J. C. Tothill 144* (holotype, UC; fragment, GH).

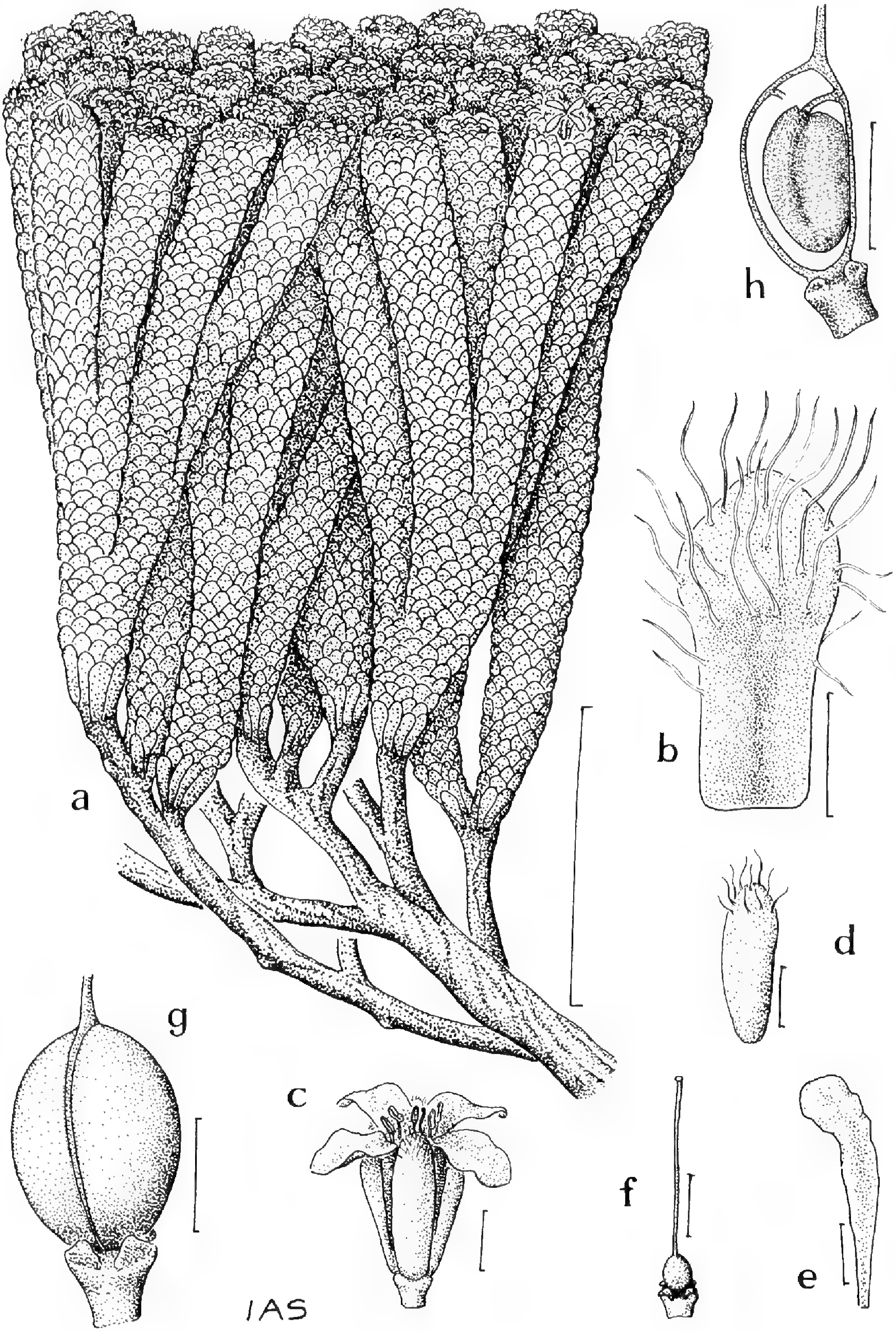

FIGURE 3. *Dactylocardamum imbricatifolium*: a, portion of plant; b, leaf; c, flower (one stamen removed); d, sepal; e, petal; f, pistil; g, fruit with part of style; h, opened fruit. Scale bars: a, 1 cm; b–h, 1 mm. Drawn from the holotype by the author.

Additional field notes on the type read: "Mat plant forming rather tight cushions over rocks of lower talus slope. South exposure, associated with other mat plants."

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I am most grateful to Reed C. Rollins for his critical review of the manuscript, and to Donald H. Pfister for obtaining funds from the Harvard University Herbaria that supported the SEM portion of the research. I am thankful to Elizabeth A. Shaw for correcting the Latin description, to Thomas Duncan and Barbara Ertter for permitting the deposition at GH of fragments of the holotype, to Trisha Rice for the SEM work, to Barbara Nimblett for typing the manuscript, to Michael A. Canoso for obtaining the loan, to Elizabeth B. Schmidt and Stephen A. Spongberg for their editorial advice, and last, but certainly not least, to my wife, Mona, for her continuous support.

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BOOK REVIEW

Grass Systematics and Evolution, edited by Thomas R. Soderstrom, Khidir W. Hilu, Christopher S. Campbell, and Mary E. Barkworth. Smithsonian Institution Press, Washington, D. C., 1988. xiv + 474 pp. illustrations. ISBN 0-87474-300-1. $45 hardcover.

In July, 1986, some 150 students of grass systematics from North and South America, Europe, Africa, Asia, Australia, and New Zealand gathered at the Smithsonian Institution's Natural History Museum to discuss the systematics and evolutionary biology of grasses. The genuinely international character of the International Symposium on Grass Systematics and Evolution should not have been a surprise, for the principal organizer was Thomas Soderstrom. Soderstrom was known for his enthusiastic encouragement of—and collaboration with—numerous members of the worldwide community of grass systematists. His death in 1987 prevented him, however, from witnessing the publication of this attractive, cleanly edited volume of papers from the symposium.

The book's 33 papers are organized under seven headings (Structural Diversity; Biochemical Diversity; Reproductive Biology; Evolution; Systematics of Major Groups; Taxonomic Data and Analysis; and Grasses: Past, Present, and Future). The majority of the contributions are review papers, and with few exceptions the coverage under each heading is rather complete (e.g., under Biochemical Diversity are treatments of photosynthetic pathways, chloroplast DNA, nuclear DNA, amino-acid profiles, and isozymes). Following the papers are a composite 71-page bibliography and an index to taxonomic names. The organization of this volume directly reflects that of the symposium, with each major section more or less corresponding to the proceedings of a given morning or afternoon of the conference.

The conveners apparently called for a survey of grass systematics, and the contributors provided it. While symposium volumes often comprise odd combinations of articles that take off in their own directions, this one represents a theme developed. Unfortunately, comprehensiveness and consistency seem to have been provided at the cost of original analysis and synthesis. Even as reviews, several of the articles discuss little that is new; they repeat the contents of earlier reviews, cite a few of the most recent papers, and sign off. Others do present fresh overviews of segments of the literature that were in need of such treatment. Although the majority of the offerings are reviews, the volume also includes some significant original contributions (e.g., Barkworth and Everett on generic delimitation and alignments in the Stipeae, Campbell and Kellogg on cladistic structure of the Poales, Kellogg and Campbell on cladistic structure of the Poaceae, Soderstrom and Ellis on tribal delimitation in the Bambusoideae, and Zuloaga on infrageneric classification of *Panicum*).

Journal of the Arnold Arboretum **70:** 523, 524. October, 1989.

This volume also gives the reader a sense of the level of satisfaction in the agrostological community with the now-conventional five-subfamily system; it seems to me that there is more complacency than there should be. The Festucoid/Panicoid dichotomy, which served agrostologists well in its time, has finally passed away. Indeed, the 1959 Montreal grass symposium, to which the Washington symposium might be compared, is remembered today in large part for the boost it gave to the five-subfamily system, which was then emerging. One could not have expected a new synthesis to appear on cue in 1986, but a little more questioning of the current system might have gone a long way. The subfamily Arundinoideae, for instance, is widely acknowledged to be an unnatural assemblage. Most of the authors surveying particular sorts of characters mention this in passing but seem content to catalog the odd character combinations that occur in the group, note the need for further analysis, and then move on to the other, more clearly defined subfamilies. Specific attention to the realignment of arundinoid elements, and to other outstanding problems with the current system, would have evidenced a greater interest in progress.

Despite these problems, the volume does include many useful reviews, as well as a handful of original contributions. Even the weaker reviews provide citations of the key literature. Consequently, the book's greatest success is as a wide-ranging survey of grass systematics, and as the best available point of entry into the enormous literature of this discipline. Properly supplemented, it might even serve as the principal text for a course on the subject. Agrostologists would be well advised to have a copy close at hand.—JERROLD I. DAVIS, L. H. Bailey Hortorium, Cornell University, Ithaca, New York 14853.

INDEX

JOURNAL OF THE
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HARVARD UNIVERSITY VOLUME 70 1989

Dates of Issue

No. 1 (pp. 1–152) issued 10 January 1989.
No. 2 (pp. 153–306) issued 25 April 1989.
No. 3 (pp. 307–442) issued 14 July 1989.
No. 4 (pp. 443–542) issued 11 October 1989.

Contents of Volume 70 *1989*

The *Journal of the Arnold Arboretum* is a refereed botanical journal that presents the results of original research in systematic and evolutionary botany and related disciplines. Beginning in 1988, critical, in-depth reviews of major books published in the above fields will also be included on a periodic but timely basis. In addition to Arboretum staff and associates, we encourage botanists worldwide to submit manuscripts to the *Journal.* We particularly welcome those that record the results of studies utilizing Harvard University Herbaria (A and GH) collections or focusing on geographic areas of traditional interest to Arboretum staff. A guide for potential contributors, periodically published in the *Journal,* is available on request.

Journal of the Arnold Arboretum *October, 1989*

CONTENTS OF VOLUME 70, NUMBER 4

Volume 70, Number 3, including pages 307–441, was issued 14 July 1989.