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PHYLOGENETIC IMPLICATIONS OF LEAF ANATOMY IN SUBTRIBE MELITTIDINAE (LABIATAE) AND RELATED TAXA

MONES S. ABU-ASAB AND PHILIP D. CANTINO[1]

Leaf anatomy was surveyed in 39 species of Labiatae, including representatives of all six genera of subtribe Melittidinae. When subjected to cladistic analysis, variation in stomatal subsidiary-cell configuration, glandular-trichome morphology, and leaf histology provides evidence for phylogenetic relationships among these genera. Peculiar saclike idioblasts in the mesophyll of *Physostegia* and *Brazoria* appear to represent a synapomorphy. This clade is further corroborated by the shared absence of bundle-sheath extensions, probably a derived state. Support for a more inclusive clade comprising *Physostegia, Brazoria,* and *Macbridea* is provided by the shared presence of a particular type of trichome and absence of keels on the secondary veins. Two other apparently derived states, diallelocytic stomata with four subsidiary cells and subsessile glandular trichomes with partial radial walls, suggest that the sister group of the *Macbridea-Physostegia-Brazoria* clade is *Galeobdolon* or *Synandra.* Leaf anatomy provides no evidence that subtribe Melittidinae is monophyletic.

There is relatively little published information on the anatomy of the Labiatae, a rather surprising situation given the size and economic importance of the family. We are aware of only a few works on leaf anatomy in particular. The broadest in taxonomic scope are Solereder's (1908) general anatomical survey and Inamdar and Bhatt's (1972) study of stomatal types in the family. Other works, more intensive but narrower in taxonomic scope, are those of Bokhari and Hedge (1971) on tribe Meriandreae, Rudall (1979, 1980) on subtribe Hyptidinae, Azizian and Cutler (1982) on *Phlomis* L. and *Eremostachys* Ledeb., and Shah and Naidu (1983) on "tribe Ocimoideae."

The primary focus of this paper is the leaf anatomy of subtribe Melittidinae, but the study collection was selected to include a variety of other Labiatae so

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that it would be possible to evaluate the systematic significance of characters that vary within the Melittidinae. The work was undertaken with two objectives: first, to seek anatomical evidence for the monophyly (*sensu* Hennig, 1966) of subtribe Melittidinae and/or its suprageneric subgroups; and second, to contribute to the body of information available on the leaf anatomy of the Labiatae.

TAXONOMIC BACKGROUND

LABIATAE

The most widely used classification of the Labiatae today is that of Briquet (1895–1897), which is heavily based on a series of comprehensive treatments of the family by Bentham (1832–1836, 1848, 1876). Briquet's classification differs from Bentham's mainly in the ranking and interrelationships of suprageneric groups rather than in the content of those groups (Cantino & Sanders, 1986). The suprageneric groups of both authors are based principally on gross floral morphology.

An alternative classification of the Labiatae was proposed by Erdtman (1945) on the basis of palynological features. He subdivided the family into two subfamilies: Lamioideae, with tricolpate pollen that is shed in a two-celled stage; and Nepetoideae, with hexacolpate pollen shed in a three-celled stage. A variety of other characters have since been found to correlate with these (Wunderlich, 1967; Zoz & Litvinenko, 1979; Cantino & Sanders, 1986). Subfamily Lamioideae is characterized by albuminous seeds containing a spatulate embryo, the production of iridoid glycosides, the absence of rosmarinic acid, a low volatile terpenoid content (the leaves hence usually not aromatic), moderately unsaturated seed oils, and a nonmucilaginous pericarp. Subfamily Nepetoideae is characterized by exalbuminous seeds containing an "investing" embryo (terminology of Martin, 1946), the absence of iridoid glycosides, the production of rosmarinic acid, high volatile terpenoid content (the leaves hence aromatic), highly unsaturated seed oils, and a frequently mucilaginous pericarp. Erdtman's subfamilial classification (1945), with its strong character support, conflicts markedly with Briquet's (1895–1897) widely used system but is highly congruent with Bentham's (1876) tribal classification (Cantino & Sanders, 1986). In the present study, Erdtman's subfamilial classification has been adopted.

TRIBE LAMIEAE

Inasmuch as a primary objective of this study is to investigate whether subtribe Melittidinae is monophyletic, it is necessary to delimit a monophyletic study group that includes (but is not limited to) the subtribe. The Melittidinae fall within Erdtman's subfamily Lamioideae. Although this subfamily is a primary phenetic subgroup of the Labiatae, it has not been possible to demonstrate its monophyly through the identification of synapomorphies (Cantino & Sanders, 1986). There is, however, a less inclusive group that includes subtribe Melittidinae and appears to be monophyletic. It is composed of Bentham's (1876) tribes Lamieae and Prasieae, excluding *Anisomeles* R. Br., *Scutellaria*

L., and probably *Salazaria* Torrey. This group is similar in circumscription to Wunderlich's (1967) subfamily Lamioideae ("Stachyoideae"; corrected nomenclature follows Sanders & Cantino, 1984), but if it is recognized at the tribal level it must be called Lamieae. Except where otherwise stated, all future use of the name Lamieae will refer to the group thus circumscribed.

The monophyly of tribe Lamieae is supported by one clear synapomorphy, one probable synapomorphy, and a third congruent character, the polarity of which cannot currently be assessed. Hagemann and co-workers (1967) found an allenic component, which they presumed to be laballenic acid, in the seed oils of all examined members of Bentham's Lamieae and Prasieae except *Anisomeles* and *Scutellaria.* The allenic component was not found in these two genera or in the other examined members of Erdtman's subfamily Lamioideae, and it was found in only four of 122 examined species of subfamily Nepetoideae. The polarity of this character can be assessed by outgroup analysis (Watrous & Wheeler, 1981; Maddison *et al.,* 1984), using suprageneric taxa of the Verbenaceae as outgroups. (It is generally believed that the Labiatae evolved from the Verbenaceae, which would make the latter at best paraphyletic, but it is unclear which members of the Verbenaceae are the closest relatives of the Labiatae. All members of the Verbenaceae must therefore be included among the outgroups in the assessment of character polarity within the Labiatae.) In an unpublished study, Robert Kleiman (pers. comm.) found the allenic component to be absent from the seed oils of all 24 species of Verbenaceae examined, including representatives of three subfamilies and eight tribes. Occurrence of the allenic component therefore appears to be a derived trait within the Labiatae and represents a synapomorphy of a monophyletic group composed of Bentham's tribes Lamieae and Prasieae (excluding *Scutellaria* and *Anisomeles*). Because *Salazaria* appears to be closely related to *Scutellaria* on morphological (Epling, 1942) and chemical (Kooiman, 1972) grounds, it should perhaps be excluded from the Lamieae as well, although its seed oils have not been investigated.

Embryological peculiarities of the Lamieae offer two other possible synapomorphies. The mature embryo sac in the Labiatae tends to be two-lobed, with distinct micropylar and chalazal sections. Genera differ in the relative size and shape of these lobes. Wunderlich (1967) reported that the micropylar lobe is much longer and broader than the chalazal one in Bentham's Lamieae and Prasieae (except *Scutellaria* and *Anisomeles*), whereas the micropylar lobe is shorter than or equal to the chalazal in the rest of the Labiatae, except two genera of Nepetoideae. *Salazaria* was not examined. Embryo-sac shape has been reported for ten genera of Verbenaceae representing three subfamilies and six tribes (Junell, 1934; Misra, 1939; Tatachar, 1940; Pal, 1951; Maheshwari, 1954; Khaleel & Nalini, 1972; Spies & Stirton, 1982; Spies, 1984a, 1984b; Thirumaran & Lakshmanan, 1984). In only one species, *Clerodendrum ugandense* Prain, does the embryo sac resemble those found in the Lamieae (Junell, 1934). In all other Verbenaceae examined, including four other species of *Clerodendrum* L. (Junell, 1934; Misra, 1939), the micropylar end of the embryo sac is usually little if at all broader (in some species narrower) than the chalazal end; if it is much broader, it is shorter than the chalazal end. The characteristic embryo-sac shape of the Lamieae is thus probably derived, although more Verbenaceae need to be studied before character polarity can be assessed with confidence.

Wunderlich (1967) reported the presence of what Schnarf (1918) called "Lamium-type" glandular trichomes (identical to our "type 4"; see trichome classification below) on the outside of the integument in recently fertilized ovules of all examined genera of Bentham's Lamieae and Prasieae except *Scutellaria* and *Anisomeles*; no such glandular trichomes were found in other Labiatae (but *Salazaria* was not examined). It is not possible to assess the polarity of this character because of lack of data for the Verbenaceae, but its distribution in the Labiatae closely parallels that of the other two characters.

Although a strong case can be made for the existence of a monophyletic tribe Lamieae (as circumscribed above), one must remain aware that the characters delimiting the group have been examined in a minority of its members. Seed-oil chemistry was studied (Hagemann *et al.*, 1967) in 18 of the 42 genera of Bentham's (1876) Lamieae and Prasieae, and the two embryological characters cited above were studied in 16 genera of these tribes (Wunderlich, 1967). There are 11 genera for which data are available for all three characters. Because the congruence between the three characters is perfect in these genera, we are assuming that the characters are highly correlated in the group as a whole. Examination of more genera may demonstrate, however, that others besides *Scutellaria* and *Anisomeles* are not members of the monophyletic group. Our tentative inclusion of all of Bentham's Lamieae and Prasieae (except *Scutellaria, Anisomeles,* and possibly *Salazaria*) reflects our confidence in Bentham's usually excellent taxonomic judgment—i.e., we are assuming that those genera not yet examined for embryology and seed-oil chemistry really are closely related to those that have been.

SUBTRIBE MELITTIDINAE

The historical changes in the circumscription of subtribe Melittidinae have been summarized by Cantino (1985a). As currently circumscribed, the subtribe comprises six genera, four of them (*Brazoria* Engelm. ex A. Gray, *Macbridea* Elliott ex Nutt., *Physostegia* Bentham, and *Synandra* Nutt.) North American, one (*Chelonopsis* Miq.) Asian, and one (*Melittis* L.) European. The group is delimited on the basis of a set of calyx and corolla characters that were proposed by Bentham (1876) and adopted by Briquet (1895–1897): calyx broadly campanulate, membranaceous or herbaceous, 3- or 4-lobed or 5-toothed, with venation scarcely visible; corolla tube long-exserted from calyx, broad at base or markedly dilated distally, with upper lip broad and scarcely concave.

A survey of these characters in subfamily Lamioideae (Cantino, unpublished data) revealed that none is diagnostic of subtribe Melittidinae. Three states used by Bentham and Briquet (calyx broadly campanulate, calyx membranaceous or herbaceous, and corolla tube long-exserted from the calyx) are present throughout the Melittidinae but are also common elsewhere in the subfamily. The other character states cited by these authors are not only found elsewhere in the subfamily but also occur in only some members of the Melittidinae.

Weak calyx venation at anthesis is characteristic of *Physostegia, Brazoria,* and (to a degree) *Synandra,* but not the other three genera. The upper lip of the corolla is broad and only barely concave in *Physostegia, Chelonopsis,* and three species of *Brazoria* but markedly concave in *Macbridea, Synandra,* and *Brazoria scutellarioides.* The number of calyx lobes varies from three to five, with no two genera having the same calyx morphology. Corolla-tube shape is similarly variable. It is, of course, insufficient to consider characters only singly. In groups in which parallel and/or reticulate evolution have been common, taxa are often distinguished by combinations of character states, with no single state unique to any taxon ("kaleidoscopic variation"; see Cantino, 1982). However, the combination of the three character states that occur throughout the Melittidinae is also found in some or all species of at least ten other genera in subfamily Lamioideae (*Colquhounia* Wallich, *Gomphostemma* Bentham, *Lamium* L., *Microtoena* Prain, *Phyllostegia* Bentham, *Scutellaria, Stenogyne* Bentham, *Tetraclea* A. Gray, *Thuspeinanta* T. Durand, and *Trichostema* L.), seven of them in tribe Lamieae as circumscribed above.

We are unaware of any morphological feature or combination of features that would distinguish subtribe Melittidinae from the rest of tribe Lamieae, let alone a clearly derived feature. Nor does cytology provide evidence for the monophyly of the subtribe. Chromosome number is extremely variable among the genera, chromosome size is moderately variable, and other karyotypic features are restricted to particular species or species groups (Cantino, 1985a). The present study was undertaken to investigate whether leaf anatomy might provide evidence for the monophyly of subtribe Melittidinae, where morphology and cytology have not.

STOMATAL TERMINOLOGY

Because of the variety of stomatal classifications now available and the sometimes conflicting use of terms contained therein, a brief review of the situation is necessary if the reader is to understand our adopted terminology. For a more comprehensive and very enlightening review, see Rasmussen (1981).

Stomata have been classified on the basis of three criteria: the configurations of neighboring and subsidiary cells in mature stomata (Vesque, 1889; Metcalfe & Chalk, 1950; Payne, 1970), stomatal ontogeny (Pant, 1965; Stevens & Martin, 1978; Payne, 1979), and a combination of the above (Fryns-Claessens & Van Cotthem, 1973; Stevens & Martin, 1978).

The first criterion is relatively uncomplicated and has the advantage that it can be applied when one is working with mature leaves. Its principal disadvantage is that the same stomatal morphology may develop through different ontogenetic pathways in different plants and may therefore not be homologous (Rasmussen, 1981, and references cited therein). Classifications based partly or completely on stomatal ontogeny are more difficult to apply, and some of the terms used are defined differently by different authors.

Pant (1965) classified stomata on the basis of their ontogenetic pathways: mesogenous stomata, in which the guard-cell mother cell and all subsidiaries are derived from the same meristemoid; perigenous stomata, in which all neighboring and subsidiary cells are derived from protodermal cells other than the meristemoid that produces the guard-cell mother cell; and mesoperigenous stomata, in which the surrounding cells are of dual origin, some mesogenous and others perigenous.

The guard-cell mother cell is the immediate progenitor of the guard cells. Subsidiary cells surround the guard cells and clearly differ from other epidermal cells; neighboring cells immediately surround the guard cells but do not differ in shape from the remaining epidermal cells (Fryns-Claessens & Van Cotthem, 1973; Rasmussen, 1981). Unfortunately, the ambiguity of the term "meristemoid" has rendered Pant's and other ontogenetic classifications difficult to use.

Stomatal ontogeny starts with the unequal division of a protodermal cell. The smaller daughter cell, which contains a denser cytoplasm, divides again unequally or directly produces (by an equal division) the pair of guard cells (Fryns-Claessens & Van Cotthem, 1973; Payne, 1979; Rasmussen, 1981). The term "meristemoid" was used by Fryns-Claessens and Van Cotthem (1973) and Rasmussen (1981) to refer to the smaller daughter cell of the original protodermal cell, whereas Payne (1979) referred to the protodermal cell itself as the meristemoid. If the latter usage is adopted, there is always at least one neighboring or subsidiary cell that is derived from the meristemoid (i.e., mesogenous), so a true perigenous type cannot exist (Fryns-Claessens & Van Cotthem, 1973; Payne, 1979). A consequent disadvantage of Payne's terminology is that it is less precise; i.e., a wider variety of ontogenetic pathways is necessarily subsumed under the same term, mesoperigenous (see *fig. 3* in Rasmussen, 1981). For this reason, and because the meristemoid *sensu* Payne can only be recognized after it has divided and hence no longer exists (Rasmussen, 1981), the ontogenetic terminology of Fryns-Claessens and Van Cotthem (1973) rather than that of Payne (1979) is adopted in this study. The more complex system of Stevens and Martin (1978) is even more precise but is not used here because of the difficulty in distinguishing "agene" cells (Rasmussen, 1981) from perigene cells *sensu* Rasmussen.

MATERIALS AND METHODS

Leaf material was obtained from 53 specimens representing 39 species (see APPENDIX 1), including all species of *Brazoria, Macbridea, Melittis,* and *Synandra,* seven of the 12 species of *Physostegia,* and two of the approximately 16 species of *Chelonopsis.* Leaf material of most species was collected from living plants, with herbarium specimens prepared as vouchers. Leaf material of *Chelonopsis, Melittis,* and some species of *Physostegia* was obtained directly from herbarium specimens.

Fresh leaves were fixed in Carnoy's solution (3 parts ethanol to 1 part acetic acid). Dried leaves were revived by soaking them in 5 percent sodium hydroxide for three days at room temperature. Both types of material were then stored in 70 percent ethanol. To prepare the material for study, we used the whole-mount method as well as transverse sectioning of the lamina. In the former method leaves or leaf pieces were stained with ferric tannate (2.5% tannic acid in 50% ethanol, followed by 2.5% ferric chloride in 50% ethanol; modified from Berlyn & Miksche, 1976) and mounted in surface view. In the latter, leaves were infiltrated with and embedded in paraffin (Cutler, 1978) and sectioned at 10-μm thickness with an AO rotary microtome. After sectioning, the leaves were stained with toluidine blue or with safranin O and fast green FCF. The procedure using toluidine blue is outlined in Sakai (1973). The double-staining procedure, adapted from Johansen (1940), required deparaffination of the sections, staining with safranin (1% in 50% ethanol) and fast green (0.1% in 50% ethanol), dehydration through a series of ethanol, xylene : ethanol (1 : 1), and xylene, and mounting in Permount.

A set of permanent slides has been deposited in the Bartley Herbarium of Ohio University (BHO). Drawings were prepared by means of a microprojector or the camera-lucida attachment of an Olympus BH-2 microscope.

RESULTS

STOMATA

Based on shapes and arrangements of mature subsidiary and neighboring cells, the following types of stomata were found in the species examined (see FIGURE 1) (definitions follow Payne, 1970, 1979; and Wilkinson, 1979): anomocytic (stoma surrounded by a limited number of cells that are indistinguishable from other epidermal cells); paracytic (stoma bordered on both sides by one or more subsidiary cells whose long axes lie parallel with the long axis of the guard cells; subsidiary cells sometimes meeting over the poles and sometimes laterally elongated); anisocytic (stoma surrounded by three cells, one of which is markedly smaller than the other two); diacytic (stoma enclosed by a pair of subsidiary cells whose common radial walls are at right angles to the guard cells); and diallelocytic (stoma enclosed by three or more C-shaped cells at right angles to the guard cells).

Two subtypes of diallelocytic stomata were found in the species examined, one with three subsidiary cells and the other with four. The two have not been distinguished by previous authors, including Payne (1970), who discussed the ontogeny of diallelocytic stomata. Since the two types do not always occur together (see TABLES 1, 2), they are worth distinguishing. The three-celled type will be referred to as diallelocytic-1 and the four-celled type as diallelocytic-2.

The ontogenetic pathways of several stomatal types were documented through examination of young leaves in various stages of development (see FIGURE 1). The diallelocytic-1 type was studied in *Scutellaria lateriflora, Stachys riddellii,* and *Stachys tenuifolia* and is mesoperigenous in all. Because the diallelocytic-2 type occurs only with the diallelocytic-1 type in the species examined (although the latter may occur without the former), and the former differs from the latter in having one more subsidiary cell, the ontogenetic pathway reported by Payne (1970) for the diallelocytic-2 type is presumed to occur in the taxa examined in this study. The ontogenetic pathway for the diacytic type was also adopted from Payne (1970). The ontogeny of the anomocytic type was studied in *Scutellaria lateriflora, Stachys tenuifolia,* and *Stachys riddellii* and is perigenous

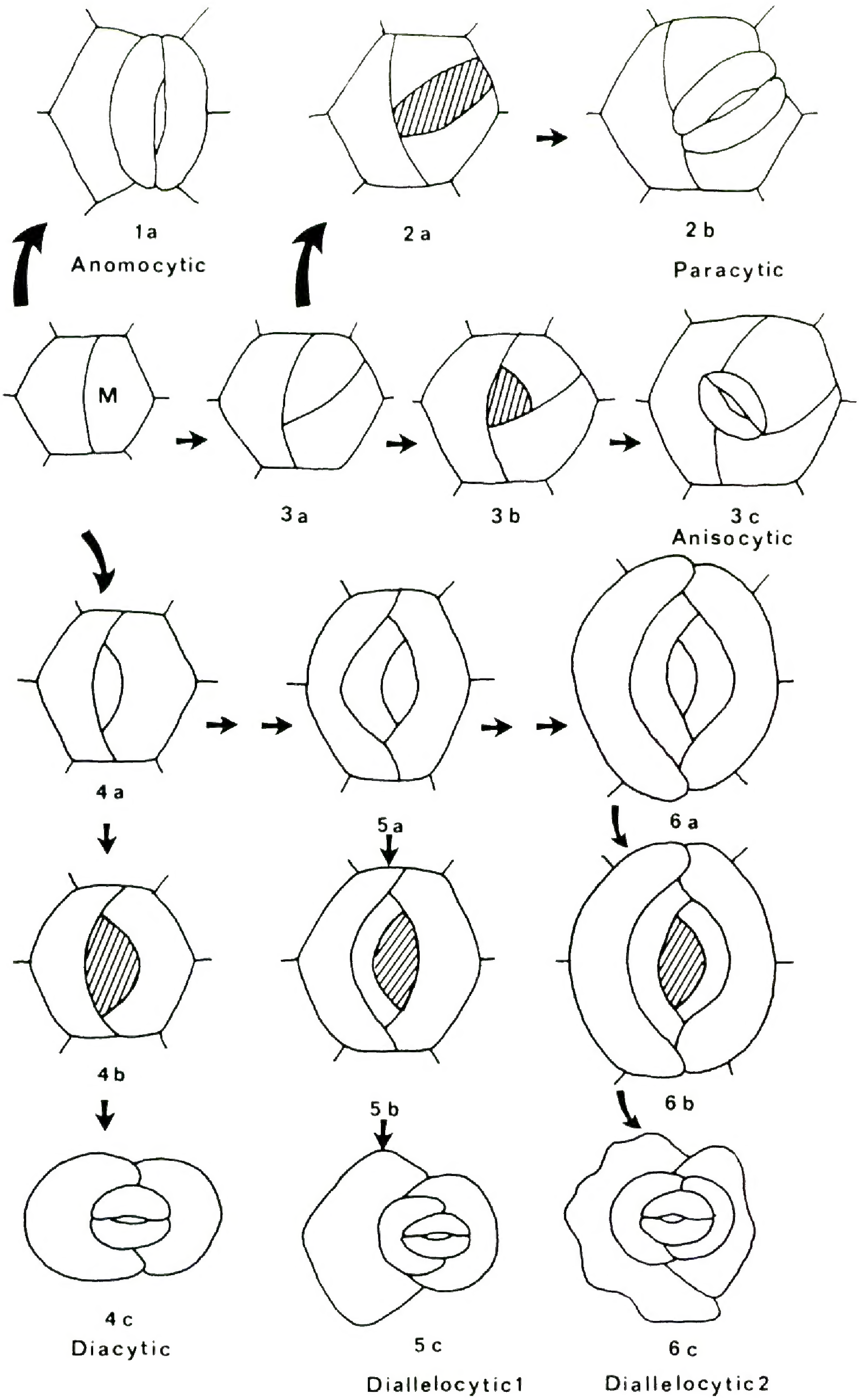

FIGURE 1. Stomatal ontogenetic pathways: anomocytic (1a), paracytic (2a, b), anisocytic (3a–c), diacytic (4a–c), diallelocytic-1 (5a–c), and diallelocytic-2 (6a–c). M = meristemoid (*sensu* Fryns-Claessens & Van Cotthem). Diacytic and diallelocytic-2 ontogenies adopted from Payne (1970).

in all. The ontogeny of the paracytic and anisocytic types was studied in *Trichostema dichotomum.* Both are mesoperigenous, and they share a common initial step in their ontogenetic pathways.

Other stomatal features examined included distribution (viz., both leaf surfaces or abaxial surface only), position in relation to general level of epidermis (viz., sunken or raised), and presence of stomatal ledges. Stomatal ledges are elevated extensions of the cuticle that rise from the guard-cell surface "like an incompletely roofed dome" (Wilkinson, 1979, p. 97). They extend over the stomatal pore, delimiting an outer cavity (see *fig. 10.1* in Wilkinson, 1979). In some taxa similar inner ledges project from the guard cells, forming an inner cavity (Wilkinson, 1979), but only outer ledges were found in the present study.

Published data on stomatal types in Labiatae and Verbenaceae are scarce, and the authors do not always clearly indicate the taxonomic distribution of stomatal types. Data from Inamdar (1969), Ramayya and Rao (1969), Payne (1970), and Inamdar and Bhatt (1972) are summarized in TABLE 1; our own observations are shown in TABLE 2.

Diacytic, diallelocytic-1, and anomocytic stomata are all common in the Labiatae. Of the 39 species we examined, diallelocytic-1 stomata were found in 31, diacytic in 33, and anomocytic in 24. Diacytic and anomocytic stomata occur widely in both the Labiatae and the Verbenaceae, but diallelocytic-1 stomata are apparently rare in the Verbenaceae, having been reported only from *Lippia lanceolata.*

Diallelocytic-2 stomata have been observed in seven genera of Labiatae and one of Verbenaceae. Specifically, we observed this type in six of seven examined species of *Physostegia,* both species of *Macbridea,* one of the four species of *Brazoria,* the single species of *Galeobdolon* Adanson, and two of the seven examined species of *Scutellaria*; it has also been reported from *Ocimum* L., *Plectranthus* L'Hér., and *Lippia* L.

Anisocytic stomata appear to be rare in the Labiatae. We found them only in *Trichostema* and *Prostanthera* Labill. In previous studies anisocytic stomata have been reported from three species of Verbenaceae but not in any Labiatae. We found paracytic stomata only in *Trichostema, Prostanthera,* and *Melittis,* and in the latter two they are rare; they have also been reported from three species of Verbenaceae. Parallelocytic stomata (Payne, 1970), which resemble the diallelocytic-2 type but have the subsidiary cells parallel to the guard cells, have been found in *Lippia lanceolata* (Abu-Asab, 1984) but not in any Labiatae. Helicocytic stomata (Payne, 1970) were included in the drawing of *Lavandula gibsonii* in Inamdar and Bhatt (1972, *fig. 13*).

Leaves are amphistomatic in the North American Melittidinae, *Scutellaria integrifolia,* and the examined species of *Ajuga* L., *Trichostema, Lamium, Marrubium* L., and *Prostanthera.* They are hypostomatic in the rest of the Labiatae examined, including *Chelonopsis* and *Melittis* of subtribe Melittidinae. Most species of Labiatae and Verbenaceae investigated in previous studies have hypostomatic leaves. We found intrageneric variation in this character in *Scutellaria,* and such variation has also been reported in *Leucas* R. Br. and *Ocimum* (Inamdar & Bhatt, 1972), *Eriope* Humb. & Bonpl. ex Bentham (Rudall, 1979), and *Phlomis* (Azizian & Cutler, 1982).

TABLE 1. **Published data on stomatal types in Labiatae and Verbenaceae.**[a]

Species	Stomatal Types[b]								St. Loc.[c]	Ref.[d]
	1	2	3	4	5	6	7	8		
Labiatae										
Subfamily Lamioideae										
Tribe Lamieae										
Leonotis nepetifolia R. Br.	+	–	–	+	–	–	–	–	H	3
Leucas aspera Sprengel	+	+	–	+	–	–	–	–	A	3
L. biflora R. Br.	+	–	–	+	–	–	–	–	H	3
L. cephalotes Sprengel	+	+	–	+	–	–	–	–	H	3
L. linifolia Sprengel	+	–	–	+	–	–	–	–	H	3
L. urticifolia R. Br.	+	–	–	+	–	–	–	–	H	3
L. zeylanica R. Br.	+	–	–	+	–	–	–	–	A	3
Phlomis bracteosa Royle ex Bentham	–	+	–	+	–	–	–	–	H	3
Other Lamioideae										
Anisomeles heyneana Bentham	+	–	–	+	–	–	–	–	H	3
A. ovata R. Br.	+	+	–	+	–	–	–	–	H	3
Dysophylla auricularia Blume	–	+	–	+	–	–	–	–	H	3
Pogostemon parviflorus Bentham	+	–	–	+	–	–	–	–	H	3
P. purpurascens Dalz.	+	+	–	+	–	–	–	–	H	3
Subfamily Nepetoideae										
Tribe Mentheae										
Mentha viridis L.	+	+	–	+	–	–	–	–	H	3
Micromeria capitata Bentham	+	–	–	+	–	–	–	–	H	3
Tribe Ocimeae										
Acrocephalus capitatus Bentham	+	+	–	+	–	–	–	–	H	3
Coleus amboinicus (Bentham) Lour.	+	–	–	+	–	–	–	–	H	3
C. blumei Bentham	+	+	–	+	–	–	–	–	H	3
Hyptis suaveolens (L.) Poit.	+	–	–	+	–	–	–	–	H	3
Lavandula burmanii Bentham	+	–	–	+	–	–	–	–	H	3
L. gibsonii J. Graham	+	–	–	+	–	–	+	–	H	3
Moschosma polystachyum Bentham	+	–	–	+	–	–	–	–	H	3
Ocimum adscendens Willd.	+	+	–	+	–	–	–	–	?	5
O. basilicum L.	+	+	–	+	–	–	–	–	A	3
O. basilicum L.	+	+	+	+	–	–	–	–		5
O. canum Sims	+	+	–	+	–	–	–	–	H	3
O. gratissimum L.	+	–	–	+	–	–	–	–	H	3
O. kilimandscharicum Gürke	+	–	–	+	–	–	–	–	H	3
O. sanctum L.	+	–	–	+	–	–	–	–	H	3
O. sanctum L.	+	–	–	+	–	–	–	–		5
Orthosiphon pallidus Royle ex Bentham	+	+	–	+	–	–	–	–	H	3
Plectranthus australis R. Br.	–	–	+	–	–	–	–	–	?	4
P. incanus Link	+	–	–	+	–	–	–	–	H	3
P. mollis (Burman) Kuntze	+	–	–	+	–	–	–	–	H	3
Tribe Salvieae										
Salvia plebeia R. Br.	+	+	–	+	–	–	–	–	H	3
S. santolinifolia	+	–	–	+	–	–	–	–	H	3
Verbenaceae										
Subfamily Verbenoideae										
Tribe Citharexyleae										
Citharexylum subserratum Sw.	–	–	–	+	–	–	–	–	A	2
Duranta plumieri Jacq.	–	–	–	+	+	+	–	–	H	2
Tribe Lantaneae										
Lantana camara L.	+	–	–	+	–	–	–	–	A	2
Lippia lanceolata Michaux	+	+	+	+	–	–	–	+	A	1
Stachytarpheta jamaicensis (L.) M. Vahl	+	–	–	–	–	–	–	–	A	2
Tribe Petreeae										
Petrea volubilis L.	+	–	–	+	–	–	–	–	H	2
Tribe Verbeneae										
Verbena hastata L.	–	–	–	+	–	–	–	–	H	1
V. urticifolia L.	–	–	–	+	–	–	–	–	H	1
V. venosa Gillies & Hooker	+	–	–	+	–	–	–	–	A	2

TABLE 1 (*continued*).

Species	Stomatal Types 1	2	3	4	5	6	7	8	St. Loc.	Ref.
Verbenaceae (continued)										
Subfamily Viticoideae										
Tribe Clerodendreae										
Clerodendrum fragrans R. Br.	+	-	-	+	-	-	-	-	H	2
C. inerme (L.) Gaertner	-	-	-	+	-	+	-	-	H	2
C. phlomoides L.f.	-	-	-	+	-	+	-	-	H	2
C. splendens Don	+	-	-	+	-	-	-	-	H	2
C. umbellatum Poiret	+	-	-	+	-	-	-	-	H	2
Holmskioldia sanguinea Retz.	+	-	-	+	+	-	-	-	H	2
Tribe Viticeae										
Gmelina arborea Roxb.	-	-	-	+	-	-	-	-	H	2
Vitex negundo L.	-	-	-	+	+	-	-	-	H	2

[a] Diallelocytic types in Inamdar (1969) and Inamdar and Bhatt (1972) were interpreted from their drawings. Subfamilial classification of Labiatae follows Cantino and Sanders's (1986) circumscription of Erdtman's (1945) subfamilies. Tribal classification within subfamily Nepetoideae follows Bentham (1876), with nomenclature corrected by Sanders and Cantino (1984). Tribe Lamieae is circumscribed as discussed in text. Verbenaceae classification follows Briquet (1895).

[b] Stomatal types: 1 = diacytic, 2 = diallelocytic-1, 3 = diallelocytic-2, 4 = anomocytic, 5 = anisocytic, 6 = paracytic, 7 = helicocytic, 8 = parallelocytic. +, present; -, absent.

[c] Stomatal location: A = amphistomatic, H = hypostomatic.

[d] References: 1 = Abu-Asab, 1984; 2 = Inamdar, 1969; 3 = Inamdar & Bhatt, 1972; 4 = Payne, 1970; 5 = Ramayya & Rao, 1969.

Outer stomatal ledges were present in all genera except *Trichostema.* Stomata were found to be at the same level as the epidermis in 24 species, slightly elevated in 12, and markedly elevated in four. Stomatal position varied within a number of genera and within one species (*Physostegia virginiana*). It is probably of little taxonomic value at the generic level and of none in delimiting suprageneric groups.

Our data do not support the observations of El-Gazzar and Watson (1968, 1970) regarding the stomata of Bentham's tribe Lamieae. These authors (1970, p. 476) maintained that if *Prunella* L., *Cleonia* L., and the North American Melittidinae are excluded, anomocytic stomata "are the rule" in Bentham's "Stachydeae" (Lamieae). This is not the case, however, in the Lamieae that we examined. All 16 investigated species of Bentham's Lamieae (including *Scutellaria* but not the North American Melittidinae) had anomocytic stomata; however, all but one also had diacytic stomata, and 12 of them had diallelocytic stomata as well. In most species in which both diacytic and anomocytic stomata were found, the former type was more abundant. El-Gazzar and Watson's (1970) generalization about Bentham's Lamieae thus appears to be incorrect. (On the other hand, anomocytic stomata are at least present in all examined Lamieae except three genera of North American Melittidinae.) Our data also disagree with regard to particular genera in *table 1* of El-Gazzar and Watson (1968). They included *Ajuga, Galeobdolon, Teucrium* L., and most species of *Pogostemon* Desf., *Scutellaria,* and *Stachys* L. in their list of taxa whose stomata

TABLE 2. **Stomatal characters in Labiatae examined.**[a]

Taxa	Stomatal Types[b]						St. Loc.[c]	Ldg.[d]	St. Pos.[e]
	1	2	3	4	5	6			
Subfamily Lamioideae									
Tribe Lamieae									
Subtribe Melittidinae									
Brazoria arenaria	+	+	–	–	–	–	A	+	b
B. pulcherrima	+	+	–	–	–	–	A	+	a
B. scutellarioides	+	+	+	–	–	–	A	+	a
B. truncata	+	+	–	–	–	–	A	+	a
Chelonopsis forrestii	–	–	–	+	–	–	H	+	a
C. moschata	+	–	–	+	–	–	H	+	a
Macbridea alba	+	+	+	–	–	–	A	+	a
M. caroliniana	+	+	+	–	–	–	A	+	a
Melittis melissophyllum	+	+	–	+	–	+	H	+	a
Physostegia angustifolia	+	+	+	–	–	–	A	+	b
P. digitalis	–	+	+	–	–	–	A	+	b
P. godfreyi	+	+	–	–	–	–	A	+	b
P. leptophylla	+	+	+	–	–	–	A	+	a
P. longisepala	–	+	+	–	–	–	A	+	b
P. purpurea	+	+	+	–	–	–	A	+	a
P. virginiana									
subsp. *praemorsa*	+	+	+	–	–	–	A	+	a
subsp. *virginiana*	–	+	+	–	–	–	A	+	b
Synandra hispidula	+	+	–	+	–	–	A	+	a
Other Lamieae									
Galeobdolon luteum	+	+	+	+	–	–	H	+	a
Lamium purpureum	+	+	–	+	–	–	A	+	a
Leonurus cardiaca	+	–	–	+	–	–	H	+	b
Marrubium vulgare	+	–	–	+	–	–	A	+	b
Stachys riddellii	+	+	–	+	–	–	H	+	b
S. tenuifolia	+	+	–	+	–	–	H	+	a
Other Lamioideae									
Ajuga reptans	+	+	–	+	–	–	A	+	b
Pogostemon cablin	–	+	–	–	–	–	H	+	a
Prostanthera rotundifolia	+	–	–	+	+	+	A	+	a
Scutellaria elliptica	+	+	+	+	–	–	H	+	a
S. incana	+	+	–	+	–	–	H	+	c
S. integrifolia	+	+	–	+	–	–	A	+	b
S. lateriflora	+	+	–	+	–	–	H	+	a
S. nervosa	+	+	–	+	–	–	H	+	a
S. ovata	+	+	+	+	–	–	H	+	a
S. serrata	+	+	–	+	–	–	H	+	a
Teucrium canadense	+	+	–	+	–	–	H	+	c
T. chamaedrys	+	–	–	+	–	–	H	+	c
Trichostema dichotomum	–	–	–	+	+	+	A	–	a
T. lanceolatum	+	–	–	+	+	+	A	–	a
Subfamily Nepetoideae									
Blephilia hirsuta	+	+	–	+	–	–	H	+	b
Monarda fistulosa	–	+	–	–	–	–	H	+	c

[a] Subfamilial classification follows Cantino and Sanders's (1986) circumscription of Erdtman's (1945) subfamilies. Tribe Lamieae is circumscribed as discussed in text.
[b] Stomatal types: 1 = diacytic, 2 = diallelocytic-1, 3 = diallelocytic-2, 4 = anomocytic, 5 = anisocytic, 6 = paracytic.
[c] Stomatal location: A = amphistomatic, H = hypostomatic.
[d] Ldg. = outer ledges: +, present; –, absent.
[e] Stomatal position: a = level with the epidermis, b = slightly elevated, c = strongly elevated.

are predominantly anomocytic and/or anisocytic. We found the stomata of all of these genera to be predominantly to entirely diacytic and/or diallelocytic.

TRICHOMES

NONGLANDULAR TRICHOMES. Simple, uniseriate trichomes were found on the leaves of most species. Only *Physostegia* (all species examined), *Macbridea* (both species), and *Prostanthera rotundifolia* lacked nonglandular foliar trichomes and could be described as having glabrous leaves if the minute, subsessile glands were ignored (see below). Of these three genera, only *Physostegia* consistently has glabrous leaves (Cantino, 1982). Species of *Prostanthera* not examined in this study have pubescent leaves (Conn, 1984), as do some individuals of both *Macbridea alba* (Godfrey & Wooten, 1981; Kral, 1983) and *M. caroliniana* (Godfrey & Wooten, 1981). The leaves of *Brazoria* are nearly glabrous, with the usually sparse trichomes concentrated toward the base of the blade (the leaves of *B. scutellarioides* are essentially glabrous throughout).

The only other nonglandular trichomes observed were dendritic in form and confined to *Marrubium vulgare*. These are stalked and basally branched, with the stalk composed of several cells, a ray arising from each stalk cell, and each ray composed of one to six cells. Similar trichomes were reported by Solereder (1908) and Theobald and colleagues (1979) from other species of *Marrubium* and were illustrated in the latter publication.

The simple trichomes vary in cell number (see TABLE 3). Unicellular trichomes were found in eight genera and 12 species, while multicellular ones were observed in all species. The variation in cell number may prove on further study to be of taxonomic use within genera or in distinguishing among closely related genera, but it appears to be of no value in delimiting suprageneric taxa in the Labiatae.

GLANDULAR TRICHOMES. Two distinct classes of glandular trichomes were observed. Clavate glandular trichomes (see FIGURE 2), found in 14 species, consist of a unicellular or multicellular head resting on a relatively long, multicellular, uniseriate stalk, the uppermost cell of which is usually discoid. Subsessile glandular trichomes (see FIGURE 3), found in nearly all species, consist of a unicellular or multicellular head borne on one (rarely two) short, discoid stalk cell(s) resting on one or more foot cells. The foot cells are generally sunken below the level of the adjacent epidermis, the gland as a whole lying in a tiny depression on the leaf surface. The cuticle is fused to the wall of the stalk cell but appears to separate from the wall of the head, leaving a space in which secretions accumulate. (For excellent photographs, plus evidence that the separated cuticle is provided with a noncellulosic framework derived from the outermost wall layer of the head cells, see Bruni & Modenesi, 1983.)

There is considerable variation in size and morphology of clavate glandular trichomes (see FIGURE 2). Those of *Synandra hispidula* and the four species of *Scutellaria* in which clavate glandular trichomes were observed (*S. elliptica, S. nervosa, S. ovata,* and *S. serrata*) are quite similar, with a four-celled head atop a more or less discoid stalk cell, and three to six elongate stalk cells. Clavate

TABLE 3. **Simple, nonglandular trichomes in Labiatae examined.**[a]

Species	Trichomes[b]			
	1	2	3	4
Subfamily Lamioideae				
Tribe Lamieae				
Subtribe Melittidinae				
Brazoria arenaria	-	+	+	+
B. pulcherrima	-	+	+	-
B. scutellarioides	+	+	-	-
B. truncata	-	+	+	+
Chelonopsis forrestii	-	+	+	-
C. moschata	-	-	+	+
Melittis melissophyllum	-	+	+	+
Synandra hispidula	-	+	+	+
Other Lamieae				
Galeobdolon luteum	-	+	+	+
Lamium purpureum	+	+	-	-
Leonurus cardiaca	-	+	+	-
Marrubium vulgare	-	+	+	+
Stachys riddellii	+	+	-	-
S. tenuifolia	+	+	-	-
Other Lamioideae				
Ajuga reptans	-	+	+	+
Pogostemon cablin	-	+	+	+
Scutellaria elliptica	-	+	+	+
S. incana	+	+	+	+
S. integrifolia	+	+	+	-
S. lateriflora	-	+	+	+
S. nervosa	+	+	+	+
S. ovata	-	+	+	+
S. serrata	-	+	+	+
Teucrium canadense	-	+	+	+
T. chamaedrys	+	+	+	+
Trichostema dichotomum	+	+	+	+
T. lanceolatum	+	+	+	+
Subfamily Nepetoideae				
Blephilia hirsuta	+	+	+	+
Monarda fistulosa	+	+	+	+

[a] Species with glabrous leaves omitted; see text. Classification of suprageneric taxa as in TABLE 2.

[b] Types of trichomes: 1, one-celled; 2, two-celled; 3, three-celled; 4, with more than three cells; +, present; -, absent.

trichomes with heads composed of more than four cells were found only in *Brazoria truncata* and *B. scutellarioides* but resemble those on the calyx and inflorescence axis in *Physostegia* (Cantino, 1979, 1982). Clavate trichomes with single-celled heads were observed in *Marrubium vulgare* and *Trichostema lanceolatum.*

Subsessile glandular trichomes are very characteristic of the Labiatae and occur in many Verbenaceae as well (Solereder, 1908; Metcalfe & Chalk, 1950). They have been referred to by a variety of names, including shortly-stalked bladder-like glands (Metcalfe & Chalk, 1950), sunken glandular dots (Huang & Cheng, 1971), glandular scales (Bosabalidis & Tsekos, 1982), and glandular capitate sessile trichomes (Shah & Naidu, 1983). The term subsessile seems appropriate to us since the glands appear to be sessile unless examined very closely. Because of their nearly universal occurrence in the Labiatae and the extensive variation in their complexity, subsessile glandular trichomes offer considerable potential as a taxonomic character in the family. They have been little used for this purpose, perhaps in part due to lack of a satisfactory classification of the glands on which to base taxonomic comparisons. We have developed such a classification (see APPENDIX 2), based on number of cells and cell-wall configurations (FIGURE 4) in the head of the gland.

Terms used to describe cell-wall configurations are adopted from Stace (1973). A primary radial wall originates from the center of the head of a gland and ends at the periphery. A secondary radial wall originates on a primary radial wall and ends at the periphery. A tertiary radial wall originates on a secondary radial wall and ends at the periphery. A tangential wall connects two radial walls. A partial radial wall originates on a tangential wall and ends at the periphery.

Subsessile glandular trichomes (see FIGURE 5) were found on the leaves of all species examined except *Trichostema lanceolatum* (see TABLE 4). Gland types 4 and 5 were encountered in nearly all species, both within and outside of subtribe Melittidinae. Types 2 and 3 are rare and type 1 absent in the Melittidinae. Type 1 was found only in *Pogostemon,* while type 2 was commonest in *Teucrium* and *Pogostemon.*

The more complex gland types (6–10) were most frequently encountered in *Scutellaria* and the North American Melittidinae. Glands with partial radial walls (types 7 and 10) were restricted to subtribe Melittidinae, where they were found in all species of *Brazoria, Macbridea,* and *Synandra,* as well as in two species of *Physostegia.* Type 7 was found only in *Synandra.* The systematic value of the complex gland types in subtribe Melittidinae is discussed below.

LEAF HISTOLOGY

All species examined have a uniseriate epidermis composed of unsclerified, thin-walled cells and a midrib consisting of an arcuate collateral bundle; all lack a hypodermis. Of the other characters investigated, two (number of cell layers in palisade parenchyma and shape of palisade cells) are too variable on individual specimens to be of any taxonomic use. Histological characters that

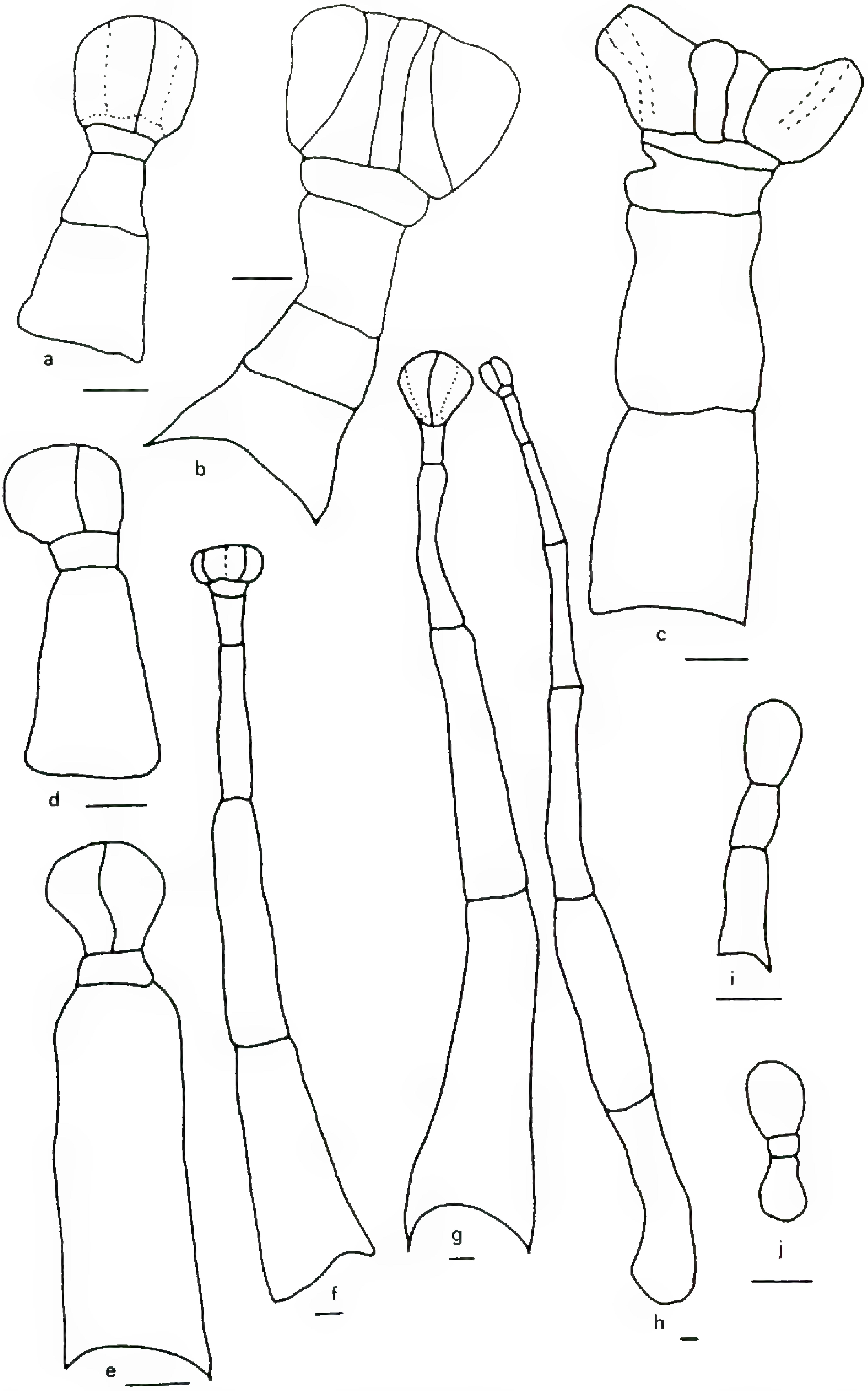

FIGURE 2. Clavate glandular trichomes: a, *Brazoria arenaria*; b, *B. scutellarioides*; c, *B. truncata*; d, *Melittis melissophyllum*; e, *Stachys riddellii*; f, *Synandra hispidula*; g, *Scutellaria nervosa*; h, *S. elliptica*; i, *Trichostema lanceolatum*; j, *Marrubium vulgare*. Scale bars = 15 μm.

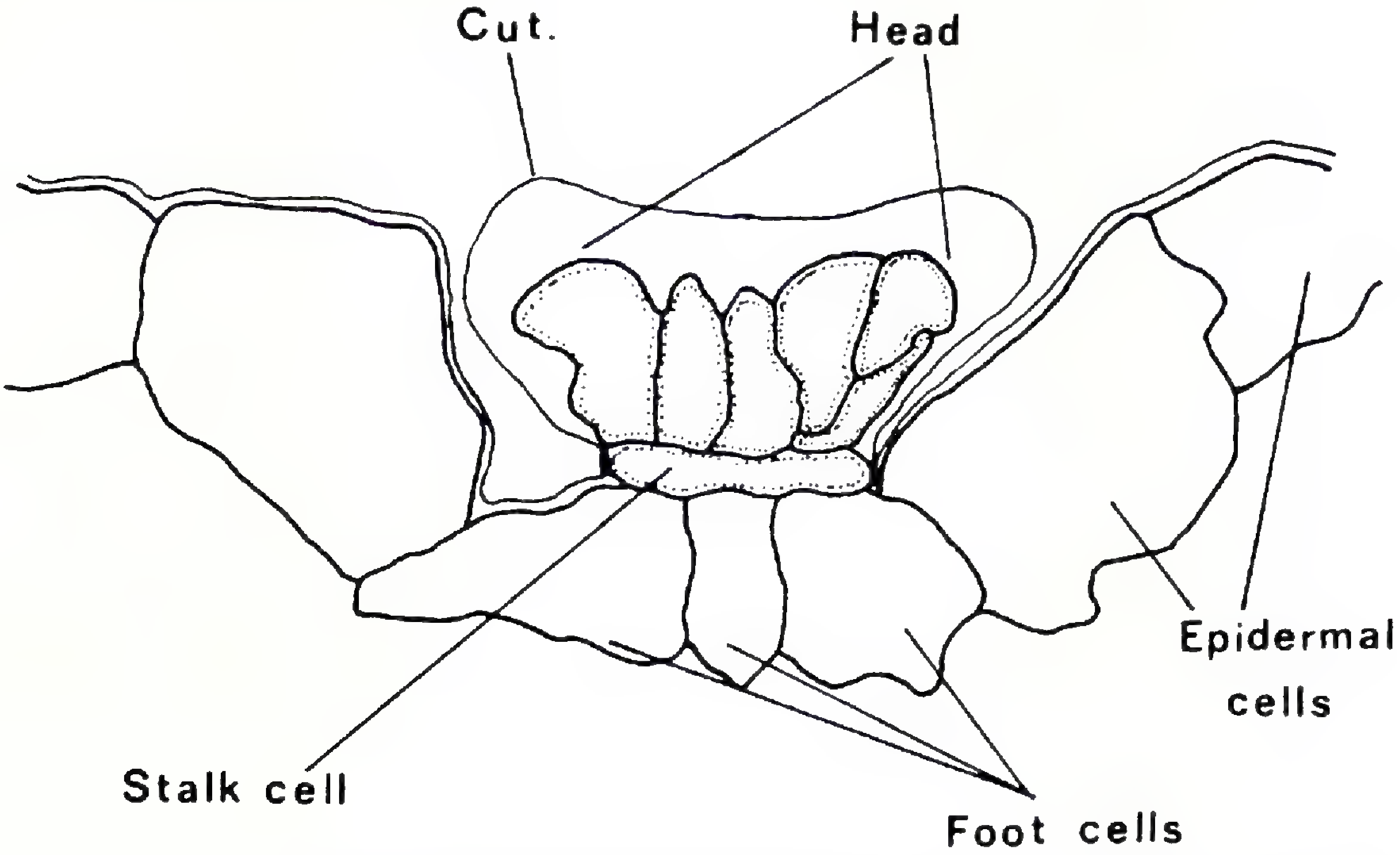

FIGURE 3. Subsessile glandular trichome (*Macbridea alba*), transverse section. Cut. = cuticle.

may be of some taxonomic value are listed in APPENDIX 3, and the distribution of their character states is summarized in TABLE 5.

Most of these characters vary too much within genera to be of much value in circumscribing suprageneric groups. They may prove useful, however, in distinguishing species or species groups within certain genera (i.e., characters 2 and 6 in *Brazoria*; 1, 2, 4, 5, 6, and 7 in *Physostegia*; 2 and 4 in *Scutellaria*; and 1 in *Trichostema*). A much more extensive sample will be necessary before even tentative conclusions can be drawn at this taxonomic level.

In the assessment of phylogenetic relationships above the genus level, presence of idioblasts in the mesophyll appears to be the character with the greatest potential because it varies among but not within genera. Two kinds of idioblasts were observed. One of them, seen only in *Pogostemon*, resembles a glandular trichome but occurs inside the leaf (FIGURE 6h). These structures were also noted by Solereder (1908, p. 1022), who described them as "internal glandular hairs" provided with a short stalk of two or three suberized cells and a unicellular, cuticularized head projecting into the intercellular spaces. He also noted that a secretion accumulates under the cuticle, which is raised like a bladder, just as in an external trichome.

The second kind of idioblast is a large, saclike cell, presumably secretory in function (FIGURE 6a–g). These were observed in all species of *Brazoria* and all investigated species of *Physostegia*. They were also noted by Solereder (1908) in *Physostegia intermedia*, a species that we did not examine. Our observations and those of Solereder suggest that within the Lamiales such saclike idioblasts are unique to these two genera. They vary in shape and thus may offer a good

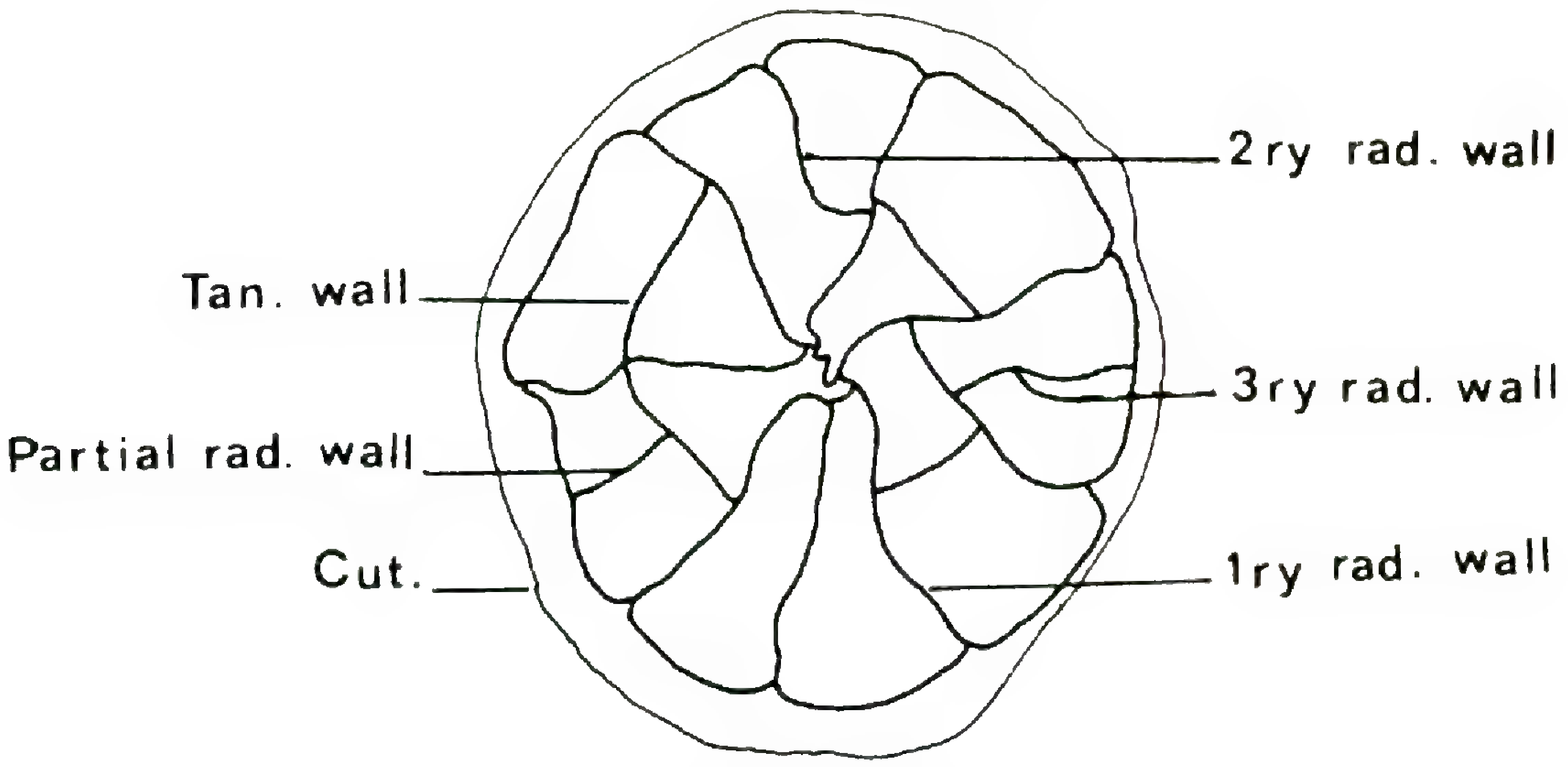

FIGURE 4. Subsessile glandular trichome, surface view, showing cell-wall configurations in head. Cut. = cuticle, tan. = tangential, rad. = radial. (Adapted from Stace, 1973.)

taxonomic character at the species level, in addition to providing evidence for a close relationship between *Physostegia* and *Brazoria.*

DISCUSSION

Discussion will center on the question of whether leaf anatomy provides evidence for the monophyly of subtribe Melittidinae as a whole and/or of subgroups within it. The existence of shared, derived character states (synapomorphies) would constitute such evidence (Hennig, 1966; Wiley, 1981).

The identification of synapomorphies is a two-step procedure. First, an evolutionary transformation series (Wiley, 1981) is hypothesized for each character, usually on the basis of ontogeny and structural complexity of the character states. (This step is trivial when the character is binary.) Second, the evolutionary polarity of the characters must be assessed. Of the many criteria that have been used to determine polarity (see review by Stevens, 1980), outgroup comparison is now the most widely accepted (see, for example, Eldredge & Cracraft, 1980; Stevens, 1980; Arnold, 1981; Wiley, 1981; Farris, 1982) and is the sole criterion used here. Outgroup comparison, in its simplest form, can be explained as follows: "For a given character with 2 or more states within a group, the state occurring in related groups [the outgroups] is assumed to be the plesiomorphic state" (Watrous & Wheeler, 1981). (For a thorough discussion of the underlying logic of outgroup comparison, which is based on the principle of parsimony, see Maddison *et al.,* 1984.)

Because the monophyly of the Melittidinae is in question, the ingroup must be a demonstrably monophyletic group that includes (but is not limited to) this subtribe. The least-inclusive such group is tribe Lamieae, as circumscribed above (i.e., Bentham's tribes Lamieae and Prasieae minus *Anisomeles, Scutellaria,* and probably *Salazaria*; see "Taxonomic Background" for evidence

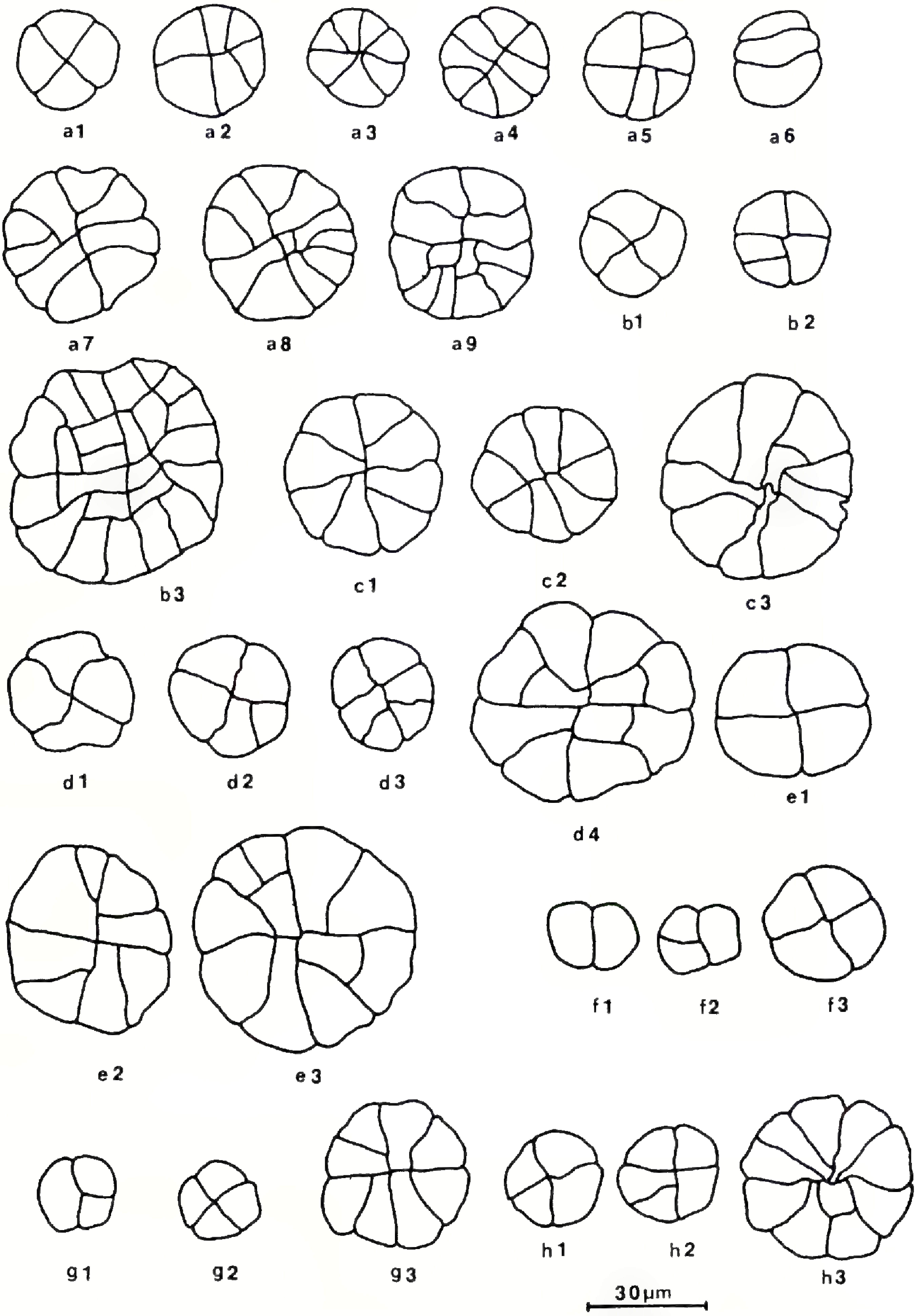

FIGURE 5. Subsessile glandular trichomes, surface view: a1–a9, *Brazoria arenaria*; b1–b3, *Physostegia virginiana* subsp. *praemorsa*; c1–c3, *Macbridea alba*; d1–d4, *M. caroliniana*; e1–e3, *Synandra hispidula*; f1–f3, *Teucrium canadense*; g1–g3, *Marrubium vulgare*; h1–h3, *Scutellaria incana*.

TABLE 4. **Distribution of subsessile glandular trichomes.**[a]

Taxa	Trichomes[b] 1	2	3	4	5	6	7	8	9	10
Subfamily Lamioideae										
Tribe Lamieae										
Subtribe Melittidinae										
Brazoria arenaria	–	–	a	+	+	–	–	+	+	+
B. pulcherrima	–	–	–	+	+	–	–	+	+	+
B. scutellarioides	–	–	–	+	+	+	–	–	+	+
B. truncata	–	–	–	+	+	–	–	+	+	+
Chelonopsis forrestii	–	+	–	+	+	–	–	–	–	–
Macbridea alba	–	–	–	+	+	+	–	+	+	+
M. caroliniana	–	–	–	+	+	+	–	–	+	+
Melittis melissophyllum	–	–	–	+	+	–	–	–	–	–
Physostegia angustifolia	–	–	–	+	+	–	–	+	+	+
P. digitalis	–	–	–	+	+	–	–	–	–	–
P. godfreyi	–	–	–	+	+	–	–	+	–	–
P. leptophylla	–	–	–	+	+	+	–	–	–	–
P. longisepala	–	–	–	+	+	–	–	–	–	–
P. purpurea	–	–	–	+	+	–	–	–	–	–
P. virginiana										
subsp. *praemorsa*	–	–	–	+	+	–	–	–	+	+
subsp. *virginiana*	–	–	–	+	+	–	–	–	–	+
Synandra hispidula	–	–	–	+	+	+	+	–	+	–
Other Lamieae										
Galeobdolon luteum	–	–	–	+	+	+	–	–	+	–
Lamium purpureum	–	+	b	+	+	+	–	–	–	–
Leonurus cardiaca	–	+	b	+	+	+	–	+	+	–
Marrubium vulgare	–	+	b	+	+	–	–	–	–	–
Stachys riddellii	–	–	–	+	+	–	–	–	–	–
S. tenuifolia	–	–	–	+	+	–	–	–	–	–
Other Lamioideae										
Ajuga reptans	–	+	–	+	–	–	–	–	–	–
Pogostemon cablin	+	+	–	–	–	–	–	–	–	–
Prostanthera rotundifolia	–	–	b	+	–	–	–	+	–	–
Scutellaria elliptica	–	–	–	+	–	–	–	+	–	–
S. incana	–	–	–	+	+	+	–	+	+	–
S. integrifolia	–	–	–	+	+	–	–	+	–	–
S. lateriflora	–	+	b	+	+	–	–	–	–	–
S. nervosa	–	–	–	+	+	–	–	+	–	–
S. ovata	–	–	b	+	+	+	–	+	–	–
S. serrata	–	+	b	+	+	–	–	–	–	–
Teucrium canadense	–	+	b	+	+	–	–	–	–	–
T. chamaedrys	–	+	b	+	–	–	–	–	–	–
Trichostema dichotomum	–	–	b	+	–	–	–	–	–	–
Subfamily Nepetoideae										
Blephilia hirsuta	–	–	–	–	+	–	–	–	–	–
Monarda fistulosa	–	–	–	–	+	–	–	–	–	–

[a] Classification of suprageneric taxa as in TABLE 2.
[b] Numbers (1-10) and letters (a, b) refer to trichome classification in APPENDIX 2; +, present; –, absent.

TABLE 5. **Leaf histological characters as recorded from transverse sections.**

	Characters[b]						
Taxa	1	2	3	4	5	6	7
Subfamily Lamioideae							
Tribe Lamieae							
Subtribe Melittidinae							
Brazoria arenaria	b	b	b	a	a	b	b
B. pulcherrima	b	b	b	a	a	c	b,e
B. scutellarioides	b	a	b	a	a	b	b
B. truncata	b	b	b	a	a	a	b
Chelonopsis forrestii	b	a	a	a	a	c	e
Macbridea alba	b	a	a	a	a	b	a
M. caroliniana	b	a	a	a	c	c	e
Melittis melissophyllum	b	a	a	a	a	c	e
Physostegia angustifolia	b	a	b	d	a	c	c
P. digitalis	b	a	b	d	a	a	c
P. godfreyi	a	a	b	d	a	a	a
P. leptophylla	b	a	b	a	a	a	b
P. longisepala	b	b	b	a	b	a	b
P. purpurea	b	a	b	d	a	a	b
P. virginiana							
subsp. *praemorsa*	b	a	b	d	a	c	b
subsp. *virginiana*	b	a	b	b?	a	c	e
Synandra hispidula	b	b	a	a	a	c	e
Other Lamieae							
Galeobdolon luteum	b	b	a	a	a	c	e
Lamium purpureum	b	a	a	a	a	c	d
Leonurus cardiaca	b	a	a	a	c	c	e
Marrubium vulgare	b	a	a	a	b	c	e
Stachys riddellii	b	a	a	a	b	c	e
S. tenuifolia	b	a	a	a	b	c	e
Other Lamioideae							
Ajuga reptans	b	a	a	a	a	b	d
Pogostemon cablin	b	a	c	a	a	c	e
Prostanthera rotundifolia	b	a	a	a	a	a	a
Scutellaria elliptica	b	b	a	a	a	c	e
S. incana	b	a	a	a	a	c	e
S. integrifolia	b	a	a	a	a	c	d
S. lateriflora	b	b	a	a	a	c	e
S. nervosa	b	b	a	c	a	c	d
S. ovata	b	a	a	a	a	c	e
S. serrata	b	b	a	a	a	c	d
Teucrium canadense	b	a	a	a	a	c	e
T. chamaedrys	b	a	a	a	a	c	d
Trichostema dichotomum	b	a	a	a	a	b	d
T. lanceolatum	c	a	a	a	a	c	d
Subfamily Nepetoideae							
Blephilia hirsuta	b	a	a	a	a	c	e
Monarda fistulosa	b	a	a	a	a	c	e

[a] Classification of suprageneric taxa as in TABLE 2.
[b] Characters explained in APPENDIX 3.

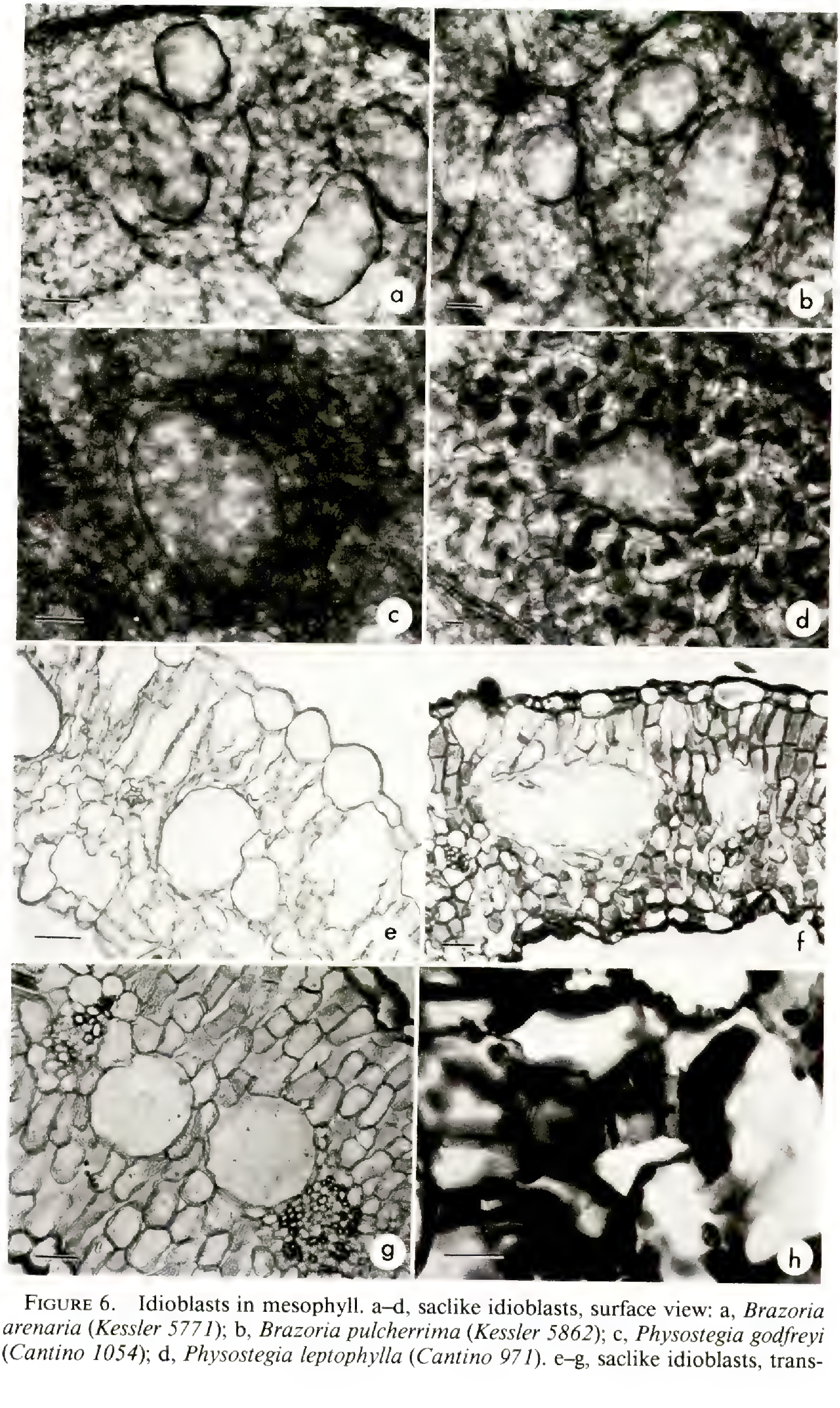

FIGURE 6. Idioblasts in mesophyll. a–d, saclike idioblasts, surface view: a, *Brazoria arenaria* (*Kessler 5771*); b, *Brazoria pulcherrima* (*Kessler 5862*); c, *Physostegia godfreyi* (*Cantino 1054*); d, *Physostegia leptophylla* (*Cantino 971*). e–g, saclike idioblasts, trans-

supporting the monophyly of this group). The ingroup is represented in our study by all six genera of subtribe Melittidinae plus five others (*Galeobdolon, Lamium, Leonurus* L., *Marrubium,* and *Stachys*). Anatomical data for two additional genera (*Phlomis* and *Eremostachys*) have been provided by Azizian and Cutler (1982). For stomatal characters the ingroup sample includes *Leonotis* (Pers.) R. Br. and *Leucas,* as well (Inamdar & Bhatt, 1972).

Choice of outgroups is constrained by both the uncertainty about cladistic relationships within the family and the paucity of anatomical data for the Labiatae. We have selected as outgroups those few non-ingroup taxa of subfamily Lamioideae for which we have collected anatomical data (*Ajuga reptans, Pogostemon cablin, Prostanthera rotundifolia, Scutellaria* [7 spp.], *Teucrium* [2 spp.], and *Trichostema* [2 spp.]), plus subfamily Nepetoideae as a whole. The latter must be included because, as discussed above, there is no evidence that subfamily Lamioideae is monophyletic. If it were paraphyletic by exclusion of subfamily Nepetoideae, the latter might be more closely related to tribe Lamieae (the ingroup) than are some of the other selected outgroups. Subfamily Nepetoideae is represented by our own data for *Monarda fistulosa* and *Blephilia hirsuta* and by published data for *Zhumeria* Rech. f. & Wendelbo (Bokhari & Hedge, 1976), tribe Meriandreae (Bokhari & Hedge, 1971), and subtribe Hyptidinae (Rudall, 1979, 1980). For stomatal characters (see TABLE 1) ten other genera can be added as representatives of subfamily Nepetoideae, two other species can be added as representatives of *Pogostemon,* and *Dysophylla* Blume and *Anisomeles* can be added to the list of outgroups. For subsessile glands, nine other genera can be added as representatives of subfamily Nepetoideae (Bruni & Modenesi, 1983; Werker, Putievsky, & Ravid, 1985; Werker, Ravid, & Putievsky, 1985). Each of the outgroups is thought to be monophyletic, and no two of them can be combined into a more inclusive monophyletic group. For example, there is no evidence that tribe Ajugeae *sensu* Bentham, represented in this study by *Ajuga, Teucrium,* and *Trichostema,* is monophyletic.

The outgroups must be used in combination, because even the more distant outgroups may affect polarity assessment in the ingroup (Maddison *et al.,* 1984). The analysis is complicated, however, by the lack of resolution of phylogenetic relationships among the outgroups and by uncertainty about which outgroups are most closely related to the ingroup. If a state that occurs in the ingroup occurs in none of the outgroups, it is clearly derived within the ingroup, but if it occurs in some outgroup taxa (the most frequent situation), polarity assessment is more problematic. The outgroup-substitution approach (Donoghue & Cantino, 1984) is applicable to this situation but difficult to apply here because of the large number of plausible outgroup combinations that must be considered. Moreover, both this approach and the global parsimony approach of Maddison and colleagues (1984) require a full cladistic analysis using all

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verse section: e, *Brazoria pulcherrima* (*Kessler 5865*); f, *Physostegia angustifolia* (*Cantino 1058*); g, *Physostegia godfreyi* (*Cantino 1054*). h, internal glandular trichome, transverse section, *Pogostemon cablin* (*Cantino 1262*). Scale bars = 60 μm (a–g) and 20 μm (h).

available characters, whereas the intent here is simply an evaluation of the possible phylogenetic significance of a few specific characters.

An alternative method will therefore be used to evaluate polarity of characters that vary within the outgroups. This approach, developed by Frohlich (1983, 1987), involves calculation of the probability that the commonest state among the outgroups could parsimoniously be treated as ancestral in the ingroup if the cladistic relationships of the outgroups to each other and to the ingroup were known. Frohlich has developed an algorithm that considers all possible arrangements of the outgroups, determines for each arrangement which state of a binary character it is most parsimonious to consider as ancestral within the ingroup, and then calculates the percentage of arrangements that assign each state as ancestral in the ingroup. This can be converted to probability if all outgroup combinations are assumed to be equally probable, a necessary assumption when one is ignorant of the true outgroup relationships. Thus, according to Frohlich, if a state occurs in only one of seven outgroups, the probability is 0.909 that the alternative state could parsimoniously be treated as ancestral within the ingroup if outgroup relationships were known (i.e., 90.9% of the outgroup arrangements yield this polarity assessment, while the rest yield an equivocal one). Frohlich's "tree-count method" turns out to be helpful in determining the polarity of several characters (see below).

A derived character state that occurs in some, but not all, members of a monophyletic group is called a nonuniversal derived state (Cantino, 1985b). A nonuniversal derived state shared by two or more groups, each known to be monophyletic on the basis of other characters, provides evidence that these groups together constitute a clade, but it is weaker evidence than if monophyly is inferred on the basis of a synapomorphy that occurs in all members of the clade it delimits (Cantino, 1985b). Both synapomorphies and shared nonuniversal derived states are used in the following analysis.

TRANSFORMATION SERIES

Most characters examined in this study are binary. Of the multistate characters only two, stomatal type and subsessile glandular trichomes, display variation of phylogenetic significance at the suprageneric level.

Based on ontogenetic studies (see FIGURE 1), a transformation series for stomatal types is proposed (FIGURE 7a). The anomocytic type is the simplest ontogenetically. The diacytic and diallelocytic stomata form a transformation series from the anomocytic type. The anisocytic and paracytic types, which form a second transformation series from the anomocytic type, share the initial step in their ontogenies (FIGURE 1) but diverge after that point.

Bosabalidis and Tsekos (1984) studied the ontogeny of subsessile glandular trichomes in *Origanum* L. They found that a single initial protodermal cell divides to give in succession what we have called trichome types 2, 4, 5, and 6. Based on this study, as well as on a comparison of the structural complexity of the mature trichomes, a transformation series for the subsessile glandular trichomes is hypothesized (FIGURE 7b). Type 1 is the simplest structurally and ontogenetically, while type 10 is the most complex. Tangential walls occur in the heads of types 6, 7, 9, and 10. Partial radial walls occur only in types 7

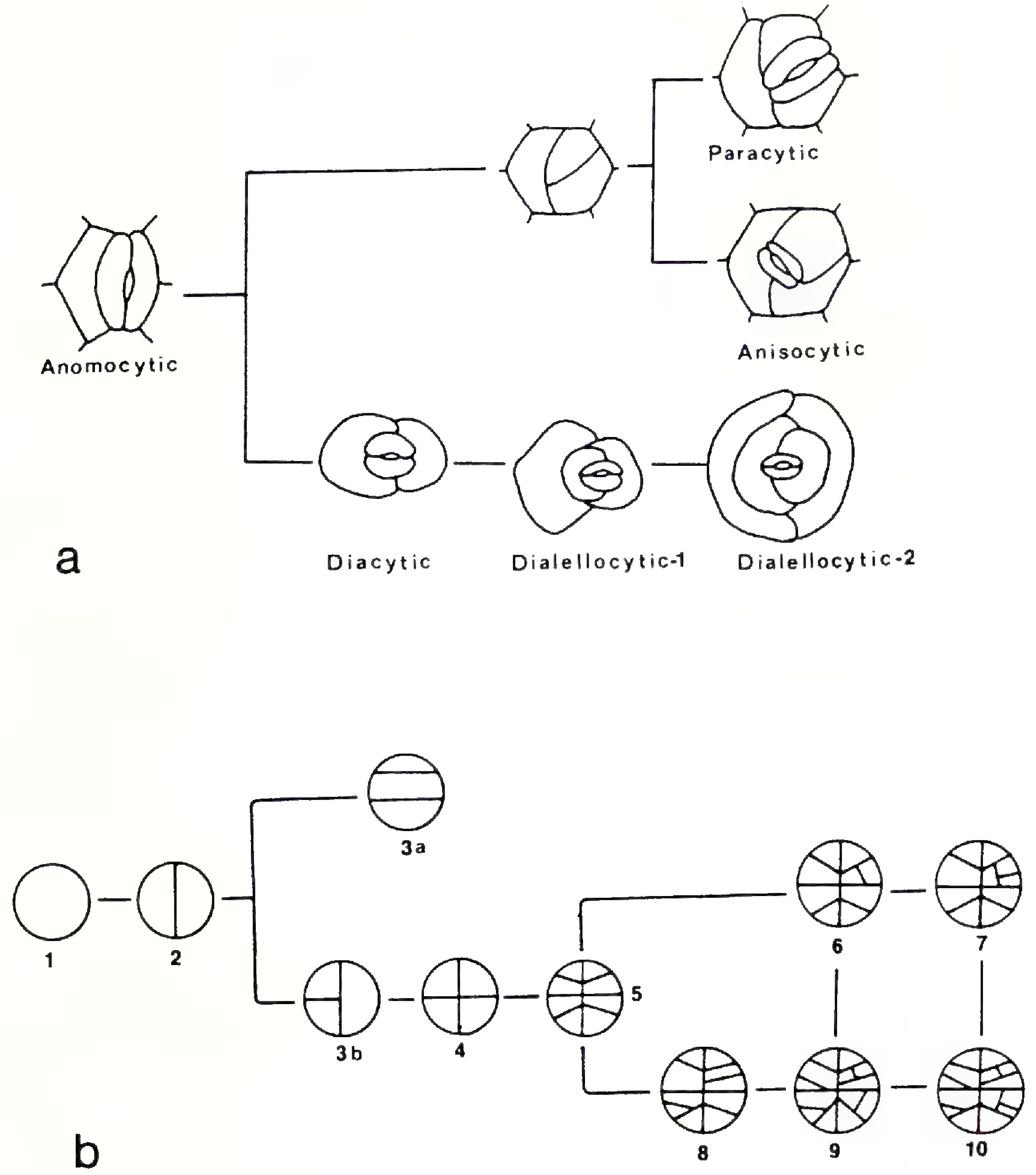

FIGURE 7. Hypothesized transformation series: a, stomatal types; b, subsessile glandular trichomes.

and 10. Types 5, 6, and 7 differ from types 8, 9, and 10 in that the former have no more than one secondary radial wall on a given side of any primary radial wall and lack tertiary radial walls, while the latter have more than one secondary radial wall on a given side of at least one primary radial wall and/or have tertiary radial walls. Types 9 and 10 trichomes can develop by more than one ontogenetic pathway and are therefore not necessarily homologous in all taxa in which they occur.

CHARACTER POLARITY

Anomocytic and diacytic stomata are widely distributed in both the Verbenaceae and the Labiatae (see TABLES 1, 2). Diallelocytic-1 stomata are widespread among the Labiatae, including the outgroups to tribe Lamieae. Diallelocytic-2 stomata are known to occur in four genera of tribe Lamieae plus four species among the outgroups (*Scutellaria elliptica, S. ovata, Ocimum basilicum,* and *Plectranthus australis*). Both diallelocytic types appear to be rare in the Verbenaceae. The anisocytic and paracytic types occur mainly in the Verbenaceae and the primitive Labiatae (i.e., tribes Prostanthereae and Ajugeae).

The above distribution suggests that although both diallelocytic types are probably derived within the Labiatae, the diallelocytic-1 type is plesiomorphic in tribe Lamieae. Based on Frohlich's (1987) probability table, there is a probability of over 0.984 that the diallelocytic-2 type can parsimoniously be hypothesized to be derived within tribe Lamieae. This calculation is based on its occurrence in two of the seven examined species of one outgroup (*Scutellaria*) and in two of the four examined species of another (subfam. Nepetoideae), and on its absence from the other five outgroups. The many other species of subfam. Nepetoideae in TABLE 1 (in none of which were diallelocytic-2 stomata reported) are ignored in this analysis because the sample for each consisted only of published drawings. If these species were to be included, the probability that the diallelocytic-2 type is derived in the Lamieae would be even greater.

Among the subsessile glandular trichomes (see TABLE 4), types 4 and 5 are common throughout the Labiatae and thus plesiomorphic within tribe Lamieae. Types 1, 2, and 3b are of scattered occurrence but apparently do not occur in the North American Melittidinae. Of the more complex glands, types 6, 8, and 9 appear to be too common in the outgroups, particularly in subfamily Nepetoideae in the case of types 6 and 9 (Werker, Putievsky, & Ravid, 1985; Werker, Ravid, & Putievsky, 1985), to permit polarity assessment in the ingroup. Glands with partial radial walls (types 7 and 10) were found only in the Lamieae, however, where they apparently represent a derived state.

The saclike idioblasts in the mesophyll of *Brazoria* and *Physostegia* appear to be unique to these genera and thus represent a synapomorphy. Undifferentiated mesophyll has been observed only in *Physostegia godfreyi* and may represent an autapomorphy of the species. Bundle-sheath extensions are absent (state a of character 6, TABLE 5) in some Lamieae (one species of *Brazoria* and five of *Physostegia*) but are present in all but one outgroup. Similarly, keels on the secondary veins are absent (states a–c of character 7, TABLE 5) in some Lamieae (*Brazoria* and some species of *Macbridea* and *Physostegia*) but present in all but one outgroup. According to Frohlich's (1987) probability table, there is a 0.909 probability that a state occurring in six of seven outgroups can be parsimoniously hypothesized to be ancestral within the ingroup. If this level of probability is deemed acceptable, absence of bundle-sheath extensions and of secondary-vein keels can tentatively be treated as derived in the Lamieae.

PHYLOGENETIC HYPOTHESES

Since the samples of both ingroup and outgroup taxa are small and only leaf anatomy is being considered, phylogenetic hypotheses must be considered very preliminary. The characters that offer apparent synapomorphies should be

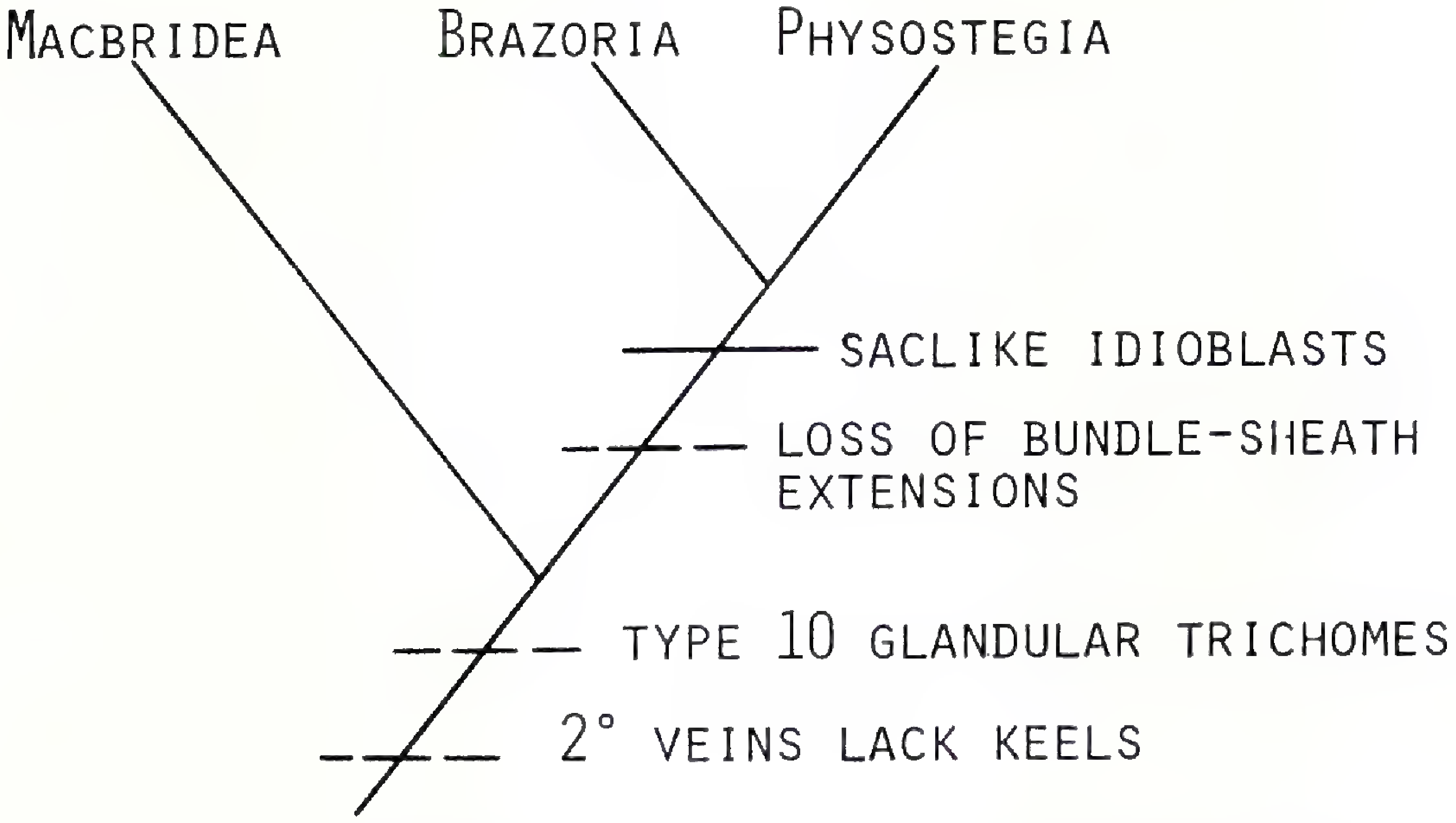

FIGURE 8. Cladogram showing hypothesized phylogenetic relationships between *Brazoria, Physostegia,* and *Macbridea.* Solid bar = synapomorphy; dashed bars = shared nonuniversal derived states.

examined in a broader survey of both tribe Lamieae and the outgroups. The latter may force reassessment of character polarity in some cases, while expansion of the ingroup sample may increase the membership of certain clades. Moreover, other sets of characters may support conflicting hypotheses. At the very least, however, this analysis should help focus future investigations on particular characters and taxa.

Shinners (1953) suggested that *Brazoria* and *Physostegia* are close relatives. In the numerical phenetic analysis of El-Gazzar (1969), these two genera paired on the phenogram at a very high similarity level. Until now, however, no strong evidence that they form a monophyletic group (i.e., the occurrence of synapomorphies) has been reported. In the present study an apparent synapomorphy—the occurrence of saclike idioblasts in the mesophyll of all examined species of both genera—has been documented. No other taxon in the Lamiales is known to have this feature. Weaker additional support for the monophyly of this clade is provided by a shared nonuniversal derived state (Cantino, 1985b), absence of bundle-sheath extensions. As discussed above, there is a 0.909 probability that this state can parsimoniously be hypothesized to be derived since it occurs in one of seven outgroups (*Prostanthera*).

Cantino (1982) suggested that *Brazoria, Physostegia,* and *Macbridea* may form a monophyletic subgroup within the Melittidinae. No synapomorphy was found to corroborate this hypothesis, but it is supported by two nonuniversal derived states (FIGURE 8). Type 10 glandular trichomes, the most complex subsessile glands, occur in all species of *Brazoria* and *Macbridea* and two species of *Physostegia,* but they were not observed in any other taxa of either the ingroup or the outgroup. Weaker additional support for the *Brazoria-Physostegia-Macbridea* clade is provided by another nonuniversal derived state that occurs in one outgroup as well as in this clade, but nowhere else in the ingroup. Secondary veins lack keels in three species of *Brazoria* (and may or may not lack them in the fourth), *Macbridea alba,* most species of *Physostegia,* and the outgroup species *Prostanthera rotundifolia.* This is probably a reflection of the relatively succulent nature of the leaves of these taxa. As discussed above, there is a 0.909 probability that the loss of secondary-vein keels can be parsimoniously hypothesized to be derived in the ingroup. However, the independent evolution of this character state in the outgroup and ingroup indicates that it may be particularly subject to parallelism, which reduces its value as a phylogenetic indicator (Gosliner & Ghiselin, 1984). If absence of secondary-vein keels is indeed a function of leaf succulence, it can be expected in other succulent Labiatae that have not yet been examined. Such a character state can provide only weak support for the *Brazoria-Physostegia-Macbridea* clade.

Leaf anatomy has provided strong support for a *Physostegia-Brazoria* clade and weaker support for a clade composed of these plus *Macbridea.* The question still remains whether there is any anatomical evidence to link these three genera to the rest of subtribe Melittidinae or to other genera within tribe Lamieae. Two ingroup genera, *Galeobdolon* and *Synandra,* are suggested as possible relatives of the *Physostegia-Brazoria-Macbridea* clade on the basis of shared nonuniversal derived states; an expanded survey of the Lamieae may reveal other relatives. Diallelocytic-2 stomata are shared by *Physostegia, Brazoria, Macbridea,* and *Galeobdolon.* Subsessile glands with partial radial walls (types 7 and 10) occur in *Physostegia, Brazoria, Macbridea,* and *Synandra.*

Leaf anatomy has provided no evidence that subtribe Melittidinae is monophyletic. The four North American genera may form a clade, but *Galeobdolon* (which has never been treated as belonging to the subtribe) is no less strongly implicated than *Synandra* as the sister group of the *Physostegia-Brazoria-Macbridea* clade. No anatomical characters suggest a relationship between *Chelonopsis* or *Melittis* and the rest of the Melittidinae. Since leaf anatomy, floral morphology, and karyology (Cantino, 1985a) do not provide any convincing evidence that subtribe Melittidinae is monophyletic, nor does any other character we are aware of, its abandonment should be seriously considered.

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APPENDIX 1. **Abbreviated collection data for voucher specimens.***

Ajuga reptans L. Ohio, Athens Co., Athens, *Cantino 1217.*

Blephilia hirsuta (Pursh) Bentham. Ohio, Vinton Co., Lake Alma State Park, *Cantino & Abu-Asab 1249.*

Brazoria arenaria Lundell. Texas: Aransas Co., Aransas National Wildlife Refuge, *Kessler 5773*; Refugio Co., *Kessler 5771.*

Brazoria pulcherrima Lundell. Texas, Leon Co., *Kessler 5862, 5865.*

Brazoria scutellarioides Engelm. & Gray. Texas, Travis Co., *Sanders 76168* (TEX), *76179* (TEX).

Brazoria truncata (Bentham) Engelm. & Gray. Texas, Live Oak Co., 2 km SW of Whitsett, *Sanders 76122* (TEX).

Chelonopsis forrestii Anthony. China, Szechwan Prov., *Rock 5515* (A).

Chelonopsis moschata Miq. Japan, Prov. Iwashiro, Pref. Fukushima, *Furuse s.n.,* 7-IX-1957 (A).

Galeobdolon luteum Hudson. Ohio, Athens Co., greenhouse plant from commercial source, *Cantino 1271.*

Lamium purpureum L. Ohio, Athens Co., Athens, *Cantino 1214.*

Leonurus cardiaca L. Michigan, Ingham Co., East Lansing, *Cantino 1224.*

Macbridea alba Chapman. Florida, Bay Co., E of Callaway, *Godfrey 79884.*

Macbridea caroliniana (Walter) Blake. North Carolina, Pender Co., near Long Creek, *Cantino 1204.*

Marrubium vulgare L. Ohio, Athens Co., Athens, in garden, *Cantino 1242.*

Melittis melissophyllum L. Czechoslovakia, Brünn [Brno], *Piskoi 667* (GH); France, between Capendu and Moux, *Neyraut s.n.,* 12-VI-1888 (GH).

Monarda fistulosa L. Ohio, Vinton Co., Vinton Twp., *Cantino & Abu-Asab 1251.*

Physostegia angustifolia Fern. Louisiana, St. Tammany Parish, 10 mi SW of Covington, *Cantino 1058.*

Physostegia digitalis Small. Louisiana, Rapides Parish, 3 mi N of Elizabeth, *Cantino 1070* (GH).

Physostegia godfreyi Cantino. Florida, Gulf Co., 12 mi S of Wewahitchka, *Cantino 1054.*

Physostegia leptophylla Small. North Carolina, Hertford Co., 4 mi W of Winton, *Cantino 971* (GH).

Physostegia longisepala Cantino. Louisiana, Lafayette Parish, garden plant transplanted from vicinity of Mauriceville, Orange Co., Texas, *Vincent 4291.*

Physostegia purpurea (Walter) Blake. North Carolina, Harnett Co., 3 mi SE of Bunnlevel, *Cantino 939.*

Physostegia virginiana (L.) Bentham subsp. *praemorsa* (Shinners) Cantino. North Carolina: Transylvania Co., 4 mi SW of Lake Toxaway, *Cantino 946*; Montgomery Co., 0.5 mi N of Blaine, *Cantino 943* (GH).

Physostegia virginiana (L.) Bentham subsp. *virginiana.* Ohio, Athens Co., York Twp., *Cantino 1260.*

Pogostemon cablin Bentham. Ohio, Athens Co., greenhouse plant from commercial source, *Cantino 1262.*

Prostanthera rotundifolia R. Br. Ohio, Athens Co., greenhouse plant from commercial source, *Cantino 1261.*

Scutellaria elliptica Muhlenb. Ohio, Jackson Co., Lake Alma State Park, *Cantino & Abu-Asab 1222.*

*Vouchers at BHO unless otherwise indicated. Herbarium abbreviations follow Holmgren *et al.* (1981).

Scutellaria incana Biehler. Ohio: Athens Co., Athens, *Cantino & Abu-Asab 1236*; Hocking Co., Ward Twp., *Cantino & Abu-Asab 1247*.

Scutellaria integrifolia L. Ohio, Vinton Co., Lake Alma State Park, *Cantino 1227*.

Scutellaria lateriflora L. Ohio. Vinton Co.: Lake Alma State Park, *Cantino & Abu-Asab 1248*; Lake Hope State Park, *Cantino & Abu-Asab 1257*.

Scutellaria nervosa Pursh. Ohio: Athens Co., Athens, *Cantino 1231*; Perry Co., Monroe Twp., *J. Young s.n.* (no voucher).

Scutellaria ovata Hill. Ohio, Athens Co., Athens Twp., *Cantino 1232*.

Scutellaria serrata Andrz. Ohio. Vinton Co.: Brown Twp., *Cantino & Abu-Asab 1219*; Lake Alma State Park, *Cantino & Abu-Asab 1221*.

Stachys riddellii House. Ohio, Vinton Co., Lake Alma State Park, *Cantino 1229, 1230*.

Stachys tenuifolia Willd. Ohio. Athens Co.: Athens, *Cantino 1235*; Waterloo Twp., *Cantino & Abu-Asab 1253*. Vinton Co., Lake Hope State Park, *Cantino & Abu-Asab 1256*.

Synandra hispidula (Michaux) Baillon. Ohio, Morgan Co., Union Twp., *Cantino 1151*.

Teucrium canadense L. Ohio, Athens Co., Dover Twp., *Cantino & Abu-Asab 1243, 1244*.

Teucrium chamaedrys L. Ohio, Athens Co., Athens, in garden, *Cantino 1240*.

Trichostema dichotomum L. Ohio, Perry Co., Monroe Twp., *J. Young s.n.*, 24-VIII-1983.

Trichostema lanceolatum Bentham. Ohio, Athens Co., greenhouse plant from commercial source, *Cantino 1259*.

APPENDIX 2. **Classification of subsessile glandular trichomes in the Labiatae.***

Type 1.	Head composed of one cell.
Type 2.	Head composed of two cells (FIGURE 5f1).
Type 3.	Head composed of three cells.
3a.	Head divided by two transverse walls (FIGURE 5a6).
3b.	Head divided by three radial walls (FIGURE 5f2, g1).
Type 4.	Head composed of four cells (FIGURE 5a1, b1, d1, e1, f3, g2, h1).
Type 5.	Head of more than four cells, usually divided by four primary radial walls that are more or less perpendicular to each other; tertiary and tangential walls absent; no more than one secondary radial wall arising on a given side of any primary radial wall (FIGURE 5a2–5, b2, c1, c2, d2, d3, e2, g3, h2).
Type 6.	As in Type 5, but with tangential walls present (FIGURE 5d4).
Type 7.	As in Type 6, but with partial radial walls present (FIGURE 5e3).
Type 8.	Head of more than four cells; tertiary radial walls present and/or more than one secondary radial wall arising on the same side of at least one primary radial wall; tangential walls absent (FIGURE 5a7).
Type 9.	As in Type 8, but with tangential walls present; partial radial walls absent (FIGURE 5a8, c3).
Type 10.	As in Type 9, but with partial radial walls present (FIGURE 5a9, b3).

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*Cell-wall configurations are defined in the text and illustrated in FIGURE 4.

APPENDIX 3. **Leaf histological characters of possible taxonomic value.**

1. Mesophyll differentiation: a, undifferentiated; b, bifacial; c, isobilateral.
2. Compactness of palisade cells: a, compact; b, loose.
3. Idioblasts in mesophyll: a, absent; b, saclike; c, resembling internal glandular trichomes.
4. Fibers associated with midrib: a, absent; b, present only on adaxial side of midrib; c, present only on abaxial side of midrib; d, present on both sides of midrib.
5. Collenchyma associated with midrib: a, absent; b, present only on abaxial side of midrib; c, present on both sides of midrib.
6. Bundle-sheath extensions: a, absent; b, present only on abaxial side of bundle; c, present on both sides of bundle.
7. Prominence of keels associated with vascular bundles as viewed in transverse section of lamina: a, keels absent; b, secondary veins lacking keels, midrib keel protruding slightly; c, secondary veins lacking keels, midrib keel protruding greatly; d, secondary veins keeled, midrib keel protruding slightly; e, secondary veins keeled, midrib keel protruding greatly.

Erratum—The *Pogostemon* used in this study was *P. heyneanus* Bentham, not *P. cablin* Bentham.

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

THOMAS J. ROSATTI[2]

PONTEDERIACEAE Kunth in Humboldt, Bonpland, & Kunth, Nova Gen. Sp. Pl. **1:** 211 (folio ed.); 265 (quarto ed.). 1816, "Pontedereae," nom. cons.

(PICKEREL-WEED FAMILY, WATER-HYACINTH FAMILY)

Submersed, emersed, or floating aquatic herbs, sometimes on wet ground because of lowered water levels. Stems sympodial, successive axes terminating in inflorescences, stout or elongate. Juvenile leaves, especially if submersed, usually sessile and linear. Adult leaves simple, alternate [or whorled in *Hydrothrix*]; stipulate or exstipulate; the bases mostly sheathing, either open or fused basally around the stem; sessile or petiolate, the petioles sometimes inflated; the blades linear [filiform in *Hydrothrix*] to orbicular, sometimes sagittate or cordate, the veins parallel, usually arching. Inflorescence a terminal spike, raceme, panicle, or single flowered; sessile or pedunculate, subtended and enclosed to various degrees by a sheathing bract that is sometimes surmounted by a variously reduced petiole and/or blade, each flowering stem (i.e., that which is not part of the sympodium) also bearing a single leaf that some-

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I am indebted to Norton Miller and Carroll Wood for the many ways they contributed to this treatment. George K. Rogers and Ihsan A. Al-Shehbaz have continued to be valuable colleagues in Cambridge, and Gordon C. Tucker has been a welcome addition to our staff in Albany. Spencer C. H. Barrett, Michael G. Simpson, and Charles N. Horn provided helpful information from their research on the Pontederiaceae. Elizabeth B. Schmidt and Stephen A. Spongberg improved the final manuscript with their editorial expertise. This investigation was based on collections in the libraries and herbaria associated with the New York State Museum and Harvard University.

The illustration of *Pontederia* was drawn in 1956 and 1957 by Dorothy H. Marsh from living materials collected by Carroll Wood and Richard J. Eaton and dissected by Wood.

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times differs from the others. Flowers perfect (some species of *Eichhornia* and *Pontederia* tristylous); perianth petaloid, biseriate, usually funnelform to salverform [parts nearly distinct in *Monochoria*], zygomorphic, subactinomorphic, or actinomorphic, the 6 [4, rarely 3, in *Scholleropsis*] lobes imbricate, often unequal. Stamens usually 6 (in 2 series of 3) or 3 [4 in *Scholleropsis*], 1 in some cleistogamous flowers [and in *Hydrothrix*], staminodes sometimes present when stamens fewer than 6; filaments inserted on the perianth tube at various levels; anthers held at various levels, basifixed, auriculate and somewhat movable on filaments (and therefore appearing dorsifixed), bilocular, with introrse, longitudinal dehiscence [rarely terminal pores]; pollen bi- or trinucleate when shed, with 1 to 3 distal or subequatorial colpi. Gynoecium of 3 united carpels; style single, of various lengths (i.e., some species tristylous); stigma terminal, entire or variously toothed and/or lobed (often 3- or 6-parted); ovary superior, with 3 locules, each locule with an axile placenta, or with 1 locule and 3 intrusive parietal placentae, or with 1 locule (through abortion of 2 locules) and a terminal placenta (in *Pontederia*); ovules in each locule numerous (solitary in *Pontederia*), anatropous, crassinucellar, and bitegmic; nectaries septal (lacking in *Heteranthera*). Fruit a many-seeded, loculicidal capsule or a 1-seeded utricle (in *Pontederia*). Seeds small, ovoid, at least those in capsules with longitudinal ridges or ribs; endosperm starchy; embryo axile, cylindrical, with a terminal cotyledon and a lateral plumule. (Including Heterantheraceae J. G. Agardh, Theoria Syst. Pl. 36. 1858, "Heteranthereae.") TYPE GENUS: *Pontederia* L.

A small family of fresh-water aquatics comprising about six genera and 30 species, mostly pantropical but extending into the temperate zones as well. Although of diverse habit (submersed, emersed, or free floating; erect or prostrate; rhizomatous, stoloniferous, or neither), the plants are all more or less obviously sympodial in structure: each successive axis terminates in an inflorescence that may appear to be axillary.

Plants in the family are most readily distinguished by a combination of characters, including (in addition to the sympodial structure) herbaceous stems enveloped to various extents by sheathing leaf bases; inflorescences subtended by a single sheathing bract; usually six petaloid, nongreen tepals in two series of three, variously connate basally; stamens adnate to the perianth; and superior ovaries.

Three tribes, each represented in the Southeast, were recognized in the Pontederiaceae by Schwartz (1927, 1930). Although both the Eichhornieae Schwartz and the Heteranthereae Schwartz have three-locular ovaries (appearing one-locular at maturity in *Hydrothrix* Hooker f.) and many-seeded capsules, the Pontederieae (*Pontederia* L. and *Reussia* Endl.) have a single fertile locule and a one-seeded, indehiscent fruit. Mostly funnelform perianths and six stamens characterize the monogeneric Eichhornieae; flowers in the Heteranthereae normally have either mostly salverform perianths and three or fewer stamens (*Heteranthera* Ruiz & Pavón, with three stamens of two more or less distinct kinds; *Scholleropsis* H. Perr., with three stamens of two kinds; and *Hydrothrix*, with one stamen and two staminodes) or initially campanulate but ultimately spreading to almost rotate perianths of nearly separate tepals and six stamens (*Monochoria* Presl). Extraregional genera of Heteranthereae include *Scholleropsis* (one species in Madagascar with four or rarely three tepals), *Hydrothrix* (one or two Brazilian species with filiform leaves), and *Monochoria* (perhaps five species ranging from northeastern Africa to Manchuria, Japan, and Australia; one of these established in experimental rice plots in California, according to Mason). The monotypic genera *Eurystemon* E. J. Alex. (Texas and northern Mexico) and *Zosterella* J. K. Small (widely distributed in Mexico and North America) are included here in *Heteranthera. Reussia* (two or three species in South America) is treated as a subgenus of *Pontederia.*

The systematic position of the Pontederiaceae has long been a subject of controversy. The group is considered by many to be most closely related to the Philydraceae (e.g., Casper & Krausch, Dahlgren & Clifford, and Thorne) and/or the Haemodoraceae (e.g., Cronquist; Dahlgren; Simpson, in press) and has been variously allied at higher levels with, among other families, the Bromeliaceae and/or Commelinaceae by some and the Liliaceae by others.

In Thorne's system the Pontederiineae (Pontederiaceae and Philydraceae) were included as one of seven suborders in the Commelinales; the Commeliniflorae and the Liliiflorae were placed as far apart as possible among the five superorders of monocotyledons recognized. Thorne further proposed (p. 100) that the Pontederiineae and Bromeliineae share a "rather close common origin" and thought that misplacement of the former with groups included in his Liliiflorae was probably due to the presence in the Pontederiineae of a petaloid (although biseriate) perianth that is often connate at the base and mostly zygomorphic, as well as to a cylindrical embryo centrally placed in abundant, starchy endosperm. Castellanos, on the other hand, considered the Pontederiaceae to be related to the Commelinaceae because both exhibit zygomorphy and androecial reduction. On the basis of starch grains, Czaja recognized three groups of monocots, one including the Bromeliaceae, Commelinaceae, Haemodoraceae, Philydraceae, and Pontederiaceae, and another the Liliaceae and their close relatives. Likewise, Huber suggested that the superorder Pontederiiflorae (Pontederiales and Philydrales) had more in common with the Bromeliiflorae, Haemodoriflorae, and Commeliniflorae than with the Liliiflorae.

A number of systematists have considered the Pontederiaceae to be more closely allied to the Liliaceae than to either the Bromeliaceae or the Commelinaceae. Although Bentham (in Bentham & Hooker) thought that the flowers indicated a close relationship with the Liliaceae, Baillon and Solms-Laubach (1883a) were among the first to suggest unification with that family. Such a proposal was later at least tacitly accepted by Schwartz (1930), who nevertheless considered the floral zygomorphy, androecial reduction, and mealy endosperm to indicate a relationship with the Commelinaceae and Philydraceae. Hamann (in Melchior) suggested on embryological (starchy endosperm) and anatomical (unspecified) evidence that the Pontederiaceae should be separated from the Liliaceae but maintained as one of five suborders (including the Philydrineae) comprising the order Liliiflorae (Liliales), although he pointed out that in some characters the family is in agreement with the Commelinaceae (Commelinales) and Philydraceae.

Takhtajan stated that the Pontederiaceae probably originated from liliaceous stock, because of the presence of septal nectaries and similarities in vegetative anatomy and embryology (neither specified). Accordingly, he included a unifamilial Pontederiineae as one of six suborders (between the Haemodorineae and a unifamilial Philydrineae, the latter considered to be somewhat isolated but related to the Pontederiineae) in the Liliales, one of 14 orders (the Bromeliales and Commelinales among them) comprising the subclass Liliidae. Cronquist included the Pontederiaceae in his Liliales (subclass Liliidae), far removed from both the Bromeliaceae (Zingiberidae) and Commelinaceae (Commelinidae). Dahlgren, on the other hand, incorporated a unifamilial Pontederiales (between the Haemodorales and the Philydrales) as one of 12 orders with the Bromeliales in his Liliiflorae and placed the Commelinaceae in a separate superorder (Commeliniflorae). Dahlgren & Clifford envisioned a series of taxa, the members of which (e.g., Haemodorales, Philydrales, Pontederiales, Bromeliales, Commelinales) formed a gradual transition between the Liliiflorae and the Commeliniflorae and combined significant features of both. The Pontederiales were indicated to have substantially more attributes in common with "core" Liliiflorae (11 of 21) than with "core" Commeliniflorae (3 or 4 of 21) and a profile of features agreeing most closely with that of the Philydrales.

What little is known about the chemistry of the Pontederiaceae has been compiled and reviewed by Gibbs, and the following is based largely on that account. The plants are among only six monocot families (including none of those discussed here) for which the Mäule test (which is positive for all but weakly lignified tissues) is negative or doubtful. Calcium oxalate crystals, usually raphides, are present. Although cyanogenesis has been reported in *Monochoria,* Gibbs obtained negative results for *Eichhornia speciosa* Kunth, *Heteranthera dubia* (Jacq.) MacM., and *Pontederia cordata* L. He determined that mucilage was present in *Pontederia,* doubtfully so in *Heteranthera,* and absent in *Eichhornia.* Gibbs observed strong reactions between ferric ammonium citrate and the leaves of *E. speciosa* and *P. cordata,* indicating the likely presence of tannins or tanninlike substances; Cronquist (p. 1202) characterized the family as having "scattered tanniferous cells containing proanthocyanins." Saponins are reportedly absent or probably absent from *Eichhornia* and *Pontederia.* Lipids of *Eichhornia crassipes* (Mart.) Solms have been analyzed by Lakshminarayana and colleagues.

Various kinds of phenolic compounds are represented in the Pontederiaceae. Caffeic acid, cyanidin, and ferulic acid have been reported in *Eichhornia speciosa* and *Pontederia lanceolata* Nutt., while *p*-coumaric and synaptic acids are evidently known only from the latter (Bate-Smith). Leucoanthocyanins (which produce anthocyanidins when heated with mineral acids) were indicated for *P. cordata* by Gibbs and considered to be abundant in the family by Bate-Smith. The anthocyanins cyanidin, malvidin, delphinidin, and eichhornin have been reported in *E. crassipes* (see Krishnaveni *et al.*), as has been delphinidin in *P. lanceolata* (Bate-Smith). A number of other flavonoids, including the flavones apigenin and luteolin as well as the flavonols quercetin and isorhamnetin, were isolated from various species of *Heteranthera* by Horn (1985a).

Lowden compared the phenolic profiles of several genera of Pontederiaceae in his revision of *Pontederia* (see discussion of that genus).

Cheadle studied the vessel elements in a number of species (including five occurring in the Southeast) belonging to several genera of Pontederiaceae and found that they normally had long, obliquely oriented, scalariform perforation plates with many perforations and were mostly confined to the roots. Some, however, indicated a more advanced condition, because of either their structure (five or fewer perforations in nearly transverse plates) or their location (stems of *Eichhornia crassipes, Heteranthera limosa* (Sw.) Willd., and possibly *Pontederia cordata*). Cheadle concluded that while relatively unspecialized vessel elements are typical of aquatic angiosperms in general, the more advanced structure of some in the Pontederiaceae suggested that the family was primitively terrestrial. Nevertheless, he also allied the Pontederiaceae with the Philydraceae, even though the vessel elements in this group, which is terrestrial, are somewhat less specialized.

Anthers in the Pontederiaceae are tetrasporangiate (the normal condition among angiosperms); they are bisporangiate in the Philydraceae according to Bhandari, but are tetrasporangiate by Cronquist's account. The microspore mother cells undergo successive divisions to form either isobilateral or decussate tetrads (Davis), and the pollen grains are binucleate when shed (Brewbaker; see, however, Cronquist, who indicated that they are sometimes trinucleate).

The Pontederiaceae were not well known palynologically before Simpson's recent electron micrographic (both TEM and SEM) studies of the group (pers. comm.; 1986), which featured comparisons with the pollen of both the Haemodoraceae and the Philydraceae. Despite earlier reports to the contrary (Erdtman; Rao & Rao; Simpson, in press), pollen with two furrow-shaped apertures (orientation yet to be determined) appears to be the only type represented in the family. In part because this condition is unknown in either the Haemodoraceae or the Philydraceae (and presumably elsewhere), its derivation was considered to have been uniquely shared by members of the Pontederiaceae.

Internal exine structure is variable within the Pontederiaceae, according to Simpson (in press), but the variation does not correspond well to the tribes recognized here. For example, what was termed a "modified tectate-columellate" exine is shared by species of both the Heteranthereae (*Monochoria vaginalis* (Burman f.) Presl, *Scholleropsis lutea* H. Perr.) and the Pontederieae (*Pontederia cordata*), a "two-layered" exine characterizes members of both the Heteranthereae (*Zosterella dubia* (Jacq.) Small = *Heteranthera dubia*) and the Pontederieae (*Reussia rotundifolia* (L. f.) Castell. [here put in *Pontederia* subg. REUSSIA]), and a "one-layered" exine corresponding to the outer layer of the two-layered type was depicted for genera of the Eichhornieae (*Eichhornia crassipes*) and the Heteranthereae (*Hydrothrix Gardneri* Hooker f.). A condition described as intermediate between the modified tectate-columellate type and the two-layered type was reported for *Heteranthera reniformis* Ruiz & Pavón (see, however, Simpson, 1984).

On the basis of palynological evidence, Simpson also concluded that the Pontederiaceae are more closely related to the Haemodoraceae than to the

Philydraceae. The distinctive verrucate sculpturing reported for all the Pontederiaceae studied (except *Pontederia cordata,* which has psilate to scabrate pollen) is identical to that found in tribe Haemodoreae of the Haemodoraceae. In addition, two genera of Haemodoreae have a one-layered exine identical to that of *Eichhornia* and *Hydrothrix,* while four others in the Haemodoreae and all six genera of the Conostylideae have a two-layered exine very similar to that reported by Simpson for *Reussia* and *Zosterella.* The Philydraceae generally have reticulate grains and typical tectate-columellate internal exine structure.

The pontederiaceous ovule is anatropous, bitegmic (with both integuments forming the micropyle), and crassinucellar (Davis). The chalazal megaspore (see, however, Ono) of a linear tetrad develops into a Polygonum-type megagametophyte in which the synergids (at least in *Monochoria hastifolia* Presl) may have a filiform apparatus; the degree to which the three antipodals persist has been controversial (see Coker, R. W. Smith, W. R. Smith). Endosperm formation is, according to Davis, helobial, with free-nuclear divisions and subsequent wall formation normally taking place in both the micropylar and chalazal chambers (the chalazal chamber remains free-nuclear in *Monochoria*). Two haustorial arms are developed laterally in the micropylar chamber in *Monochoria* and presumably the remainder of the family as well (Davis). Embryogeny in the Pontederiaceae is of the Asterad type (see, for example, Souèges). The embryos, along with those of *Amomum* Roxb. (Zingiberaceae), are reportedly unique in their complete extension to both poles of the seed (Martin). According to information compiled by Davis, the most substantial embryological differences between the Pontederiaceae and the Philydraceae are that the former have an amoeboid (vs. glandular) tapetum and unhooked (vs. hooked) synergids.

Tristyly has been reported in the Pontederiaceae and three other flowering plant families (Lythraceae, Oxalidaceae, and Rubiaceae; see Vuilleumier). Species with this condition are characterized by individuals with one of three floral forms (morphs), each differing in the arrangement of anthers and stigmas. (For the condition in *Pontederia cordata,* see FIGURE 1, c–e.) Three levels (short, medium, and long) are occupied by two groups of anthers and the single stigma; thus, pollen is partitioned on a pollinator in such a way that its delivery to the stigma of another flower of the same morph is unlikely. For example, pollen from short and long stamens of mid-styled flowers normally would not be delivered to the stigmas of other mid-styled flowers. Transfers of pollen from anthers to stigmas of the same level are termed legitimate pollinations, while all intraform and some interform pollinations are illegitimate. Populations of tristylous Pontederiaceae (and perhaps other families) vary from isoplethy, a condition in which the three morphs are equally represented, to monomorphy, in which only a single floral form is present.

The mechanical barrier to pollinations leading to either self-fertilization or assortative (like genotype) crossing effected by the tristylous condition is normally accompanied by a physiological self-incompatibility system, as well as by a marked pollen trimorphism, and since the time of Darwin it has been thought to promote animal-mediated cross-pollination and subsequent outcrossing. Under one argument tristyly and self-incompatibility are mutually reinforcing, while another holds that the former is secondarily reinforced by the latter, even though self-incompatibility would appear to be superfluous if the pollen partitioning effected by tristyly were as effective as it appears to be. It may be more reasonable to suppose that in groups with both conditions, self-incompatibility, which is relatively widespread in plants in general, evolved first and is secondarily reinforced by tristyly in the sense that pollen partitioning would minimize the wasteful placement of pollen on incompatible stigmas. The selective advantage of tristyly evidently does not involve reduction of interference on the stigma by illegitimate pollen or adjacent stamens, according to experiments on *Pontederia cordata* by Barrett & Glover. The pollen trimorphism accompanying tristyly in the Pontederiaceae, which involves differences in both pollen size and degree of self-incompatibility, appears to be physiological and/or developmental in nature and dependent on anther level (see discussions of *Eichhornia* and *Pontederia*).

Four species of *Pontederia* (*P. cordata, P. rotundifolia* L. f., *P. sagittata* Presl, *P. subovata* (Seub.) Lowden) and three of *Eichhornia* (*E. azurea* (Sw.) Kunth, *E. crassipes, E. paniculata* (Sprengel) Solms) are tristylous (Barrett, 1978a, 1979; Lowden; Richards & Barrett). The condition in *Pontederia* and *E. azurea* is accompanied by physiological self-incompatibility, strong pollen trimorphism, and populations in which all three floral morphs are usually represented, but it is characterized in *E. crassipes* and *E. paniculata* by a high degree of self-fertility, weakly developed pollen trimorphism, and populations that are frequently monomorphic. Self-fertilizing, semihomostylous (upper set of anthers adjacent to stigma) races of each of the tristylous species of *Eichhornia,* including *E. azurea,* have been reported (see also discussions of the genera).

Progeny tests have indicated that the determination of floral morph in *Eichhornia crassipes* is governed by two diallelic loci (Barrett, 1977). While the M locus determines whether styles are midlength (MM or Mm) or long (mm), the S locus controls whether they are short (SS or Ss) or nonshort (ss) and is epistatic to the M locus. Barrett, Price, & Shore have assumed that this pattern of inheritance characterizes all tristylous Pontederiaceae. (See further discussion under *Eichhornia* and *Pontederia.*)

The economic significance of the Pontederiaceae lies chiefly with *Eichhornia crassipes,* possibly the world's most serious aquatic weed; other members of the family also occur as weeds, especially in rice fields. A number of species have ornamental value, and many are used in one way or another by fish, waterfowl, aquatic mammals, and humans.

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KEY TO THE GENERA OF PONTEDERIACEAE IN THE SOUTHEASTERN UNITED STATES

General characters: *Rooted or floating herbs, submersed, emersed, or sometimes on wet ground; stems sympodial, either stout and sometimes connected by stolons or elongate; leaves simple, alternate, sessile and ligulate or petiolate, venation parallel, a distinct midvein absent, bases sheathing; inflorescences terminal (often appearing axillary), spicate, racemose, paniculate, or single flowered, sessile or pedunculate, each subtended and enclosed to various extents by a sheathing bract that is sometimes surmounted by a reduced petiole and/or blade, each flowering stem with a single leaf sometimes differing from the others; flowers perfect (some species tristylous); perianth of 6 petaloid tepals in 2 series, the lobes imbricate, fused to various degrees basally, actinomorphic to zygomorphic (then with 2 lips of 3 lobes each); stamens usually 6 or 3 (and then sometimes with 3 staminodes), the filaments adnate to perianth tube, inserted at various levels (often in the same flower), the anthers usually with introrse, longitudinal dehiscence; carpels 3, united; style single; ovary superior with 1 or 3 fertile locules; nectaries septal or absent;*

ovules solitary (in unilocular ovaries) or numerous in each locule, anatropous, bitegmic; fruit a 1-seeded utricle or a many-seeded capsule; seeds small, those in capsules with longitudinal ridges.

A. Inflorescences usually several- to many-flowered; perianths zygomorphic; stamens 6 (at least in chasmogamous flowers), long axes of anthers and filaments not parallel; nectaries septal.
  B. Ovaries with 3 fertile, many-ovulate locules; fruit a capsule; plants usually floating. .... 1. *Eichhornia.*
  B. Ovaries with 1 fertile, 1-ovulate locule (and 2 aborted locules); fruit a utricle; plants rooted in substrate. ....3. *Pontederia.*
A. Inflorescences usually 1- to few-flowered; perianths actinomorphic or subactinomorphic; stamens 3 (at least in chasmogamous flowers), long axes of anthers and filaments parallel; nectaries absent. .... 2. *Heteranthera.*

Tribe EICHHORNIEAE Schwartz, Bot. Jahrb. **61**(Beibl. 139): 32. 1927.

1. **Eichhornia** Kunth, *Eichhornia,* Genus Novum [Diss.]. 1842; Enumeratio Pl. **4:** 129. 1843, nom. cons.

Perennial [or annual], submersed, emersed, or floating herbs. Stems stout, more or less vertical, often connected by stolons. Adult leaves exstipulate, either sessile, linear, and thin (if submersed), or petiolate, with the petioles longer than the blades and usually more or less inflated, the blades broadly elliptic to orbicular. Inflorescence a spike or panicle [or single flowered], pedunculate, the subtending bract of each with a highly reduced petiole and blade, the single leaf on each flowering stem with a large, sheathing base, little or no petiole, and a reduced blade. Flowers perfect, some species tristylous; perianth mostly funnelform, zygomorphic, with 2 lips of 3 lobes each. Stamens 6, unequal in length; filaments curved; anthers oblong, auriculate and somewhat movable on the filaments, much shorter than the filaments, the adaxial 3 either included deep within the perianth tube or near its summit, lower than the abaxial 3, which are either near the summit of the perianth tube or exserted. Ovary with 3 locules, each with numerous ovules on an axile placenta; stigma (depending on style length) included deep within the perianth tube, or near its summit, or exserted. Fruit a many-seeded, membranaceous capsule with loculicidal dehiscence; seeds longitudinally ribbed. (*Eichornia* A. Rich., 1850, orthographic variant; *Piaropus* Raf., 1837, nom. rejic.) TYPE SPECIES: *E. azurea* (Sw.) Kunth (*Pontederia azurea* Sw.), typ. cons. (Named for Johann Albrecht Friedrich Eichhorn, of Berlin, 1779–1856.)—WATER HYACINTH.

A genus of about seven species native to the American tropics and perhaps subtropics, including one, *Eichhornia natans* Solms, that appears to be closely related to (if not conspecific with) plants that may occur naturally in tropical Africa and Madagascar, and another, *E. crassipes* (Mart.) Solms, that through introductions has spread throughout the tropics and to adjacent warm-temperate areas. *Eichhornia* can be distinguished from other genera of Pontederiaceae by a combination of floral characters including a mostly funnelform perianth, six stamens, and an ovary with three fertile, many-ovulate locules.

Schwartz (1927, 1930) placed *Eichhornia* in the monogeneric tribe Eichhornieae Schwartz and proposed two sections in the genus that were neither adequately defined by him nor widely accepted by later workers (e.g., Alexander, Castellanos, Schulz), although they may have some utility. Section PROTOEICHHORNIA Schwartz (paniculate inflorescences, plants rooted in the ground) included *E. paniculata* (Sprengel) Solms and *E. paradoxa* (Mart.) Solms, while sect. *Eueichhornia* Schwartz (= EICHHORNIA) (spicate inflorescences, plants free floating) included *E. azurea* (Sw.) Kunth, *E. natans,* and *E. crassipes.* Additional names, and perhaps species, exist, and the genus is in need of taxonomic attention on a worldwide basis.

Two species of *Eichhornia* have been reported from the southeastern United States, each an introduction, apparently from Brazil. *Eichhornia paniculata* differs from *E. crassipes,* $2n = 32$, in the characters by which the two sections are distinguished and in its complete lack of inflated petioles. It was at least at one time naturalized in peninsular Florida from plants in cultivation (Alexander; Muenscher, 1944), but I have seen no specimens from the area and the species is not included in recent floristic accounts (e.g., Godfrey & Wooten, Long & Lakela, and Ward). *Eichhornia azurea,* $2n = 32$, also lacking inflated petioles, is an introduction in southern Texas (Correll & Correll).

Perianths in *Eichhornia,* including those of our plants, are various intensities of blue, violet-blue, or lilac, with those of *E. crassipes* often pale and rarely even white; those of *E. paniculata* are often darker in the lower three lobes. The upper-middle perianth lobe in *E. crassipes* usually bears a deep violet-blue area with a yellow spot inside, while that of *E. paniculata* has an unbordered, bilobed yellow spot (Alexander).

Eichhornia crassipes, the water hyacinth, is generally considered to be the world's most serious aquatic weed. An enormous amount of research has been conducted in an effort to understand many aspects of its biology, with the ultimate but perhaps unattainable goal of eradicating it from areas and habitats in which it is not native. The literature on this species, which has been reviewed by Sculthorpe and more recently by Pieterse, is correspondingly immense. The *Hyacinth Control Journal* (now the *Journal of Aquatic Plant Management*), the existence of which underscores the significance and extent of the problem, contains only a portion of what has been published.

Problems caused by the water hyacinth, although multifarious, are all more or less direct results of the tremendous, rapidly accumulated biomass generated by the plants. Floating mats are frequently large enough to obstruct navigation completely, to impede drainage to the point of flooding, to contribute in various ways to eutrophication, and to cause wastage of impounded water by displacement and transpiration. It was conservatively estimated that in Louisiana damage and losses attributable to the foregoing probably exceeded five million dollars per year in the 1940's (Penfound & Earle). The water hyacinth has been reported to have detrimental effects on rice paddies (Sculthorpe) and to provide excellent conditions for mosquitoes and other disease-carrying organisms (Vietmeyer). The floating mats are thought to accelerate greatly and perhaps alter fresh-water succession (see Sculthorpe) and to prevent the occupancy of lakes, ponds, and streams by various kinds of waterfowl (Vietmeyer).

Methods of controlling the water hyacinth have been both numerous and varied. Removal of the plants by hand has been effective in small waterways and rice fields, but this may be hazardous if disease-carrying organisms are present and is impractical if the mats have attained even relatively small sizes. Various devices (including lasers) have been constructed either to cut temporary paths through the mats or to destroy them completely, but the costs involved have been high. Numerous chemicals, most commonly 2,4-dichlorophenoxyacetic acid (2,4-D), have been employed, but effects on the environment have usually been detrimental. Drainage of infested areas has been effective in killing the plants, but this may ultimately prove to be unwise because it favors seed production, which could enhance the adaptability of the species. Many control methods result in the accumulation of dead and decaying plant material that must be removed in order to prevent eutrophication.

Attempts at biological control have included the use of fungi, snails, mites, insects, fish, and manatees. Significant control by the host-specific weevil *Neochetina eichhorniae* Warner has been reported in Louisiana (Goyer & Stark) and in Florida (Center & Durden); *N. bruchi* Hustache and the pyralid moth *Sameodes albiguttalis* (Warren) have also been released in Florida (Center & Durden). Center & Durden (p. 28) note that "recent successes with biological control of water hyacinth. . .have now been reported worldwide."

Accounts regarding the first appearance of *Eichhornia crassipes* in the United States are somewhat varied (see Penfound & Earle). Despite some evidence that it was cultivated shortly after the Civil War, it was, according to some, first shown at an exposition in New Orleans in 1884. The plant attracted a great deal of attention as a beautiful, easily grown ornamental. Because of its popularity and vigorous growth, its escape from cultivation and subsequent naturalization were probably inevitable. In Louisiana, and elsewhere in the world, its introduction to nature was commonly effected by exasperated gardeners who, in attempting to rid cultivated pools and ponds of this initially desirable but soon troublesome aquatic, threw living material into local waterways in the hope that it would be carried away. Unfortunately, the plants thrived out of cultivation in areas where natural enemies were lacking. The species was reported from Florida in 1890, was known from each of the coastal states in the Southeast (its maximum and present range in our area) by the early 1900's, and was first recorded in California in 1904 (Bock, 1968). Nevertheless, in North America it appears to have been and continues to be a serious problem only in Louisiana, Mississippi, and Florida (Sculthorpe).

The water hyacinth, a native of the South American tropics, has been introduced and is now naturalized throughout most tropical and subtropical areas of the world, with an adventive range extending into such warm-temperate areas as the southeastern United States, California, Japan, southeastern China, northern Africa, Portugal, Uruguay, and South Africa (for distribution map, see Barrett, 1977, or Sculthorpe, p. 462). Although it is called the "Florida devil" in South Africa (Vietmeyer), and although its introduction throughout the Old World seems to postdate its first occurrences in North America, it is unclear whether the species spread secondarily from that continent or was introduced outside of the Western Hemisphere directly by plants obtained from

South America. It seems likely that both contributed (see also discussion of style morph distribution, below). It was introduced into Malaysia in 1894 (Backer).

The plants can rapidly cover stagnant or slow-moving bodies of fresh water because of their remarkable capacity for vegetative growth and reproduction. A single plant reportedly developed in one season into a patch of about 600 m^2 through the production of a radiating system of stolons and associated rosettes (Aston; see also Batanouny & El-Fiky). The foliage is killed by frost or generally cold conditions, but the stems may survive and resume growth when temperatures rise. Unconfirmed reports indicate that although the plants are sensitive to salt water, stems protected by sheathing leaf bases may survive exposure long enough for dispersal along sea coasts (Vietmeyer); stems so protected may also withstand periods out of water. Seeds remain viable for up to 15 years and may aid in dispersal of the plants, as well as in their reestablishment following extermination of the parental plants.

Although it has been difficult to assess the relative importance of reproduction by seeds in the spread of *Eichhornia crassipes,* there is now little doubt that it has been very much underestimated in the past. While Hitchcock and colleagues reported very few seedlings in Louisiana despite extensive seed production, tremendous numbers of young plants were discovered along the banks of the White Nile in November, 1963, less than six years after the species was first seen in the region (Pettet). Ironically, the massive establishment is thought to have resulted from attempts to eradicate the species with 2,4-D. The seedlings were most abundant on the decomposed material left by the killed mats of *E. crassipes* and were absent from adjacent banks of natural, sandy soil. The free-floating habit of *E. crassipes* often limits sexual reproduction, particularly in the adventive range of the species, by enabling the plants to reach and then occupy habitats that never become favorable for germination and seedling establishment. In habitats with seasonally fluctuating water levels, which are more commonly occupied in the native range of the species, sexual reproduction may be very important, since seeds germinate and seedlings become established in warm, shallow water during periods of extensive desiccative damage to vegetative parts.

Barrett (1980a, 1980b) determined that clones of *Eichhornia crassipes* from Louisiana, Florida, California, Mexico, South America, Africa, and India all retained the potential for sexual reproduction and that observations to the contrary were due to environmental and not genetic factors. Sexual reproduction in nature is evidently limited by inadequate pollination and unsuitable conditions for seed germination and seedling growth and not by the inbreeding depression, self-incompatibility, and accumulation of deleterious mutations often characteristic of largely vegetative species.

The free-floating habit and vigorous asexual reproduction of *Eichhornia crassipes* have been held responsible in one way or another for the reported disruption of tristyly in the species. These features have often resulted in populations that are either monomorphic (particularly in the adventive range of the species) or dominated by a single floral form. In either case selection has presumably favored the development of self-compatibility, high levels of which have been detected in many populations (Barrett, 1977; François; Mulcahy). Barrett (1979) studied a marshland population in Costa Rica consisting of both mid- and long-styled forms and determined that within each, seed production following illegitimate pollinations was only slightly less than that associated with legitimate pollen deposition, indicating both self-compatibility and weak and/or residual self-incompatibility. The results of progeny tests involving seeds obtained from these plants revealed low levels of disassortative (unlike genotype) crossing for each floral form. While this pattern of crossing is at least in part due to pollinator behavior (foraging bees tended to visit most of the flowers of an inflorescence before departing), it also indicates high levels of self-compatibility.

The habit and growth characteristics mentioned above have further contributed to the disruption of tristyly in *Eichhornia crassipes* by allowing the plants to occupy extensive areas, particularly within the adventive range of the species where pollinators are supposedly ill adapted and/or limiting (Barrett, 1977). Flowers within the native range of *E. crassipes* are usually visited by insects large enough to partition the different pollen types effectively and thereby to cross-pollinate the three floral forms (e.g., *Ancyloscelis gigas*, a species of long-tongued bee, is the major pollinator in the lower Amazon). Flowers in the adventive range, on the other hand, have apparently been attracting smaller pollinators, so there has been selective pressure to bring the anthers and stigmas closer together. Such floral modifications would also be favored if pollinating vectors were numerically limiting because they would increase the chances of self-pollination. Barrett (1979) reported that four percent of the mid-styled flowers sampled from a Costa Rican population considered to be outside the native range of the species were semihomostylous (upper set of anthers adjacent to stigma; also reported by François) and that this condition was accompanied by increases in pollen deposition. The development of semihomostyly and related phenomena is probably responsible at least in part for the weakened pollen trimorphism observed as another aspect of the breakdown of tristyly in *E. crassipes* in that size and number of pollen grains are dependent on anther level (Barrett, 1979).

Semihomostyly in *Eichhornia crassipes* is generally thought to have been derived from tristyly because its occurrence is restricted and because it evidently has not been detected in the native range of the species. Reports of the condition throughout *E. heterosperma* E. J. Alex., *E. natans*, and *E. diversifolia* (Vahl) Urban (see Barrett, 1979), as well as in races of *E. azurea* (Barrett, 1978a), prompted Barrett (1979) to conclude that it developed a number of times within the genus. Its relative infrequency in *E. crassipes* appears to be the result of limited sexual reproduction and consequently slow evolutionary rates within the species (Barrett, 1979).

Investigations into the distribution of style-morphs among New World populations of *Eichhornia crassipes* have suggested that the species is native to the Amazon basin and perhaps to parts of the Paraguay and Paraná river systems, as well, instead of to the tropics and subtropics of the New World in general, as has been widely thought (see primarily Barrett & Forno). Trimorphic populations, which if of limited occurrence would be expected primarily in areas of ancient occupancy (assuming that the species is indeed primitively tristylous), have been reported only from the Amazon basin in Brazil (where the species is thought to have originated) and from lagoons near the confluence of the Paraguay and Paraná rivers in Argentina (to which it is thought to have spread by natural means). Populations in Paraguay, Uruguay, Guyana, Venezuela, and Colombia, as well as throughout the Caribbean, Central America, and warm-temperate North America, evidently lack the short-styled morph and are therefore considered to have resulted from introductions. (The lack of specialized pollinators in Central America also implies that the species is introduced there.)

Distribution data on style-morphs may provide insights into the spread of *Eichhornia crassipes* when considered in conjunction with the genetic basis of tristyly in the species. Since the short-styled morph (S__M__ or S__mm) cannot be segregated from crossings involving the mid- (ssM__) and/or long-styled (ssmm) morphs, its presence in the adventive range of the species would have required separate introduction(s). The fact that it is evidently absent from these areas suggests that the spread of the species throughout the world has involved only a very few and perhaps even a single introduction, unless the short-styled morph for some reason either was not selected by man from nature or is ill equipped to become introduced and established outside its native range. Otherwise, one would expect at least some introductions to have involved the short-styled morph. The predominance of the mid-styled form in the adventive range and of the short-styled morph in the native range (Barrett & Forno) would then be explained by simple genetics. That seed production of the short-styled morph in the Lower Amazon was found to be 44–75 percent higher than that of the other two style-morphs (Barrett, 1977, 1980a) is not only consistent with the foregoing but may imply that it de-emphasizes vegetative reproduction and is therefore less well adapted to establishment outside its native range.

Considerable effort has been expended to find uses for *Eichhornia crassipes* on the assumption that exploitation would constitute the most economically sound form of control (see primarily Pieterse). Plants have been investigated as animal fodder (silage, hay, pelletized feed), but their high water content has made harvesting, storage, and processing difficult. The costs of using the water hyacinth as fertilizer and mulch have also been prohibitive. The plants have been utilized with some success as sources of plant hormones and other chemicals and have been fermented to produce methane. Because the roots of *E. crassipes* are effective in absorbing nitrates, phosphates, and potassium, the species has been used to purify water that has been polluted by fertilizers. Fishermen in the Philippines and in Bangladesh maintain circular mats that provide shade and shelter and therefore attract fish, and farmers in Bangladesh and Burma transform mats into floating gardens by the application of fertile bottom muck. Neither the water hyacinth if grown for a crop nor the plants grown on the floating gardens require manufactured fertilizer, irrigation, or land. Leaves of water hyacinth are used in Thailand to wrap cigars and are utilized by the Chinese in wicker and basket work.

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iae, in Canal-M, Palm Beach County, Florida, in 1983–1984. *Neochetina bruchi* and the pyralid moth *Sameodes albiguttalis* also present and probably effective. Citation of several other recent successes in biological control throughout the world.]

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VIETMEYER, N. D. The beautiful blue devil. Natural History **84:** 64–73. 1975. [Despite several inaccuracies, an interesting account with several good photographs.]

Tribe HETERANTHEREAE Schwartz, Bot. Jahrb. **61**(Beibl. 139): 35. 1927.

2. **Heteranthera** Ruiz & Pavón, Fl. Peruv. Chil. Prodr. 9. 1794, nom. cons.

Perennial or annual, submersed, emersed, or floating herbs. Stems stout and more or less vertical to elongate and more or less horizontal. Adult leaves stipulate or exstipulate, either sessile, linear (strap shaped) and thin, or petiolate, with the petioles longer than the blades and not inflated, the blades reniform, cordate, or lanceolate. Inflorescence a spike or single flowered, sessile or pedunculate, the subtending bract lacking a petiole and blade, the single leaf on each flowering-stem identical to all other leaves. Flowers perfect; perianth salverform, with 6 lobes, actinomorphic or subactinomorphic (1 lobe different in shape and/or spaces between lobes unequal). Stamens 3 (sometimes 1 in cleistogamous flowers), equal in length or the lateral 2 shorter, inserted on adjacent adaxial tepals; filaments straight or curved; anthers oblong or ovate, sometimes auriculate and somewhat movable on the filaments, sometimes nearly equal in length to the filaments, exserted, in subgen. *Zosterella* becoming circinately coiled after anthesis. Ovary with 1 locule, the ovules numerous in 2 or more rows on each of 3 more or less completely intrusive placentae; stigma usually exserted. Fruit a many-seeded membranaceous capsule with loculicidal dehiscence; seeds longitudinally ribbed. (*Schollera* Schreber, 1791, not Roth, 1788; *Heterandra* Beauv., 1799; *Leptanthus* Michx., 1803, nom. superfl. [includes type of *Heterandra* Beauv.]; *Zosterella* Small, 1913; *Eurystemon* E. J. Alex., 1937.) TYPE SPECIES: *H. reniformis* Ruiz & Pavón, Fl. Peruv. Chil. **1:** 43. 1798. (Name from Greek *heteros,* different, and *antheros,* anther, in reference to the unequal anthers of most species, including the type.)—MUD-PLANTAIN, WATER STAR-GRASS, BUFFALO-GRASS.

A small genus of about 12 species native to tropical and temperate regions of the New World and Africa. *Heteranthera* is distinguished from other Pontederiaceae by a suite of floral characters, including salverform perianths with six equal or nearly equal lobes, one- or imperfectly three-loculate ovaries with numerous ovules, and three stamens.

Infrageneric classifications of *Heteranthera* have been varied. Persoon (1805) evidently was the first to subdivide the genus (as *Leptanthus* Michx.), establishing two subgenera (see Brizicky) based on androecial morphology: *Heteranthera* (including the types of both *Heteranthera* Ruiz & Pavón and *Heterandra* Beauv.), with dimorphic stamens ("Filam. longitudine inaequalia, antherae biformes"); and *Leptanthus,* with stamens of only one form ("Antherae uniformes lineares, filamenta aequalia"). Solms-Laubach later (1883a) established two sections: *Leptanthus* Solms (including the type of *Heteranthera*), with petiolate leaves; and *Schollera* Solms, with strap-shaped (ligulate) leaves. Schwartz (1927) recognized three sections on entirely different grounds. Section *Protoheteranthera* (= sect. HETERANTHERA) was characterized by three- to many-flowered inflorescences with no cleistogamous flowers; sect. *Heterantheropsis,* by one- or two-flowered inflorescences with no cleistogamous flowers; and sect. *Euheteranthera,* by many-flowered inflorescences with one or more cleistogamous flowers.

Small (in Small & Carter) segregated the monotypic genus *Zosterella* from *Heteranthera* on the basis of monomorphic (vs. dimorphic) stamens and linear (vs. broad) leaf blades. Although such a treatment generally agrees with that of Persoon, neither has been widely accepted. Recent studies by Horn (1985a), however, suggest that division of *Heteranthera* along these lines may be most tenable. Neither leaf morphology, on which the classification of Solms-Laubach was based, nor the presence or absence of cleistogamous flowers, by which Schwartz's sections were partially delimited, has proven to be taxonomically significant. Horn (1984a) reported that all species in the group initially produce strap-shaped (linear) leaves and that the mature leaf form is habitat dependent. Horn (1985a) also determined that all species produce cleistogamous flowers, usually in response to development under water, and that such structures are for the most part morphologically identical to chasmogamous flowers (see also Thieret). Underwater development commonly results in reduced numbers of flowers per inflorescence as well, unless the species is one that normally produces only one- or two-flowered inflorescences.

Horn (1985a) recently completed a revision of *Heteranthera* sensu lato that employed a number of biosystematic methods (e.g., flavonoid chemistry, cytology, pollen and seed morphology, vegetative anatomy, developmental biology), as well as numerical (cluster and principal component) and cladistic analyses of populations and species, respectively. Although a fairly convincing case for the existence of two groups was presented, I do not agree that the data support their recognition at the generic level (*viz., Heteranthera* and *Zosterella*). Horn's decision to do so may have resulted from a failure to incorporate outgroup comparisons in the analyses: the characters by which *Heteranthera* and *Zosterella* were reported to differ (e.g., internode length on flowering stem, length of time flowers stay open, perianth pubescence, androecial morphology [monomorphic or dimorphic stamens], filament inflation, anther shape and coiling, seed size) seem much less significant than those by which other genera in the Pontederiaceae differ (e.g., fusion of perianth parts, number of stamens, attachment and dehiscence of anthers, number of locules per ovary and of ovules per locule, and fruit type). In addition, the stamens of *H. limosa* (Sw.) Willd. and *H. peduncularis* Bentham are only slightly dimorphic (indeed, Persoon included *Leptanthus ovalis* Michx. [= *H. limosa*] in subg. *Leptanthus*; Horn, however, has correctly placed it with the other species having dimorphic stamens), further lessening the distinction between the two groups. I am, therefore, recognizing as subgenera the two groups treated as genera by Small and

Horn.[3] The species concepts of Horn appear to be sound, and much of the following is based on his revision. (Unless otherwise indicated, material attributed to Horn is taken from his dissertation.)

Subgenus HETERANTHERA (annuals with dimorphic stamens and noncoiling anthers) comprises the eleven species placed by Horn in *Heteranthera* sensu stricto; all but one (*H. callifolia* Reichenb. ex Kunth, of sub-Saharan Africa) are native to the New World. Two groups were identified in subg. HETERANTHERA by Horn's cladistic analysis, although they were not given names (see, however, Horn, 1986b). One group of species, all $2n = 14$, is represented in the Southeast by *H. limosa* and probably by *H. rotundifolia* (Kunth) Griseb. The other group, in which $x = 8$, has among its members *H. multiflora* (Griseb.) Horn, $2n = 32$, and *H. reniformis* Ruiz & Pavón, $2n = 48$, both found in our area. All species of the subgenus in our area produce petiolate leaves.

Heteranthera limosa and *H. rotundifolia,* each with single-flowered inflorescences, are identical in flavonoid chemistry, chromosome number, and pollen and seed morphology. Plants of *H. limosa* commonly form rosettes and have ovate to elliptic leaf blades, actinomorphic perianths, and nearly monomorphic stamens, while those of *H. rotundifolia* do not form rosettes and have at least some round leaf blades, subactinomorphic perianths (one lobe cordate at the base), and clearly dimorphic stamens (the lateral filaments curved). Plants of *H. limosa* usually occur in shallow water, commonly at the edges of ponds and in roadside ditches, and are submersed as seedlings. Rosette-forming individuals and others with elongate, horizontal stems occur in the Southeast and may represent two biologically meaningful taxa, according to Correll & Correll, although Horn considered the latter condition to be induced by growth in water 10 cm or more deep. The distribution of *H. limosa* extends from California and the central United States (including Tennessee, Mississippi, Arkansas, and Louisiana) to central South America. Plants of *H. rotundifolia* grow in small bodies of water or on mudflats. With the exception that the species has not been reported either from California or from our area, it has a distribution almost identical to that of *H. limosa.* Although Steyermark did not report *H. rotundifolia* from Missouri (he apparently did not consider it to be distinct from *H. limosa*), Horn indicated that it occurs throughout the state and along the Missouri side of the Arkansas border.

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[3] Although *Schollera* Schreber is a later homonym and is therefore illegitimate at the generic level, it could be used as a new name for the subgenus with monomorphic stamens recognized here. However, *Zosterella* Small is also available, and since it is the more familiar name for these plants, it is appropriate to make the following new combination at the level of subgenus.

Heteranthera subg. **Zosterella** (J. K. Small) Rosatti, comb. et stat. nov.

Zosterella J. K. Small in J. K. Small & J. J. Carter, Fl. Lancaster County [Pennsylvania], 68. 1913. TYPE SPECIES: *Z. dubia* (Jacq.) J. K. Small (*Commelina dubia* Jacq.).

Leptanthus Michaux (1803) is a superfluous name, since Michaux cited *Heterandra* Palisot de Beauvois (Trans. Am. Philos. Soc. **4:** 175. 1799) (as "*Heteranthera*"), for which the type species is *Heterandra reniformis* Beauv., 1799, not *Heteranthera reniformis* Ruiz & Pavón, 1798, although both names apply taxonomically to the same species.

Heteranthera multiflora and *H. reniformis* both have spicate inflorescences, and they are difficult to distinguish vegetatively. However, in *H. multiflora* the flowers are purple, and the inflorescence is more than twice as long as the subtending bract, while in *H. reniformis* the perianths are white and the spike is usually about as long as the bract. In the United States *H. reniformis* occurs from Connecticut and southern New York southward to southeastern Virginia, western North Carolina, northern Georgia, and western Florida, and westward to Louisiana, southern and western Missouri, and southern Illinois, with disjunct localities along the Rio Grande in Texas. It is also found in Mexico and Central America, Cuba, Hispaniola, and Jamaica. In South America it is known from Venezuela and Colombia, southward to northern Argentina, Paraguay, and southern and eastern Brazil. *Heteranthera multiflora* has a similar but more disrupted distribution. In the United States it is known from New Jersey south to northeastern North Carolina; from southwestern Illinois, Missouri, southeastern Nebraska, Kansas, Oklahoma, Arkansas, and southwesternmost Tennessee; and from outlying stations in Mississippi and southernmost Texas. Disjunct localities have been found in northern Venezuela, northern Argentina, Paraguay, and southern and eastern Brazil. Although plants of both species can either float or become rooted in shallow water or moist ground, those of *H. multiflora* reportedly are able to occupy deeper water than those of *H. reniformis* because of their superior ability to produce elongate stems. *Heteranthera peduncularis,* primarily of high elevations in Mexico but also reported from southeastern Arizona and Guatemala, is very similar to *H. multiflora* and *H. reniformis* but can evidently be distinguished from them by its glabrous or glabrate (vs. pubescent) lateral staminal filaments.

Subgenus ZOSTERELLA (perennials with monomorphic stamens and coiling anthers) comprises one, or perhaps two, species, both present in the Southeast. The leaves are linear in both and resemble those of *Potamogeton* species, except that they lack a distinct midrib. *Heteranthera Liebmannii* (Buch. ex Magnus) Shinners (*Zosterella longituba* E. J. Alex.) has been recognized by some (e.g., Alexander; Correll & Correll) as being distinct from *H. dubia* (Jacq.) MacM. (*Zosterella dubia* (Jacq.) Small) because of differences in flower size and seed morphology. The perianth tubes of *H. Liebmannii* are usually much longer than those of *H. dubia* (5–12 vs. 1.5–7 cm), and the seeds of the former are nearly globose, black-brown, and 14- to 16-ribbed, while those of the latter are ellipsoid, yellow-brown, and 10- to 12-ribbed. Horn has reported, however, that from north to south there is a general increase in perianth-tube length and that, although there is a genetic component, shorter perianth tubes were produced on cooler mornings among experimental plants. He also found that seed color was related to development and that the number of ribs per seed varied within populations.

Heteranthera dubia occurs at various depths and tolerates a relatively wide range of temperatures (Steyermark) in still to swift, usually alkaline water (Hellquist & Crow; Muenscher, 1944; De Wit). The species is known from southern Quebec to North Dakota, south to Texas and Florida, and from more scattered localities in Washington, Oregon, California, Arizona, Mexico, Central America, and the Caribbean region. *Heteranthera Liebmannii* is found on mud or in relatively still water from Alabama to Mexico and the Caribbean (i.e., it has a more southern distribution than *H. dubia*) and is reportedly more abundant than *H. dubia* in Texas (Correll & Correll).

Horn (1983) determined that mature seeds of *Heteranthera dubia* sink upon being released in autumn and germinate the following spring. Plants flower in the first year and may overwinter *in toto* beneath the ice, although growth does not occur below 8°C. In shallow and/or swift water the plants may produce much shorter stems and internodes, forming denser, more circular patches (Steyermark) that may provide food and shelter for fish (Correll & Correll). Plants growing on mud develop short, stiff leaves and stems and have been recognized under various names (see Horn, 1983). Although such variants have been considered to be environmentally induced and therefore unworthy of formal taxonomic recognition (Horn, 1983; Steyermark), it is interesting and possibly significant that they are more likely to flower than those in more typical, aquatic conditions (Fassett). While emersed plants flower to some extent, most submersed ones are sterile or develop only flowers that are hidden in the leaf axils and do not open (Voss, under family references). Thieret reported that such flowers are structurally identical to chasmogamous ones and showed that they were induced when buds did not reach the surface or when they were pulled under water by the current.

Flower color, which is variable in *Heteranthera,* has been described in detail by Horn (1985a). Among species of subg. HETERANTHERA in our area, the basic perianth color is purple, lavender, pale blue, or white (yellow, or rarely blue or white in the extraregional *H. Seubertiana* Solms; blue or white in the extraregional *H. zosterifolia* Mart.), while the upper middle lobe is variously marked with dark purple, brown, green, and/or yellow. The central and lateral stamens, as well as the filament and anther of any one stamen, usually differ in color; either filaments or anthers are purple, blue, yellow, or white. Styles and (evidently) stigmas are either purple or white (the style is yellow and the stigma blue in *H. zosterifolia*). With the exception of purple stigmatic hairs, all externally visible flower parts of *H. dubia* (subg. ZOSTERELLA) are yellow or pale yellow.

There is some evidence that the stamen dimorphism (both in color and size) found in species of subg. HETERANTHERA is related to pollination biology. According to studies of *H. reniformis* by Lovell, pollen from the pale blue or greenish anther of the long central stamen is deposited on a visiting bee while it gathers pollen (the flowers lack nectaries) from the more conspicuous yellow anthers of the shorter lateral stamens. Such observations, including that of a green color for the central anther, evidently have not been corroborated by other workers.

The only economic significance of *Heteranthera* involves the occurrence of some of its members as weeds in rice fields: *H. reniformis* and *H. limosa* in the United States (Barrett, 1978b) and *H. reniformis* in northern Italy (Webb, in Valentine). The seeds of various species, including *H. dubia,* are eaten by wildfowl (McAtee; see also Fassett). Both *H. dubia* and *H. reniformis* are considered to be rare and endangered in various northeastern states (Hellquist & Crow).

REFERENCES:

Under family references see ALEXANDER; BARRETT (1978b); CORRELL & CORRELL; FASSETT; HELLQUIST & CROW; HORN (1984a, 1985a); HUNTER; LOVELL; MCATEE; MUENSCHER (1944); SCHWARTZ (1927); SOLMS-LAUBACH (1883a); STEYERMARK; VALENTINE; VOSS; and DE WIT.

AGOSTINI, G. El gênero *Heteranthera* (Pontederiaceae) en Venezuela. Acta Bot. Venez. **9**: 295–301. 1974. [Five species, including *H. limosa* and *H. reniformis.*]

BRIZICKY, G. K. Subgeneric and sectional names: their starting points and early sources. Taxon **18**: 643–660. 1969. [Generic subdivisions in PERSOON's *Synopsis Plantarum* are subgenera.]

EAST, E. M. The distribution of self-fertility in the flowering plants. Proc. Am. Philos. Soc. **82**: 449–518. 1940. [Dimorphism and heterostyly in *Heteranthera.*]

HORN, C. N. Life history of *Heteranthera dubia* (Jacq.) MacM. (Pontederiaceae) with respect to seasonal and environmental effects on morphology. 104 pp. Unpubl. Master's thesis, Ohio State Univ., Columbus. 1980.*

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———. Variation in the adaptations to the aquatic environment during seedling growth in the genus *Heteranthera* (Pontederiaceae). (Abstr.) Am. Jour. Bot. **71**(5, part 2): 172. 1984b. [Vegetative differences between *Heteranthera* and *Zosterella* appear to be due to adaptations to different habitats.]

———. *Zosterella* vs. *Heteranthera,* a little used genus in the Pontederiaceae. (Abstr.) ASB Bull. **31**: 62. 1984c. [Recognition as separate genera favored by flower and seed characters; vegetative aspects of little taxonomic value.]

———. Morphology and distribution of *Heteranthera* (sensu lato; Pontederiaceae) in the southeastern United States. (Abstr.) ASB Bull. **32**: 46. 1985b. [*H. dubia, H. limosa, H. reniformis, H. rotundifolia.*]

———. Adaptation to the aquatic environment by species of *Heteranthera.* (Abstr.) *Ibid.* **33**: 76. 1986a. [Experiments suggested that in response to growth in deeper water, plants generally produce shorter petioles and more elongate vegetative stems.]

———. Typifications and a new combination in *Heteranthera* (Pontederiaceae). Phytologia **59**: 290. 1986b. [*H. multiflora* (Griseb.) Horn; sects. *Schollera* Solms in A. DC. and *Leptanthus* Solms in A. DC. typified.]

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PERSOON, C. H. *Leptanthus.* Syn. Pl. **1**: 56. 1805. [*Leptanthus* Michx.; the earlier *Heteranthera* Ruiz & Pavón included as a subgenus.]

SMALL, J. K., & J. J. CARTER. Flora of Lancaster County [Pennsylvania]. New York. 336 pp. 1913. [Pontederiaceae, 68, 69; *Zosterella* Small, *Heteranthera, Pontederia.*]

THIERET, J. W. Observations on some aquatic plants in northwestern Minnesota. Michigan Bot. **10**: 117–124. 1971. [Induction of "pseudocleistogamous" flowers in *H. dubia,* 117, 118.]

VARALDA, G., G. FORNERIS, & F. MONTACCHINI. New findings and interesting confirmations of species in the flora of Basso, Vercellese and Oltrepo, Alessandrino, central east Piedmont, Italy. Allionia **26**: 123–130. 1983.* [*H. limosa, H. reniformis.*]

VOSS, E. G. A vegetative key to the genera of submersed and floating aquatic vascular plants of Michigan. Michigan Bot. **6**: 35–50. 1967. [Includes *H. dubia.*]

Tribe PONTEDERIEAE [Schwartz, Bot. Jahrb. **61**(Beibl. 139): 39. 1927]

3. **Pontederia** Linnaeus, Sp. Pl. **1:** 288. 1753; Gen. Pl. ed. 5. 140. 1754.

Perennial, emersed herbs. Stems stout and more or less horizontal. Adult leaves exstipulate; petiolate, petioles usually much longer than blades, not inflated; blades sagittate, cordate, ovate, or elliptic. Inflorescence a spikelike panicle,[4] pedunculate, the subtending bract sometimes mucronate, the single leaf on each flowering-stem with a large, sheathing base and a petiole much shorter than the blade. Flowers perfect, all species tristylous except the homostylous *P. parviflora*; perianth mostly funnelform, zygomorphic, with 6 lobes in 2 lips of equal [or unequal] lobe number. Stamens 6, unequal in length; filaments straight or curved; anthers oblong, auriculate, much shorter than the filaments and somewhat movable on them, the adaxial 3 either included deep within the perianth tube or near its summit, lower than the abaxial 3, which are either near the summit of the perianth tube or exserted. Ovary with 2 abortive locules and 1 fertile one with a solitary ovule pendulous from a terminal placenta; stigma (depending on style length) included deep within the perianth tube, or near its summit, or exserted. Fruit a 1-seeded utricle enclosed in the accrescent, roughened, ridged, and terminally coiled base of the perianth tube, tipped by the coiled base of the style; seeds not ribbed. (Including *Reussia* Endl., 1836, nom. cons., and *Unisema* Raf., 1808, "*Umsema.*") TYPE SPECIES: *P. cordata* L.; see Britton & Brown, Illus. Fl. No. U. S. & Canada, ed. 2. **1:** 462. 1913, and discussion below. (Named for Giulio Pontedera, 1688–1757, professor of botany in Padua, Italy; see Critica Botanica, p. 94. 1737 [p. 77 in English transl. by A. Hort, 1938].)—PICKEREL-WEED, BLACK-POTATO, WAMPEE, WILD-GENTIAN.

A small New World genus of five species (Lowden), *Pontederia* is characterized by a two-lipped perianth, a one-locular ovary (through the abortion of two locules) containing a single pendulous ovule, and six stamens. The genus is, for the most part, tropical to subtropical in its distribution. The plants grow primarily in fresh inland water and in brackish rivers and marshes near the sea.

Lowden's revision of *Pontederia* incorporated evidence from chemistry (phenolics), cytology, and morphology and also included considerations of nomenclatural history, dispersal mechanisms, breeding systems, and evolutionary development. He reviewed the controversy surrounding interpretation of the Linnaean genus *Pontederia* and concluded that of the three species listed in the first edition of *Species Plantarum,* only *P. cordata* L. belonged and must therefore be considered the type. *Pontederia ovata* L., with one stamen, was clearly out of place in a genus that was included in the Linnaean class Hexandria, and the species has since been removed to the Marantaceae. The third species, *P. hastata* L. (actinomorphic perianths of mostly free parts, six stamens in

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[4] The flowers are sessile and are grouped in sessile clusters along the main axis of the inflorescence; flowers along the axis, as well as within each cluster, are in various stages of development, suggesting that the clusters represent reduced branches or branch systems. At least partial resupination of most flowers is therefore suggested by their uniform orientation at anthesis. (Also see Leggett, 1875.)

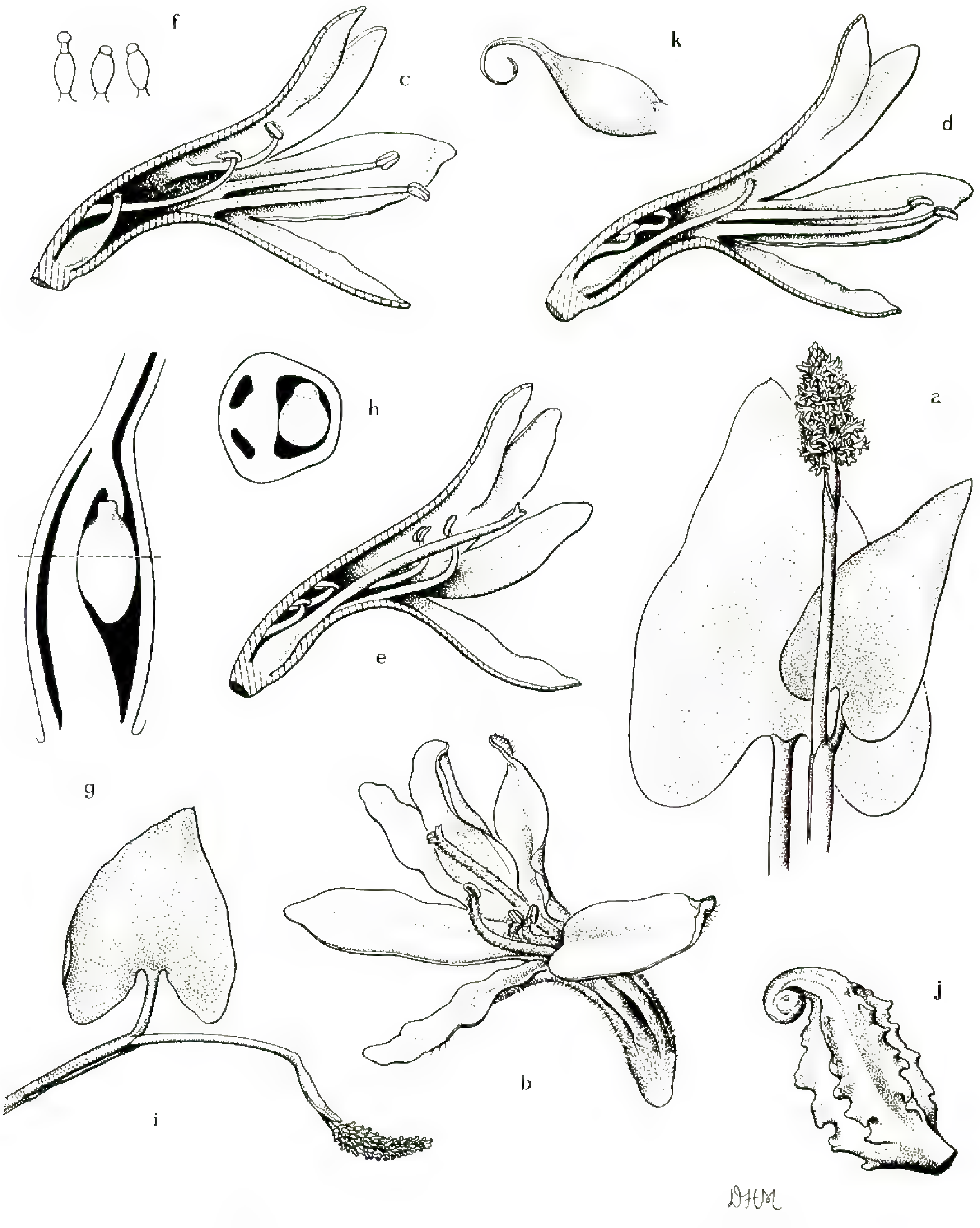

FIGURE 1. **Pontederia.** a–k, *P. cordata*: a, leaf blade and portion of petiole behind flowering stem (terminal part) with leaf and bract subtending inflorescence, × ¼; b, flower of long-styled form, with style and 3 mid-length stamens exserted, × 3; c, flower of short-styled form, in semidiagrammatic longitudinal section (e.g., hairs not shown), showing 2 of 3 adaxial, mid-length stamens and 2 of 3 abaxial, long stamens, × 3; d, flower of mid-styled form (drawn as in "c"), showing 2 of 3 adaxial, short stamens and 2 of 3 abaxial, long stamens, × 3; e, flower of long-styled form (as in "c"), showing 2 of 3 adaxial, short stamens and 2 of 3 abaxial, mid-length stamens, × 3; f, glandular hairs of staminal filaments, × 50; g, ovary, in longitudinal section, showing position of 1 aborted locule (at left) and fertile locule with its single pendulous, anatropous ovule, × 16; h, ovary, in transverse section (at level of dashed line in "g"), showing 2 aborted, adaxial locules and fertile locule with its single ovule, × 16; i, terminal part of flowering

groups of five and one based on length, and many seeds per fruit), has been placed by most botanists in the Old World genus *Monochoria* Presl.[5]

Lowden decided to treat *Reussia* Endl. as a subgenus of *Pontederia* because the supposed morphological differences between the two groups are weak and/or evidently unclear. According to him, the perianth in *Pontederia* clearly has two lips of three lobes each, while that in *Reussia* has an upper lip of four lobes and a lower of two by some accounts, but an upper of five and a lower of one by others. In addition, the genera are similar in other aspects of morphology, including an ovary with one fertile locule and a single pendulous ovule. Lowden reported haploid chromosome counts of $n = 8$ in subg. PONTEDERIA (ridges of the persistent, accrescent perianth base encasing the fruit smooth or toothed; flowering shoot erect) for *P. cordata* var. *cordata, P. parviflora* E. J. Alex., and *P. sagittata* Presl, and $n = 16$ in subg. REUSSIA (Endl.) Lowden (ridges of perianth base spinulose; flowering shoots prostrate) for *P. rotundifolia* L. f.

Chemical data provided by Lowden are consistent with the inclusion of *Reussia* as a subgenus in *Pontederia* on the basis of coefficients of similarity[6] he calculated for all pairs of the included taxa of *Pontederia* (*P. cordata* vars. *cordata, lancifolia* (Muhl.) Torrey, and *ovalis* (Mart. in Roemer & Schultes) Solms in DC., *P. parviflora,* and *P. sagittata,* of subg. PONTEDERIA; *P. rotundifolia,* of subg. REUSSIA), as well as on those I calculated for all pairings involving *Heteranthera limosa, Eichhornia crassipes,* and the foregoing taxa of *Pontederia.* Mean values for coefficients of similarity (zero indicating no resemblance, one indicating identity) were lower between genera of Pontederiaceae (*Pontederia-Eichhornia,* 0.58; *Pontederia-Heteranthera,* 0.49; *Eichhornia-Heteranthera,* 0.50) than between subgenera of *Pontederia* (subg. *Pontederia*–subg. *Reussia,* 0.69), although greater between subgenera than between included taxa of subg. *Pontederia* (0.62).

Lowden speculated that *Pontederia* originated in the American tropics from tristylous, aquatic ancestors with many-flowered spikes and flowers with zygomorphic perianths of basally connate parts, six stamens, and a single pen-

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[5] Rafinesque (Med. Repos. N. Y. II. **5**: 532. 1808) placed *Pontederia cordata,* with a single seed per fruit, in his new genus *Unisema* ("*Umsema*") and retained *P. hastata,* with many seeds per fruit, in *Pontederia,* presumably because Linnaeus had used the term "capsula" in describing his genus. Lowden maintained, however, that the term had been used to describe the accrescent base of the perianth tube surrounding the fruit and did not therefore indicate a many-seeded fruit. Fernald (Rhodora **27**: 76–81. 1925) pointed out that in dedicating the genus to Pontedera, Linnaeus primarily had plants from North America in mind, and that in the fifth edition of *Genera Plantarum* he added to *Pontederia* a tropical American plant with one-seeded fruits, thus strengthening the idea that his concept of *Pontederia* excluded plants with many seeds per fruit.

[6] Between any two taxa, the coefficient of similarity is the number of phenolic compounds in common divided by the sum of this number and the number of phenolics present in only one or the other.

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stem during fruit maturation, which occurs under water, × ⅛; j, accrescent, terminally coiled base of perianth tube enclosing utricle, × 3; k, 1-seeded utricle with persistent, coiled base of style, × 3.

dulous ovule. He proposed that sometime during the Tertiary the genus spread from Central to North America, where it initially occurred farther west than it does at present. Fossils attributable to *Pontederia cordata* have been recovered from the Green River Formation in Wyoming, now considered to be early or mid-Eocene (Bradley, Knowlton).

Pontederia is represented in the Southeast by three commonly accepted but taxonomically questionable varieties of *P. cordata* (see below). The species is distinguished from others in subg. PONTEDERIA by a combination of characters, including tristyly and teeth on the ridges of the persistent, accrescent perianth bases. The plants are largely restricted to stream banks and pond edges where bare ground (required for seed germination) is exposed by fluctuating water levels; few individuals are found in "high marsh plant communities" (see Whigham & Simpson).

Variety *cordata* (leaves sagittate, cordate, reniform, or hastate; mature floral tube glabrous or sparsely glandular) occurs throughout the eastern United States and adjacent Canada but is most abundant in the Great Lakes region, in the Northeast, and on the Gulf and Atlantic coastal plains. It is also found in southern Brazil and adjacent areas, as well as in Belize, where Lowden reported specimens that suggested hybridization with *P. sagittata.* The distribution of var. *lancifolia* (*P. lancifolia* Muhl., 1813; *P. angustifolia* Pursh, 1814; *P. lanceolata* Nutt., 1818) (leaves narrowly to broadly lanceolate, mature floral tube glandular) matches that of var. *cordata,* with the exception that it appears to be rare in the Great Lakes region and otherwise less common than var. *cordata* in North America outside of southern Georgia and Florida; Lowden reported it from two localities in Cuba as well. Perry observed that var. *lancifolia* is less hardy than var. *cordata,* which perhaps explains its more southern distribution. Godfrey & Wooten reported that vars. *cordata* and *lancifolia* are not easily distinguished in Florida and southern Georgia, where each occurs in abundance, and my own observations suggest that the same is true elsewhere in the Southeast. Both varieties are popular among gardeners and have become naturalized in parts of the Old World (Aston; Casper & Krausch; Clapham *et al.*; Valentine). According to Lowden, var. *ovalis* is restricted to South America and differs from broad-leaved specimens of var. *lancifolia* in its densely pubescent upper peduncles. Nevertheless, *Mather M-277* (GH), from Marion County, Florida, was determined by Lowden to belong to var. *ovalis.* My observations indicate that the upper peduncles of many specimens of var. *lancifolia* from our area are as densely pubescent as those of this specimen.

The two subgenera of *Pontederia* differ in the relative importance of vegetative and sexual reproduction (Lowden). In subg. REUSSIA, members of which have few-flowered inflorescences and long, trailing stems, reproduction through fragmentation of adventitiously rooted stems has a greater immediate value than reproduction by seeds, especially in populations composed of a single floral form (in which all pollinations would be illegitimate and thwarted by physiological incompatibility systems). In contrast, sexual reproduction may be of greater importance in subg. PONTEDERIA because inflorescences are many flowered and the stems are more erect, above ground, and shorter.

All species of *Pontederia* are tristylous, with the exception of *P. parviflora* (subg. Pontederia), in which homostyly (semihomostyly according to Barrett, 1979) is thought to have been derived from the tristylous condition (Lowden). Ornduff studied the breeding system of *P. cordata* in a number of populations along the Atlantic Coastal Plain in the Southeast. Except for one population in North Carolina in which only short- and mid-styled flowers occurred, all three floral morphs were represented in each population. Populations varied, however, in the relative proportions of each morph, presumably because of a combination of founder effects and vegetative reproduction (see, however, Price & Barrett, 1982).

Although data regarding the genetic basis for tristyly in the diploid *Pontederia cordata* are not yet completely available, Barrett, Price, & Shore assumed it was the same as that observed in the diploid *Eichhornia paniculata,* in which two alleles are present at each of two loci, one of which is epistatic to the other. Essentially the same is true of *E. crassipes,* except that this species is a tetraploid (see also Barrett, 1985a [under *Eichhornia*], Charlesworth; see, however, Barrett & Anderson).

In *Pontederia cordata,* as in the majority of other tristylous plants investigated, legitimate pollinations are most effective in producing seed. Illegitimate pollinations are less productive both because they are less frequent and because of the existence of a physiological incompatibility system. Ornduff provided data from artificial pollinations indicating that in *P. cordata* the incompatibility is due to "carpellary factors" (i.e., is of the sporophytic type) and is strongest in the short-styled form, slightly weaker in the long-styled, and clearly weakest in the mid-styled (see also Barrett *et al.*). Barrett & Anderson summarized data from *P. cordata* vars. *cordata* and *lancifolia, P. rotundifolia,* and *P. sagitatta* showing that in each the level of self-compatibility, as determined by percentage of seed set in flowers pollinated with the most compatible pollen (i.e., that from short, medium, or long stamens), is clearly and consistently greatest in the mid-styled form, with the exception that seed set in the long-styled form of *P. rotundifolia* is approximately equal to that of its mid-styled form. These data also suggest that the relationships between self-compatibility levels in the short- and long-styled forms are rather inconsistent among the four taxa. Barrett & Anderson proposed several hypotheses to explain their observations.

Price & Barrett (1982) investigated tristyly in 74 North American populations of *Pontederia cordata,* including 45 from the Southeast, and for the most part substantiated the findings of Ornduff. They also determined, however, that the mid-level (medium) stamens of short-styled flowers produced about twice as many pollen grains as those of long-styled ones. Although the basis of this difference could not be established, Barrett, Price, & Shore later suggested that it could result from differences in the time of anther development, since the mid-level stamens of the short-styled morph are the lower set, while those of the long-styled morph are the upper set (i.e., the lower set of anthers develops first, so these are therefore larger and more productive of pollen). Price & Barrett (1982) also suggested that pollen from short-styled flowers fertilizes more ovules of the mid-styled morph than does pollen from the long-styled morph (although Barrett, Price, & Shore later reported that field studies provided only limited evidence that this was so) and that this difference may influence the composition of natural populations in favor of the short-styled form.

On the basis of data gathered from the same 74 populations mentioned above, Barrett, Price, & Shore reported that of 69 trimorphic populations, 76.8 percent were significantly anisoplethic (although morph frequencies varied among populations, presumably because most had not yet reached equilibrium). Most frequently encountered were a predominance of the short-styled morph and a deficiency of the long-styled one, regardless of variety (var. *cordata* or var. *lancifolia*), habitat type (permanent or temporary), locality (Ontario and Wisconsin or the Carolinas, Georgia, Florida, and Louisiana), population size (more or fewer than 500 inflorescences), location within a population (divided into 10 × 2 m sections), or time (populations observed for five years). Because of the large sample of populations employed, they considered it unlikely that historical factors (e.g., dispersal, disturbance, establishment) alone could be responsible for the anisoplethy observed in *Pontederia cordata*; they proposed instead the existence of some selective advantage for the short-styled morph and a corresponding disadvantage for the long-styled one. It is interesting that Price & Barrett (1984) reported that legitimate pollinations were most frequent in the long-styled morph, followed in order by the mid- and short-styled morphs, possibly due at least in part to differences in amount of surface area available for pollen deposition (e.g., the pollinator's proboscis tip, which normally delivers pollen to short styles, is smaller than its head, which delivers to mid-length styles). Nevertheless, Price & Barrett (1982) reported no statistically significant differences among floral morphs in flowering phenology, fruit weight, germination percentage, number of inflorescences per individual, or flowers (all or chasmogamous only) and seeds per inflorescence. It is notable that while the situation in *P. sagittata* appears to be almost identical to that in *P. cordata*, it is considerably different in *Eichhornia* (see discussion of that genus).

Perianths in species of *Pontederia* (including *P. cordata* as represented in the Southeast) are purple, blue-purple, blue, pale blue, or white, and the anthers are blue. The extraregional *P. subovata* (Seub. in Mart.) Lowden differs from this pattern in sometimes having blue-green perianths, while *P. parviflora* (the only homostylous species of *Pontederia*, see above) has greenish white to white perianths and black to brown anthers (Lowden). The upper-middle perianth lobe in species of *Pontederia* bears a single bilobed yellow spot (Lowden) or two separate yellow spots (Lovell).

The flowers of *Pontederia cordata* attract a number of insect visitors, primarily bees of the genera *Bombus, Melissodes,* and *Xylocopa* (Price & Barrett, 1982, 1984). The emergence of *Dufourea novaeangliae* (Robertson), a small solitary bee, coincides remarkably well with the onset of flowering in *P. cordata,* and the insect is not known to visit any of the many other species concurrently available (Lovell, Percival; see, however, Hurd). According to Hazen, the numerous insects that visit *P. cordata* do so primarily for nectar, which is produced by three septal nectaries, but some hymenopterans also collect pollen. Price & Barrett (1982) determined that the frequency of visits to *P. cordata* by bumblebees (*Bombus* spp.) in a Canadian (Ontario) population was independent of floral form.

Evidence provided by Price & Barrett (1984) suggests that the frequency of legitimate pollinations in populations of *Pontederia cordata* may be dependent on the type of pollinators involved and may therefore vary geographically. In northern North America, species of *Bombus,* which have broad preferences and are therefore probably not highly co-adapted to the breeding system of *P. cordata,* are the most important pollinators. In the South, on the other hand, a diverse set of more specific (long-tongued) pollinators is involved, perhaps most importantly species of *Melissodes.* These observations may help to explain why significant levels of legitimate pollination (i.e., levels significantly greater than those predicted by a model that assumes random pollination) appear to become less frequent with increasing latitude in the species as a whole. In Florida, populations of all three morphs experienced significant levels of legitimate pollination, in the Carolinas only some did, and in Ontario none did.

The fruits and associated perianth bases of *Pontederia* are buoyant because of the presence of aerenchyma in the latter and normally float for more than 15 days, according to Schulz. Transport by water is considered to be the primary means of dispersal. Dissemination by ducks and other animals is less important and probably involves only relatively short distances (see Sculthorpe). *Pontederia cordata* has been recorded as a food source for the southern black or mottled duck (*Anas fulvigula*), and the seeds have been found in the stomachs of wood ducks (*Aix sponsa*) (Ridley). Lowden observed that the spinulose perianth bases encasing the fruits of *P. rotundifolia* become attached to livestock in El Salvador and Costa Rica, but in subg. PONTEDERIA (including our plants) such surfaces are smooth or only toothed, and the fruits are probably less effectively dispersed in this way.

Pontederia cordata is widely grown as an aquatic ornamental, and it sometimes escapes cultivation. It is reportedly naturalized in Britain (Clapham *et al.*) and southern Europe (Valentine). In South America and perhaps elsewhere it frequently occurs as a weed in rice fields (Barrett, 1978b).

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Note added in proof. Since this treatment was completed, a paper of considerable significance has appeared in the literature. Various cladistic analyses reported by Eckenwalder & Barrett (under family references; annotation based on a manuscript copy of the abstract) suggested that the Pontederiaceae and Philydraceae are sister groups and that the former is divisible into two groups of two genera each. *Pontederia* (including *Reussia* as a subgenus) and *Eichhornia* were depicted as one clade, while *Heteranthera* (including *Eurystemon, Hydrothrix, Scholleropsis,* and *Zosterella*) and *Monochoria* comprised the other. The family, the two clades, three of the four genera, and both subgenera were considered to be monophyletic, while *Eichhornia* was said to be paraphyletic. The cladograms generally indicated that tristyly is not the primitive breeding system in the Pontederiaceae and that it did not arise more than once in the family. Although it was shown to be a synapomorphy of the *Pontederia-Eichhornia* clade, its evolutionary relationship to homostyly in *Eichhornia* was not resolved. The possibility that the dimorphic stamens of the *Heteranthera-Monochoria* clade were not derived from a tristylous condition was also suggested. A base chromosome number of $n = 8$ for the family was favored, from which $n = 7$ and $n = 15$ would have been repeatedly derived. The cytological diversity in the family was thought to have resulted from both aneuploidy and polyploidy.—T. J. R.

REPRODUCTIVE STRUCTURE OF LITHOCARPUS SENSU LATO (FAGACEAE): CYMULES AND FRUITS

Robert B. Kaul[1]

Seventy-three species were examined for structural and developmental details of the cymules and fruits. The cymules bear one to seven or more flowers and are subtended by one to nine or more bracteoles. Generally, the number of flowers and bracteoles in the pistillate cymules is the same or less than in the staminate ones. Some of the latter have an inner set of bracteoles that could be homologous to the pistillate cupule. Scales are present at anthesis on the cupules of all species examined, but in some species they fail to enlarge, are torn or disintegrate, or fall away as the cupule matures, leaving the cupule essentially naked. In species with scaly cupules at maturity, the scales enlarge and sometimes also become adpressed, thickened, or elongated. Some cupules are intermediate between the naked and scaly ones. Apparently adventitious flowers borne on the outer walls of some cupules are often abortive flowers of the same cymule that have been elevated by the maturing cupule of the fertile flower, but in some cases they could be developed from latent primordia that are axillary to the cupular scales.

Nearly all that is known of the reproductive structure of *Lithocarpus* Blume comes from studies done for taxonomic purposes. Most notable are the contributions of Camus (1948, 1952–1954) and Soepadmo (1968, 1970, 1972), which contain numerous illustrations and some discussion of reproductive structure and its possible phylogeny. Hjelmqvist (1948) detailed floral and cymular structure in several species and provided some phylogenetic assessments. Nevertheless, only a few species have been investigated for reproductive detail, and no comprehensive overview of the genus is available. Here I report on morphological, developmental, and evolutionary aspects of partial inflorescences (cymules) and fruits in 73 species that represent eight of the 14 subgenera proposed by Camus (1952–1954). I give particular attention to the organization of the cymules and cupules. Details of floral structure will be presented elsewhere.

Lithocarpus, with perhaps 300 species when taken in its broadest sense, is second in the Fagaceae only to *Quercus* L. in number of species. The genus ranges from northeastern India across central China to Korea and southern Japan, south to southeastern Asia, the Philippines, and the East Indies as far east as New Guinea. There is one American species, *L. densiflora,* which occurs in the coastal mountains from Douglas County, Oregon, south to Ventura

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Journal of the Arnold Arboretum **68:** 73–104. January, 1987.

County, California, and at scattered locations in the Sierra Nevada of California (Little, 1971). The range of the genus is almost exactly congruent with that of the third largest genus of Fagaceae, *Castanopsis* (D. Don) Spach, but it is much less than that of *Quercus.*

Lithocarpus is found on a variety of soil types from sea level to about 4000 m, but it is most abundant at middle elevations, where it is sometimes one of the dominant forest genera, often with *Quercus* and members of the Lauraceae.

Some taxonomists (e.g., Barnett, 1940, 1944; Camus, 1952–1954; Soepadmo, 1972) have recognized *Lithocarpus* in the broad sense, but others (e.g., Li, 1963; Lin & Liu, 1965; Liao, 1969) have preferred to restrict that name to some species and to place others in segregate genera. Those favoring the broad interpretation justify their position by noting that there are intermediate species between the groups. Further taxonomic complications arise from the fact that certain species are intermediate in many respects between *Lithocarpus* s.l. and both *Castanopsis* and *Quercus.*

Camus (1952–1954) recognized 14 subgenera in *Lithocarpus,* most of them with fewer than 15 species. Because her subgeneric classification covers the entire genus in its broadest sense, it is the basis of reference for the work presented here. Soepadmo (1970, 1972), in his treatment of *Lithocarpus* for the *Flora Malesiana,* described some new species and reduced or did not accept some of Camus's species; of the 136 species recognized by Camus for Malesia, he accepted only 64 as good species but did not assign them to subgenera. His nomenclature is used for the southeastern Asian species discussed here.

The classification of *Lithocarpus* is based mostly upon cupule and fruit characters (Barnett, 1940, 1942, 1944; Camus, 1952–1954; Li, 1963; Lin & Liu, 1965; Liao, 1969; Soepadmo, 1970, 1972), as it is in other Fagaceae. Gross inflorescence and flower characters are useful in separating genera (Soepadmo, 1970; Kaul & Abbe, 1984) but not in distinguishing species.

Camus (1952–1954) believed *Lithocarpus* to be one of the most primitive members of the family. She cited seven reproductive characters as primitive (but was not clear about the reasons for those assessments): the abortive ovules apical in the nut (known elsewhere only in *Quercus* subg. *Cyclobalanopsis* and one section of subg. *Quercus*); the scar of the nut large in some species; the cupule asymmetric in some species; the tomentum that lines the cupule dense (known elsewhere only in *Quercus* subg. *Cyclobalanopsis* and some sections of subg. *Quercus*); the cupule poorly developed at anthesis, as is also the case in *Quercus*; the cupule fused for much or all of its length to the nut in some species; and the partitions of the nut absent or poorly developed in some species. Schottky (1912) and Hjelmqvist (1948) believed *Lithocarpus* to be the most primitive genus of the family, and they suggested that it gave rise—or is a sister group—to *Quercus* s.s. and *Cyclobalanopsis* (*Quercus* s.l. subg. *Quercus* and subg. *Cyclobalanopsis,* respectively). Forman (1966; see also Elias, 1971), however, postulated separate origins of *Quercus* and *Lithocarpus* from hypothetical ancestors and thus implied morphological parallelisms of the two; *Trigonobalanus* Forman was seen as having some intermediate characteristics.

Camus (1952–1954, p. 1188) also noted the "affinités indéniables" of *Lithocarpus* subg. *Cyclobalanus* with *Quercus* subg. *Cyclobalanopsis.* Both have more than three styles per flower in many instances, annular cupules, apical abortive ovules, rudimentary perianthopodia in some instances, and entire, evergreen leaves. The stigmas, styles, and stamens of each subgenus are typical of their genera, however, and their characteristics are not shared by the two subgenera. It is mostly because of these distinct floral characteristics that Barnett (1940), Camus (1952–1954), and Soepadmo (1968, 1970, 1972) maintained *Lithocarpus* distinct from *Quercus* despite the similarities in fruits and cupules. I have shown all these and other differences between the two genera elsewhere (Kaul, 1985, *t. 2*).

The cupules of *Lithocarpus* and *Quercus* are often indistinguishable, but those of *Lithocarpus* have a greater variety of shapes and ornamentation. Further, although there is a rather sharp distinction between the lamellate cupules of *Quercus* subg. *Cyclobalanopsis* and the scaly ones of subg. *Quercus,* in some species of *Lithocarpus* there are intermediate cupular patterns.

Further complications to generic delimitation of *Lithocarpus* arise when some of the species that strongly suggest *Castanopsis* sect. *Pseudopasania* are examined. These were placed in *Lithocarpus* subg. *Pseudocastanopsis* by Camus (1952–1954) and resemble *Castanopsis* because of cupular and foliar similarities (i.e., the scales in three groups, the castanopsoid hairs on the abaxial leaf surface, and the cupules of *L. fissa* opening by three valves). Soepadmo (1970) noted several differences between the two genera: *Castanopsis* has the inner bark surface smooth, the wood rays only uniseriate, and the cupules solitary (but enclosing one to three nuts). The cupule has a definite number of growing points separated by vertical rows of scales, and its vascular system shows a dichasial pattern. *Lithocarpus* has the inner bark surface longitudinally ridged, the wood rays both uni- and multiseriate, the cupules solitary or clustered and each enclosing a single nut, and the cupular vascular system not dichasial. The cupule has a continuous, circular growing edge, and there are no sutures.

Barnett (1940) believed that *Lithocarpus* and *Castanopsis* are very close and that their separation is perhaps more artificial than natural. Nevertheless, she believed their fruit structure distinct enough to treat the two as genera. She noted that in species of *Lithocarpus* with spiny cupules (e.g., *L. garrettiana, L. lappacea, L. longispina, L. recurvata*), the spines are certainly recurved scales. The spines and tubercles of *Castanopsis,* however, do not appear to be the original cupular scales but develop later, often in the axils of the original scales. She included in *Lithocarpus* those species with oblique cupular lamellae, whether tuberculate or not, in which the fruit is oblique (e.g., *L. blumeana, L. encleisacarpa*). She placed *C. acuminatissima* in *Castanopsis,* however, because it has oblique cupules with irregular whorls of short spines or tubercles and because it has some castanopsoid anatomical characters.

In *Lithocarpus* each pistillate flower has its own cupule (as is the case in *Quercus*), but sometimes the cupules are grouped and even fused. In extreme cases of fusion, the combined cupules appear almost as a single cupule enclosing several nuts. Soepadmo (1970) showed that in organization of the vascular system of the cupule, *Lithocarpus* is the same as *Quercus* but markedly different from *Castanopsis.* Where adjacent cupules are fused, the unified wall that separates the flowers retains the separate vasculature of each cupule.

Forman (1966) interpreted the one-flowered cupule of *Lithocarpus* as being derived from a three-flowered cymule whose valves fused to form one cupule around each flower; the one-flowered cupule of *Quercus* became so by loss of some valves and the lateral flowers. Thus the one-flowered cupules of both genera were seen as convergently evolved. This interpretation was illustrated by Elias (1971).

Camus (1952–1954) and Soepadmo (1970) noted the variety of patterns of cupular fusion to the nut. In some subgenera the mature cupule entirely encloses the nut and is totally fused to it for its entire length (subg. *Oerstedia,* some sections of subg. *Lithocarpus*); in others the cupule entirely covers the nut but is only partially fused to it (subgenera *Lithocarpus* (sect. *Costatae*), *Pachybalanus, Synaedrys*) or is not fused except for the basal scar (subg. *Pseudosynaedrys,* and some species of subgenera *Pasania* and *Pseudocastanopsis*). In the unique subgenus *Corylopasania* the cupule not only encloses the nut but also is much prolonged beyond it into a narrow tube; the cupule is only basally fused to the nut. In many taxa (subgenera *Cyrtobalanus* and *Gymnobalanus,* as well as many species of subgenera *Cyclobalanus* and *Pasania*) the cupule covers just part of the nut and is not fused to it but the basal scar is large. Camus believed that the greater degree of fusion is the more primitive condition in the genus.

In some species of *Lithocarpus* the cotyledons are free, but in others they are fused. The latter condition is found in some species of *Quercus,* too, and Nixon (1985) considered it to be the derived condition in that genus. The endocarp is tomentose in many species, as it is in some members of *Quercus.*

MATERIALS AND METHODS

I have examined more than 1000 specimens that my colleagues and I collected in Asiatic and southwestern Pacific island forests. We took special care to collect developmental as well as mature material. Most of the specimens were identified by E. Soepadmo, the most recent monographer of southeastern Asiatic *Lithocarpus* (Soepadmo, 1970, 1972) and by other taxonomists residing in the areas of provenance of the specimens.

Most of the specimens were stored in FAA, quinoline-sulfate solution, or glycerin-alcohol. All are documented by dried voucher specimens in my collection, for which various sets of duplicates are deposited in A, BH, G, K, L, MIN, SING, and US.

OBSERVATIONS

Gross Structure of the Inflorescences

The overall structure of the inflorescences of *Lithocarpus* has been dealt with in some detail (Kaul & Abbe, 1984; Kaul, 1986). The genus was shown to have the most elaborate gross inflorescence structure among *Lithocarpus, Castanopsis, Castanea,* and *Quercus.* It was suggested that this elaborate structure is the least specialized condition—one that gave rise to more advanced inflorescences by loss of branching and separation of staminate from pistillate flowers first within the spike and ultimately, in *Quercus,* into separate spikes.

Spikes bearing usually sessile cymules are variously aggregated into reproductive branches that are caducous or persistent. In a few species some spikes, especially the staminate ones but occasionally the pistillate as well, are branched at a cymule (Kaul, 1986). The spikes are variously entirely staminate, entirely pistillate, androgynous, or androgynecandrous, and more than one pattern often occurs on a given tree. Furthermore, some cymules contain various combinations of staminate, pistillate, or perfect flowers (see Kaul & Abbe, 1984, *fig. 4*). Those cymules at the transition point on a spike between staminate and pistillate cymules more often have both flower sexes or perfect flowers than do more proximal or distal cymules. Within a spike, the pistillate flowers are more likely to occur proximally than distally, but the spikes bearing pistillate flowers are more abundant distally in the total spike-bearing shoot system. In a few instances the staminate and pistillate cymules are mixed for short distances along the spike. These phenomena are illustrated in the papers cited above, while details of cymule and fruit structure are emphasized here. There is much infraspecific variability in reproductive structure both locally and throughout the ranges of the species, and variant morphological patterns are likely to be found in specimens of the species illustrated here that are collected from other parts of their ranges.

CYMULES IN LITHOCARPUS

The groups of flowers spaced along a spike are often called cymules, dichasia, or partial inflorescences. "Cymule" is used here generally for the presumably condensed pleiochasia and dichasia that characterize *Lithocarpus* and other Fagaceae.

In the specimens examined for this study, the number of flowers in a cymule ranged from one to seven (or more in a few instances), but one, three, and five were the usual numbers (TABLE). (Downward departures from the typical numbers are common in a few cymules at the extreme proximal and distal ends of a spike in most species; such exceptions are not included in the data presented here.) Often the staminate and pistillate cymules on a specimen contain the same number of flowers (this was true for 29 of the 73 species shown in the TABLE), and where the number of flowers is variable and rather high in the staminate cymules it is also that way in the pistillate cymules (e.g., *Lithocarpus elegans* and *L. harmandii,* TABLE). However, the number of flowers in a pistillate cymule never exceeds that in the staminate cymules on the same plant and, in fact, is frequently lower (see TABLE). There is some variability in cymule flower number from tree to tree and even from branch to branch within some species (e.g., *L. celebica, L. dealbata, L. fenestrata, L. harlandii, L. lucida, L. reinwardtii,* and *L. sootepensis*).

In most cases all the flowers of a staminate cymule are fully formed at anthesis. Only occasionally do clearly abortive flowers appear, as in *Lithocarpus buddii,* where the central (uppermost) flower is fully developed but the two lateral ones are abortive. Likewise, all the flowers of the pistillate cymules are usually nonabortive at anthesis, but many of them abort later due to apparent lack of pollination or fertilization. The abortive pistillate flowers are often readily observed attached to or just below the cupule of a fully formed nut.

Cymule characteristics of Lithocarpus.

SUBGENUS species	Pistillate cymules		Staminate cymules	
	No. of flowers	No. of evident bracteoles	No. of flowers	No. of bracteoles
CYCLOBALANUS A. Camus				
aggregata Barnett	3	5+	3	5
bullata Hatusima ex Soep.	1	3	3	3
clementiana A. Camus	1,3	3	1,3	3
conferta Soep.	1	3	1	3
conocarpa Rehder	1	1	–	–
cyclophora A. Camus	–	–	3	5
daphnoidea A. Camus	1	3+	–	–
eichleri A. Camus	1	3+	–	–
encleisacarpa A. Camus	1	3	3	5
ewyckii Rehder	1	3	1,3	3
korthalsii (Endl.) Soep.	3	5+	3	5+
lampadaria A. Camus	5–7	7	5	7
lucida Rehder	1–3	1	3	3
lutea Soep.	1	3+	3	3
macphailii A. Camus	1–3	5+	3	5
mariae Soep.	1	3+	1	3
meijeri Soep.	1	1,3	1,3	3,5
neorobinsonii A. Camus	1	3	1	3
nieuwenhuisii A. Camus	1	3	–	–
pattaniensis Barnett	1–3	5–7	1	3–7
philippinensis A. Camus	–	–	1,3	1,3
rassa (Miq.) Rehder	1	3	1	3
reinwardtii A. Camus	1,3	3,5	1,3	3
sericobalanus Warb.	1	3	–	–
suffruticosa (Ridley) Soep.	1	3	3	3
GYMNOBALANUS A. Camus				
havilandii Barnett	1	3	1	3
kingiana A. Camus	1	3	1	3
konishii Rehder	1	3	3	5
lauterbachii Markgraf	1	3	1	3
LIEBMANNIA A. Camus				
hendersoniana A. Camus	3–5	5+	3–5	5+
LITHOCARPUS Markgraf				
beccariana A. Camus	1	1	1	1
maingayi Rehder	–	–	3	–
perakensis Soep.	1	3	–	–
turbinata (Stapf) Forman	1	3	1	3
PACHYBALANUS A. Camus				
amygdalifolia Hayata	1–3	3–7	3	5
nantoensis Hayata	1	1	1	5
truncata Rehder & Wilson	5	ca. 7	5	ca. 7
PASANIA A. Camus				
buddii (Merr.) A. Camus	3	3	3	3,7
caudatifolia Rehder	1	3	3+	3
celebica Rehder	1,3	3+	3	3
cooperta (Blanco) Rehder	1	3	1,3	3
curtisii (King ex Hooker f.) A. Camus	1	3	1	1
dasystachya (Miq.) Rehder	1,3	3,5	3	3
dealbata A. Camus	3,5	3+	3,5	9+
densiflora Rehder	1	1	3,5	5,7
edulis Nakai	1	–	1,3	1,3

Cymule characteristics of Lithocarpus (*continued*).

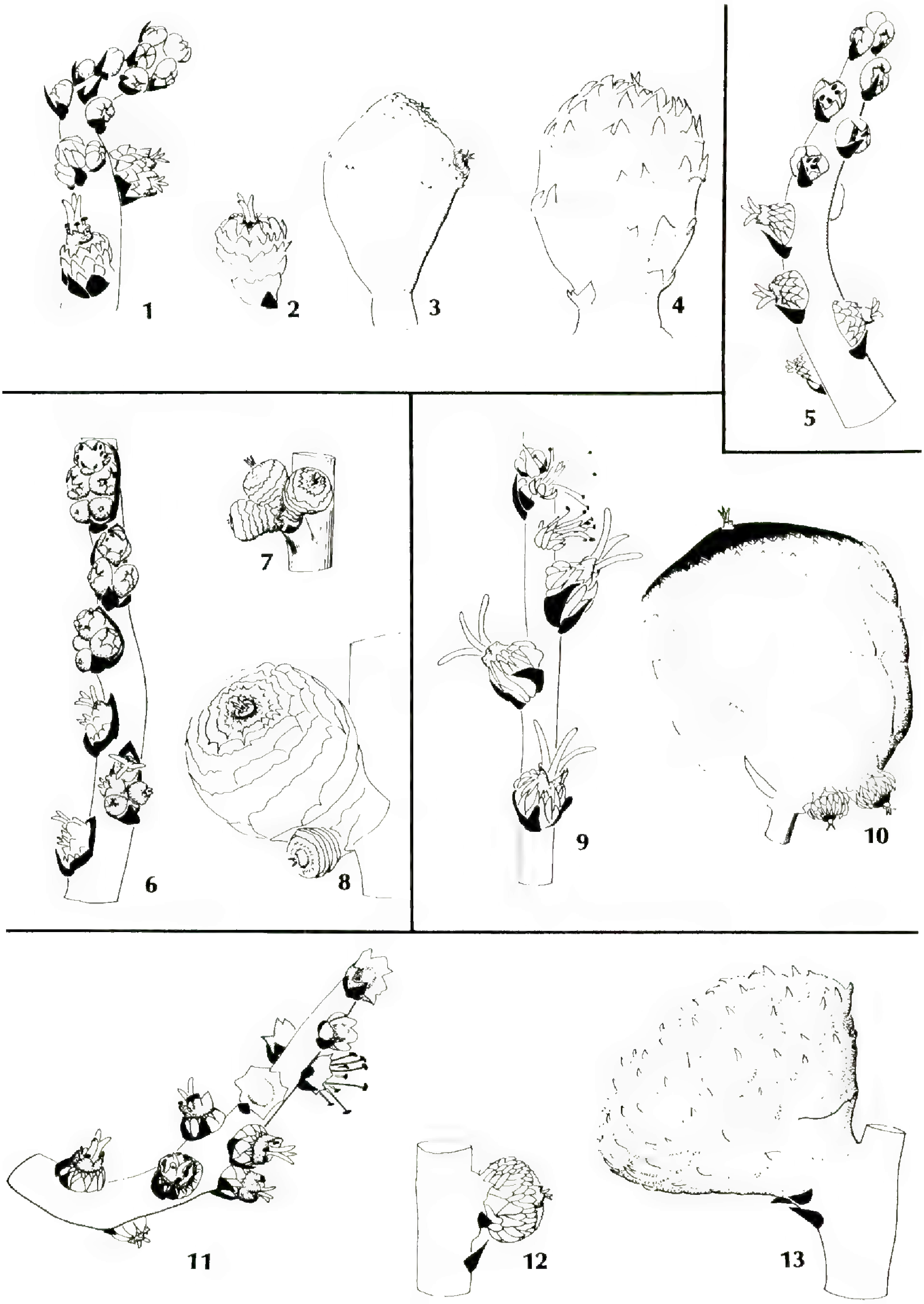
	Pistillate cymules		Staminate cymules	
SUBGENUS *species*	No. of flowers	No. of evident bracteoles	No. of flowers	No. of bracteoles
elegans (Blume) Hatusima ex Soep.	3-5	3	3-5	5+
elephantum A. Camus	1	3	1	3
falconeri Rehder	1	3	1	3
fenestrata Rehder	3	3	3	9+
formosana Hayata	3	3+	3	5
garrettiana A. Camus	3	3+	3	1
hancei Rehder	3	3+	3	3
harlandii Rehder	1,3	3	1,3	3,5
harmandii A. Camus	3-5	3?	4-7+	3
kawakamii Hayata	3-5	3+	-	-
papillifer Hatusima ex Soep.	1	1	2,3	-
polystachya Rehder	1-3	3+	3	3,5
rufovillosa Rehder	1	3	1,3	3
sabulicola A. Camus	1	3+	1	3
scortechinii A. Camus	1	3+	3	7+
soleriana Rehder	1	1	3	7+
sootepensis A. Camus	1,3	3	3	3
spicata Rehder & Wilson	3	3	3	5+
sundaica Rehder & Wilson	1	3+	1,3	1,3
ternaticupula Hayata	3	3+	3	3
thomsonii Rehder	3	3+	3	5
wallichiana Rehder	3	3	3	3
wrayi A. Camus	1	3+	3	3
PSEUDOCASTANOPSIS Hickel & A. Camus				
fissa A. Camus	1	1	1,3	4
SYNAEDRYS A. Camus				
cornea Rehder	1	3	3	3
kodaihoensis Hayata	1	3	1	3
pulchra Markgraf	1	3	1	3

In multi-flowered cymules the sequence of anthesis begins with the central (uppermost) flower and progresses to the subjacent pair and then to the lowest pairs (see, for example, FIGURES 29, 30). In three-flowered cymules the central (upper) flower opens first and the subjacent pair soon afterward.

The bracteoles that subtend the cymules vary within subgenera and species and sometimes between staminate and pistillate cymules in the same inflorescence (see TABLE). The number of bracteoles sometimes equals but more often exceeds the number of flowers in the cymule, but it is rarely less (see TABLE).

In both pistillate and staminate cymules there is a single, usually larger, primary bracteole centered below the cymule (see, for example, FIGURES 16, 17). Subsequent bracteoles are often smaller, sometimes progressively so, and are usually paired across the cymule.

The subtending bracteoles of the pistillate cymules sometimes grade into the cupular bracteoles (hereinafter called "scales"), but for the most part they are



FIGURES 1–13. 1–4, *Lithocarpus turbinata:* 1, spike tip at anthesis, staminate cymules above, pistillate and perfect below (bracteoles in black and perianth stippled in most figures); 2, pistillate flower in cupule at anthesis; 3, mature cupule with adventitious, abortive flower; 4, immature cupule. 5, *L. beccariana:* spike tip at anthesis, staminate (upper) and pistillate (lower) cymules with 1 flower. 6–8, *L. hendersoniana:* 6, spike tip at anthesis, staminate (upper) and pistillate (lower) cymules with 3 to 5 flowers; 7, pistillate cymule after anthesis, somewhat raised upon peduncle; 8, immature cupules, 1 abortive.

distinguished by their size (as the illustrations show), their greater thickness, and occasionally their coloration. In some cases the uppermost bracteoles are connate and form an entire or serrate border above the pistillate cymule, but usually all the bracteoles are free. While some of the bracteoles are deciduous or break off as the cupule expands after fertilization, the primary, and often other, bracteoles persist below the matured cupule. At least the primary bracteole is usually readily apparent at cupular maturity, although it is often greatly exceeded by the cupule and its scales.

The bracteoles of the staminate cymules are more easily seen because they are not crowded by cupular scales. They are more often connate than are those of the pistillate cymules, even within a species, and sometimes the connation is so extreme that an accurate count is impossible (see, for example, FIGURES 89, 94). In rare instances the partially connate upper bracteoles enclose smaller bracteoles that suggest a rudimentary cupule enclosing the staminate flowers (see FIGURE 62, uppermost cymule).

In staminate and pistillate cymules that have more than four bracteoles, it is usually possible to enumerate the bracteoles and bracteole pairs at least to the quaternary level or, if there is no connation, beyond. In many pistillate cymules, however, the intergradation of subtending cymule bracteoles with the cupular scales often makes such distinctions arbitrary beyond the primary or secondary bracteoles. Even in the earliest developmental stages of a few species that have been studied, it is not always possible to distinguish the first cupular scales from the subtending bracteoles.

PISTILLATE CYMULE ORGANIZATION AND CUPULAR STRUCTURE

Among and within subgenera, there are great differences in the relative contributions of the cupular scales to the mature cupules, which vary more than those of *Quercus.* The flowers, cymules, and immature and mature cupules are shown in FIGURES 1–111 for 38 species from seven subgenera. Camus (1948), in Volume 3 of her *Atlas,* illustrated many species but did not include details of cymule bracteoles or cupule development. Her plates are cited below to complement my illustrations.

SUBGENUS LITHOCARPUS. In both species that were studied developmentally (*Lithocarpus beccariana, L. turbinata*), the fruits are large, elongate, and figlike; the cupule encloses the nut almost entirely (FIGURE 4; Camus, 1948, *pl. 355*). In *L. turbinata* there are three obvious cymule bracteoles, above which the cupular scales are prominent at anthesis (FIGURE 1). These scales are pushed upward as the cupular lamellae extend, and some of the lamellae become excentric and disrupted in the process (FIGURES 2–4); the scales become widely

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9, 10, *L. cornea:* 9, upper portion of spike at anthesis, showing staminate and pistillate, 1-flowered cymules; 10, mature cupule with 2 abortive cupules fused to it. 11–13, *L. pulchra:* 11, spike tip at anthesis, showing staminate and perfect flowers; 12, lateral view of pistillate cymule some time after anthesis, showing 2 of 3 bracteoles; 13, immature cupule, showing scale-bearing tubercles and all 3 bracteoles. Figures 1, 2, 4, 10, 13, × 2; Figure 3, × 0.3; Figures 5–9, 11, 12, × 4.

separated, but many of them persist on the mature cupule (FIGURE 3). At maturity the primary bracteole also usually persists, but the secondary bracteoles do not; however, some scales remain near the base of the cupule. *Lithocarpus beccariana* has but one bracteole below each pistillate cymule, and above it are the cupular scales (FIGURE 5). At maturity the cupule is virtually scaleless, and the scale-bearing lamellae are greatly extended (Camus, 1948, *pl. 355*). FIGURE 3 shows an apparently adventitious, abortive flower and cupule borne well up on the mature, nut-enclosing cupule.

SUBGENUS LIEBMANNIA. The three-or-more-flowered pistillate cymules of *Lithocarpus hendersoniana* have an obvious primary bracteole below them, and a low ring of overlapping bracteoles above that forms a pointed cowl at the distal end of the cymule (FIGURE 6). After pollination the cymule becomes pedunculate, and the primary bracteole is elevated on the peduncle (FIGURE 7). The cupular lamellae are continuous at first but later become interrupted (FIGURE 8), perhaps because of the rupturing stresses of diametric growth. The mature nut is included in the cupule.

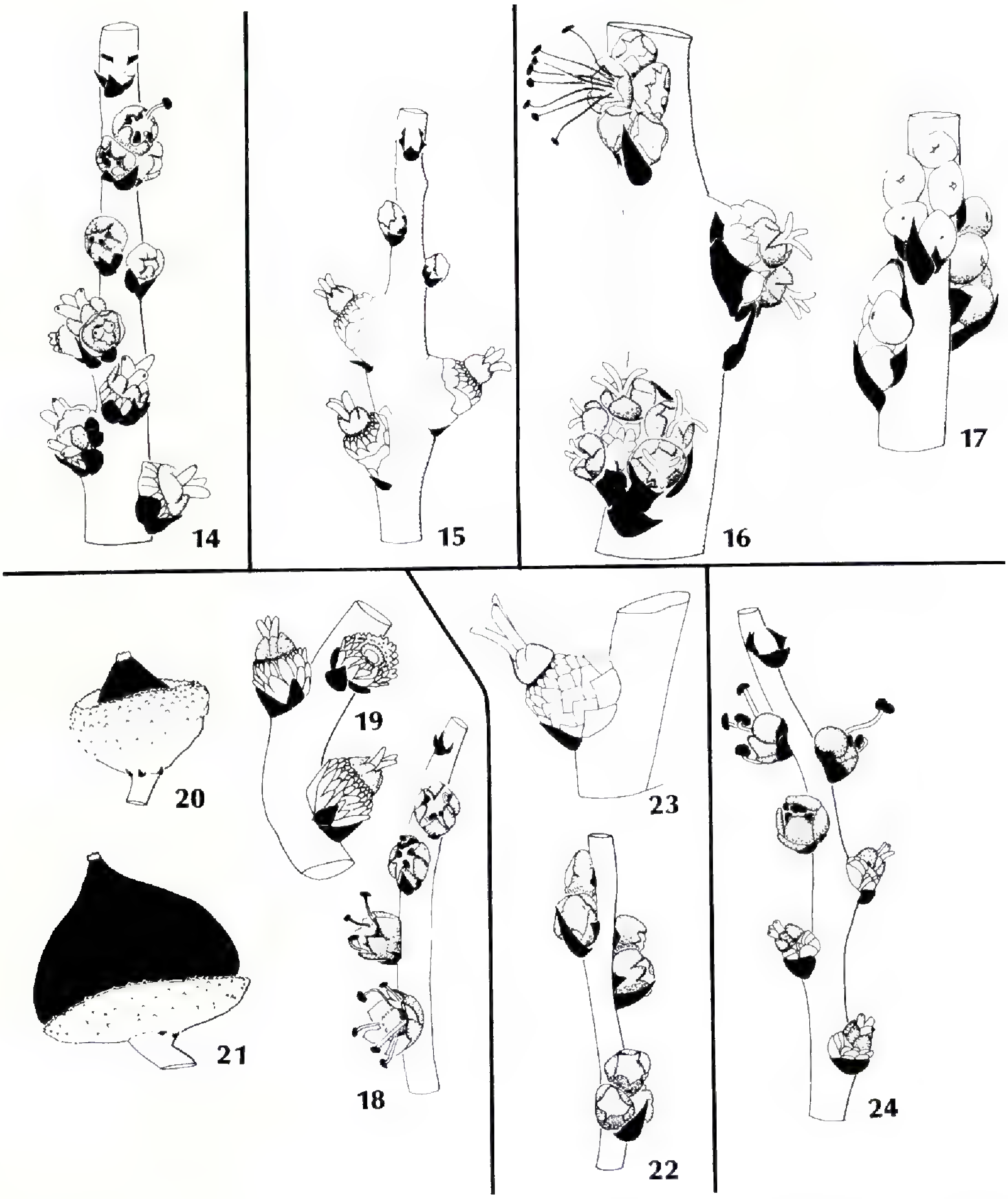
SUBGENUS SYNAEDRYS. The cupular scales of *Lithocarpus cornea* are prominent at anthesis, and the three subtending bracteoles are clearly distinguished (FIGURE 9). Enormous expansion of the cupular lamellae is accompanied by great growth in the scales, which become appressed and fused to the lamellae (FIGURE 10). The mature cupule covers most of the nut, except for a broad polar area. FIGURE 10 shows two abortive flowers and cupules attached at the base of the cupule.

In *Lithocarpus pulchra* the three bracteoles of the one-flowered cymule are evident at anthesis (FIGURES 11, 12) and in fruit (FIGURE 13), but an additional ring of bracteoles that surrounds the cupular scales quickly loses its identity as the cupule enlarges. The scales of the mature cupule are widely separated, each of them raised upon a mound of cupular tissue (FIGURE 13; Camus, 1948, *pl. 370*).

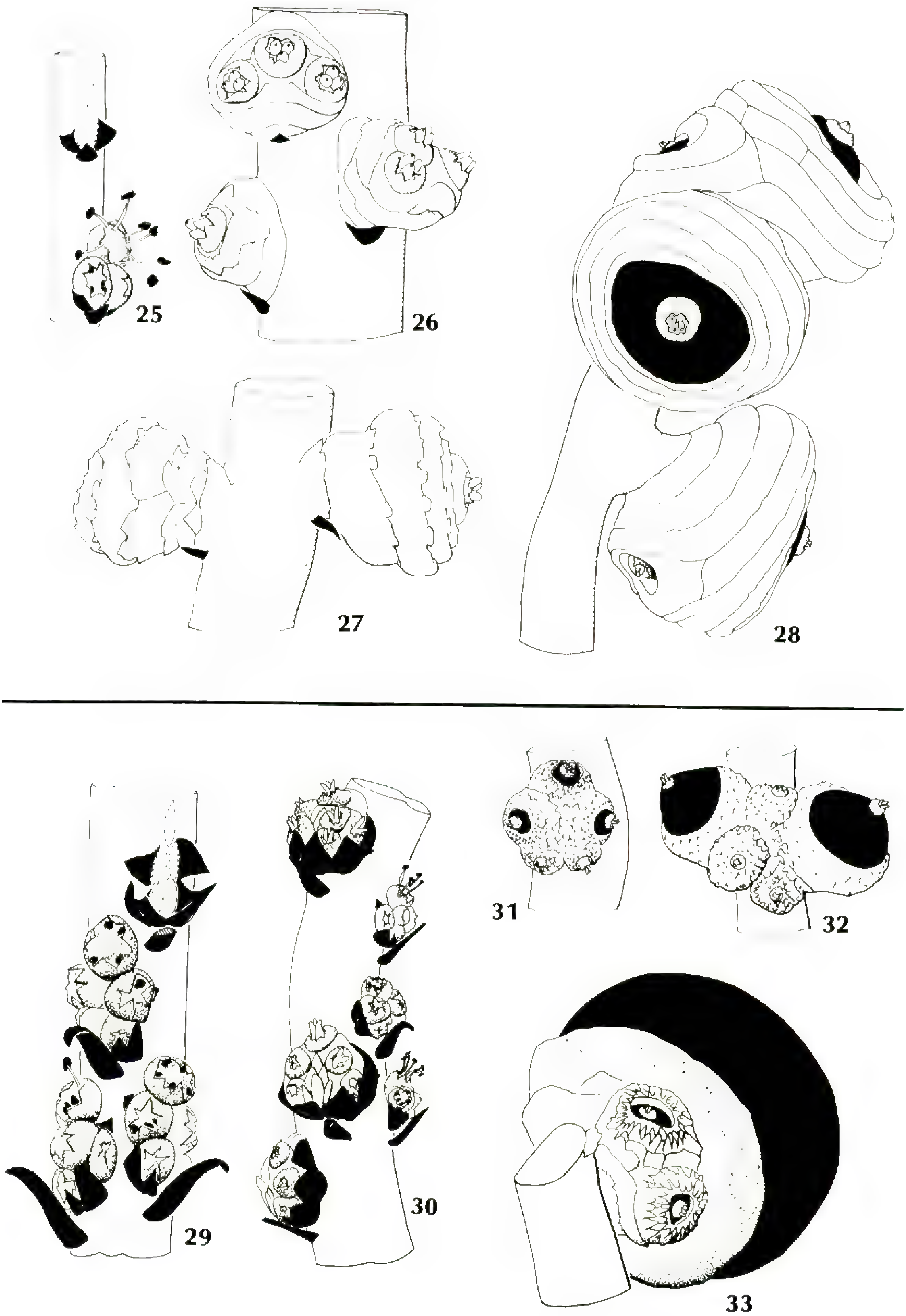
SUBGENUS PACHYBALANUS. In both *Lithocarpus amygdalifolia* and *L. truncata* at least seven bracteoles subtend the multi-flowered cymules (FIGURES 14, 16); in the former species the one-flowered cymules have but three (FIGURE 14). There are other bracteoles within the multi-flowered cymules. The cupular scales are hidden at anthesis by all these bracteoles, but they quickly become evident afterward. The mature cupule encloses much of the nut and is adorned with large, widely spaced cupular scales (Camus, 1948, *pl. 377*). The cymules of *L. nantoensis* have just one bracteole, the primary, and above it is a ring of presumably fused bracteoles that entirely encircles the cupule (FIGURE 15).

SUBGENUS GYMNOBALANUS. Three distinct bracteoles subtend each one-flowered cymule of *Lithocarpus havilandii* at anthesis (FIGURE 19), and they usually persist below the mature cupule (FIGURES 20, 21). The numerous cupular scales are prominent at anthesis (FIGURE 19) but are mostly adnate to the cupule at maturity (FIGURE 21), at which time they are not obviously arranged in concentric rings. The nut is enclosed by the cupule when immature but is mostly exposed at maturity (FIGURES 20, 21).

The one-flowered cymules of *Lithocarpus konishii* and *L. lauterbachii* have



Figures 14–24. 14, *Lithocarpus amygdalifolia:* spike tip at anthesis, staminate and pistillate cymules 1- to 3-flowered, flowers removed from uppermost staminate cymule to reveal 5 bracteoles. 15, *L. nantoensis:* spike tip at anthesis, staminate and pistillate cymules 1-flowered, uppermost staminate cymule with flower removed to reveal 5 bracteoles. 16, 17, *L. truncata:* 16, portion of spike at anthesis with 1 staminate and 2 pistillate cymules, all 5-flowered; 17, portion of staminate spike, showing 5-flowered staminate cymules with bracteoles and unopened flowers. 18–21, *L. havilandii:* 18, 19, segments of staminate and pistillate spikes at anthesis, all cymules 1-flowered; 20, 21, immature and mature fruits, showing persistent bracteoles below cupule. 22, 23, *L. konishii:* portions of staminate and pistillate spikes, showing 3-flowered staminate and 1-flowered pistillate cymules. 24, *L. lauterbachii:* near-terminal segment of spike at anthesis, all cymules 1-flowered. Figures 14, 20, 21, × 2; all others, × 4.



FIGURES 25–33. 25–28, *Lithocarpus lucida:* 25, segment of staminate spike with 2 3-flowered cymules, upper 1 with flowers removed to reveal 3 bracteoles; 26, segment of pistillate spike with 1 1-flowered and 2 3-flowered cymules after anthesis; 27, 2 1-flowered cymules with immature fruits, cupular scales evident; 28, immature fruits, older than those of Figure 27, cupular lamellae now devoid of scales, abortive fruit visible at lower end of lower cupule. 29–33, *L. lampadaria:* 29, segment of staminate spike,

a primary bracteole and, above it, a ring of free but overlapping bracteoles around the cupule (FIGURES 23, 24). In both species the mature cupule covers less than half of the broad, low nut, and it is heavily invested with overlapping cupular scales (Camus, 1948, *pl. 385*).

SUBGENUS CYCLOBALANUS. The mature cupule is often devoid of cupular scales (FIGURES 28, 33, 35, 41, 44, 55–57, 66), or it may have weakly developed scales that are widely separated (FIGURES 47, 51). In all the species of this subgenus illustrated, the early developmental stages clearly show the presence of cupular scales (FIGURES 27, 31, 32, 34, 38, 42, 43, 45, 46, 49, 50, 52, 59, 65). Many scales are deciduous or become distorted and exceeded by the massive growth of the cupule, and the mature cupule is then naked or nearly so. The cupular lamellae are more or less concentric in many species, but in a few they are not distinguishable at maturity (FIGURES 33, 35). In these the mature cupule consists of random or vaguely concentric scaleless enations. In some multi-flowered cymules the lowest few lamellae embrace all the flowers (FIGURES 26, 33, 39), but each flower eventually develops its own cupule (FIGURES 28, 33, 39). Other multi-flowered cymules lack such collectively embracing lamellae, and the flower cupules are distinct from the earliest stages (FIGURES 49, 50, 64).

The pistillate cymules of *Lithocarpus lucida* (FIGURES 26–28) are one- or three-flowered. All three flowers do not ordinarily mature in the latter case (FIGURE 28), nor do some of the one-flowered cymules. There is but one discernible subtending bracteole below each cymule, whether it is one- or three-flowered. Above it is a ring of tissue that perhaps represents fused bracteoles and that forms the first lamella of the cupule embracing all the flowers. The next structures to appear are partial lamellae that collectively embrace all the flowers (FIGURES 26, 27). It is not until well after pollination that the truly concentric, cupular lamellae arise in acropetal sequence. The scales are readily visible at these early stages. As the cupules near maturity, the scales have fallen or have become split and stretched beyond recognition; the cupule then appears to be scaleless (FIGURE 28). The massive growth of the cupular lamellae causes distortions among the contiguous cupules so that at least the first-formed (lowest) lamellae are often distinctly excentric. Abortive flowers become partially or completely buried in the maturing cupule (e.g., the central flower in the upper cymule and the lateral flowers in the lower cymule of FIGURE 28). At maturity the cupule covers less than half of the nut (Camus, 1948, *pl. 386*).

In *Lithocarpus reinwardtii* the cymules are also one- or three-flowered (FIGURES 37–40). The one-flowered cymules are subtended by three distinct bracteoles, above which the scale-bearing concentric lamellae appear in acropetal sequence. The last few lamellae to form are weakly developed and show no external evidence of scales (FIGURES 40, 41). The mature cupule is scaleless, although

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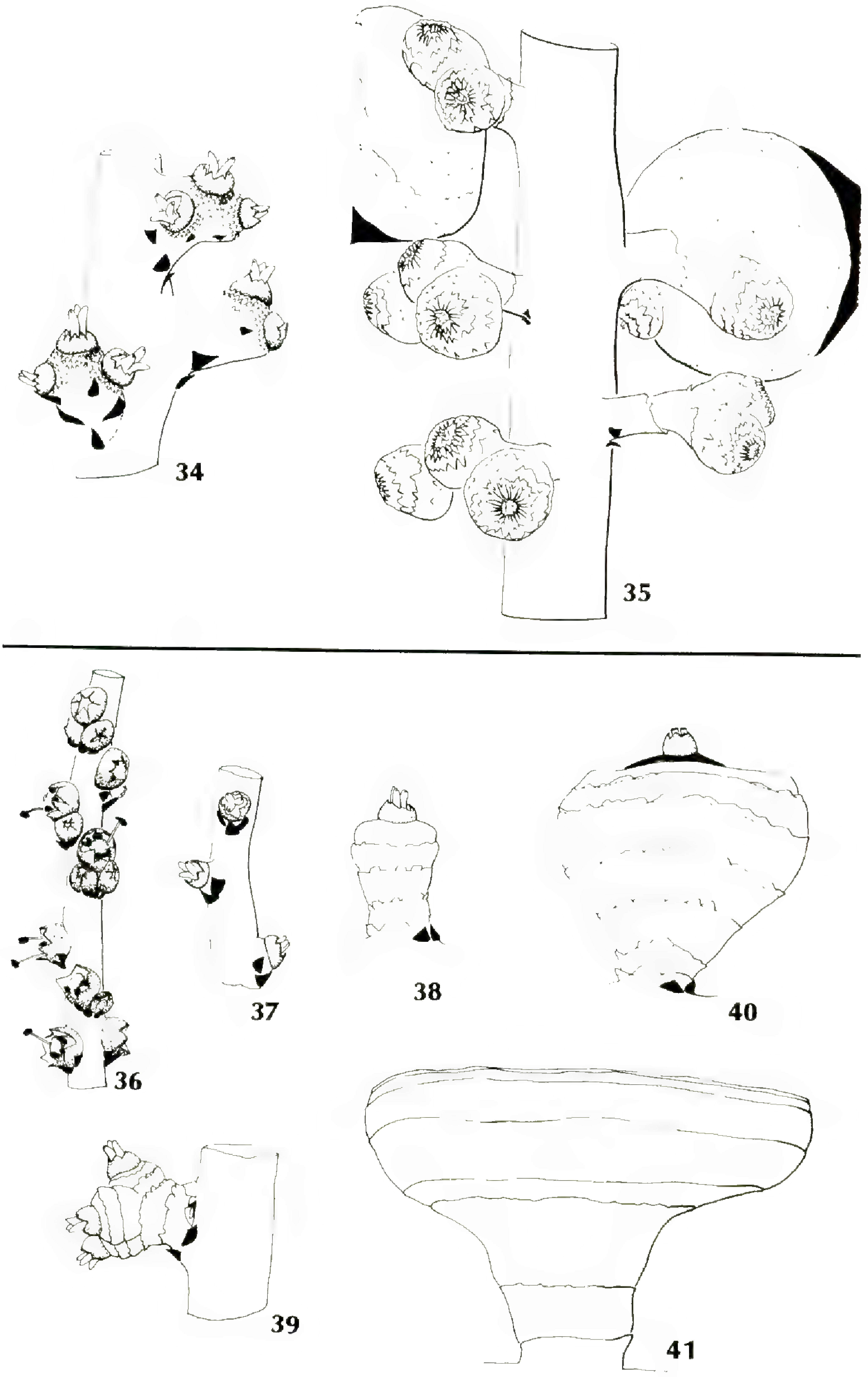
showing 5-flowered cymules, upper 1 with flowers removed to reveal 7 bracteoles; 30, segment of spike showing mixture of staminate and pistillate cymules, all multi-flowered; 31, 32, maturing pistillate cymules after anthesis, some flowers and their cupules abortive; 33, mature fruit with 2 basal, abortive flowers in cupules. Figures 28, 33, × 2; all others, × 4.



FIGURES 34–41. 34, 35, *Lithocarpus aggregata:* 34, segment of pistillate spike at anthesis, showing pedunculate 3-flowered cymules and their bracteoles; 35, segment of pistillate spike bearing mature fruits and abortive cupules. 36–41, *L. reinwardtii:* 36, segment of staminate spike at anthesis, showing 1- and 3-flowered cymules; 37, 1-flowered pistillate cymules at anthesis; 38–40, maturing cupules with evident scales; 41, mature cupule (nut removed), showing essentially scaleless lamellae. Figure 41, × 2; all others, × 4.

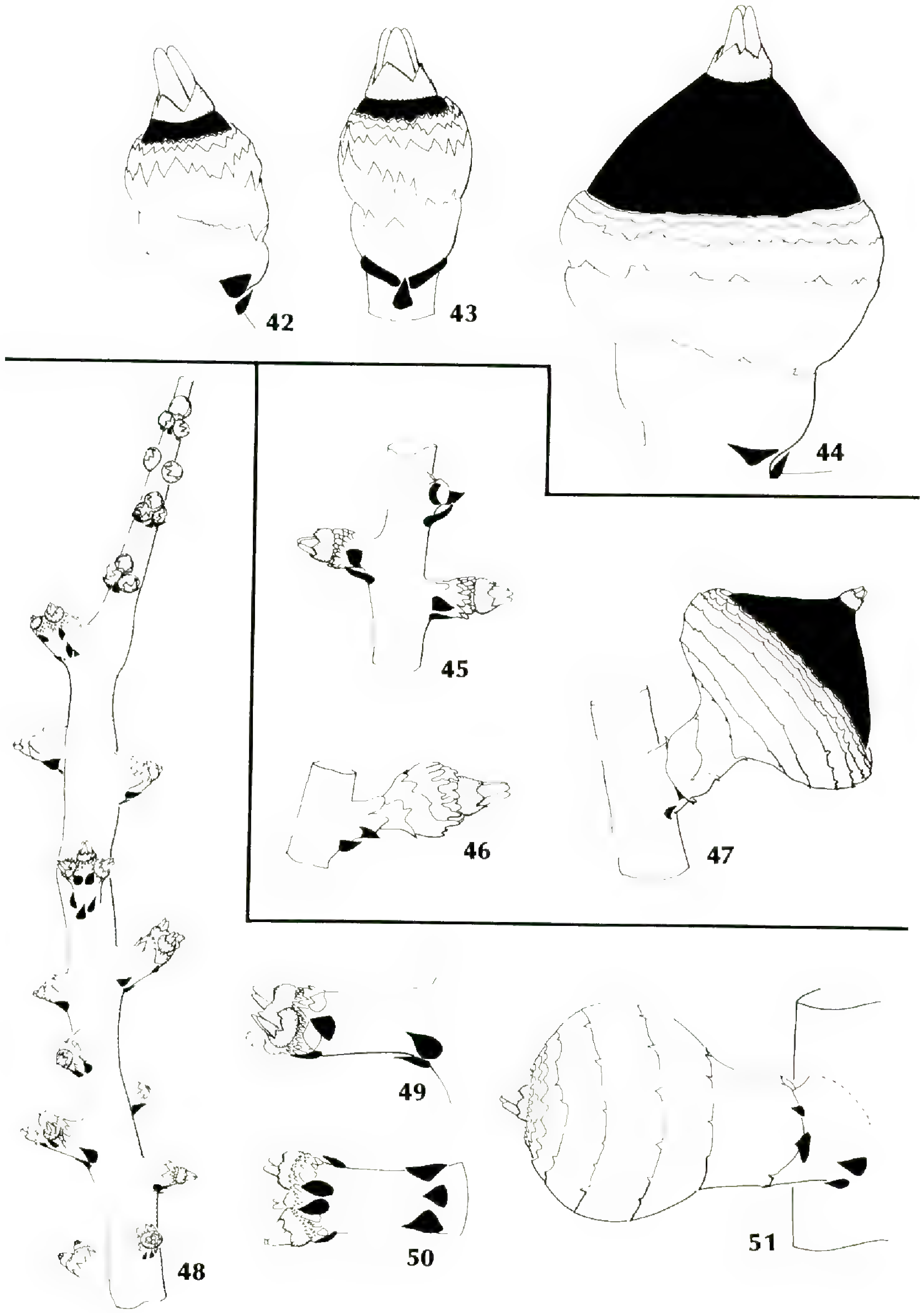
some evidence of scales can be seen in the lowest few lamellae (Figure 41). The three-flowered cymules, which are less common in my specimens than the one-flowered, are subtended by at least five distinct bracteoles (Figure 39), and there are other structures at the base of the cymule that may also represent subtending bracteoles. The first two lamellae to form surround all three flowers, but later lamellae embrace only one. Further details are shown by Camus (1948, *pl. 397*).

The one-flowered cymules of *Lithocarpus bullata* and *L. ewyckii* are also subtended by three obvious, distinct bracteoles (Figures 42–47) that persist below the mature cupule. The first lamella to form above the bracteoles of *L. bullata* bears a few scales (Figures 42, 43) that persist to maturity of the cupule. Succeeding lamellae have more scales, many of which persist but become widely separated as the diameter of the cupule increases (Figure 44). The uppermost lamellae are scaleless from their earliest stages. The first lamellae of *L. ewyckii* are more irregular than those of *L. bullata,* but they, too, are scaly. The later lamellae are regular and concentric and retain many of their scales into maturity, at which time the scales are widely spaced, sometimes reflexed, and often broken (Figure 47).

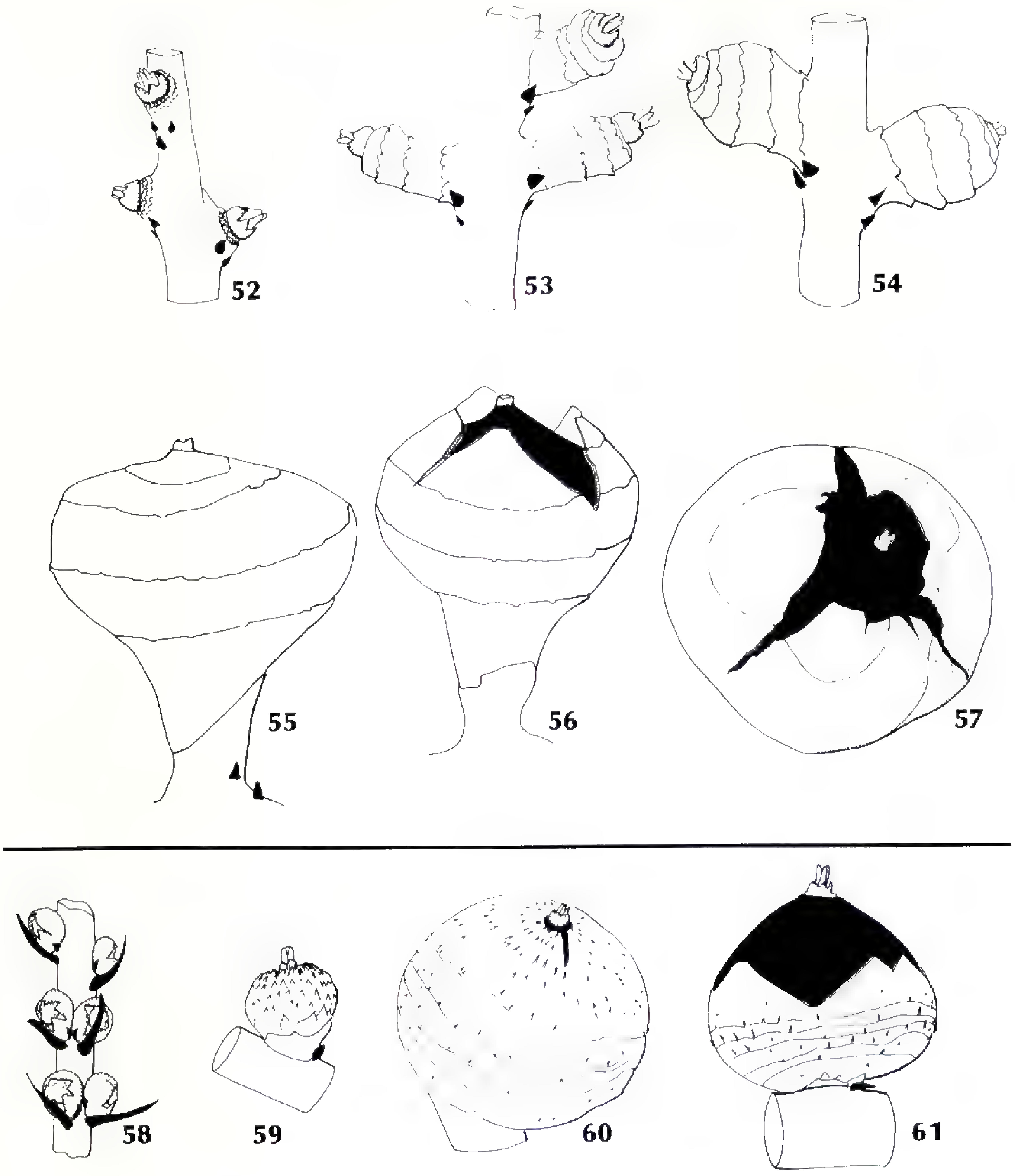
The cymules of *Lithocarpus macphailii* are distinctly pedunculate at anthesis (Figures 49, 50), but the peduncle does not lengthen very much as the cupule matures. There are three basal bracteoles (shown in lateral and ventral views in Figures 49 and 50, respectively). Another series of distinct bracteoles is evident at the distal end of the peduncle, just below the individual flowers (these are shown in black for emphasis in Figures 48–51). These, too, persist into maturity of the cupule (Figure 51), and they are readily distinguished by their location, thickness, and color from the other bracteoles below the flowers. Each flower develops its own cupule, but there is a loose ring of distinct or partially fused bracteoles that embraces all the flowers below their cupules (Figures 49, 50). As the cupular lamellae expand, the scales become widely separated but (as in the other species of this and many other subgenera) do not enlarge (Figure 51). At full maturity, only a small upper portion of the nut is visible (Camus, 1948, *pl. 407*).

Most of the cymules of *Lithocarpus encleisacarpa* are one-flowered, and each is subtended by three bracteoles (Figures 52–55). At anthesis the cymules are sessile, but they become pedunculate by elongation of the first few lamellae of the cupule (Figures 52–56); succeeding lamellae increase in diameter more than in length, and the mature cupule is turbinate. The cupular scales are evident at anthesis (Figure 52) but are barely apparent when the cupule matures (Figures 55–57). As the nut enlarges, the cupule ruptures, usually along three irregular arcs that cut through some of the upper lamellae (Figures 56, 57; Camus, 1948, *pl. 406*).

The pistillate cymules of *Lithocarpus neorobinsonii* have one primary bracteole at the base (Figures 59, 61); above this is an irregular lamella that may represent other, fused bracteoles. The somewhat irregular lamellae (even the uppermost, poorly developed ones) of the cupule retain their scales to maturity. The upper part of the cupule ruptures irregularly as the nut enlarges, with the tears extending only into the region of weak development of the lamellae (Figures 60, 61; Camus, 1948, *pl. 410*).

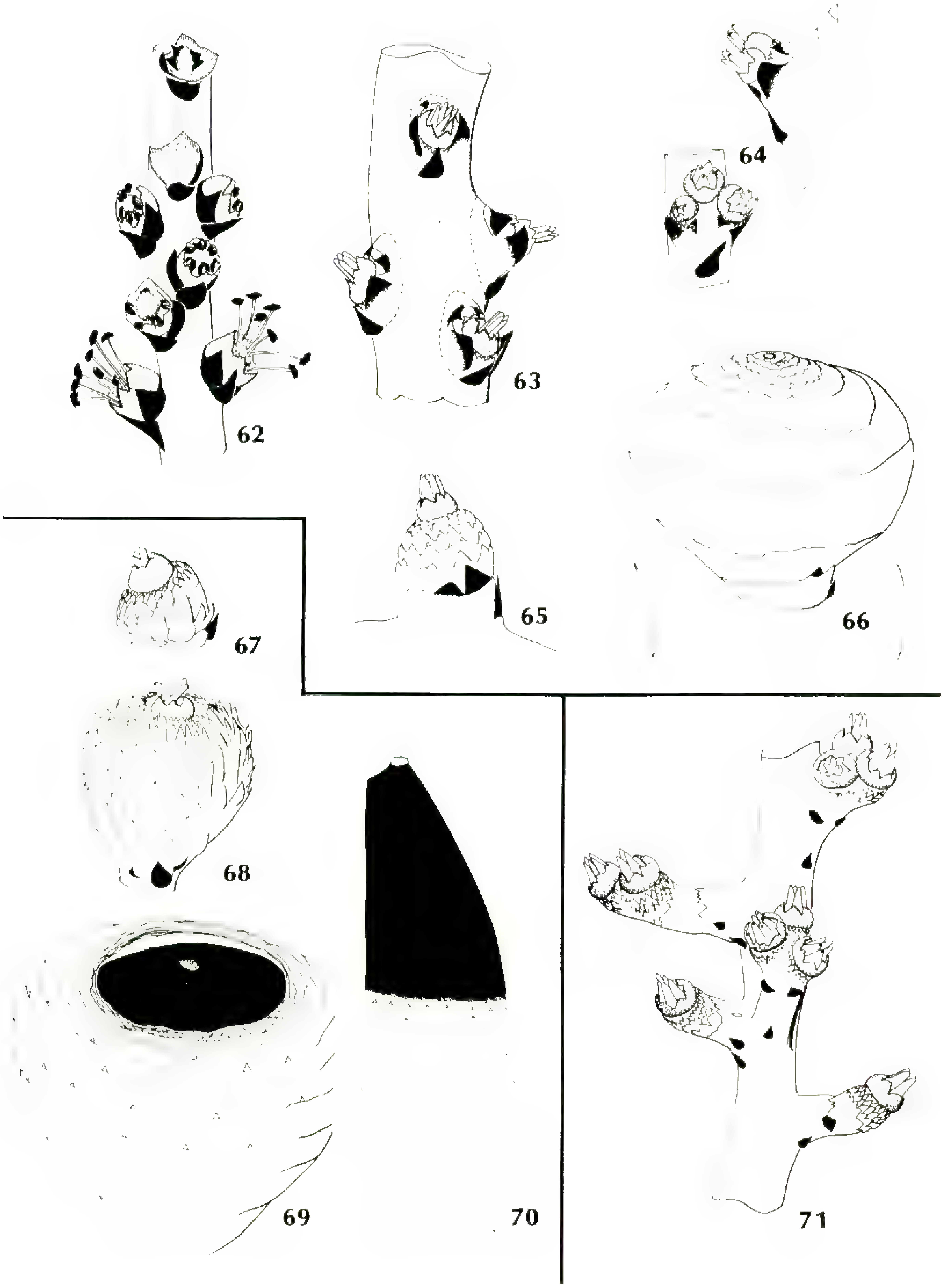


FIGURES 42–51. 42–44, *Lithocarpus bullata:* 42, 43, lateral and basal views of 1-flowered pistillate cymule somewhat beyond anthesis, showing bracteoles and young cupule; 44, nearly mature fruit, showing bracteoles and cupular scales during cupular enlargement. 45–47, *L. ewyckii:* 45, segment of pistillate spike at anthesis, showing 1-flowered cymules and their 3 bracteoles; 46, pistillate cymule somewhat after anthesis, showing early, scaly stages of cupular lamellae; 47, nearly mature fruit, showing retained bracteoles and cupular lamellae with their remote scales. 48–51, *L. macphailii:* 48, spike tip at anthesis with 1- and 3-flowered cymules, staminate above and pistillate below; 49, 50, pistillate,



FIGURES 52–61. 52–57, *Lithocarpus encleisacarpa:* 52–54, 1-flowered pistillate cymules at anthesis and in early fruit, 3 bracteoles evident below each cymule, cupular scales evident at anthesis (FIGURE 52) but becoming remote and ruptured as cupule matures; 55, mature cupule with nearly scaleless lamellae; 56, 57, dehiscing cupule in lateral and polar views. 58–61, *L. neorobinsonii:* 58, segment of staminate spike at anthesis, cymules 1-flowered and with 3 bracteoles; 59, pistillate, 1-flowered cymule after anthesis, cupular scales evident; 60, nearly mature cupule with scales now remote and lamellae weakly developed; 61, mature cupule, upper portion dehisced irregularly and revealing nut. Figures 52–54, 58, × 4; all others, × 6.

3-flowered cymules at anthesis, lateral and basal views (cymules pedunculate from anthesis); 51, nearly mature cupule with persistent bracteoles and remote cupular scales. Figures 47, 51, × 2; all others, × 4.



FIGURES 62–71. 62–66, *Lithocarpus pattaniensis:* 62, segment of staminate spike, showing 1-flowered cymules, each with 3 or more bracteoles, upper 2 cymules with flower removed, uppermost cymule showing presence of inner set of bracteoles; 63, 64, 1- and 3-flowered pistillate cymules at anthesis; 65, 1-flowered pistillate cymule some time after anthesis, showing beginnings of lamellar growth of cupule, scales evident; 66, nearly mature cupule with lamellae prominent, scales now remote and ruptured, bracteoles evident. 67–70, *L. rufovillosa:* 67–69, maturing 1-flowered pistillate cymule with 3 bracteoles, scales prominent near anthesis (FIGURE 67) but lamellae prominent in fruit (FIGURES

Above the obvious primary bracteole of the one- and three-flowered cymules of *Lithocarpus pattaniensis* are other, basally fused bracteoles that encircle the flower(s) (FIGURES 63–65). There are usually four of these in the one-flowered cymules but more in the three-flowered ones. Some of these bracteoles persist into maturity of the cupule (FIGURE 66). The cupular scales are evident at anthesis (FIGURES 63, 64) but are tiny and often ruptured on the massive lamellae of the mature cupule (FIGURE 66). The scales are adjacent at anthesis but become separated during cupular expansion (FIGURES 65, 66). When the cupule is fully mature, it reveals a small portion of the nut (Camus, 1948, *pl. 517*).

The mature cupule of *Lithocarpus aggregata* does not show the obvious lamellae of the above-described species. Instead, it bears vaguely defined rows of enations that carry little or no evidence of cupular scales (FIGURE 35). However, cupular scales and lamellae are clearly evident in earlier developmental stages (FIGURES 34, 35). At anthesis the three-flowered cymules are pedunculate, and the peduncle is evident through maturity of the fruit (FIGURE 35). There are three bracteoles under each cymule, and above them are two more, each near a lateral flower; there is no bracteole immediately below the central flower (FIGURE 34). These persist into fruit. There is one lamella (or sometimes two) encircling the peduncle, but above it the lamellae embrace single flowers (FIGURE 35). After several obvious lamellae have formed, the succeeding ones are, from their inception, indistinct; it is they that form the irregular rows of enations in the upper part of the cupule.

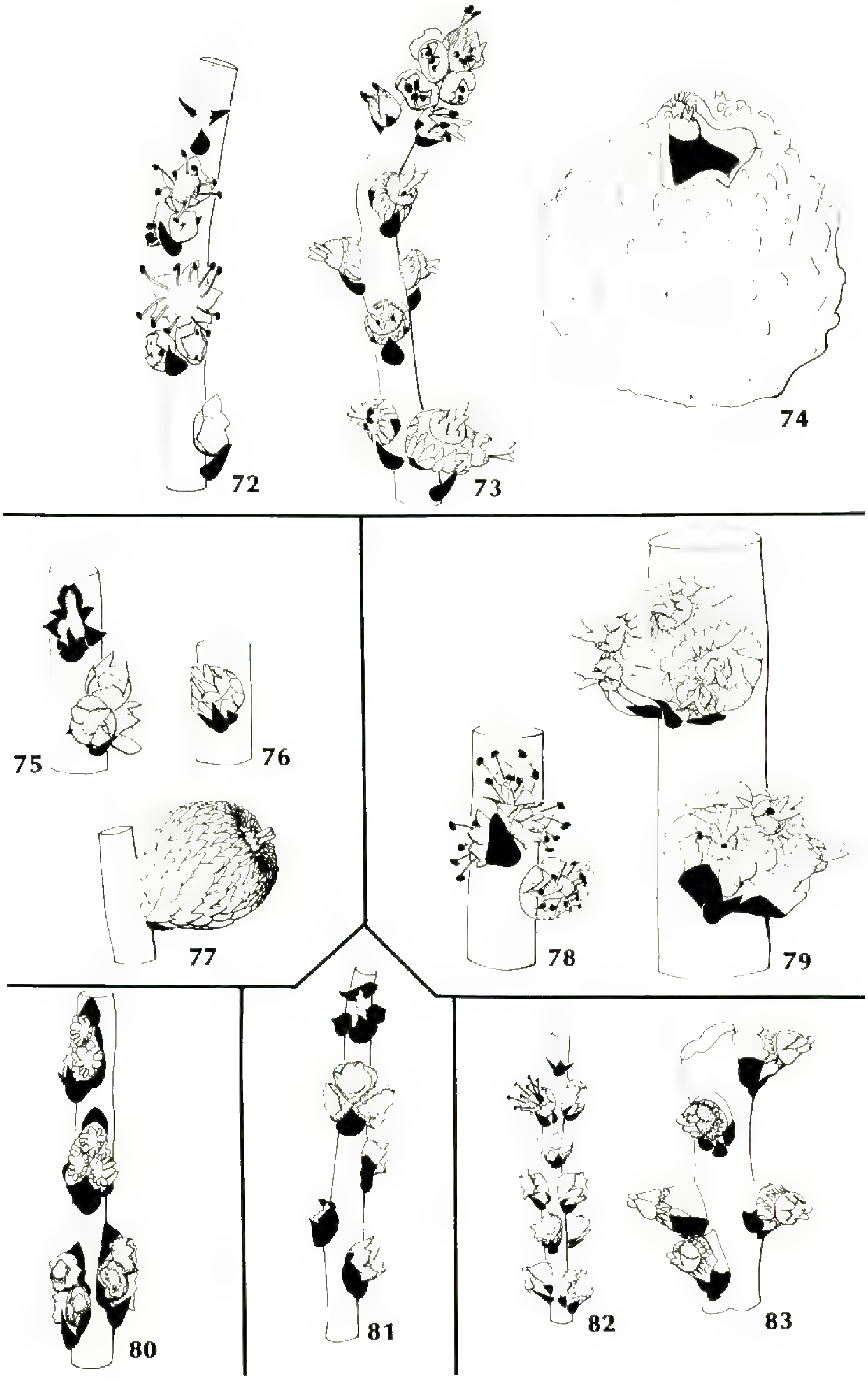
The pistillate cymules of *Lithocarpus lampadaria* often have five flowers, but more or fewer are common. Below each cymule is a single, distinct primary bracteole, above which is a series of six or so free but overlapping paired bracteoles (FIGURE 30). The primary bracteole and some of the others persist into fruit, but they are often completely distorted by the massive growth of the cupules and the resulting juxtaposition of the abortive flowers (FIGURES 32, 33). Of the hundreds of fruiting cymules examined, none bore more than three fully developed nuts, and most had none, one, or two.

SUBGENUS PASANIA. The cymule bracteole patterns of this subgenus resemble those of the other subgenera, but the cupular ornamentation is very diverse.

There are three bracteoles subtending the one-flowered pistillate cymule of *Lithocarpus rufovillosa* (FIGURE 68), and they persist into fruit. The cupular scales are evident at anthesis (FIGURE 67), and soon thereafter their alignment in rows is apparent (FIGURE 68). The massive growth of the lamellae separates the scales, many of which fall, leaving the cupule barely scaly at maturity (FIGURES 69, 70). In fact, many of the lower lamellae are scaleless (FIGURES 69, 70).

The distinctively pedunculate one- and three-flowered cymules of *Lithocar-*

69, 70); 70, segment of mature fruit, cupule covering about half of nut, scales retained only on upper lamellae. 71, *L. sootepensis:* segment of pistillate spike very soon after anthesis, cymules 1- and 3-flowered and with 3 bracteoles, peduncle evident at anthesis and eventually carrying mature fruits. Figures 66, 70, × 2; all others, × 4.



FIGURES 72–83. 72–74, *Lithocarpus wrayi:* 72, segment of staminate spike at anthesis, showing 1- and 3-flowered cymules, uppermost 1 with flowers removed to reveal 3 bracteoles; 73, spike tip with distal, 1-flowered staminate cymules and 1- and 2-flowered pistillate cymules, all with 3 bracteoles; 74, nearly mature cupule, scales basally adnate, upper portion broken away to reveal nut within. 75–77, *L. scortechinii:* 75, segment of staminate spike with 3-flowered cymules, upper 1 with flowers removed to reveal complex bracteole pattern; 76, 1-flowered pistillate cymule at anthesis, 3 bracteoles shown; 77, pistillate cymule after anthesis, showing extensive growth of cupular scales. 78, 79, *L.*

pus sootepensis each have a basal primary bracteole and a pair of secondary bracteoles that become elevated on the elongating peduncle (FIGURE 71). The cupular scales are well developed soon after anthesis and are evident in the mature cupule (Camus, 1948, *pl. 416*).

Three bracteoles subtend the one- or several-flowered cymules of *Lithocarpus wrayi* (FIGURE 73), and at least the primary bracteole can be seen below the mature cupule. The scales of the cupule are large at anthesis, and they remain prominent on the cupule in fruit, eventually becoming reflexed (Camus, 1948, *pl. 441*). The cupule does not show lamellae, although the persisting, subulate scales are aligned in concentric rows (FIGURE 74).

A primary bracteole and a pair of secondary ones subtend the pistillate cymules of *Lithocarpus hancei* (FIGURE 84). Most of the cymules have three flowers, but some of the more distal ones are one-flowered (FIGURE 84). A ring of connate bracteoles surrounds the flowers, and within that (but not visible in FIGURE 84) are the young cupules. As the nut and cupule begin to grow, the cupular scales emerge (FIGURE 86, lower, abortive cymule); at maturity the relatively small cupule shows irregular rings of annular enations, most of which bear a tiny cupular scale (FIGURE 86, mature nut and cupule; Camus, 1948, *pl. 415*).

The numerous scales of *Lithocarpus papillifer* (FIGURE 87), so evident at anthesis, remain small and adpressed on the mature cupule. There is but one obvious bracteole below each one-flowered cymule.

The long cupular scales of *Lithocarpus garrettiana* are evident from anthesis onward (FIGURES 79, 90–92), elongating considerably during cupular growth so as to be trichomelike at maturity. In the lower part of the mature cupule, the scales are in concentric rows (FIGURE 92); those higher up are usually crowded, and their arrangement in rows is not evident. The drying, dehiscing cupule splits open along three radial arcs (FIGURE 91) that extend halfway or less down the cupule, the upper part of the cupule sometimes breaking away in a crudely circumscissile dehiscence (FIGURE 92). There is some variation in dehiscence pattern of the cupule; only the usual one is illustrated in FIGURES 91 and 92 (cf. Camus, 1948, *pl. 434*).

As in many species of subg. *Cyclobalanus,* the mature cupule of *Lithocarpus soleriana* has concentric lamellae bearing vestiges of cupular scales (FIGURE 96; Camus, 1948, *pl. 467*). The primary bracteole subtends the one-flowered cymule and is surmounted by a ring of partially connate bracteoles that enclose the cupule; the cupular scales are evident at anthesis (FIGURE 95). With ex-

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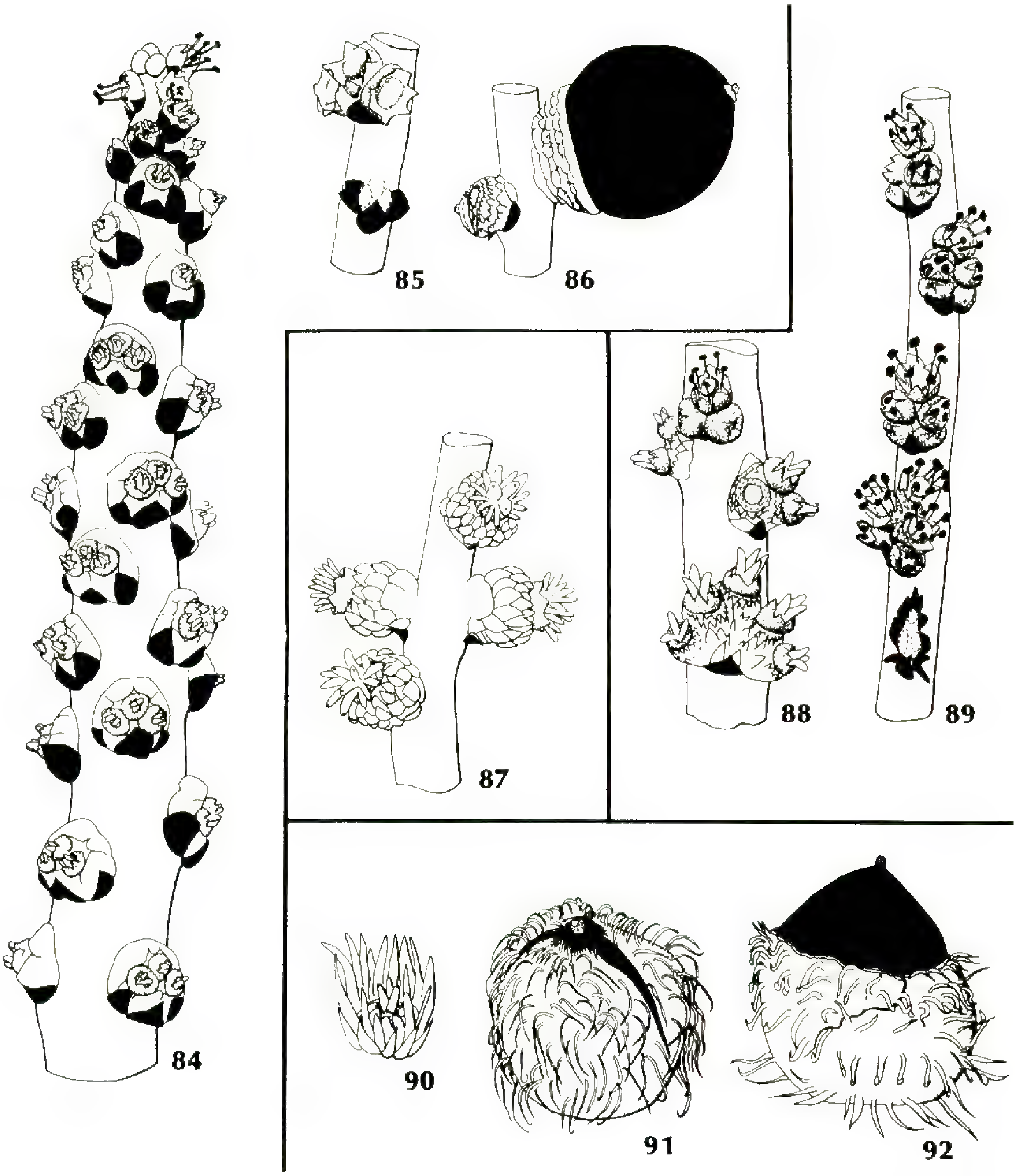
garrettiana: 78, segment of staminate spike, showing 3-flowered cymules with 1 bracteole; 79, segment of pistillate spike at anthesis, showing 3- and 4-flowered cymules, each subtended by 3 bracteoles. 80, *L. fenestrata:* segment of staminate spike in anthesis, showing 3-flowered cymules, upper 2 with flowers removed to reveal interior sets of bracteoles (not in black). 81, *L. harlandii:* segment of staminate spike at anthesis with 1- and 3-flowered cymules, uppermost 1 with flower removed to reveal bracteoles. 82, 83, *L. sabulicola:* 82, segment of staminate spike at anthesis, showing 1-flowered cymules, uppermost 1 with flower removed to reveal 3 bracteoles; 83, segment of pistillate spike at anthesis showing 1-flowered cymules with 3 bracteoles. Figures 74, 77, × 2; all others, × 4.



FIGURES 84–92. 84–86, *Lithocarpus hancei:* 84, spike tip at anthesis, showing few distal, staminate, 1-flowered cymules, each with 3 bracteoles, pistillate cymules 3-flowered and with 3 bracteoles; 85, segment of staminate spike with 3-flowered cymules, each with 3 bracteoles, lower cymule with flowers removed; 86, segment of fruit-bearing pistillate spike, 1 cymule with only abortive flowers and cupules, mature cupule with scale-bearing enations. 87, *L. papillifer:* segment of pistillate spike soon after anthesis, 1-flowered cymules each with 1 obvious bracteole, numerous styles on each flower. 88, 89, *L. dealbata:* 88, segment near tip of spike, with 1 3-flowered staminate cymule, pistillate cymules 3- and 5-flowered, each with 1 obvious bracteole; 89, segment of staminate spike at anthesis, most cymules 5-flowered, lowest 1 with 3 flowers removed to reveal complex bracteole pattern. 90–92, *L. garrettiana:* 90, flower in cupule soon after anthesis, cupular scales already very long; 91, mature cupule invested with elongate, recurved scales and showing 3 lines of dehiscence from upper pole; 92, mature cupule, dehisced upper portion fallen away. Figures 86, 91, 92, × 2; all others, × 12.

pansion of the cupule as maturity nears, the scales are separated and often ruptured, but most of them persist.

The pistillate cymules of *Lithocarpus harmandii* are among the most complex in the genus. They have one to seven flowers and are surrounded by a mass of bracteoles (FIGURES 97, 98). Below each cymule is a single obvious primary bracteole, above which is a complex ring of barely connate bracteoles. At anthesis the cupular scales are not evident because they are hidden by the ring of bracteoles (FIGURE 97), but soon thereafter they become prominent (FIGURE 98). Each flower develops its own cupule, but only one or two—very rarely three—mature into fruit. The abortive flowers continue to grow for some time and develop obvious but small cupules (FIGURE 100). The cupule surrounding a mature nut is a mass of more or less concentrically arranged enations, most of which bear a tiny cupular scale (FIGURE 100; Camus, 1948, *pls. 470, 471*).

The pistillate cymules of *Lithocarpus elegans* are also complex. They usually hold three to five flowers, with a few having one or six or more (FIGURE 101). A primary bracteole and a lateral pair of secondary ones are attached to the elevated buttress that bears the flowers (FIGURES 101, 103). There are no other obvious bracteoles in the cymule at anthesis, but there are faint ridges on the buttress that suggest a ring of reduced bracteoles (not visible in FIGURE 101). There are no readily discernible cupular scales at anthesis, but they appear soon thereafter. Their arrangement in concentric rows is then evident. The rings of scales are very tightly compressed, and the scales are appressed but readily visible in the mature cupule (FIGURE 103; Camus, 1948, *pl. 481*). As the nut matures, the partially enclosing cupule ruptures along four or five arcs (FIGURE 103).

One primary bracteole and a pair of lateral bracteoles, one below each lateral flower, are characteristic of the three-flowered cymules of *Lithocarpus wallichiana*. There is also a ring of partially connate bracteoles that partially surrounds the cymule (FIGURE 105). The cupular scales are not entirely concealed by these bracteoles at anthesis, and they later become prominent (FIGURE 106). Although it is not obvious in FIGURE 106, the scales are aligned in concentric rows. At maturity of the cupule, the scale-bearing concentric lamellae are evident; they have persistent, separated, torn scales (FIGURE 107; Camus, 1948, *pl. 503*). The abortive flowers and cupules are shown in FIGURE 107. Any one of the three flowers in a cymule can mature into a fruit. The upper cymule in FIGURE 107 shows the matured cupule of the central flower (the nut is removed to show the scar) subtended by two abortive lateral flowers; the lower cymule has one abortive and one fertile lateral flower and an abortive central flower. Occasionally, more than one flower matures a nut.

Although the cupular scales of *Lithocarpus scortechinii* are hidden by the bracteoles at anthesis (FIGURE 76), they quickly become prominent (FIGURE 77); by cupular maturity they are long and reflexed (Camus, 1948, *pl. 442*). The mature cupule covers much less than half of the nut. There are one primary and two distinct lateral bracteoles below the one-flowered cymule, and a ring of barely connate bracteoles above that (FIGURE 76). When the cupular scales enlarge, the ring of bracteoles is not readily distinguishable from the scales (FIGURE 77).

FIGURES 93–100. 93, *Lithocarpus densiflora:* segment near spike tip at anthesis, upper 4 cymules staminate, with 3 to 5 flowers and 5 to 7 bracteoles (not all visible here), pistillate cymules with 1 flower and 1 bracteole. 94–96, *L. soleriana:* 94, segment of staminate spike with 1- and 3-flowered cymules, 2 with flowers removed to show numerous bracteoles; 95, segment of pistillate spike at anthesis, showing 1-flowered cymules, each with 1 bracteole, cupular scales prominent; 96, mature cupule covering about half of nut, lamellae somewhat scaly. 97–100, *L. harmandii:* 97, 98, segments of pistillate

As in *Lithocarpus scortechinii* and other species, the mature cupule of the only American member of the genus, *L. densiflora,* covers little of the nut and is thickly invested with rather long, often recurved scales (Camus, 1948, *pl. 444*). The cymules are one-flowered and are subtended by a large primary bracteole (FIGURE 93); above this is a ring of slightly overlapping bracteoles that enclose the cupular scales, which are evident at anthesis (FIGURE 93).

The one-flowered pistillate cymules of *Lithocarpus sabulicola* have three bracteoles, one primary and two secondary, and there is a ring of strongly connate bracteoles that surrounds the remainder of the cymule. The ring does not entirely conceal the cupular scales at anthesis (FIGURE 83). At maturity the nut projects well beyond the scaly cupule (Camus, 1948, *pl. 464*).

The cymule bracteoles of *Lithocarpus dealbata* are not clearly distinguishable from the cupular scales. Although the primary bracteole is easily observed, the secondary ones are less so (FIGURE 88). Beyond them is a series of structures that are not clearly bracteoles or scales. The cupule encloses most of the nut at maturity, and it is invested with concentric rows of widely spaced, appressed, slightly elongate scales (Camus, 1948, *pls. 450, 451*).

SUBGENUS PSEUDOCASTANOPSIS. The cymules of *Lithocarpus fissa* subsp. *fissa* are one-flowered, and each has one bracteole (FIGURE 109). At anthesis the cupular scales and lamellae are obscured, but they are evident at maturity, at which time the cupule dehisces and the nut emerges (FIGURES 110, 111).

THE STAMINATE CYMULES

The staminate cymules are borne on staminate spikes, as well as above and below the pistillate cymules on mixed-sex spikes (Kaul & Abbe, 1984). On the latter spikes there are sometimes a few cymules that bear both staminate and pistillate flowers at the area of transition from entirely pistillate to entirely staminate cymules. The flowers in that area may be perfect, while those away from it are imperfect. Such transitional conditions are especially evident in species with multi-flowered cymules.

The staminate cymules are subtended by one or more bracteoles whose number and arrangement are the same as or different from those of the pistillate cymules of the same species. Often there are more bracteoles subtending the staminate than the pistillate cymules (see TABLE).

FIGURES 1 and 11 show the one-flowered staminate cymules of *Lithocarpus turbinata* and *L. pulchra* on the rachis beyond the pistillate cymules. Each staminate cymule has one long primary and two shorter secondary bracteoles, a condition often found in one-flowered staminate cymules in other subgenera. However, by contrast, the one-flowered cymules of *L. beccariana* (FIGURE 5) have only a primary bracteole. The situation is more complex in *L. hender-*

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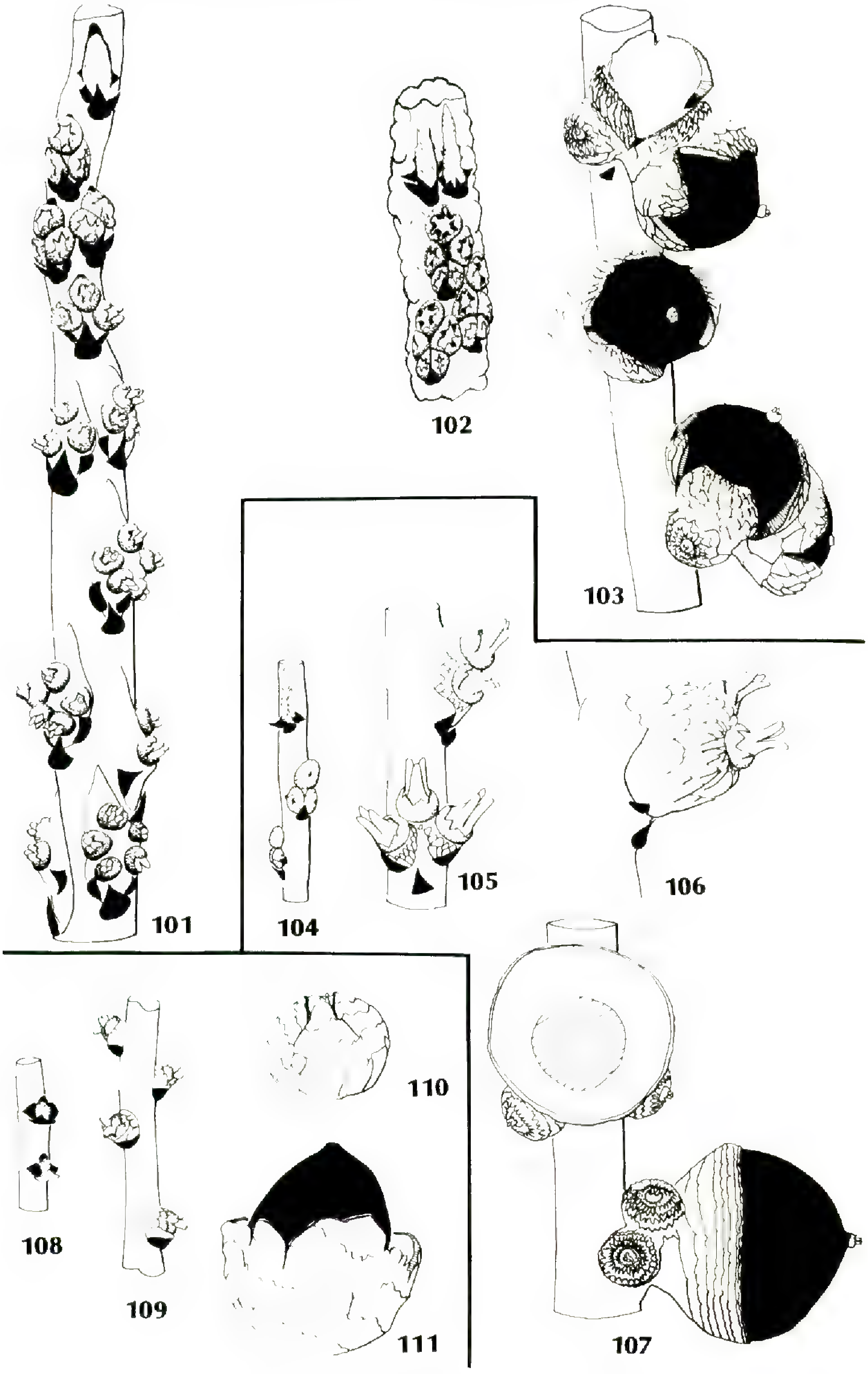
spikes at and shortly after anthesis, respectively, cymules 3- to 7-flowered, each with 1 prominent bracteole, well-developed staminodia present in flowers of uppermost cymules of FIGURE 97; 99, segment of staminate spike just before anthesis, cymules 7-flowered, each 3-bracteolate; 100, mature cupule and nut, each scale borne on enation. Figures 96, 99, 100, × 2; all others, × 4.



FIGURES 101–111. 101–103, *Lithocarpus elegans:* 101, segment near tip of androgynous spike at anthesis, upper 4 cymules staminate, uppermost with all 3 flowers removed to show bracteoles, pistillate cymules 3- to 5-flowered, each with 3 bracteoles and raised upon buttress; 102, segment of staminate spike at anthesis, 5-flowered cymules subtended by numerous bracteoles, upper 2 cymules with flowers removed; 103, mature, fruit-bearing pistillate spike, 1 cupule split and with parts fallen away, each cymule with 1 abortive flower and cupule. 104–107, *L. wallichiana:* 104, segment of staminate spike nearing anthesis, each cymule with 3 flowers and 3 bracteoles; 105, segment of pistillate spike at anthesis, each cymule with 3 flowers and 3 bracteoles, cupular scales evident; 106, pistillate cymule after anthesis; 107, mature cymules, each with 2 abortive flowers and cupules, mature cupule covering about half of nut and barely scaly. 108–111, *L.*

soniana (FIGURE 6): above the primary bracteole there is a series of low, basally connate bracteoles that encircle the entire cymule, just as they do in the pistillate cymules of that species. In all these species the bracteole pattern is the same in staminate and pistillate cymules.

The one- and three-flowered staminate cymules of *Lithocarpus amygdalifolia* and *L. nantoensis* (FIGURES 14, 15) have five bracteoles, with the primary always the largest. The five-flowered staminate cymules of *L. truncata* usually have seven bracteoles (FIGURE 17). The quaternary pair extends completely over the distal end of the cymule (not visible in figures).

In the three species illustrated from subg. *Gymnobalanus,* the staminate cymules are one- and three-flowered and three-bracteolate, and three-flowered and five-bracteolate (FIGURES 18, 22, 24).

In the large subgenus *Cyclobalanus* the bracteoles of the staminate cymules range from three to seven or more per cymule. A complex example is shown for *Lithocarpus lampadaria* in FIGURE 29. The staminate cymules are mostly five-flowered, and there is an elongate primary bracteole below each one. Above it, in pairs, are six additional bracteoles, some overlapping and some not (FIGURE 29, top). Four of the flowers of the cymule have one or more bracteoles beside them, but the distal flower does not. The bracteole pattern of the pistillate cupule is likewise complex (FIGURE 30).

Simpler bracteole patterns exist in *Lithocarpus reinwardtii,* where both the one- and the three-flowered staminate cymules have three bracteoles (FIGURE 36), as do some of the pistillate cymules (FIGURE 37). In *L. macphailii* the three-flowered staminate cymules have five bracteoles, and the pistillate cymules have that many or more (FIGURES 48–51). The simplest case is that of *L. neorobinsonii* (FIGURE 58), in which the staminate and pistillate cymules both have one flower and three bracteoles.

The bracteole pattern is somewhat complex in *Lithocarpus pattaniensis* because, although the cymules are always one-flowered, there are three or sometimes more bracteoles present, even on the same specimen (FIGURE 62). When the single flower is removed from the bracteoles, as in the upper two cymules in FIGURE 62, it can be seen that the secondary bracteoles are slightly confluent above the cymule, where they form a point that suggests another, reduced bracteole. Furthermore, within that encircling series of bracteoles there is sometimes a second set of four (two to six) tiny ones that suggest a rudimentary cupule (FIGURE 62, uppermost cymule).

The largest subgenus, *Pasania,* also has a great range of bracteole patterns in the staminate cymules. Some three-flowered cymules have but one bracteole (e.g., in *Lithocarpus garrettiana,* FIGURE 78), and some have three bracteoles (e.g., in *L. lucida,* FIGURE 25; *L. wrayi,* FIGURE 72; *L. hancei,* FIGURE 85; and *L. wallichiana,* FIGURE 104). Some cymules with five or more flowers also have

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fissa: 108, 109, segments of staminate and pistillate spikes at anthesis, each cymule with 1 flower, staminate with 3 or more bracteoles, pistillate with 1; 110, cupule nearing maturity and showing early signs of dehiscence; 111, mature, dehisced cupule revealing part of nut, lamellae prominent and barely scaly. Figures 103, 107, 110, 111, × 2; all others, × 4.

only three bracteoles (e.g., in *L. harmandii,* FIGURE 99), but so do some one-flowered cymules (e.g., in *L. wrayi,* FIGURE 73; *L. sabulicola,* FIGURE 82; *L. hancei,* FIGURE 84).

Complex bracteole patterns in the staminate cymules of subg. *Pasania* are illustrated here by seven species. *Lithocarpus scortechinii* (FIGURE 75), *L. harlandii* (FIGURE 81), *L. dealbata* (FIGURE 89), *L. soleriana* (FIGURE 94), and *L. elegans* (FIGURES 101, 102) illustrate a common arrangement: an identifiable primary bracteole and usually an identifiable pair of secondary ones. Beyond these three bracteoles is a series of smaller, sometimes irregular ones that are not always obviously paired. At the distal end of the cymule, the bracteoles are reduced and apparently fused; they usually surmount the cymule. Such complexity occurs in these species in one-, three-, and multi-flowered cymules, as shown in the figures. The three- and five-flowered staminate cymules of *L. densiflora* have five and seven bracteoles, respectively.

The most complex staminate bracteole pattern among the species studied is that of *Lithocarpus fenestrata.* In addition to having a series of complex bracteoles similar to those of the species discussed in the preceding paragraph, each flower is subtended by a whorl of small bracteoles that suggests a rudimentary cupule (FIGURE 80, upper two cymules, the small bracteoles not darkened).

Lithocarpus fissa, of subg. *Pseudocastanopsis,* has one-flowered staminate cymules, each with four subtending bracteoles, the fourth one located at the distal end of the cymule (FIGURE 108).

DISCUSSION

Some aspects of the bracteole patterns and the floral arrangement support the interpretation that the groups of flowers provisionally called cymules are actually that. Evidence is provided by the sequence of opening of the flowers in both staminate and pistillate cymules. In every instance the distal flower opens first, with the subjacent pair next, and the lowest pair last (i.e., the sequence is strictly basipetal within the cymule). Where more than five flowers are present in a cymule, the sequence of opening beyond the fifth flower is also generally basipetal, but the pattern is less obvious.

The primary bracteole and the paired secondary, tertiary, and subsequent bracteoles, as well as the absence of a bracteole immediately below the central flower, all suggest a condensed cyme. When the cymule has a single flower, sometimes one and sometimes three or more bracteoles subtend it. Where the number of bracteoles exceeds the number of flowers subtended, it is possible that each excess bracteole represents the single bracteole subtending a lost flower or branch of a complex, now-condensed branching system.

The bracteoles subtending the pistillate cymules are undoubtedly homologous with the cupular scales above them. The bracteoles merely represent the lowest bracteoles of the condensed branching system, while the scales are the bracteoles of the branches whose phylogenetic condensation formed the cupule. Some evolutionary increase in scale number could have occurred after sterilization of bracteoles and while the cupule was evolving.

Fey and Endress (1983) interpreted the fagaceous cupule as a complex, cymose branching system with shortened, united axes and with persistent bracteoles that form the cupular scales. They showed that, at least in earlier ontogenetic stages, the scales are regularly arranged in a pattern suggesting that of branched cymes. The subtending bracteoles discussed in this paper are then merely the lowest bracteoles of the much-reduced cymose system (cf. Fey & Endress, 1983, *fig. 21*). In many pistillate cymules the subtending bracteoles intergrade with the cupular scales, as would be expected with this interpretation.

In every instance where the ontogeny has been observed, the cupular scales are present at anthesis (but are sometimes obscured by the bracteoles). They may persist and even enlarge with the cupule, fully investing it at maturity, as in many species of subg. *Pasania*. In extreme cases (e.g., *Lithocarpus garrettiana*, FIGURE 91) the scales elongate greatly and the cupule becomes coarsely hirsute. They may also persist without enlarging, so that the mature cupule has obvious but small and often widely spaced scales, as in many species of subgenera *Lithocarpus, Synaedrys,* and *Gymnobalanus* and in some species of subg. *Cyclobalanus*. The extreme condition is seen especially in the last subgenus, where in many species the scales are lost during ontogeny because they either fall from the cupule or become ruptured during cupular expansion. Such mature cupules essentially lack scales, consisting of massively enlarged axial tissue of the cupule. The morphological nature of this axial tissue is yet to be defined, however.

Special conditions exist in subg. *Synaedrys* and in a few species of other subgenera. For example, in *Lithocarpus cornea* of subg. *Synaedrys* (FIGURE 10), the scales enlarge with the cupule and become totally adnate to it so that at maturity the cupule is mostly covered by them. In *L. pulchra* of the same subgenus (FIGURE 13), the scales or scale tips become elevated on tubercles, which completely cover the cupule. The morphological nature of these tubercles is unknown.

Soepadmo (1970) studied the vascular anatomy of the cupule of *Lithocarpus* and found the same vascular organization as that in the *Quercus* cupule (Kaul, 1985, *fig. 36*). In pistillate cymules that mature more than one fruit, the cupules usually become connate laterally. When this occurs, the vascular systems of the individual cupules remain distinct in the fused, "interseminal" cupular walls. The more or less regular patterns of dichotomous branching of the cupular vascular bundles, ultimately serving each scale with a vascular trace, could be interpreted as evidence of the cymose history of the cupule (Kaul, 1985), but the extreme condensation in the cupule and the lack of intermediate forms make any interpretation of vascular evidence tentative.

The function of the cupule is probably protection, first of the flower and later of the fruit, and in this aspect its evolutionary history resembles that postulated for the inferior ovary. However, the ovary of *Lithocarpus* is inferior and the ovary wall at anthesis is not especially thick, although it becomes so with maturity. Additional, often formidable, protection is possibly provided by the cupule from anthesis onward, not only by the scales but also by the large amounts of tannins, crystals, and sclereids present.

In all species the cupule provides complete coverage of the immature nut, but in many the maturing nut emerges from the cupule, by which time its own pericarp is very strong.

As in *Quercus,* effective dissemination of the fruits of *Lithocarpus* requires animals (but see Boucher, 1981). Monkeys, squirrels, and similar mammals are known to be especially important in burying the nuts (Camus, 1952–1954; pers. obs.), which have hypogeal germination. Some nuts are, of course, eaten by those animals, but many are buried and not exhumed.

The real or apparent dehiscence of some cupules recalls the more obvious dehiscence of the cupules of *Castanea* and *Castanopsis.* The pattern is regular in some species of *Lithocarpus* (e.g., *L. encleisacarpa, L. garrettiana*) but irregular in others. Correspondence of dehiscence lines to sutures between valves is unknown for *Lithocarpus* but is understood for some other fagaceous genera.

Some mature cupules of *Lithocarpus* bear abortive pistillate flowers at various sites (see, for example, FIGURES 3, 8, 10). Often it is clear that these abortive flowers are merely other flowers of the cymule that have been elevated somewhat by the overwhelming growth of the cupule of the fertilized flower (FIGURES 8, 10, 35). In other instances such abortive flowers have probably actually formed upon the cupule itself from latent floral primordia of the ancestral, now-condensed, cymose branching system that produced the cupule (see FIGURE 3). Fey and Endress (1983) stated that apparently adventitious staminate flowers upon the cupule of *Fagus sylvatica* L., as reported by Cole (1923), are not unexpected if each cupular valve is interpreted as a modified branching system. That concept also seems valid for the presence of pistillate flowers on the upper regions of mature cupules.

In such a large genus as *Lithocarpus,* there has undoubtedly been substantial adaptive radiation, parallelism, and convergence leading to a plethora of patterns of reproductive structure. There is very little published information that relates reproductive structure in the genus to habitat or pollination specializations, making interpretations of structure/function relationships difficult.

The homology of staminate with pistillate cymules, as suggested by Kaul and Kaul (1981), is corroborated by the evidence presented here. Not only do those cymules have similar bracteole patterns in general, but they also occupy interchangeable sites in some spikes. In a few staminate cymules, such as those of *Lithocarpus fenestrata* and *L. pattaniensis,* there is a set of bracteoles interior to the main ones. These are probably additional residual bracteoles of a condensed branching system and may represent a rudimentary system of cupular scales in the staminate cymules, perhaps fully homologous with the cupular scales of the pistillate cymules. In some cymules the flowers are both staminate and pistillate, or perfect, or perfect and imperfect (sometimes all of these on a single spike), indicating that separation of the sexes is not complete at flower and cymule levels. In *Quercus,* by contrast, the functional sexes are strictly separated into different spikes (except in obviously aberrant specimens), but the pistillate flowers often have well-developed staminodia, especially in the tropical species (Kaul, 1985). Neither *Quercus* nor *Lithocarpus* is dioecious.

ACKNOWLEDGMENTS

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CONTRIBUTIONS TO A FLORA OF ANGUILLA AND ADJACENT ISLETS

Richard A. Howard and Elizabeth A. Kellogg[1]

The small island of Anguilla is north of St. Martin and with it comprises the westernmost of the "limestone Caribbees," separated from the British Virgin Island group of Anegada, Tortola, Jost Van Dyke, and Virgin Gorda by the Anegada passage (166 km wide and 604 m deep). A brief checklist of the vegetation of Anguilla was published by Boldingh (1909), listing 150 species as his collections, sight records, or literature references; subsequent additions are few. Père Le Gallo visited Anguilla in 1955 and 1956 and prepared a new flora of the island, which was available for our study but has never been published. Our visit in 1985 produced 125 collections with additional sight records for a total flora of 443 species. Previously three taxa had been considered endemic to Anguilla, but all are now known from other islands. *Rondeletia anguillensis* is described as new and is considered endemic to Anguilla. Comparisons are made with the Virgin Islands to the west of Anguilla.

The small island of Anguilla[2] lies about 10 km (6 mi) north of St. Martin; together the two islands form the western extension of the Leeward Island complex, known as the "limestone Caribbees" (Harris, 1965). Anguilla is separated from the British Virgin Island group of Anegada, Tortola, Jost Van Dyke, and Virgin Gorda by the Anegada passage, 166 km (100 mi) wide and over 604 m (2000 ft) deep. Shoals extend north to Sombrero. Close to Anguilla are Anguillita, Dog Island, Prickly Pear Cays, Seal Island, Scrub Island, and Little Scrub Island. Road Bay offers the only large and partially protected harbor for fishing boats and visiting yachts.

Anguilla is at latitude 18°13′12″N and longitude 65°4′22″W. It is approximately 28 km (16 mi) long and 8 km (4 mi) wide at its broadest point, with an area of 90 sq. km (35 sq. mi) (see Map 1). The highest point is Crocus Hill, with an elevation of 59 m (192 ft). The center of the island is mildly depressed to form a basin, in which the principal town of The Valley is located. The island's population is about 7000. According to Southey (1827), the island of Anguilla, then called Snake Island, was colonized by the British about 1650 and remained a part of the British Commonwealth. In 1967 Anguilla separated from the independent state of St. Kitts–Nevis and Barbuda.

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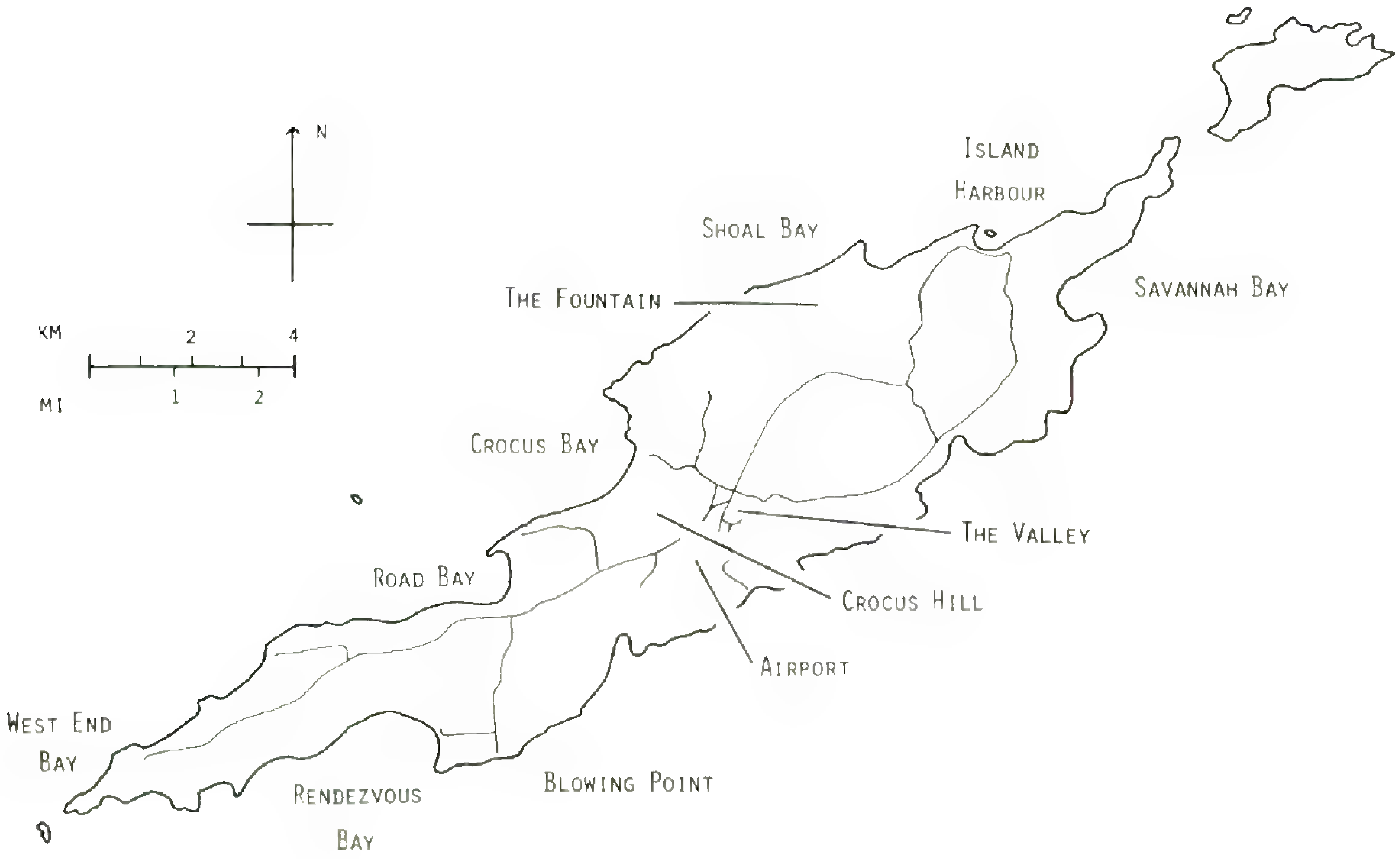
[2] This island should not be confused with the Anguilla Cays of the southern Bahama Islands. The Anguilla Cays are the southeastern exposure of the Cay Sal Bank between Florida and Cuba. Percy Wilson, for example, visited the Anguilla Cays but not Anguilla, and his collections have been cited incorrectly in *Flora Neotropica* monographs.

Journal of the Arnold Arboretum **68:** 105–131. January, 1987.



MAP 1. Island of Anguilla.

The geology of the island was most recently studied by Christman (1953). From the sea, the island appears almost flat (see FIGURE 1)—a raised platform of coralline limestone. The beds of limestone and marl are underlain with andesite tuffs equivalent to and contemporaneous with the Pointe-Blanche Formation on St. Martin. Vaughan (1926) has described it as the lowest Miocene type in the Caribbean. Scattered old volcanic boulders are found near Crocus Bay, near Old Road Bay, and on Dog Island (Le Gallo, unpubl. ms.). Weathered limestone pavement is evident in many places, devoid of soil cover and pitted by broad, shallow solution hollows or penetrated by tubular channels where most plants are rooted. The existing soil on the limestone is terra rossa, an alkaline, reddish brown clay of low fertility. Elsewhere, a blackish, highly alkaline clay called rendzina has accumulated in poorly drained depressions. The limestone forms sea cliffs on the north coast estimated to approach 30 m (100 ft). Several karstic sinkholes, the most famous being "The Fountain," are present near Shoal Bay. Uplifted coastal limestone benches are few and relatively low; they were seen only on the south coast. Coastal embayments have been cut off by sand bars (see FIGURE 2) and exist as salt ponds (see FIGURE 3) that are only occasionally activated. Inland lakes are shallow and brackish. Drinking water is obtained from roof catchments, although a public water supply from several shallow wells produces mildly brackish water. Average annual rainfall is 1026 mm, with the peak months being May and August through November. The figures for average monthly rainfall in mm for the years 1931–1981 (with data for 1982 in parentheses) are as follows:

January	62	(35)	April	64	(29)
February	39	(173)	May	102	(121)
March	37	(32)	June	65	(105)

FIGURE 1. View looking west from Shoal Bay hotel development. Note plant of *Scaevola plumieri* established on sandy beach (left).

July	79	(89)	October	130	(184)
August	102	(39)	November	130	(39)
September	130	(55)	December	83	(108)

VEGETATION

Harris (1965) has termed the vegetation of Anguilla an evergreen woodland. By Beard's (1955) classification, it would be called an evergreen bushland, more popularly known in the area as thorn scrub. Although Beard believed that the Anguillan thorn scrub is the natural vegetation of the island, Harris suggested that it represents a subclimax created by biotic processes of impoverishment and selection of xerophytic, sclerophyllous species. Harris (1965, p. 137) admitted, however, that in "Anguilla, the communities of native plants are more complex, and aliens much less abundant." He emphasized (p. 137) a "moderately large population dependent mainly on shifting cultivation, together with considerable development of plantations which resulted in the complete or partial clearance of the whole island." Our observations led to a somewhat different conclusion. It appeared to us that agriculture is at best tenuous on the shallow soils; the extensive exposed limestone pavement, with plants rooting in solution holes, indicates that the thorn-scrub vegetation has always been dominant.

On a special trip to aid West Indian agriculture, Morris (1891) recommended that the thorn-scrub areas be cleared as a work-relief project and that such fiber

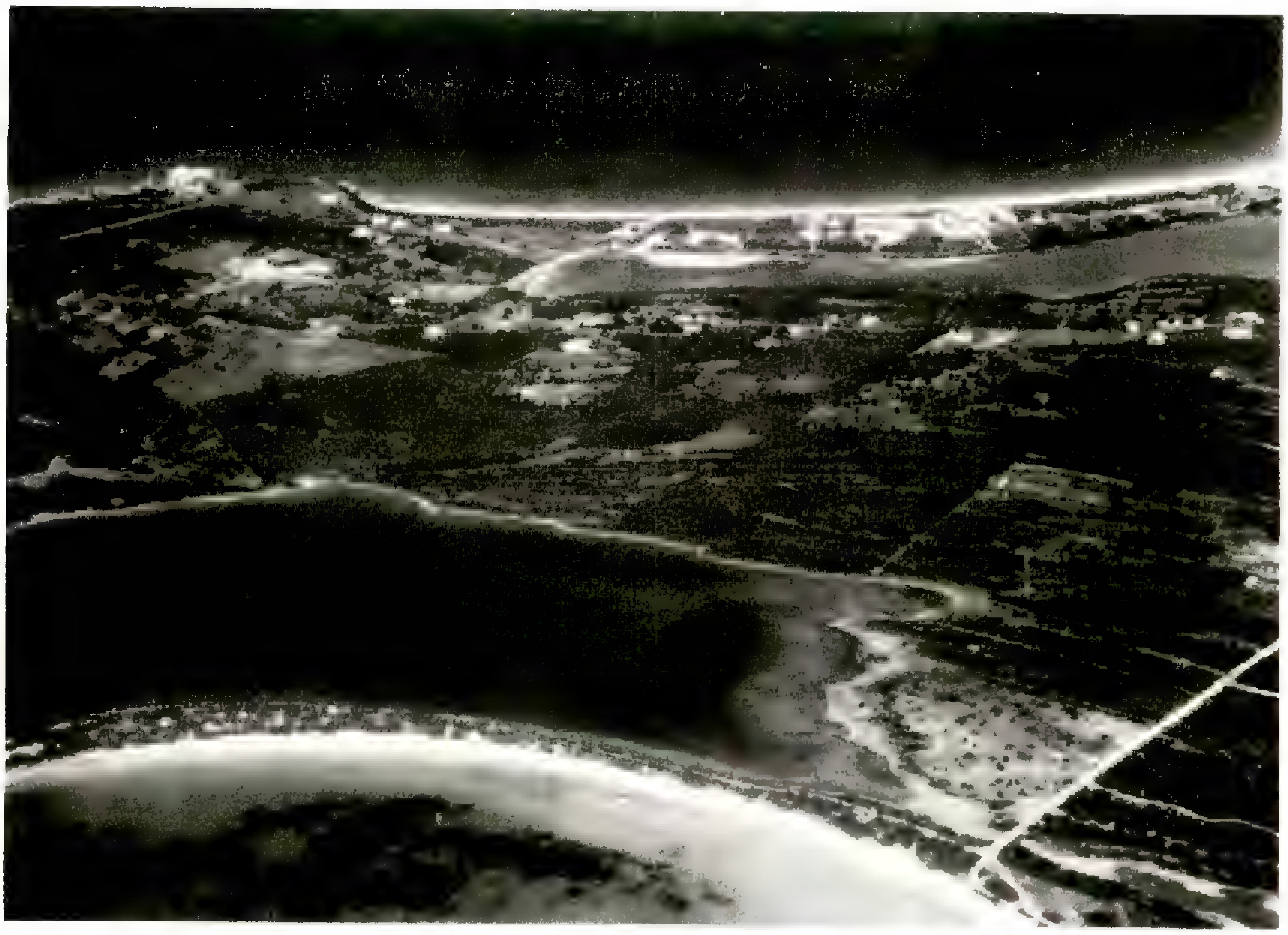


FIGURE 2. Aerial view of west end of the island near Rendezvous Bay.

sources as *Agave* and *Furcraea* be planted, but this was never developed. A government-sponsored planting of *Aloë vera* has long been abandoned. Historical records show that the cultivation of sugar cane and cotton and the planting of mahogany were unsuccessful in the low-rainfall climate. Subsistence agriculture today consists of small home gardens and an occasional larger plot of cassava, pigeon peas, sweet potatoes, okra, and pumpkins.

Boldingh (1909a), in the only existing list of plants of Anguilla, reported (p. 2) "a vegetation that consisted chiefly of prickly plants resembling in superficial appearance the *Croton* vegetation of the Dutch Antilles. I did not see any tropical wood." In 1985 a low shrub vegetation dominated most of the uncultivated areas and no active charcoal pits were observed, suggesting a paucity of appropriate charcoal wood or the complete acceptance of kerosene and electricity for cooking. Cattle were certainly fewer than in the past, and goats and sheep were mostly tethered in appropriate feeding locations and had little effect on most of the thorn scrub.

The neem, *Azadirachta indica*, has been introduced relatively recently and is perhaps the most common shade tree. Large specimens of *Mangifera indica, Meliococcus bijugatus, Swietenia mahagoni, Tamarindus indica,* and *Zizyphus mauritiana* exist around habitations. Occasional trees of *Ficus citrifolia, Guapira fragrans, Pisonia subcordata,* and *Tabebuia pallida* are the largest native species.

In coastal areas and around salt ponds, the dominant woody plants are *Argusia gnaphalodes, Avicennia germinans, Coccoloba uvifera, Conocarpus erecta, Erithalis fruticosa, Hippomane mancinella, Laguncularia racemosa,*

FIGURE 3. Road Bay harbor looking north, with salt pond development to right. *Canella, Capparis,* and *Exostema* species growing on distant point.

Scaevola plumieri, and *Suriana maritima.* Very few individuals of *Casuarina equisetifolia, Chrysobalanus icaco,* or *Thespesia populnea* were encountered. Although Harris (1965) indicated "mangrove swamps" at Little Harbour and Sea Feathers Bay, we found *Rhizophora mangle* only in Road Bay pond, where there were a few isolated individuals.

Locally dominant shrubs included *Antirhea acutata, Bourreria succulenta, Byrsonima lucida, Canella winterana, Castela erecta, Coccoloba krugii, Comocladia dodonaea, Croton flavens, Eugenia axillaris, E. foetida, Exostema caribaeum, Gyminda latifolia, Jacquinia arborea, J. berterii, Malpighia emarginata, Phyllanthus epiphyllanthus, Pithecellobium unguis-cati, Plumeria alba, Randia aculeata,* and *Reynosia uncinata.* These may be in mixed populations, and occasionally a single large specimen may dominate an area. *Coccoloba krugii* and *C. uvifera* are known to hybridize on other islands (Howard, 1957). On Puerto Rico, St. Thomas, St. Croix, and Virgin Gorda the hybrids resembled *C. uvifera.* Three distinct plants on Anguilla were called to our attention by Andrew Parker and shown to us by Oliver Hodge. They were isolated individuals with leaves more like those of a very large *C. krugii.* One plant had been coppiced; its leaves were intermediate in shape but with the texture of *C. krugii* and the abundant pubescence of *C. uvifera.* One plant had fruits comparable to those of *C. krugii,* while the other two had sterile fruits resembling those of *C. uvifera.*

The most abundant spiny plants on Anguilla were *Acacia macracantha, Castela erecta, Clerodendrum aculeatum, Comocladia dodonaea, Pithecello-*

Comparisons of island size, altitude, and recorded flora.

ISLAND	AREA (sq. mi)	MAXIMUM ALT. (ft)	NUMBER OF SPECIES Indigenous	Introduced/ cultivated	Endemic/ restricted*
Anegada	14	15	198	33	0
Anguilla	35	192	321	122	1 [3]
Barbuda	62	47	229	32	[1]
Jost Van Dyke	4	1054	73†	12	0
St. Bartholomew	10	800–1000	336	53	[4]
St. Martin	38	1119, 1391	392	41	1
Tortola	24	1263, 1780	484‡	152	2
Virgin Gorda	8	1539	372	63	1

*Bracketed numbers represent species now in synonymy.
†Trees only.
‡Dicotyledons only.

bium unguis-cati, Randia aculeata, Reynosia uncinata, Zanthoxylum flavum, Z. punctatum, and *Z. spinifex.* The scramblers *Caesalpinia crista* and *C. divergens,* with extremely spiny fruits, may be added to this list. Other scramblers forming local entanglements include *Boerhavia scandens, Cissus verticillatus, Heteropteris purpureus, Merremia dissecta, Passiflora foetida, P. suberosa, Plumbago scandens, Rhynchosia minima, R. reticulata, Stigmaphyllon diversifolium, S. emarginatum, S. lingulatum, Tournefortia volubilis,* and *Urechites lutea.* Parasitic plants were *Cassytha filiformis, Cuscuta americana, Dendropemon caribaeus,* and *Phoradendron trinervium.*

Existing floristic studies (Box, 1939; D'Arcy, 1967, 1975; Le Gallo, 1957; Little, 1969; Little *et al.*, 1976; Monachino, 1941) of the small northern islands are not comparable, and significant comparisons are difficult to make (see TABLE).

The following taxa were originally described as endemic.

ANEGADA: *Cynanchum anegadensis* (Britton) Alain. Type: *Britton & Fishlock 962* (NY). Current status: endemic. *Fishlockia anegadensis* (Britton) Britton & Rose. Type: *Britton & Fishlock 990* (NY). Current status: the basionym, *Acacia anegadensis* Britton, is preferred. Endemic.

ANGUILLA: *Bouteloua vaneedeni* Pilger. Type: *Boldingh 3521B* (B?). Current status: now known from St. Bartholomew and from Camaguey province, Cuba. *Myrtus anguillensis* Urban. Type: *Boldingh 3509B* (B?) (= *Psidium longipes* (Berg) McVaugh var. *orbicularis* (Berg) McVaugh). Current status: now known from the eastern Bahamas, the Turks and Caicos islands, Jamaica, St. Bartholomew, Barbuda, and Antigua. *Rondeletia anguillensis* R. Howard & E. Kellogg. Type: *R. Howard & E. Kellogg 20105* (A). Current status: endemic. *Thrinax morrisii* Wendl. Type: *H. A. A. Nicholls s.n.,* 1890 (K). Current status: known from Florida, Cuba, Haiti, Puerto Rico, the Bahamas, and the Turks and Caicos islands.

BARBUDA: *Coccothrinax boxii* Bailey. Type: *Box 669* (BH) (= *Coccothrinax barbadensis* (Lodd.) Bec). Current status: known from the Lesser Antilles, Trinidad and Tobago.

St. Bartholomew: *Peperomia barthelemyana* Trel. Type: *Questel 275* (not located) (= *Peperomia myrtifolia* (Vahl) Dietr.). Current status: known from St. Croix and the Lesser Antilles. *Peperomia barthelemyana* Trel. var. *reducta* Trel. Type: *Questel 361* (not located) (= *Peperomia myrtifolia* (Vahl) Dietr.). Current status: known from St. Croix and the Lesser Antilles. *Peperomia questeliana* Trel. Lectotype: *Questel 2518* (NY) (= *Peperomia humilis* Dietr.). Current status: known from Florida, Central America, and the Greater and Lesser Antilles. *Peperomia myrtifolia* (Vahl) Dietr. var. *major* Trel. Type: *Questel 803* (NY) (= *Peperomia myrtifolia* (Vahl) Dietr.). Current status: known from St. Croix and the Lesser Antilles.

St. Martin: *Calyptranthes boldinghii* Urban. Type: published as *Boldingh 2370B* (B?) but *3270B* on label. Current status: endemic and known only from the type collection.

Tortola: *Calyptranthes kiaerskovii* Krug & Urban. Type: *Eggers 3217* (B?). Current status: original material sterile and identification uncertain; now also reported from Virgin Gorda. *Sida eggersii* E. G. Baker. Type: *Eggers 3183* (BM?, K?). Current status: known only from a single tree on Jost Van Dyke. D'Arcy (1967) reported the species from Tortola and Culebra but did not encounter it.

Virgin Gorda: *Croton fishlockii* Britton. Type: *Fishlock 311* (NY). Current status: endemic.

It can be estimated that the floras of the "limestone Caribbees" and adjacent islands each consist of about 500 species. With the few exceptions of species whose distribution is limited to adjacent islands, the species that dominate the vegetation of any island can also be found on Puerto Rico and the drier areas of Hispaniola, occasionally Cuba, and to a lesser extent Guadeloupe. The islands with peaks of 1000 feet or more are likely to have a rain shadow that affects the island and niches where zonation of the vegetation can be established. The lower islands of Barbuda, Anguilla, and Anegada are more apt to receive fortuitous rain showers. Barbuda and Anegada have been more extensively cultivated or grazed in the past, and a larger percentage of the existing vegetation is adventive and secondary. Anguilla stands out in the amount of limestone pavement area having what we concluded to be a natural and less disturbed vegetational type.

BOTANISTS WHO HAVE VISITED ANGUILLA

L.-C. Richard, 1786. Urban (1902) reported that Richard had collected on Anguilla during his voyage north from Cayenne in the spring of 1867. We have seen no collections or citations of such specimens. Box (1939) located citations for four type specimens from Antigua and for one specimen from Barbuda.

D. Morris, 1890. Morris visited the Lesser Antilles as an agricultural consultant in 1890 and gathered 30 to 40 living plants of a dwarf palm, later named *Thrinax morrisii* by Wendland, during a visit to Anguilla on December 14 and 15.

H. A. A. NICHOLLS, 1891. Nicholls, a medical doctor and specialist on yaws, was on Barbuda in August, 1891, and wrote on November 11, 1891 (*in* Wendland, 1892), "I went again to Anguilla." His collections, sent to Kew, are unnumbered. They have not been encountered except for fruiting specimens of *Thrinax morrisii,* one of which is now the lectotype, that he gathered to permit the description to be completed and published.

W. R. ELLIOTT, 1891. Elliott had been a gardener on Jamaica and later Grenada. The reason for his trip to Anguilla (1891) is not known, but his small collection of 34 numbers was identified by Box (1940).

I. BOLDINGH, 1906. Boldingh was preparing a report of the vegetation of the Dutch Antilles (1909b, 1913) and visited Anguilla on September 6 and 7, 1906. His publication (1909a) remains the only paper on the flora of Anguilla and is based on his collections numbered between *3449* and *3599.*

G. G. GOODWIN, 1926. Goodwin, accompanied by his wife, visited Anguilla between April 1 and 9, 1926, as part of the Ottley Puerto Rican expedition of the American Museum of Natural History, in search of recent and fossil mammals. A single specimen numbered *12* was found in the herbarium of the New York Botanical Garden. Botanical collections are not mentioned in the catalogs and journals of the expedition.

P. WAGENAAR HUMMELINCK, 1949, 1973. Hummelinck visited Anguilla and Dog Island June 16–20, 1949, and June 30–July 3, 1973. He collected two species of *Agave,* as well as algal and faunal specimens. The algal collections are listed in Vorman (1968). Hummelinck (1981) also published observations on "land and fresh-water localities," with photographs of Anguilla.

I. VELEZ, 1950. Prior to the publication of his *Herbaceous Angiosperms of the Lesser Antilles* in 1957, Velez spent fiscal year 1949–1950 collecting between the Virgin Islands and Grenada. He reported (p. 2) Anguilla to be among the islands that "were thoroughly studied." A single specimen, *Velez 3749* (US) (*Thrinax morrisii*), collected in January, 1950, was reported in the literature encountered. Velez (1957, p. 2) reported that "a complete set was deposited in the Herbarium of the Inter American University of Puerto Rico. Duplicates of most of them were sent to the Herbarium of the Imperial College of Tropical Agriculture, Trinidad." Velez's citations of species distribution were taken from the literature, were sight records, or were supported by specimens. They have been troublesome to untangle. On a visit to the Inter American University, one of us (R. A. H.) discovered that his herbarium, through neglect, had been completely destroyed by insects. The set sent to Trinidad was later given to Kew, where we have seen specimens from other islands. Lists of determinations, preserved at Kew, are not complete but cite specimens numbered *3006* to *3158* from the Virgin Islands, *3159* to *3287* from Grenada and the Grenadines, *3290* to *3337* from St. Lucia, and *3338* to *3386* from St. Vincent. A few specimens have been found in GH, NY, and US, but nothing from Anguilla.

C. LE GALLO, 1955, 1956. Le Gallo collected on Anguilla September 1–5, 1955, and on the adjacent islets of Scrub and Dog March 3, 1956. His unpublished and undated manuscript must have been written sometime in 1959. His plant specimens as cited are numbered *2053* to *2071* and *2470* to *2521*. Le Gallo is not listed in Barnhart (1965), so it is of interest to record here the biographical information we obtained first from Ms. Céline Arseneault, botanist-librarian of the Montreal Botanic Garden, and subsequently from the tribute to Le Gallo by Père Maurice Barbotin (1976), of Guadeloupe.[3]

G. R. Proctor, 1958–1959. Proctor collected extensively in the Leeward Islands; between December 30, 1958, and January 18, 1959, he gathered 250 numbers, *18518* to *18704* and *18731* to *18816*, on Anguilla. Complete sets of his specimens are at A and IJ.

D. R. Harris, 1960. Harris spent part of August, 1960, on Anguilla prior to publication of his "Plants, Animals, and Man in the Outer Leeward Islands, West Indies" in 1965. His collections of about 50 species were given to the British Museum (Natural History). We have included all the species in our listing, but since we have not seen specimens, they are not cited.

R. W. Read, 1974. Read, of the Smithsonian Institution, visited Anguilla on June 7, 1974, to find and collect *Thrinax morrisii*. He made no other collections there (pers. comm.).

R. A. Howard and E. A. Kellogg, 1985. We collected on Anguilla February 5–9, 1985. Our specimens numbered *20043* to *20168* are deposited in the herbarium of the Arnold Arboretum (A).

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We are grateful for the help of Oliver Hodge, of the Public Health Department on Anguilla, who accompanied us in the field and supplied local names and uses of the plants we encountered. Andrew Parker, of Powys, Great Britain, was recently stationed on Anguilla and called our attention to the hybrid pop-

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[3] Père Casimir Le Gallo was born June 25, 1906, at Erdeven, diocèse of Vannes, France. He took his holy orders in the Congregation of St.-Esprit October 1, 1933. He was a professor at Collège St.-Alexandre, Touraine, Quebec, from August 30, 1934, to January, 1935. He served as Vicar Apostolic at St. Pierre and Miquelon from January 23, 1935, to April 29, 1946. He returned to Quebec in May, 1946, to serve as Vicar Apostolic at Lac-au-Saumon until he returned to France in August, 1950. Seeking a warmer clime, he went to the West Indies in 1951 as curate of St. Bartholomew, where he also taught natural science at the seminary-college of Blanchet. In 1958 he was made curate of Vieux Fort, although he continued weekly teaching at Blanchet. Eight years later the bishop entrusted him with several successive assignments in Sacré-Coeur, in Fatima, at the Moule, and finally in Baie-Mahault. He returned to France in 1969, but not ready to retire, he requested and was granted an assignment in St. Pierre and Miquelon. He was not to occupy this position, however, for an injury to his foot developed into gangrene and his leg was amputated. He spent long and painful months in the hospital before his residence in the religious community at Wolxheim. He yearned for his native Brittany and so was taken to Langonnet, where he died peacefully June 22, 1976.

His primary botanical interest was in mosses, but he collected algae and lichens as well as vascular plants. Twenty-one papers by Le Gallo appeared in *Le Naturaliste Canadien* between 1945 and 1965, with others in specialty journals. Many of his later papers were biographical reviews of the lives of priests who were botanists. Proctor collected with Le Gallo in Guadeloupe in 1959 and as a result of that trip named *Diplazium legalloi* in his honor.

ulations of *Coccoloba*; subsequently in correspondence he supplied additional information we have incorporated. His interest in the local vegetation may lead to an illustrated ethnobotanical publication. George R. Proctor, who has collaborated with us in the production of the *Flora of the Lesser Antilles,* supplied lists of his collections from Anguilla. Père Le Gallo gave Proctor his unpublished manuscript notes on Anguilla, which we have been privileged to use. Céline Arseneault, of the Montreal Botanical Garden, and Jacques Portecop, Université des Antilles, Guadeloupe, located biographical information on Le Gallo for us. Finally, our travel and work on this flora was made possible through the support of National Science Foundation grant BSR-8307701 and a grant from the Atkins Fund of Harvard University, for which we are appreciative.

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APPENDIX. **The known flora of Anguilla.**

The collections cited below are referred to by the following abbreviations: B = Boldingh, E = Elliott, GG = Goodwin, H = Hummelinck, HK = Howard and Kellogg, LG = Le Gallo, P = Proctor. According to Le Gallo's manuscript, the Boldingh collections are at Utrecht and were at Berlin. They were also sought in NY, but very few of the cited numbers could be found. Le Gallo's (unpubl. ms.) collections were studied by Monachino (NY) and by Miss G. J. A. Amshoff. Again, a search at NY located very few of the numbered collections. Those seen, as well as those of Proctor and our own, are indicated by the herbarium acronym, most frequently A. Common names are included only when they were provided by local residents.

GYMNOSPERMAE

ARAUCARIACEAE

Araucaria heterophylla (Salisb.) Franco, Christmas plant. Cultivated. HK sight.

ANGIOSPERMAE

MONOCOTYLEDONEAE

AGAVACEAE

Agave beauleriana Jacobi. Cultivated. HK sight.
Agave karatto Miller. Cultivated. HK sight.
Agave scheuermaniana Trel. *H 160, 161, 162.*
Agave sisalina Perrine, fiber pole, pita, sisal plant. Cultivated. HK sight; *H 111, 112.*
Sansevieria hyacinthoides (L.) Druce. Naturalized. HK sight; *P 18760* (A).
Sansevieria trifasciata Prain. Naturalized. HK sight.
Yucca guatemalensis Baker, Spanish needle. Cultivated. HK sight.

AMARYLLIDACEAE

Crinum sp. Cultivated. HK sight.
Hymenocallis caribaea (L.) Herbert, spider lily. *P 18630* (A).
Zephyranthes candida (Lindley) Herbert, crocus, snowdrop. Parker sight.

ARACEAE

Alocasia plumbea C. Koch. Cultivated. HK sight.
Colocasia esculenta (L.) Schott. Cultivated. HK sight.
Dieffenbachia seguine (Jacq.) Schott. Cultivated. HK sight.
Monstera acuminata C. Koch. Cultivated. HK sight.
Rhaphidophora aurea (Linden & André) Birdsey. Cultivated. HK sight.
Xanthosoma sagittatifolium (L.) Schott. Cultivated. HK sight.

ASPARAGACEAE

Asparagus setaceus (Kunth) Jessop. Cultivated. HK sight.
Asparagus sprengeri Regel. Cultivated. HK sight.

BROMELIACEAE

Tillandsia recurvata L., wild pine. *B s.n.*; *P 18566* (A).
Tillandsia usneoides L., jumbie beds. Parker sight.
Tillandsia utriculata L., wild pine. *P 18634* (A).

COMMELINACEAE

Aploleia monandra (Sw.) Moore. Cultivated. HK sight.
Callisia fragrans (Lindley) Woodson. Cultivated. *HK 20108* (A).
Commelina elegans Kunth. *P 18752* (A).
Rhoeo spathacea (Sw.) Stearn. HK sight.
Tradescantia pallida (Rose) Hunt. Cultivated. HK sight.

CYMODOCEACEAE

Syringodium filiforme Kütz. *P 18626* (A).

CYPERACEAE

Bulbostylis pauciflora (Liebm.) Clarke. *LG 2485*; *P 18804* (A).
Cyperus calcicola Britton. *LG 2501.*
Cyperus laevigatus L. *P 18770* (A).
Cyperus oxylepis Nees ex Steudel. *P 18749* (A).
Cyperus rotundatus L. *B s.n.*; *P 18772* (A).
Eleocharis geniculata (L.) Roemer & Schultes. *P 18771* (A).
Eleocharis mutata (L.) Roemer & Schultes. *P 18769* (A).
Fimbristylis cymosa R. Br. subsp. *spathacea* (Roth) T. Koyama. *B 3527*, as *Fimbristylis spathacea* Roth; *HK 20151* (A); *P 19659* (A).
Fimbristylis ferruginea (L.) Vahl, pond grass. *B 3495.*
Fimbristylis ovata (Burman f.) Kern. *B 3514, 3573,* both as *Fimbristylis monostachya* Hassk.; *P 18666* (A).
Mariscus brunneus (Sw.) Clarke. *LG 2484*, as *Cyperus planifolius* Rich. var. *brunneus* (Sw.) Kük.; *P 18690* (A), *18777* (A).
Mariscus capillaris (Sw.) Vahl. *B s.n.*
Mariscus fulgineus (Chapman) Clarke. *LG 2512* (NY), as *Cyperus fulgineus* Chapman; *P 18608* (A), *18635* (A).
Mariscus squarrosus (L.) Clarke. *P 18810* (A).
Scleria lithosperma (L.) Sw. *LG 2503*; *P 18803* (A).

GRAMINEAE

Aristida adscensionis L. *LG 2488, 2489, 2509*; *P 18699* (A).
Bothriochloa ischaemum (L.) Keng. *P 18784* (A).

Bothriochloa pertusa (L.) A. Camus. *P 18784* (A), *18791* (A), both as *Andropogon pertusus* (L.) Willd.
Bouteloua americana (L.) Scribner. *B 3533*; *P 18757* (A).
Bouteloua vaneedeni Pilger. *B 3512* (type collection); *LG 2474.*
Brachiaria adspersa (Trin.) Parodi. *P 18643,* as *Panicum adspersum* Trin.
Brachiaria fasciculata (Sw.) S. T. Blake. Reported by Gould (1979).
Brachiaria reptans (L.) Gardner & Hubb. *B 3543,* as *Panicum reptans* L.
Cenchrus echinatus L., burr grass. *P 18762* (A).
Cenchrus incertus M. Curtis. *HK 20155* (A); *P 18693* (A), as *Cenchrus gracillimus.*
Cenchrus tribuloides L. *B s.n.*
Chloris gayana Kunth, Rhodes grass. Reported by Harris as cultivated.
Chloris inflata Link. *P 18621* (A).
Cymbopogon citratus (DC. ex Nees) Stapf, lemon grass. Cultivated and naturalized. *B 3454,* as *Andropogon schoenanthus.*
Dactyloctenium aegyptium (L.) Beauv. *P 18761* (A).
Digitaria bicornis (Lam.) Roemer & Schultes. *P 18970* (A).
Digitaria decumbens Stent, pangola grass. Reported by Harris as cultivated.
Digitaria insularis (L.) Mez. LG sight (Dog Is.), as *Trichane insularis* (L.) Nees.
Digitaria sanguinalis (L.) Scop. *B 3456*; *P 18790* (A).
Eleusine indica (L.) Gaertner. *B s.n.*; *P 18619* (A).
Eragrostis ciliaris (L.) Link. *HK 20119* (A); *LG 2518*; *P 18746* (A).
Eragrostis tenella (L.) Beauv. ex Roemer & Schultes. HK sight.
Heteropogon contortus (L.) Beauv. *LG 2521.*
Oplismenus hirtellus (L.) Beauv. subsp. *setarius* (Lam.) Mez. *B s.n.,* as *Oplismenus setarius* (Lam.) Roemer & Schultes.
Panicum diffusum Sw. *B 3457, 3459, 3538*; *P 18684* (A).
Panicum geminatum Forsskål. *B 3494.*
Panicum maximum Jacq. *P 18620* (A).
Panicum molle Sw. *B 3453.*
Panicum paniculatum L. *B 3539, 3550.*
Paspalidium geminatum (Forsskål) Stapf. *B 3494,* as *Panicum geminatum* Forsskål.
Paspalum fimbriatum Kunth. *B 3455*; *P 18618* (A).
Paspalum laxum Lam. *B 3550*; *LG 2516*; *P 18652* (A), *18767* (A).
Paspalum paniculatum L. *B s.n.,* as *Paspalum hemisphericum* Poiret.
Rhynchelytrum repens (Willd.) C. E. Hubb., red-headed grass. LG sight, as *Tricholaena rosea* Nees; *P 18789* (A).
Saccharum officinarum L. Cultivated. HK sight.
Sorghum halepense (L.) Pers. Cultivated. HK sight.
Sporobolus indicus (L.) R. Br. *LG 2519, pro parte.*
Sporobolus jacquemontii Kunth. *LG 2519, pro parte.*
Sporobolus pyramidatus (Lam.) A. Hitchc. *HK 20126* (A); *LG 2519, pro parte.*
Sporobolus virginicus (L.) Kunth. *B 3537, 3548, 3562.*
Tragus berteronianus Schultes. *B 3534*; *LG 2520.*
Vetiveria zizanioides (L.) Nash. *B 3549*; HK sight.
Zea mays L., corn. Cultivated. HK sight.

HYDROCHARITACEAE

Thalassia testudinum Banks & Sol. ex König. *P 18627* (A).

LILIACEAE

Aloë vera (L.) Burman, aloe, sempervive. Cultivated and naturalized. HK sight.

MUSACEAE

Musa sapientum L. Cultivated. HK sight.

ORCHIDACEAE

Epidendrum kraenzlinii Bello. *HK 20149* (A); LG sight, as *Epidendrum bifidum* Aublet.
Tetramicra canaliculata (Aublet) Urban. LG sight.

PALMAE

Coccothrinax barbadensis (Lodd. ex Martius) Becc. Cultivated. HK sight.
Cocos nucifera L. Cultivated. HK sight.
Phoenix dactylifera L. Cultivated. HK sight.
Thrinax morrisii Wendl., broom palm, thatch palm. *HK 20150* (A); *H. A. A. Nicholls s.n.* (lectotype, K); *P 18667* (A).

PANDANACEAE

Pandanus utilis Bory. Cultivated. HK sight.

RUPPIACEAE

Ruppia maritima L. *HK 20130* (A); LG sight (Scrub Is.); *P 18773* (A).

DICOTYLEDONEAE

ACANTHACEAE

Asystasia gangetica (L.) T. Anderson. Cultivated. HK sight.
Blechum brownei L. *P 18531* (A).
Oplonia spinosa (Jacq.) Raf. LG sight.
Pseuderanthemum carruthersii (Seemann) Guillaumin var. *reticulatum* (Bull) Fosb. Cultivated. HK sight.
Ruellia tuberosa L., snagdragon. *P 18598* (A).
Thunbergia fragrans Roxb. *P 18758* (A).

AIZOACEAE

Sesuvium microphyllum Willd. *P 18656* (A).
Sesuvium portulacastrum L., pondweed. *B 3526a.*

AMARANTHACEAE

Achyranthes aspera L. *B s.n.*, as *Achyranthes obtusifolia* Lam.; *P 18794* (A).
Alternanthera brasiliana (L.) Kuntze. Cultivated and naturalized. HK sight.
Alternanthera caracasana Kunth, yard-pussley. *B 3555* (NY), as *Alternanthera repens* Kuntze; *P 18754* (A).
Amaranthus crassipes Schldl. *P 18682* (A).
Celosia nitida Vahl. *P 18732* (A).
Lithophila muscoides Sw. *HK 20125* (A); LG sight (Dog Is.); *P 18687* (A).

ANACARDIACEAE

Anacardium occidentale L., cashew. HK sight.
Comocladia dodonaea (L.) Urban, hollow-wood, wild mango. *B 3556*, as *Comocladia ilicifolia* Sw.; LG sight (Dog Is., Scrub Is.); *P 18648* (A).
Mangifera indica L., mango. Cultivated. HK sight.
Spondias mombin L., golden apple, plum. Cultivated. Parker sight.
Spondias purpurea L., fig, hog plum. Cultivated. Parker sight.

ANNONACEAE

Annona muricata L., soursop. Cultivated. HK sight.
Annona squamosa L., sugar apple. Cultivated. HK sight.

APOCYNACEAE

Catharanthus roseus (L.) G. Don, old maid. HK sight.
Nerium oleander L., oleander. Cultivated. HK sight.
Plumeria alba L., pigeonwood, snakewood. LG sight (Dog Is., Scrub Is.); *P 18625* (A).
Plumeria rubra L., frangipani. Cultivated. HK sight.
Rauvolfia viridis Roemer & Schultes, Antigua balsam. *P 18523* (A).
Tabernaemontana divaricata (L.) R. Br. Cultivated. HK sight.
Urechites lutea (L.) Britton, lice bush. *B s.n.*, as *Urechites suberecta* Muell. Arg.; *HK 20071* (A); *LG 2056* (Scrub Is.), sight (Dog Is.); *P 18611* (A).

ARALIACEAE

Polyscias fruticosa (L.) Harms. Cultivated. HK sight.
Polyscias guilfoylei (Cogn. & Marchal) L. H. Bailey. Cultivated. HK sight.

ASCLEPIADACEAE

Asclepias curassavica L. *E 47.*
Calotropis procera (Aiton) R. Br., French cotton, milky-milky bush. *B s.n.*; *P 18623* (A).
Cynanchum parviflorum Sw. *P 18550* (A).

BATACEAE

Batis maritima L., pondweed. *B 3545a*; LG sight (Scrub Is.); *P 18744* (A).

BIGNONIACEAE

Crescentia cujete L. Cultivated. HK sight.
Podranea ricasoliana (Tanf.) Sprague. Cultivated. HK sight.
Spathodea nilotica Seemann. Cultivated. HK sight.
Tabebuia heterophylla (DC.) Britton, bark, cedar, white cedar. *B 3482, 3512, 3541,* all as *Tecoma leucoxylon* Martius; *GG 12* (NY); *HK 20104* (A); *P 18555* (A).
Tabebuia pallida (Lindley) Miers. Cultivated. Parker sight.
Tecoma stans (L.) Kunth, fever bush, torchwood. *E 42*; *P 18587* (A).

BOMBACACEAE

Ceiba pentandra (L.) Gaertner. Cultivated or naturalized. *P 18792* (A).

BORAGINACEAE

Argusia gnaphalodes (L.) Heine, wild lavender. *B s.n.*, as *Tournefortia gnaphalodes* R. Br.; *E 52*; LG sight (Scrub Is.); *P 18615* (A).
Bourreria succulenta Jacq., chink bush. *B 3518* (NY); LG sight (Dog Is.); *HK 20067* (A); *P 18579* (A).
Cordia collococca L., clamen cherry. *P 18753* (A).
Cordia sebestena L. Cultivated. HK sight.
Heliotropium angiospermum Murray, eyebright. *E 45*; *B s.n.*; *HK 20079* (A); *P 18640* (A), as *Heliotropium parviflorum* L.
Heliotropium curassavicum L. LG sight (Dog Is.); *P 18657* (A).
Heliotropium indicum L., eyebright. Parker sight.

Heliotropium microphyllum Sw. *B 3517* (NY); *HK 20137* (A); *LG 2061, 2062* (both Scrub Is.); *P 18688* (A), *18808* (A).
Rochefortia acanthophora (DC.) Griseb. LG sight (Scrub Is.).
Tournefortia volubilis L. *B 3521, 3540*; *P 18780* (A).

BURSERACEAE

Bursera simaruba Sarg., turpentine tree. *B s.n.*; *P 18532* (A).

CACTACEAE

Cephalocereus nobilis (Haw.) Britton & Rose, doodle doo. *P 18743* (A).
Epiphyllum oxypetalum (DC.) Haw. Cultivated. HK sight.
Hylocereus undatus (Haw.) Britton & Rose. Cultivated. HK sight.
Mammillaria nivosa Link. LG sight (Scrub Is.), as *Neomammillaria nivosa* (L.) Britton & Rose.
Melocactus intortus (Miller) Urban, pope's head. HK sight; LG sight (Scrub Is.), as *Cereus intortus* Miller.
Opuntia cochenillifera (L.) Miller. Cultivated. HK sight.
Opuntia dillenii (Ker Gawler) Haw. LG sight (Scrub Is.); *P 18783* (A).
Opuntia rubescens Salm-Dyck. LG sight (Scrub Is.).
Opuntia triacantha (Willd.) Sweet. LG sight (Scrub Is.).

CANELLACEAE

Canella winterana (L.) Gaertner, pepper cinnamint, pepper cinnamom. *B 3479,* as *Canella alba* Murray; LG sight (Scrub Is.); *P 18558* (A).

CAPPARACEAE

Capparis cynophallophora L., black widdy, parrotbush, snake bush. *B 3522*; *HK 20141* (A); LG sight (Dog Is.); *P 18733* (A).
Capparis flexuosa L. LG sight (Dog Is.); *P 18586* (A).
Capparis frondosa Jacq., whitescrub. *B s.n.* (NY), as *Capparis baducca* L.
Capparis hastata Jacq. *HK 20142* (A).
Cleome gynandra L. *B s.n.*; *E 59*; *HK 20110* (A).

CARICACEAE

Carica papaya L., pawpaw. Cultivated. HK sight.

CASUARINACEAE

Casuarina equisetifolia J. R. & G. Forster, lumber tree. Cultivated and naturalized. HK sight.

CELASTRACEAE

Crossopetalum rhacoma Crantz, maidenberry. *B 3489, 3500,* both as *Rhacoma crossopetalum* L.; *E 56*; *HK 20045* (A), *20065* (A); LG sight (Scrub Is.); *P 18559* (A).
Elaeodendron xylocarpum (Vent.) A. DC., cuttard. LG sight (Dog Is.); *P 18534* (A), *18695* (A).
Gyminda latifolia (Sw.) Urban. *B 3479*; *HK 20043* (A), *20156* (A), *20168* (A); *P 18664* (A), *18806* (A).
Maytenus elliptica (Lam.) Krug & Urban. LG sight.
Schaefferia frutescens Jacq. *P 18633* (A).

CHENOPODIACEAE

Atriplex pentandra (Jacq.) Standley. *LG 2717* (Dog Is.).
Chenopodium murale L. *HK 20131* (A).
Salicornia bigelovii Torrey. *HK 20118* (A).
Salicornia herbacea L. *B 3505a, 3571.*

CHRYSOBALANACEAE

Chrysobalanus icaco L., coco plum. *P 18778* (A).

COMBRETACEAE

Conocarpus erecta L., buttonwood, pond bush. *B 3545*; LG sight (Dog Is.); *P 18568* (A).
Laguncularia racemosa (L.) Gaertner. *B 3547*; *P 18745* (A).
Terminalia catappa L., almond. HK sight.

COMPOSITAE

Ambrosia hispida Pursh. Cultivated. HK sight.
Bidens cyanapiifolia Kunth. *P 18679* (A).
Borrichia arborescens (L.) DC. *E 50, 55*; LG sight (Dog Is., Scrub Is.); *P 18628* (A).
Cosmos sulphureus Cav. Cultivated. HK sight.
Dyssodia tenuifolia Cass. Naturalized. *P 18578* (A).
Emilia fosbergii Nicolson. *P 18742* (A).
Eupatorium odoratum L. *P 18588* (A).
Flaveria bidentata (L.) Kuntze. HK sight.
Lactuca intybacea Jacq. *HK 20114* (A); *P 18787* (A).
Lagascea mollis Cav., catnip. *B s.n.*; *P 18525* (A).
Parthenium hysterophorus L., mule weed, whitehead, whitetop. *B s.n.*; *E 30*; *P 18765* (A).
Pectis humifusa Sw. *B 3570*; *P 18660* (A).
Pectis linifolia L. *P 18779* (A).
Pluchea symphytifolia (Miller) Gillis. B 3563, as *Pluchea odorata* (L.) Cass.; HK sight.
Pseudogynoxis confusus (Greenman) Cabrera. Cultivated. HK sight.
Solidago microglossa DC. Cultivated. *P 18793* (A).
Sonchus oleraceus L., sowthistle. *HK 20140* (A); *P 18629* (A), *18788* (A).
Synedrella nodiflora (L.) Gaertner. *P 18674* (A).
Tridax procumbens L. HK sight.
Vernonia albicaulis Pers. *HK 20164* (A); *P 18543* (A).
Vernonia cinerea (L.) Less. *HK 20161* (A); *P 18641* (A).
Wedelia calycina Rich., marigold. *B s.n.*, as *Wedelia buphthalmoides* Griseb.; *HK 20124* (A); *P 18607* (A).
Wedelia trilobata (L.) Hitchc. Cultivated. HK sight.
Xanthium strumarium L. HK sight.
Zinnia multiflora L. Cultivated. HK sight.

CONVOLVULACEAE

Cuscuta americana L., dodder, love vine, yellow dod. *B 3480*; *E 31*; *HK 20100* (A); *P 18601* (A).
Evolvulus antillanus Powell. *B 3565, LG 2475, 2476, 2478, 2504, 2505,* all as *Evolvulus argyreus* Choisy.
Evolvulus convolvuloides (Willd.) Stearn. *P 18686* (A).
Evolvulus glaber Sprengel. *B 3564* (NY); *P 18686* (A).
Evolvulus sericeus Sw. *P 18647* (A).

Ipomoea batatas L., sweet potato. Cultivated. HK sight.
Ipomoea carnea Jacq. subsp. *fistulosa* (Martius) Austin, morning glory. Cultivated. HK sight.
Ipomoea eggersii (House) Austin, wild potato. *B 3471, 3515bis,* both as *Ipomoea arenaria* (Choisy) Steudel; *E 35*; *HK 20061* (A); *P 18542* (A).
Ipomoea nil (L.) Roth. HK sight.
Ipomoea pes-caprae (L.) R. Br. subsp. *brasiliensis* (L.) Ooststr., sea bean. *B s.n.*
Ipomoea triloba L. *P 18520* (A).
Jacquemontia cayensis Britton. *HK 20146* (A); *P 18646* (A), *18802* (A).
Jacquemontia pentantha (Jacq.) G. Don, black wiss. *B 3544.*
Jacquemontia solanifolia (L.) Hallier f. *HK 20098* (A); *P 18546* (A).
Merremia dissecta (Jacq.) Hallier f., nio, noyeaux, sprain bush. *B s.n.*; *P 18590* (A).

CRASSULACEAE

Bryophyllum pinnatum (Lam.) Kurz, Christmas plant. *B s.n.*; HK sight.
Kalanchoë blossfeldiana Poelln. Cultivated. HK sight.
Kalanchoë tubiflora (Harvey) Raym.-Hamet. Cultivated and naturalized. *HK 20051* (A).

CRUCIFERAE

Brassica carinata A. Braun. *HK 20112* (A).
Brassica oleracea L. var. *botrytis* L., cauliflower. HK sight.
Brassica oleracea L. var. *capitata* L., cabbage. HK sight.
Cakile lanceolata (Willd.) O. Schulz. *HK 20122* (A); *P 18623* (A).
Lepidium virginicum L. *B s.n.* (NY).

CUCURBITACEAE

Cucumis anguria L. *HK 20075* (A).
Cucurbita moschata Duchesne ex Poiret, pumpkin. Cultivated. HK sight.
Momordica charantia L., maiden apple. HK sight.

EUPHORBIACEAE

Acalypha amentacea Roxb. subsp. *wilkesiana* (Muell. Arg.) Fosb. Cultivated. HK sight.
Acalypha chamaedrifolia (Lam.) Muell. Arg. *HK 20127* (A).
Acalypha poiretii Sprengel. *B 3451*; *P 18797* (A).
Argythamnia candicans Sw., tea. *B 3466*; *HK 20167* (A); LG sight (Scrub Is.); *P 18565* (A).
Breynia disticha J. R. & G. Forster. Cultivated. HK sight.
Chamaesyce blodgettii (Engelm.) Small. *HK 20058* (A); *P 18651* (A), *18658* (A).
Chamaesyce hirta (L.) Millsp. *HK 20080* (A); *P 18576* (A).
Chamaesyce hypericifolia (L.) Millsp. *P 18639* (A).
Chamaesyce mesembrianthifolia (Jacq.) Dugand. *B 3561, 3567,* both as *Chamaesyce buxifolia* (Lam.) Small; *E 48*; *HK 20121* (A); LG sight (Dog Is.); *P 18809* (A).
Chamaesyce multinodis (Urban) Millsp. *P 18591* (A).
Chamaesyce pilulifera L. *B s.n.*
Chamaesyce prostrata Aiton. LG sight (Scrub Is.); *P 18591* (A).
Codiaeum variegatum (L.) Blume. Cultivated. HK sight.
Croton betulinus Vahl, nanny bunch. *B 3465, 3499*; *HK 20159* (A); LG sight (Scrub Is.); *P 18553* (A).
Croton flavens L., balsam. *B 3477, 3528, 3599*; *E 39*; *HK 20085* (A); LG sight (Dog Is., Scrub Is.); *P 18522* (A), *18532* (A).
Croton lobatus L. *B s.n.*; *HK 20147* (A); *P 18636* (A).

Croton microcarpus Ham., sweet marjoram. *B s.n.,* as *Croton ovalifolius* Vahl; *HK 20109* (A); *LG 2471, 2489, 2506, P 18665* (A), as *Croton nummulariaefolius* A. Rich.
Euphorbia cyathophora Murray. *HK 20165* (A); *P 18583* (A).
Euphorbia heterophylla L., Bethlehem star. *P 18637* (A).
Euphorbia lactea Haw. Cultivated. HK sight.
Euphorbia leucocephala Lotsy. Cultivated. HK sight.
Euphorbia pulcherrima Willd., Christmas plant. Cultivated. HK sight.
Euphorbia tirucalli L. Cultivated and naturalized. HK sight.
Gymnanthes lucida Sw., scrub bush. *P 18805* (A).
Hippomane mancinella L., manchineel. *B s.n.*; LG sight (Dog Is., Scrub Is.); *P 18807* (A).
Jatropha curcas L., barricata bush. HK sight.
Jatropha gossypifolia L., physic nut. *HK 20070* (A); LG sight (Dog Is.); *P 18680* (A).
Jatropha integerrima Jacq. Cultivated. HK sight.
Jatropha multifida L. Cultivated. HK sight.
Manihot esculenta Crantz. Cultivated. HK sight.
Pedilanthus tithymaloides (L.) Poit., bleeding heart, candle flame bush. *B 3572*; *P 18616* (A).
Phyllanthus amarus Schum. & Thonn., churchweed. *HK 20115* (A), *20148* (A); *P 18638* (A).
Phyllanthus epiphyllanthus L., bilbush. *B 32566*; *E 33*; LG sight (Scrub Is.); *HK 20078* (A); *P 18516* (A).
Ricinus communis L., castor nut. Naturalized. HK sight.

GOODENIACEAE

Scaevola plumieri (L.) Vahl, candlewood. *B 3563*; *HK 20123* (A); *P 18781* (A).

GUTTIFERAE

Clusia rosea L., autograph tree, pitch apple. *HK 20154* (A); *P 18631* (A).

LABIATAE

Leonotis nepetifolia (L.) Aiton, hollow stalk. *P 18702* (A).
Ocimum micranthum Willd., French basil. *HK 20072* (A).
Plectranthus amboinicus (Lour.) Launert, stingy time. Cultivated. *B s.n.*
Plectranthus blumei (Bentham) Launert. Cultivated. HK sight.
Salvia occidentalis L., cat mint. *P 18575* (A).
Salvia serotina L., cat mint. *B s.n.*; *HK 20144* (A); *P 18662* (A).

LAURACEAE

Cassytha filiformis L. *B 3523*; *P 18668* (A).
Persea americana Pers. Cultivated. *B 3491a.*

LEGUMINOSAE

Acacia farnesiana Willd., queen casha. LG sight (Dog Is.); *P 18528* (A).
Acacia macracantha Humb. & Bonpl., kushar. *HK 20087* (A); *P 18774* (A).
Acacia nilotica (L.) Willd., casha, cassi, kushar. *P 18596* (A).
Albizia lebbeck (L.) Bentham. Cultivated. HK sight.
Caesalpinia bonduc (L.) Roxb., nicker tree. *P 18529* (A).
Caesalpinia coriaria (Jacq.) Willd. *P 18671* (A).
Caesalpinia divergens Urban, red nicker. *HK 20128* (A); LG sight (Dog Is., Scrub Is.), as *Guilandina divergens* Urban; *P 18562* (A).

Caesalpinia pulcherrima Sw., pride of Barbados. Cultivated. *P 18759* (A).
Cajanus cajan (L.) Huth, Angola pea, pigeon pea. Cultivated. HK sight.
Canavalia rosea (Sw.) DC. *P 18782* (A).
Centrosema virginianum Bentham. *HK 20158* (A); *P 18547* (A).
Chamaecrista glandulosa (L.) Greene var. *swartzii* (Wikström) Irwin & Barneby, wild tamarind. *B 3516*; *P 18563* (A).
Crotalaria incana L. *P 18698* (A), *18734* (A).
Crotalaria retusa L., shack-shack. *P 18736* (A).
Crotalaria verrucosa L. *HK 20152* (A); *P 18655* (A).
Delonix regia (Bojer) Raf., flamboyant. Cultivated. HK sight.
Desmanthus virgatus (L.) Willd. *HK 20107* (A); *P 18604* (A).
Desmodium frutescens Schindler var. *angustifolium* Schindler. *LG 2515*.
Erythrina variegata L. var. *orientalis* (L.) Merr. Cultivated. HK sight.
Galactia dubia DC. *B 3503*; *HK 20069* (A); *P 18548* (A).
Gliricidia sepium (Jacq.) Kunth, quick set. HK sight.
Indigofera suffruticosa Miller. *P 18701* (A).
Indigofera tinctoria L. *HK 20111* (A); *P 18735* (A).
Lablab purpureus (L.) Sweet, bonavist. Cultivated. HK sight.
Leucaena leucocephala (Lam.) De Wit, mimosa, wild tamarind. *B s.n.*; *P 18764* (A).
Neptunia pubescens Bentham. *P 18750* (A).
Parkinsonia aculeata L. Cultivated and naturalized. HK sight.
Pithecellobium unguis-cati (L.) Martius, bread and cheese, crabwood, grooven-eye. *B s.n.*; *E 57*; LG sight (Dog Is., Scrub Is.); *P 18540* (A).
Rhynchosia minima DC. *B 3486*; *P 18574* (A).
Rhynchosia reticulata (Sw.) DC. *HK 20153* (A); *P 18549* (A).
Senna bicapsularis (L.) Roxb. *E 58*; *P 18530* (A).
Senna italica Miller. *B s.n.*, as *Cassia obovata* Colladon.
Senna obcordata (Wikström) Britton. *LG 2473*, as *Cassia obcordata* Sw.
Senna obtusifolia (L.) Irwin & Barneby. *P 18672* (A).
Senna occidentalis (L.) Link, bush coffee, stinkweed. *B s.n.*, as *Cassia occidentalis* L.; *HK 20133* (A); *P 18795* (A), *18816* (A).
Senna siamea (Lam.) Irwin & Barneby. Cultivated. HK sight.
Sesbania grandiflora (L.) Pers. Cultivated. HK sight.
Sophora tomentosa L. *B 3490*; *LG 2481, 2494, 2496, 2497, 2498, 2502*; *P 18580* (A).
Stylosanthes hamata (L.) Taubert, sweetweed, wild Isaac. *B 3536*; *HK 20083* (A); *P 18763* (A).
Tamarindus indica L., tamarind. HK sight.
Tephrosia cinerea Pers. *P 18700* (A).

LOGANIACEAE

Spigelia anthelmintha L. *B 3474*; *HK 20163* (A).

LORANTHACEAE

Dendropemon caribaeus Krug & Urban. *HK 20132* (A).
Phoradendron trinervium (Lam.) Griseb., mistletoe. *B s.n.*; *HK 20049* (A), *20050* (A); *P 18564* (A).

LYTHRACEAE

Lawsonia inermis L., mignonette. Cultivated. HK sight.

MALPIGHIACEAE

Byrsonima lucida Rich., gooseberry, goosie tree. *B 3501, 3511*; *E 36*; *HK 20166* (A); *P 18536* (A).

Galphimia gracilis Bartling. Cultivated. HK sight.
Heteropteris purpureus (L.) Kunth. *E 41.*
Malpighia emarginata Sessé & Mociño ex DC., sherry. *B s.n.*, as *Malpighia punicifolia* L.; *P 18777* (A).
Malpighia linearis Jacq. LG sight (Scrub Is.).
Stigmaphyllon diversifolium (Kunth) A. Juss. *B 3513*; *HK 20120* (A); *LG 2486, 2499*; *P 18581* (A).
Stigmaphyllon emarginatum (Cav.) Juss. *HK 20093* (A), *20097* (A).
Stigmaphyllon lingulatum (Poiret) Small. *B 3452*, as *Stigmaphyllon periplocifolium* A. Juss.; *P 18519* (A).

MALVACEAE

Abelmoschus esculentus (L.) Moench, okra. Cultivated. HK sight.
Abutilon indicum (L.) Sweet. *B s.n.*
Abutilon umbellatum (L.) Sweet. *P 18766* (A).
Bastardia viscosa (L.) Kunth. *P 18678* (A).
Gossypium barbadense L. Cultivated. HK sight.
Herissantia crispa (L.) Briz. *HK 20160* (A); *P 18694* (A).
Hibiscus rosa-sinensis L. Cultivated. HK sight.
Hibiscus sabdariffa L., sorrel. Cultivated. HK sight.
Malvastrum corchorifolium (Desr.) Britton. *E 46*; *P 18585* (A).
Malvastrum coromandelianum (L.) Garcke. *B 3449*, as *Malvastrum tricuspidatum* A. Gray.
Sida abutilifolia Miller. *HK 20116* (A); *P 18681* (A).
Sida acuta Burman f., jingle weed. *P 18756* (A).
Sida ciliaris L. *B 3493, 3535*; *HK 20073* (A); *P 18649* (A).
Sida glutinosa Cav. *P 18594* (A).
Sida procumbens Sw. *P 18681* (A).
Sida spinosa L., wild Isaac. *B 3461a*; *HK 20062* (A); *P 18673* (A).
Thespesia populnea (L.) Sol. ex Correa. HK sight.

MELIACEAE

Azadirachta indica A. Juss., neem. Cultivated. *HK 20113* (A).
Melia azedarach L. Cultivated. HK sight.
Swietenia mahagoni Jacq. HK sight; LG sight.

MORACEAE

Artocarpus altilis (Parkinson) Fosb., breadfruit. Cultivated. HK sight.
Ficus citrifolia Miller. LG sight (Scrub Is.); *P 18644* (A).
Ficus elastica Roxb., rubber tree. Cultivated. HK sight.

MORINGACEAE

Moringa oleifera Lam. Cultivated or escaped. HK sight.

MYRTACEAE*

Eugenia axillaris (Sw.) Willd., sneeze berry. *HK 20056* (A); LG sight (Scrub Is.); *P 18815* (A).

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*An unknown member of this family was collected by Le Gallo as nos. *2480* and *2493* (May 9, 1955) near the Catholic church. Since this time a new church was built, but the old building remains and is surrounded by dense scrub vegetation. Our intensive search failed to locate a comparable plant.

Eugenia foetida Pers., white wattling. *HK 20094* (A), *20143* (A); *P 18518* (A), *18552* (A), *18689* (A), *18748* (A).
Eugenia monticola (Sw.) DC., cuttard. *B 3461, 3477a, 3520.*
Pimenta racemosa (Miller) J. Moore, bay leaf. *P 18622* (A).
Psidium guajava L. *B s.n.*; HK sight.
Psidium longipes (Berg) McVaugh var. *orbicularis* (Berg) McVaugh. *B 3509* (NY), as *Myrtus anguillensis* Urban; *LG 2067, 2492, 2508, 2517*; *P 18801* (A).

NYCTAGINACEAE

Boerhavia coccinea Miller. *HK 20117* (A); *P 18579* (A).
Boerhavia scandens L., piecrust. *B 3451*; *HK 20091* (A); LG sight (Dog Is.); *P 18602* (A).
Bougainvillea glabra Choisy. Cultivated. HK sight.
Guapira fragrans Dum.-Cours. *P 18814* (A).
Mirabilis jalapa L. Cultivated. HK sight.
Pisonia subcordata Sw., loblolly. *B s.n.*; *P 18785a* (A), *18785b* (A).

OLEACEAE

Forestiera eggersiana Krug & Urban. *HK 20139* (A); *P 18544* (A), *18798* (A).
Jasminum fluminense Vell. Cultivated. *P 18768* (A).

PAPAVERACEAE

Argemone mexicana L., thistle. *B s.n.*; *E 80*; LG sight (Dog Is.); *P 18741* (A).

PASSIFLORACEAE

Passiflora edulis Sims, passionfruit. Cultivated. HK sight.
Passiflora foetida L., pops. *HK 20096* (A).
Passiflora suberosa L., pops. *B 3498*; *LG 2510*; *P 18538* (A).

PERIPLOCACEAE

Cryptostegia grandiflora R. Br. Cultivated and naturalized. HK sight.

PHYTOLACCACEAE

Rivina humilis L. *P 18813* (A).

PLUMBAGINACEAE

Plumbago auriculata Lam. Cultivated. HK sight.
Plumbago scandens L., doctor John. *HK 20081* (A); *P 18600* (A).

POLYGONACEAE

Antigonon leptopus Hooker & Arn. Naturalized. HK sight.
Coccoloba krugii Lindau, wild grape. *B 3472*; *HK 20052* (A), *20068* (A); *LG 2058, 2069*; *P 18521* (A).
Coccoloba krugii Lindau × *Coccoloba uvifera* (L.) L., wild grape. *HK 20135* (A), *20136* (A) (each of these collections represents a slightly different phase of the hybrid).
Coccoloba microstachya Willd. *B 3458, 3483* (NY), both as *Coccoloba diversifolia* Jacq.
Coccoloba uvifera (L.) L., sea grape. *P 18612* (A).

PORTULACACEAE

Portulaca halimoides L., pussley. *B 3552*; *E 69*; *HK 20084* (A); *P 18572* (A).
Portulaca oleracea L. *B 3553*; *P 18683* (A).

PUNICACEAE

Punica granatum L. Cultivated and naturalized. *HK 20055* (A).

RHAMNACEAE

Colubrina arborescens (Miller) Sarg., mawby bark. *E 34*; *HK 20066* (A); *LG 2051, 2068* (both Dog Is.), both as *Colubrina ferruginosa* Brongn.; *P 18645* (A).
Krugiodendron ferreum (Vahl) Urban, ebony berry. *HK 20162* (A); *P 18751* (A).
Reynosia uncinata Urban, sloe. *B 3470*; *HK 20092* (A); *P 18533* (A).
Zizyphus mauritiana Lam., doms, pommeserrette. *HK 20054* (A); *P 18654* (A).
Zizyphus rignonii Delponte, thorn. *B 3452a* (NY), *3488* (not located), *3506a* (NY), all as *Zizyphus havanensis*; *HK 20102* (A); *LG 2053, 2066*, sight (Scrub Is.), all as *Sarcomphalus domingensis* (Sprengel) Krug & Urban; *P 18535* (A).

RHIZOPHORACEAE

Rhizophora mangle L., whistle. HK sight; LG sight.

ROSACEAE

Rosa indica L., rose. Cultivated. HK sight.

RUBIACEAE

Antirhea acutata (DC.) Urban, mutton polly. *B 3475a*; *HK 20099* (A), *20101* (A); *LG 2071*; *P 18605* (A).
Erithalis fruticosa L., candlebush. *B 3486*; *E 40*; *HK 20044* (A); *P 18650* (A).
Ernodea littoralis Sw., cough bush, stinging whip. *B 3487, 3510*; *E 32*; *HK 20047* (A); *P 18545* (A).
Exostema caribaeum Roemer & Schultes, fustic. *B 3476, 3502*; *E 37*; *HK 20060* (A); *P 18557* (A).
Guettarda scabra Lam., chink, wild guava. *B 3464, 3506*; *HK 20095* (A); *P 18556* (A).
Ixora casei Hance. Cultivated. HK sight.
Ixora coccinea L. Cultivated. HK sight.
Randia aculeata L., five-finger tree. *B 3450a*; *HK 20053* (A); *P 18560* (A).

Rondeletia anguillensis R. Howard & E. Kellogg, sp. nov. FIGURES 4, 5.

Frutex cruciatus, foliis minutissimis, minoribus quam 4 mm longis, floribus distylis.

Stiff shrub up to 1 m tall; branches divaricate, spine tipped; bark smooth, grayish; young growth densely appressed-white-puberulent, glabrescent, stems reddish; leaves and flowers clustered on short shoots. Stipules interpetiolar, fused to form truncate or obtuse collar with ciliate margin. Leaves with petiole 0.2–0.5 mm long, white-puberulent; blade suborbicular when young, becoming ovate to elliptic, 1.5–3.8 × 1.2–2.7 mm, the apex rounded, the base rounded, the margin thickened-revolute, the adaxial surface shiny, dark green, glabrous, the abaxial surface white-velutinous, the midvein white abaxially. Flowers stiffly erect to horizontal, 4-merous, subtended by crateriform fused bracts 0.6–0.8 mm long and with acute to acuminate lobes, distylous; calyx campanulate, 1.5–2.8 mm long, green, appressed-puberulent, the lobes linear, 0.7–1.1 mm long; corolla salverform, pale pink, appressed-white-puberulent externally, the tube 4–5.7 mm long in short-styled plants and 3.2–3.7 mm long in long-styled ones, glabrous within, the lobes 0.8–1.6 mm long, puberulent above, with annulus of small, raised tubercles at throat; stamens inserted on corolla tube, the filament < 0.2 mm long, filiform, the anther dorsifixed, oblong to slightly cuneate, 1.4–1.6 mm long in both forms, the pollen 3-colpate in short-styled plants, 3- and 4-colpate in long-styled ones; style linear, 2–2.2 mm long and sparsely retrorse-pubescent in short-styled plants, 4–4.7 mm long and nearly glabrous in long-styled ones, the stigmas 2, 0.8 mm long

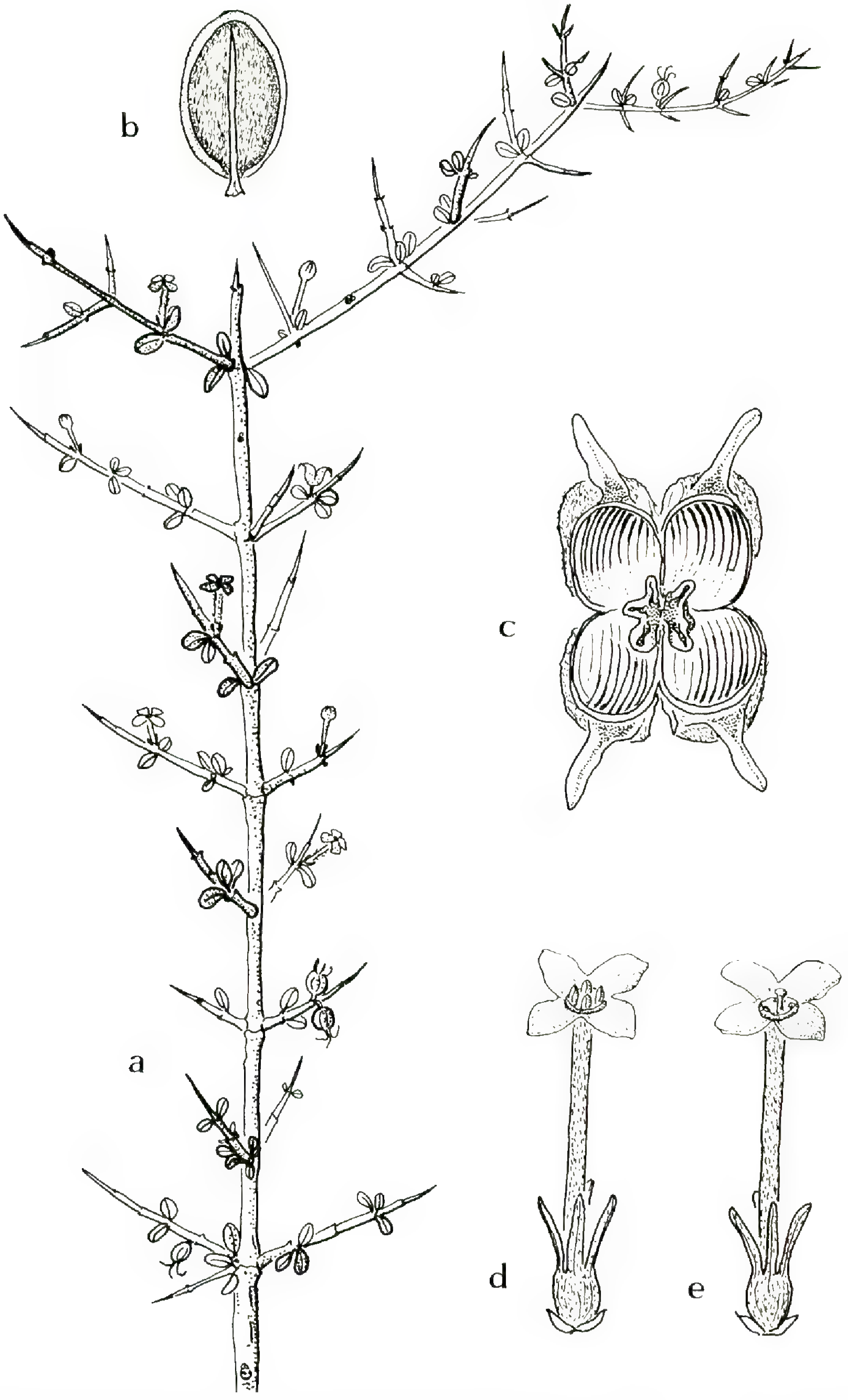

FIGURE 4. *Rondeletia anguillensis*: a, habit (*Proctor 18571,* A), × 0.75; b, lower surface of leaf (*Proctor 18571*), × 7; c, dehisced fruit (*Proctor 18571*), × 11; d, short-styled flower (*Howard & Kellogg 20105,* A), × 7; e, long-styled flower (*Howard & Kellogg 20103,* A), × 10. (a drawn by M. Dykens, b–e by I. Al-Shehbaz.)

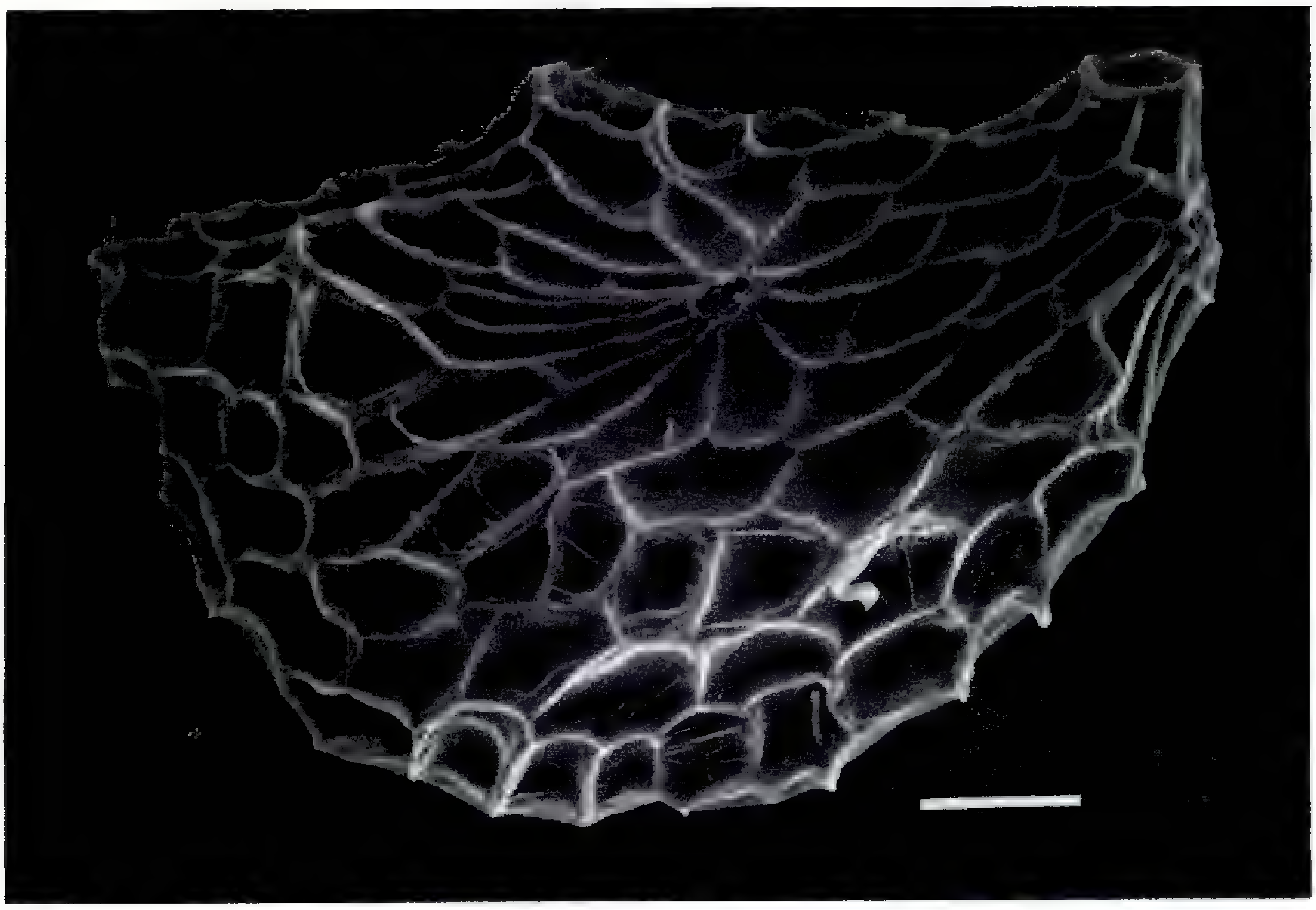

FIGURE 5. *Rondeletia anguillensis* (*Howard & Kellogg 20103*, A), seed. Scale = 100 μm.

in short-styled plants and 0.3 mm in long-styled ones; the ovary 2-locular, obconical, 1.2 mm long, stiffly erect-pubescent. Fruit capsular, globose, 1.8–2.9 mm in diameter, initially loculicidal, subsequently septicidal; calyx lobes persisting and becoming 0.8–1.7 mm long; placenta peltate, reniform in longitudinal section, becoming massive, hemispheric; seeds numerous, 0.72–0.75 mm long, imbricate upward, irregular in outline, finely reticulate.

TYPE. Anguilla, east end of island, 6 Feb. 1985, *R. Howard & E. Kellogg 20105* (holotype, A).

SPECIMENS SEEN. **Anguilla:** E end of island, *R. Howard & E. Kellogg 20103* (A); vic. of Little Bay, near Flat Cap Point, *Proctor 18571* (A).

Spermacoce confusa Rendle, chicken weed. *B 3542*; *HK 20064* (A); *P 18642* (A).
Strumpfia maritima Jacq. *B 3551*; *E 49*; LG sight (Dog Is., Scrub Is.); *P 18617*.

RUTACEAE

Amyris elemifera L., ironwood. *B 3481*; *HK 20076* (A); *LG 2056* (Scrub Is.); *P 18517* (A).
Citrus aurantifolia (Christm.), swingle lime. Cultivated. HK sight.
Citrus aurantium L., sour orange. Cultivated. HK sight.
Citrus paradisi Macfad., grapefruit. Cultivated. HK sight.
Citrus sinensis (L.) Osbeck, sweet orange. Cultivated. HK sight.
Murraya paniculata (L.) Jack. Cultivated. HK sight.
Zanthoxylum flavum Vahl, alexander. *B 3525*; *HK 20063* (A); LG sight (Scrub Is.); *P 18541* (A), *18670* (A).
Zanthoxylum punctatum Vahl, ironwood. *B 3469, 3526, 3532,* all as *Fagara trifoliata* Sw.; *HK 20077* (A).
Zanthoxylum spinifex (Jacq.) DC., ramgoat. *B 3529,* as *Fagara spinifex* Jacq.; *HK 20090* (A); *P 18584* (A), *18799* (A).

SAPINDACEAE

Cardiospermum corindum L. *P 18554* (A).
Hypelate trifoliata Sw., ironwood. *B 3508*; *LG 2410, 2477, 2479, 2514*; *P 18573* (A).
Meliococcus bijugatus L., genip. Cultivated. HK sight.

SAPOTACEAE

Bumelia obovata (Lam.) DC., thorn tree. *HK 20048* (A); LG sight (Dog Is.); *P 18589* (A).
Bumelia salicifolia (L.) Sw., mass wood. *B 3542*; *HK 20138* (A); *P 18642* (A).

SCROPHULARIACEAE

Capraria biflora L., tasane. LG sight (Dog Is.); *P 18697* (A).
Lindernia diffusa (L.) Wettst. *HK 20074* (A).

SIMAROUBACEAE

Castela erecta Turpin, cockspur. *HK 20089* (A); *LG 2054, 2065* (both Scrub Is.), *2470* (Dog Is.), *2500*; *P 18592* (A), *18606* (A).
Suriana maritima L. *B 3560*; *E 51*; LG sight (Scrub Is.); *P 18614* (A).

SOLANACEAE

Capsicum frutescens L., pepper. Cultivated. HK sight.
Datura stramonium L. *P 18738* (A).
Lycium americanum Jacq. *B 3546*; *HK 20134*; LG sight (Dog Is., Scrub Is.); *P 18747* (A).
Lycopersicon lycopersicum (L.) Karsten, tomato. Cultivated. HK sight.
Physalis angulata L. *P 18796* (A).
Solandra guttata D. Don. Cultivated. HK sight.
Solanum melongena L., bolonge, eggplant. Cultivated. HK sight.
Solanum racemosum Jacq., canker berry, cob berry, conka berry. *B s.n.*; *E 53*; *HK 20088* (A); LG sight (Dog Is., Scrub Is.); *P 18527* (A).

STERCULIACEAE

Melochia pyramidata L. *P 18524* (A).
Melochia tomentosa L. *B 3478*; *E 60*; *HK 20082* (A); LG sight (Scrub Is.); *P 18593* (A).
Waltheria glabra Poiret. *P 18569* (A).
Waltheria indica L., marshmallow. *B 3496*, as *Waltheria americana* L.; *E 43*; *P 18603* (A).

TAMARICACEAE

Tamarix chinensis Lour. Cultivated. HK sight.

THEOPHRASTACEAE

Jacquinia arborea Vahl, scrub bush. *HK 20046* (A); LG sight (Scrub Is.); *P 18567* (A).
Jacquinia berterii Sprengel. *B 3558*; *E 61*; *HK 20059* (A); *LG 2060, 2063* (both Scrub Is.); *P 18537* (A), *18632* (A).

TILIACEAE

Corchorus hirsutus L., marshmallow. *B 3473, 3519*; LG sight (Scrub Is.); *P 18570* (A), *18582* (A).
Corchorus siliquosus L., calaloo. *B 3463*; *P 18561* (A).

TURNERACEAE

Turnera ulmifolia L. *P 18731* (A).

ULMACEAE

Celtis iguanaea (Jacq.) Sarg. *B s.n.*

UMBELLIFERAE

Anethum graveolens L. *P 18676* (A).

URTICACEAE

Pilea serpyllifolia (Poiret) Wedd. Cultivated. HK sight.

VERBENACEAE

Citharexylum fruticosum L. *P 18624* (A).
Clerodendrum aculeatum (L.) Schldl. *B s.n.*; LG sight (Dog Is.); *P 18740* (A).
Duranta erecta L. *B s.n.*, as *Duranta repens* Kunth.
Lantana camara L., sage cop. *P 18786* (A).
Lantana involucrata L., sage, sage cop. *B 3476, 3504* (NY); *E 44*; *HK 20106* (A); *P 18526* (A), *18661* (A).
Lippia reptans Kunth. *B 3475*; LG sight (Dog Is.).
Lippia strigulosa Martens & Gal. *P 18677* (A).
Priva lappulacea (L.) Pers. *P 18599* (A).
Stachytarpheta jamaicensis (L.) Vahl, worry wine. *B 3497*; *HK 20157* (A); *P 18775* (A).

VIOLACEAE

Hybanthus portoricensis Urban. LG sight (Scrub Is.).

VITACEAE

Cissus verticillatus (L.) Nicolson & Jarvis. *B s.n.*, as *Cissus sicyoides* L.

ZYGOPHYLLACEAE

Guaiacum officinale L., lignum vitae. Cultivated. *P 18800* (A).
Kallstroemeria maxima (L.) Torrey & A. Gray. *P 18685* (A).

UNUSUAL POLLEN DIMORPHISM IN RONDELETIA ANGUILLENSIS (RUBIACEAE)

Elizabeth A. Kellogg and Richard A. Howard[1]

Long-styled plants of *Rondeletia anguillensis* bear a mixture of three- and four-colpate pollen, whereas short-styled plants bear only three-colpate grains. Short-styled plants have smaller pollen grains with lower pollen stainability than long-styled plants.

In the preceding paper (Howard & Kellogg, 1987) we described *Rondeletia anguillensis,* a new species collected on the Caribbean island of Anguilla in 1985. The plants were clearly distylous, a condition common in the Rubiaceae. Measurements confirmed that short-styled plants had notably longer corolla tubes than long-styled ones (4–5.7 vs. 3.2–3.6 mm, respectively); this difference in corolla size has been reported for other distylous plants (Ganders, 1979). In the process of preparing the description, we discovered that the pollen of the two stylar forms was more strongly dimorphic than is commonly the case in the family. We report our results here in the hope of stimulating further collecting and investigation of the phenomenon.

METHODS

Our observations were based on material from three collections, two short-styled plants (*Howard & Kellogg 20105,* A; *Proctor 18571,* A) and one long-styled one (*Howard & Kellogg 20103,* A) (for full specimen citations, see Howard & Kellogg, 1987). After preparing SEM photographs of pollen from each of the two forms, we continued investigations with the light microscope. Pollen was stained overnight with cotton blue in lactophenol. For each plant the diameters of 200 pollen grains from a single flower were measured and averaged. Pollen stainability was calculated from more than 200 grains for each flower observed (four flowers for each of the Howard & Kellogg collections, one for the Proctor collection). For each of these nine flowers, the number of colpi was recorded for the first 200 grains from which it could be determined.

RESULTS AND DISCUSSION

The photographs in the Figure show that the long-styled plant has a mixture of three- and four-colpate pollen (a, b), whereas the short-styled plant bears

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[1] Arnold Arboretum, Harvard University, 22 Divinity Avenue, Cambridge, Massachusetts 02138.

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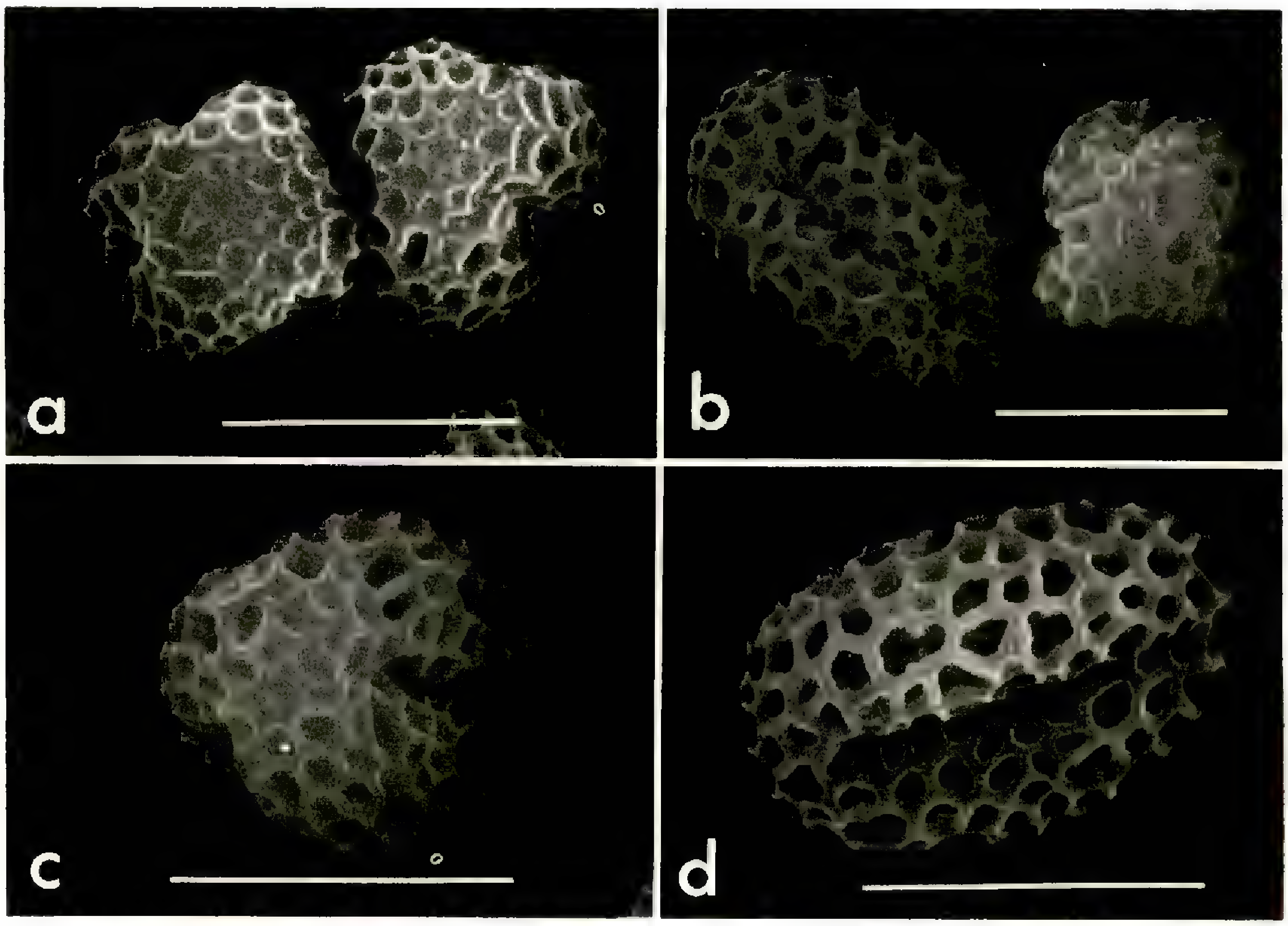

Rondeletia anguillensis, nonacetolyzed pollen (scale bars = 10 μm): a, b, long-styled plant, *Howard & Kellogg 20103*; c, d, short-styled plant, *Howard & Kellogg 20105.*

consistently three-colpate grains (c, d). Also, pollen from the short-styled plant appears to be slightly smaller than that from the long-styled one.

These observations were confirmed by light microscopy, the results of which are summarized in the TABLE. Pollen size and stainability were virtually identical for the two short-styled plants, despite the fact that they were collected 26 years apart and at different localities on the island. Unfortunately, we had only one long-styled plant, and that had very few nearly mature buds from which to take pollen, so we cannot be certain that the pollen dimorphism is characteristic of the species. There is still the possibility that *Howard & Kellogg 20103* is simply an anomalous plant.

These preliminary results show some surprising differences between the two style forms. Statistical comparison of the mean sizes of pollen of the two Howard & Kellogg collections produces $t = 8.96$, df = 398, a difference significant at $p \ll 0.005$. However, the short-styled plants have the smaller pollen, contrary to the condition in most other distylous plants. Ganders (1979) reported pollen of short-styled plants to be smaller than that of long-styled ones in *Fauria crista-galli* Makino (Menyanthaceae); this was apparently the first report of such a size relationship.

Variation in pollen stainability has been reported by Ornduff (1980) in populations of *Hedyotis caerulea* (L.) Hooker. He reported variation both between and within short- and long-styled plants, and variation between and within years. There may be similar variability in *Rondeletia anguillensis,* but its significance is unclear.

Variation in pollen size, colpus number, and stainability for three plants of Rondeletia anguillensis.

SPECIMEN	NUMBER OF COLPI	SIZE (μm) Range	Mean	SD	STAINABILITY (%)
Short-style					
Howard & Kellogg 20105	3*	11–15	13	0.75	72, 76, 93, 94
Proctor 18571	3	11–15	13	0.76	76
Long-style					
Howard & Kellogg 20103	3, 4	12–15	14	0.61	99, 99, 99.5, 99.5

*One 4-colpate grain observed out of more than 900. Most probably contamination.

The variation in colpus number is interesting for two reasons. First, morphological differences between long- and short-style pollen are usually subtle, particularly in the Rubiaceae. Major differences in shape have been reported for *Lithospermum* L. (Boraginaceae; Johnston, 1952), and differences in exine sculpturing occur in the Plumbaginaceae (Baker, 1966). The only really marked difference in pollen morphology for distylous Rubiaceae was reported by Baker (1956) for *Rudgea jasminoides* (Cham.) A. Rich., in which the pollen of long-styled plants was smooth and that of short-styled ones was spiny.

Second, four-colpate pollen is one of the major characters used by Borhidi and colleagues (1980, 1981) in distinguishing *Rondeletia* L. and the segregate genera *Roigella* Borhidi & Zequeira, *Neomazaea* Urban, and *Acuneanthus* Borhidi, Jarai-Komlodi, & Moncada; pollen of *Rondeletia* and *Acuneanthus* is three-colpate, while that of the other two genera is four- or five-colpate. The variation we have found in this character casts some doubt on its usefulness at the generic level. Its variability within species should perhaps be investigated more fully before it is relied upon for major distinctions among groups.

Four flowers from the long-styled plant were scored for percent of three-colpate pollen. The percentages were 47, 51, 59, and 62. The pooled $\chi^2 = 7.0$, indicating that the ratio of three- to four-colpate pollen was significantly different from 1:1 ($p < 0.01$). However, a test for homogeneity of χ^2 values among the flowers showed a significant lack of homogeneity, so pooling the values may not be justified. If χ^2 values are calculated separately, values for two of the flowers are not significantly different from a 1:1 ratio, whereas values for the other two are. If we assume that the two pollen morphs would indeed appear in equal proportions if the sample were sufficiently large, then we could explain the observed variation in pollen morphology by a one-locus gene with two alleles, one of which conditions for three colpi and the other for four. Under this explanation, the long-styled plant is heterozygous, the (haploid) pollen grains therefore being half three- and half four-colpate, whereas the short-styled plants are homozygous. If this proves to be the case, it would be an interesting parallel with the gene for distyly itself, which in all reported cases is also one locus with two alleles and complete dominance (Ganders, 1979).

One style morph is then homozygous recessive (ss), while the other is heterozygous (Ss). The homozygous dominant does not occur because of self-incompatibility of the heterozygotes. Although the short-styled plants are the heterozygotes in most species, long-styled heterozygotes have been reported (Ganders, 1979). It is conceivable that the gene for pollen shape could be linked with the gene for distyly to produce the pattern we have observed in *Rondeletia anguillensis.*

ACKNOWLEDGMENTS

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THE GENERA OF CINCHONOIDEAE (RUBIACEAE) IN THE SOUTHEASTERN UNITED STATES[1]

GEORGE K. ROGERS[2]

The infrafamilial classification of the Rubiaceae is in an unsettled state, with solid answers awaiting accumulation and interpretation of data on some 500 genera. Schumann's system, the only clear, comprehensive one, is followed in the present account. This is not to say that it satisfactorily reflects natural relationships, for it does not—it rests upon heavy-handed application of a few

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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-8415769 (Carroll E. Wood, Jr., principal investigator) and BSR-8415637 (Norton G. Miller, principal investigator). This treatment, the 114th 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 [ ]. References that I have not verified are marked with an asterisk.

Treatments of the first four genera were prepared at the Arnold Arboretum while I held a postdoctoral appointment there. The remainder were prepared at the Missouri Botanical Garden. I owe thanks to the Rubiaceae researchers of St. Louis, who meet occasionally for discussion. This group has broadened my perspective on the family and has been the source of a great deal of factual information. In particular, unpublished documents compiled and distributed by Walter Lewis and Steve Manning were unique references. In addition, John Dwyer's views on *Randia* and information on *Pentodon* from Robert Kral were welcome contributions. Ihsan Al-Shehbaz and Barbara Nimblett helped generously with aspects of the work at the home base in Cambridge, Massachusetts. As always, Carroll Wood supplied information, editorial expertise, guidance, and inspiration. Elizabeth Schmidt and Stephen Spongberg improved the manuscript with their good ideas. The Missouri Botanical Garden provided space and facilities.

The illustrations were drawn by Rachel A. Wheeler (*Cephalanthus*), Dorothy H. Marsh (*Casasia*), and Karen Stoutsenberger (*Hamelia*) from materials prepared by Carroll Wood. The specimens of *Cephalanthus* came from the Arnold Arboretum (Wood) and Louisiana (Joseph Ewan, GH); those of *Casasia* and *Hamelia* from Big Pine Key, Monroe County, Florida (Wood).

[2] Missouri Botanical Garden, P. O. Box 299, St. Louis, Missouri 63166.

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characters, and students of the Rubiaceae have since stressed that it breaks apart obvious alliances.

Even Schumann's fundamental division of the Rubiaceae into two subfamilies, the Cinchonoideae and the Rubioideae (Coffeoideae), is based on a single character, the number of ovules in each locule of the ovary (multiple in the former, solitary in the latter). His classification provides, nonetheless, a convenient and useful framework.

The two foremost students of the Rubiaceae since Schumann, Verdcourt (1958 and later works; see especially 1976) and Bremekamp (particularly 1966), have proposed reforms of the infrafamilial classification. Although neither assembled a comprehensive new scheme, both have added new insights, and both have laid out their concepts of the tribes and subfamilies with characterizations and discussion. Further, both have supplied thorough histories of the subject. So that their contributions do not pass ignored, a summary of the various dispositions of our genera in comparison with Schumann's follows.

Bremekamp increased the number of subfamilies from Schumann's two to eight, of which three concern us. He redefined the Rubioideae as members of the Rubiaceae having raphides and generally valvate corollas. With emphasis shifted to these characters (especially the former), the Hedyotideae (including our *Hedyotis* L. sensu lato and *Pentodon* Hochst.) were moved from the Cinchonoideae to the Rubioideae. Also, *Hamelia* Jacq., which has raphides, was transferred along with *Hoffmannia* Sw. from tribe Gardenieae in the Cinchonoideae to the resurrected Hamelieae DC. in the Rubioideae (see generic treatment).

Bremekamp did not leave the remainder of Schumann's tribe Gardenieae in the Cinchonoideae; instead, he transferred it (containing our *Randia, Casasia,* and *Catesbaea*) to the Ixoroideae Raf., a subfamily he composed of tribes showing the "ixoroid" pollination mechanism (pollen deposited on the shaft of the style). My suspicion is that the ixoroid pollination mechanism is too widespread, either by convergence or by persistence from distant common ancestry, to be a reliable character in defining a subfamily of the Rubiaceae. It shows up in *Pentodon,* clearly a member of the Hedyotideae, and in such other families as the Loganiaceae, Campanulaceae, and Compositae. Bremekamp was uncertain of the placement of *Cephalanthus.*

Verdcourt's strong Old World emphasis makes it difficult to apply his ideas to our genera. He recognized three subfamilies, including the Cinchonoideae and the Rubioideae, defined primarily by the presence or absence of raphides. Verdcourt (1958, 1976), like Bremekamp, placed *Hamelia* and our genera of Hedyotideae in the Rubioideae. He departed from Bremekamp and Schumann by merging tribe Condamineeae (containing *Pinckneya*) with the Rondeletieae (DC.) J. D. Hooker & Bentham (Fl. Nigritana, 378. 1849; note earlier authorship than that given by Darwin). Verdcourt agreed with Schumann but disagreed with Bremekamp, placing *Cephalanthus* in the Naucleeae and retaining the Gardenieae (minus *Hamelia*) in the Cinchonoideae. Among the authors of interest, he is unique in segregating tribe Catesbaeeae J. D. Hooker from the Gardenieae (see treatment of *Catesbaea*).

To summarize the present state of affairs, in my view the size of the family

Rubiaceae forces botanists concerned with its infrafamilial subunits to subdivide it "from the top down," stressing differences found in a few characters. Much discussion connected with the problem centers around the comparative (not convincingly substantiated) "importance" of various characters for this purpose. Only massive collection of new data and a new, more evolutionary emphasis will eventually allow infrafamilial groups to be built "from the bottom up," buttressed by shared derived similarities.

For those workers interested in determining the correct names of taxa of the Rubiaceae above the rank of genus, S. P. Darwin's thoroughly researched nomenclator for subfamilies, tribes, and subtribes in the family is indispensable.

RUBIACEAE subfam. CINCHONOIDEAE Rafinesque, Ann. Gén. Sci. Phys. **6**: 81 (p. 66 in reprint). 1820, "Cinchonaria."

Trees or shrubs (except *Hedyotis* sensu lato and *Pentodon*) with usually opposite, sometimes whorled or fascicled, leaves. Stipules interpetiolar, generally with 1 (sometimes bifid) lobe between adjacent petiole bases (to fimbriate in *Hedyotis* and *Pentodon,* becoming shredded in *Randia*), usually bearing colleters on the adaxial side. Flowers pentamerous or tetramerous, with tubular corollas. Ovary inferior, usually bilocular (but with up to 5 locules in *Hamelia*; *Casasia* unilocular but appearing bi- or trilocular), the locules generally multiovular (uniovular in *Cephalanthus*; *Randia* sometimes with a single seed in the fruit). TYPE GENUS: *Cinchona* L.

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KEY TO THE GENERA OF CINCHONOIDEAE IN THE SOUTHEASTERN UNITED STATES

A. Plants herbs or infrequently subshrubs; raphides present; placentae peltate; fruits dry and less than 0.5 cm long.

B. Flowers pentamerous; placentae bilobed apically; plants hygrophilous and fleshy. .... 3. *Pentodon.*
B. Flowers tetramerous; placentae entire apically; plants not hygrophilous. .... 2. *Hedyotis.*
A. Plants shrubs or trees; raphides absent (except in *Hamelia*); placentae usually axile, sometimes parietal (nearly peltate in *Exostema*), or the ovules pendulous; fruits fleshy and/or over 0.5 cm long.
  C. Flowers and fruits in globose heads; locules of ovary uniovular. .... 5. *Cephalanthus.*
  C. Flowers and fruits not in globose heads; locules of ovary usually multiovular (*Randia* sometimes with only 1 seed in a fruit).
    D. Plants armed with paired spines; leaves largely in fascicles clustered along stems.
      E. Flowers mostly tetramerous; aestivation of corolla valvate; stamens inserted at base of corolla; fruit ca. 5 mm long. .... 9. *Catesbaea.*
      E. Flowers pentamerous; aestivation of corolla imbricate-contorted; anthers inserted in throat of corolla; fruit ca. 10 mm long. .... 6. *Randia.*
    D. Plants unarmed; leaves decussate, whorled, or in terminal clusters.
      F. Fruits dehiscent; seeds winged; anthers exserted.
        G. Calyx lobes more or less uniform; seeds vertical or nearly so; flowers solitary. .... 4. *Exostema.*
        G. Some calyx lobes expanded into leaflike pink to white "flags"; seeds horizontal or oblique; flowers in compound cymes. ... 1. *Pinckneya.*
      F. Fruits indehiscent; seeds unwinged; anthers included or partly exserted.
        H. Flowers perfect; corolla red or orange, lobes a small fraction of length of tube; ovary usually 5-locular; plants pubescent; raphides present. .... 8. *Hamelia.*
        H. Flowers imperfect, plants dioecious; corolla white, lobes approximately as long as tube; ovary unilocular (or appearing bilocular); plants mostly glabrous; raphides absent. .... 7. *Casasia.*

Tribe CONDAMINEEAE Bentham & Hooker, Gen. Pl. **2:** 8, 12. 1873.

1. **Pinckneya** A. Michaux, Fl. Bor. Am. **1:** 103. *pl. 13.* 1803.

Shrubs to small trees, sometimes in colonies from root suckers. Leaves deciduous, opposite, the blades lanceolate or ovate to usually nearly elliptic, obtuse or rounded to caudate at the base, acuminate or less often acute at the apex, lateral nerves usually rather arcuate-ascending, the petiole and midrib often reddish (color fading in pressed specimens); stipules narrowly deltoid to lanceolate with acuminate apices, acting as bud scales, caducous, bearing colleters adaxially toward the base; abaxial side of blades of young leaves and the petioles, young stems, inflorescence axes, ovaries, calyces, and corollas usually abundantly provided with variably kinked to straight and spreading or parallel-appressed, tawny to almost white, incompletely septate and nonseptate, uniseriate trichomes; adaxial side of leaf blades often strigose to glabrate. Inflorescence a pyramidal or hemispheric compound cyme with a straight central axis, the lateral units sometimes repeating the form of the main axis, the branching opposite or distal pedicels alternate; distal bracts linear or greatly expanded to resemble the flaglike sepals, the basal bracts often intergrading with foliage leaves. Flowers fundamentally pentamerous, nearly actinomorphic (except for the flaglike calyx lobes), fragrant. Calyx lobes briefly connate above the ovary, the nonflaglike lobes ca. ¼–¾ the length of the corolla and subulate or linear, or somewhat broadened toward the base, pink or partly green, in certain flowers 1–3 (or all 5) calyx lobes clawed and with greatly expanded blade(s) much exceeding the corolla in length and breadth, these resembling foliage leaves in shape, but smaller and pink to white, then sometimes with reddish borders. Corolla creamy or greenish yellow to pink, mottled with (pink or) purple or brown, with a long, narrow, cylindrical or slightly flared tube and (4 or) 5 (or 6) ligulate or narrowly elliptic, reflexed lobes about ¼–½ the length of the tube, the lobes imbricate or some valvate, with particularly coarse trichomes within. Stamens exserted, the filiform filaments inserted near the base of the tube in a pilose ring, anthers dorsifixed, sagittate, elliptic-oblong or broadened below the middle; pollen grains tricolpate and reticulate (*fide* Verdcourt). Ovary surmounted by an epigynous disc, containing numerous ovules arranged more or less in 2 ranks along an axile placenta in each locule; style filiform, the stigma exserted and barely divided into 2 broad lobes. Capsules persistent, slightly longer than broad to slightly broader than long, lightly compressed perpendicular to the septum (this often appearing as a sunken vertical line), predominantly loculicidal, speckled with lenticels, the endocarp made up of light-colored fibrous cells, the apical perianth scar a broad ring around a sunken center. Seeds waferlike, with a broad wing around the embryo (except often at the hilum), wedge or fan shaped, the hilum opposite the broadest edge, the surface area considerably less than cross-sectional area of the locule, stacked horizontally or obliquely along a broadened placenta raised on a ridge running nearly the entire length of the middle of the septum (ridge and placenta T-shaped in transverse aspect, the seeds attached at various points across the head of the T), surface of seeds reticulate from outlines of testa cells, these with reticulate, straplike reinforcements on the outer walls. Embryo in a tough sac (presumably endosperm), spatulate or with cotyledons very slightly auriculate, the radicle about as long as cotyledons or shorter. TYPE SPECIES: *Pinckneya bracteata* (Bartram) Raf. (*P. pubens* Michx.). (Name commemorating General Charles Cotesworth Pinckney, 1746–1825, South Carolinian, veteran of the American Revolutionary War, statesman, presidential candidate, and benefactor of André Michaux and his son François-André.)—GEORGIA BARK, FEVER TREE, POSSUM POD.

A monotypic genus confined to the two southernmost counties of South Carolina, the southern half of Georgia (including the Okefenokee Swamp), and scattered localities in northeastern to northwestern Florida (several counties from Nassau to Volusia, west to Gulf and Jackson), but not in the western portion of the Florida Panhandle (see Little, 1977, for map). The distribution lies mostly, but by no means overwhelmingly, in the Altamaha Grit region of Georgia and is probably largely determined by edaphic factors.

Pinckneya is encountered in low, sandy, wet situations, especially at margins of swamps, stream banks, and low spots in pine barrens. According to Taylor and Uphof (independently?), it thrives best on river hummocks, where its trunk is periodically submerged.

The flowers open sequentially (possibly rarely as early as late April) through May and June (to July).

For explanation of the displacement of the well-known name *Pinckneya pubens* Michx. by *P. bracteata,* consult Merrill and Wilbur.

The most salient characteristic of these shrubs or small trees is that on many flowers one or more calyx lobes are expanded into large pink or sometimes white "flags." This occurs frequently, but sporadically, in the Rubiaceae, although not in any of the other genera indigenous to our area. Kurz & Godfrey remarked that it is "one of the most spectacularly beautiful [trees or shrubs] occurring in northern Florida." The less conspicuous, typically greenish yellow corollas are marked with purple or brown and have reflexed, internally pubescent lobes on the long tubes. The slightly flattened loculicidal capsules persist for long periods on the branches; upon opening they reveal innumerable waferlike seeds stacked horizontally in the two locules. Interpetiolar stipules with abundant colleters on the adaxial side help to distinguish *Pinckneya* from nonrubiaceous genera. The young stems, inflorescence axes, corollas, and sometimes foliage are typically conspicuously pubescent. Midribs of living leaves tend to be reddish.

Most botanists place *Pinckneya* either in the tribe Condamineeae or in infrafamilial groups named differently but consistent with the same general circle of affinity. Shared tribal or subfamilial characteristics include absence of raphides, presence of endosperm in the seeds, incompletely septate uniseriate hairs, mostly entire stipules, often "pitted" testa cells, woody habit, and—chiefly—capsular fruits containing numerous horizontal seeds. While most members of the tribe have valvate corolla lobes, an attribute sometimes ascribed to *Pinckneya,* I found the lobes to be imbricate or partly valvate in buds from the one collection available for dissection.

Among the genera of the Condamineeae, *Pogonopus* Klotzsch emerges from the literature as likely the closest relative for *Pinckneya.* Bentham & Hooker erected the subtribe "Pinkneyeae" for the pair, and Baillon merged the two genera. Their most conspicuous similarity, expanded flaglike sepals, is too widespread in the Rubiaceae to stand as strong evidence for relationship, yet *Pinckneya* and *Pogonopus* agree further in shape and size of corollas (the lobes are reflexed in *Pinckneya* only), position of anthers and stigmas, shape of capsules (although much smaller in *Pogonopus*), and indument. Their habit and leaves are similar but do not set them apart from other arborescent Rubiaceae. Beyond the differences indicated parenthetically above, *Pogonopus* has smaller seeds less drawn out marginally into wings and has stamens inserted higher in the corolla tube, although the latter difference is hardly appreciable when *Pogonopus speciosus* (Jacq.) K. Schum. is compared with *Pinckneya.* I found the basal portion of the corolla tube of flowers of *Pogonopus speciosus* and *P. tubulosus* (DC.) K. Schum. to be thickened into a woody cylinder, a feature not found in *Pinckneya.* (See Oersted for an illustrated floral dissection of *P. speciosus,* as *P. exsertus.*) In contrast with authors who list internally glabrous corolla lobes in *Pogonopus* as a distinction from *Pinckneya,* I encountered internally pubescent lobes in both genera.

Koek-Noorman & Hogeweg, in an investigation of wood anatomy of the

Condamineeae, evidently perceived no particular connection between *Pinckneya* and *Pogonopus.* They called *Pinckneya* "exceptional" among its relatives in having semi-ring-porous wood with tangential pore chains and concentric parenchyma bands. (At least the first of these exceptional features is probably due to the temperate distribution of the genus, which is in itself very unusual among woody Rubiaceae.)

A second possible close relative is the newly described monotypic Brazilian genus *Kerianthera* Kirkbride. Kirkbride held the new genus to be most similar phenetically within the Condamineeae to *Pinckneya.* He listed their shared features as foliar calyx lobes, dense pubescence on the inner faces of the corolla lobes, and winged seeds but separated *Kerianthera* from both *Pogonopus* and *Pinckneya* by its "4-merous calyx, 7–8-merous corolla, stamens separating from the apex of the corolla tube, anthers with approximately 300 locelli, septicidal capsules, and seeds irregularly biwinged" (p. 109).

It is doubtful that frequent mention of *Pinckneya* in old botanical-medical literature as a remedy for malaria has any meaningful basis. Cornatzer and colleagues related secondhand that pharmaceutical tests on extracts from *Pinckneya* revealed no antimalarial effects on infected canaries. Application of *Pinckneya* against malaria probably grew out of the perception of its relationship to *Cinchona* L., the source of the familiar antimalarial alkaloid quinine. Whether alkaloids form in *Pinckneya* remains a debatable question: Sumerford and Naudain tried and failed to detect any, but Wall and colleagues indicated the presence of at least one unnamed alkaloid. Further work is desirable.

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Tribe HEDYOTIDEAE DC. Prodromus **4:** 342, 401. 1830.

2. **Hedyotis** Linnaeus, Sp. Pl. **1:** 101. 1753; Gen. Pl. ed. 5. 44. 1754.

Annual or perennial, delicate to coarse, prostrate to stiffly erect herbs or weak subshrubs [or shrubs], highly variable in habit, sometimes rosette forming, with 1 or few delicate ascending axes, these (infrequently) unbranched to (frequently) highly branched throughout, or extensively branched at base and scoparioid, axillary growth strongly developed and often overtopping terminal growth, the branching frequently widely divergent and symmetrical. Stems winged or angled, often square, occasionally with adventitious roots when procumbent. Roots thick and woody or fasciculate. Plants usually with conspicuous raphide bundles, and with stems, leaves, and calyces pilose to glabrous. Leaves petiolate or sessile, opposite [or fasciculate or whorled], (frequently) nearly linear to (infrequently) broader than long, commonly more or less narrowly elliptic, entire or scabrous around the margins, infrequently cordate basally; stipules interpetiolar, membranaceous, emarginate or bilobed to deltoid or rounded, or frequently fimbriate, with multicellular glandular heads either adaxial or marginal. Flowers on long, threadlike peduncles or pedicels to sessile, terminal or axillary, solitary or, more often, in fundamentally cymose but highly variable inflorescences, these (usually) compound dichasial, sometimes simple dichasial or partly monochasial, lax and uncrowded to fasciculate, then sometimes tightly clustered into hemispheric heads or pseudoumbellate, flowering axes often between pseudodichotomous branches or forming pseudodichotomies with other axes. Flowers tetramerous, homostylous, heterostylous, or cleistogamous. Calyx lobes separate to top of ovary or briefly connate, usually deltoid or elliptic to subulate, exceptionally with claw and limb. Corolla white or greenish, or blue with a yellow or reddish eye, or pink, or variably purplish, extremely variable in length, usually pubescent within, the tube obsolete or very nearly so to several times longer than calyx, abruptly expanded at the level of the anthers or not expanded; in species with well-developed corolla tubes the corolla most often salverform to funnelform or sometimes obconical, the lobes ca. ⅕ as long as tube to much longer, spreading or erect, variable in shape. Anthers included or exserted, sessile or on epipetalous filaments, fusiform to orbicular, dorsifixed; pollen grains 3- or 4-colporate, reticulate. Ovary inferior, each of the 2 locules with a peltate placenta bearing numerous reportedly hemianatropous or anatropous ovules; stigmatic lobes 2, included or exserted, long and threadlike to short and stubby, nearly sessile or on a long, filiform style. Fruit a capsule usually compressed perpendicular to the generally sunken septum, much broader than long to cuneiform, often apically emarginate, inferior to almost superior, usually conspicuously belted by calyx sinuses and/or corolla scar, adorned with persistent calyx lobes, primarily loculicidally dehiscent but not rarely also septicidal; dehiscence usually restricted to the apex (but sometimes indehiscent); seeds numerous, minute, rugose to fairly smooth, dark, subglobose to angular or flattened, containing initially nuclear [or exceptionally cellular] endosperm. Megagametophyte (embryo sac) of the Polygonum type. (Including *Oldenlandia* L., *Houstonia* L.) LECTOTYPE SPECIES: *H. Auricularia* L. (discussion in text). (Name from Greek, *hedys,* sweet, and *otos,* ear, in reference to habit of plants; see Linnaeus, Philosophia Bot. 179. 1751.)

A vaguely circumscribed, polymorphic genus, possibly with 400 species when defined broadly, almost worldwide in warm regions and with extensions into temperate areas, although nearly absent from Europe and the Soviet Union;

present in Australia, Asia (including Japan and the Malay Archipelago), the Middle East (very poorly represented), almost the entire length of Africa, and the Americas from central Argentina to southern Canada. Roughly 60 species occur in the New World, about 50 of them on mainland North America and approximately 30 in the continental United States, with about two-thirds of these reaching the range of the Generic Flora. Most North American species belong to the group often recognized as the genus *Houstonia,* and with a few exceptions, the West Indian and Central and South American species belong to the group often recognized as the genus *Oldenlandia.*

The interrelationships and taxonomic status of *Hedyotis, Houstonia, Oldenlandia,* and a number of additional extralimital genera have been controversial for centuries and remain inadequately investigated, especially from a worldwide perspective. The disparate circumscriptions and diagnostic characteristics given by different authors cloud the usage of all three names and make it impossible to characterize the segregate genera crisply. The following sketch comes from the literature (see especially Gray, 1860; Lewis, 1961). It must be stressed that the validity of the distinctions changes with the varying concepts of the groups, that much of the variation is continuous, that most of the distinctions rest upon inadequate sampling, and that exceptions and overlap abound.

Oldenlandia sensu stricto is variously estimated to have from 80 to around 300 species, depending on its delimitation when recognized as a genus. Its distribution is almost worldwide in warm regions; it is best represented in the Old World tropics, with a center of diversity in Africa (see Bremekamp, 1952, for a revision of African species; also see Lewis, 1965, under subfamily references). About 15 species are distributed in America from the southern limit given above for *Hedyotis* to New York (*H. uniflora* (L.) Lam.). *Hedyotis corymbosa* (L.) Lam., *H. lancifolia* Schum., and *H. herbacea* L. are Old World species reported as weeds scattered in the American tropics. No fewer than three endemic species have been named from Cuba (see Alain). Five or six species (listed below) are found in the continental United States, all of them reaching the area of the Generic Flora.

Tendencies toward a slender, herbaceous habit, narrow leaf blades, homostylous flowers (for a list of 39 exceptions, see Bahadur, 1963), short corolla tubes, hemispheric placentae partitioned and sessile or inconspicuously stalked from the center of the septum (vs. placentae of irregular shape and stalked from base of septum in other species of *Hedyotis,* according to Hayden), completely inferior ovaries, thin, loculicidal capsules, and numerous tiny, angled or nearly spherical seeds lacking hilar ridges and containing fleshy endosperm have been set forth as distinctive features of *Oldenlandia.* (Hayden (p. 21) rejected the endosperm character as "completely useless.")

Houstonia comprises about 40 species nearly limited to North America; a few of them are rare and possibly introduced in the West Indies, and *H. serpyllacea* Schlecht. thrives in Guatemala. Roughly half the species reach the continental United States, and slightly over half of these occur in the area of the Generic Flora. The others are confined to the Southwestern States. Three species extend from the Southeast as far north as southern Canada, with the natural northern limit being about 54 degrees north latitude (see Scoggan). North of our range, Carr described from southwestern Virginia *Houstonia setiscaphia,* which Terrell (1959; also see Uttal) reduced to synonymy with *Houstonia canadensis* Willd. ex Roemer & Schultes (*Hedyotis canadensis* (Willd. ex Roemer & Schultes) Fosb.).

Species of *Houstonia* tend to have an herbaceous habit, comparatively wide leaf blades, heterostylous flowers, long corolla tubes, partly superior, fairly thin, loculicidal capsules, and relatively few, large seeds flattened parallel to the placenta, these concave toward their peltate attachments, often with hilar ridges, and containing corneous endosperm. Fosberg (1941, 1954), Fosberg & Terrell, Greenman, Lewis (most papers cited here), Lewis & Terrell, Shinners (1949), Standley (1918), Terrell (most cited papers), Terrell and colleagues, and Yelton, among others, have studied the taxonomy and related aspects of *Houstonia.*

Potentially of interest in connection with the relationship between *Houstonia* and *Oldenlandia,* the two studied species of *Houstonia* have "naked" or "undifferentiated" ovules not showing an obvious integument separated from a nucellus. Homologies of the exposed layer are not certain (cf. Lloyd; Fagerlind; Roth & Lindorf). Numerous sources (Fagerlind; Siddiqui & Siddiqui; Farooq, 1953, 1958; Farooq & Inamuddin; Raghavan & Rangaswamy; Rao & Babu; Shivaramaiah & Rajan; Shivaramaiah & Rao), on the other hand, agree that species of *Oldenlandia* have ovules with one integument and a reduced nucellus of one or a few cells. More study in *Houstonia* is needed before the difference can be given much taxonomic weight.

Hedyotis sensu stricto, comprising over a hundred species restricted to warm Asia, is ordinarily more woody and shrubby than the two preceding "potential" genera. Additional characteristics are fimbriate stipular lobes, axillary inflorescences, short corollas, sometimes hard, thick, indehiscent or septicidal fruits, and variably shaped (but not concave) seeds. Sinuses between the persistent calyx lobes on the capsules have been said to be narrower than in *Oldenlandia.*

The principal proponent of maintaining all three genera as distinct is Terrell, whose conclusions (1975b) are given credence by his study of a broad spectrum of herbarium specimens, mostly from the New World. He pointed out that *Oldenlandia* and *Houstonia* differ in base chromosome numbers, except in morphologically divergent species. His comparison of type species of the three groups does demonstrate a level of variation consistent with the recognition of three genera but leaves the question of intermediates untouched. (Note, as explained below, that Terrell and I accept different lectotype species for *Hedyotis.*) Subdividing the assemblage into three or more genera requires a willingness to draw rather arbitrary lines to break up a large, awkward, heterogeneous assemblage. Verdcourt (1976) indicated that the cumbersome nature of the complex and its heterogeneity justified partitioning it into multiple genera.

With some trepidation I interpret the case for a broad view of *Hedyotis* as slightly more convincing. In 1961 Lewis (p. 221) concluded with detailed documentation that "no character currently in use" distinguishes *Houstonia* from *Oldenlandia* and added that admittedly incomplete cytological evidence favors the union. His efforts focused chiefly on American species, and he appears to have had mixed feelings about the status of species from the Old World (see pp. 217 and 221 (footnote)). By incorporating the lectotype species of *Oldenlandia, Hedyotis corymbosa,* under *Hedyotis,* he made it necessary to regard *Oldenlandia* as a name in synonymy, although later (1964) he separated *O. corymbosa* from *Hedyotis* and recognized *Oldenlandia* as a genus. Along with Terrell and others, he coauthored a paper in 1986 explicitly holding *Oldenlandia* to be distinct (but see p. 113 for doubts).

Lewis cited palynological evidence in 1965 to support joining *Houstonia* with *Hedyotis.* Further, Fosberg (1937, 1941, 1943b, 1954; Fosberg & Terrell), stressing that the differences are weak and/or break down, followed by Shinners (1949), has maintained that *Oldenlandia, Houstonia,* and *Hedyotis* are insufficiently distinct to stand separately, a position that I find especially convincing in view of the geographic breadth of the sampling that stands behind it. McVaugh (p. 160) dismissed the differences between *Hedyotis* and *Houstonia* as evidently "largely traditional rather than morphological."

Since all three generic names have equal priority, the name to be adopted for the genus encompassing the trio depends on the choices made by the earliest authors to unite them. Lamarck selected *Hedyotis* over *Oldenlandia* in 1792, and Kunth likewise chose *Hedyotis* in 1820 upon placing *Houstonia* in synonymy.

Encircled by a crowd of potentially separate genera, mostly from the Old World, *Hedyotis* is not a sharply defined unit, even containing both of our potential segregates, and cannot be readily characterized in a universally acceptable manner. Fosberg (1943b) listed the attributes of the genus taken broadly. The following enumeration of characters is based mostly upon Fosberg's. *Hedyotis* sensu lato has tetramerous flowers with valvate corollas and equal calyx lobes; stigmatic lobes or branches receptive ventrally; expanded, fleshy, peltate placentae; and capsular or dry indehiscent fruits moderately flattened and with sclerified endocarps. The numerous seeds are often inserted peltately or are taller than broad and are neither imbricate nor horizontal. They lack lateral wings, except for thin edges at the angles. For a discussion of the position of *Oldenlandia* among its African relatives, see Bremekamp (1952).

Hedyotis and *Pentodon* are our representatives of the sizable tribe Hedyotideae (for comparison see *Pentodon*). Bremekamp (1966) and Verdcourt (1976) differed in their characterizations of the tribe, although they agreed that members usually have bilocular ovaries containing numerous ovules. Bremekamp further characterized the tribe as having valvate corolla lobes, peltate placentae inserted at the middle of the septum (Verdcourt said at the base), relatively thin testa cells, and nonconnivant anthers opening by slits. Verdcourt included capsular fruits. (See introduction for remarks on the position of the Hedyotideae.)

A handful of species in our area and several others from outside of it have been included in *Anotis* DC. (or *Anotis* auct.), which Lewis (1966b) determined to be an unnatural assemblage containing American species better placed in *Hedyotis.*

In 1962 and 1965 Lewis developed a phylogenetic hypothesis for five informal subgroups of subg. HOUSTONIA in North America, taking into consideration chromosome numbers, apertural fine structure in pollen grains, distributions, and relative levels of advancement as judged from morphological characters. Soon thereafter, Hayden added characters from seed coats. The trunk of Lewis's phylogenetic tree (1965, p. 263) culminates in "Group 2," having the base chromosome number of $x = 11$, a widespread number among Rubiaceae, and thus thought likely to have remained unchanged from the original stock of the subgenus. "Group 2" is confined to southwestern North America, the most likely port of entry and hub of radiation from the American tropics.

Lewis (1962) attributed the level of morphological specialization lower than that of "Group 2" to "Group 1," hypothetically isolated by ancient climatic changes to Baja California, an area possibly "not requiring major adaptations" (1962, p. 864). He went on in 1965 to interpret the pollen of "Group 1" as likewise least specialized and probably relictually similar to pollen in other subgenera of *Hedyotis* and other genera of Hedyotideae. If Lewis is correct, the base chromosome number of $x = 13$ in "Group 1" reflects an aneuploid climb from the ancestral $x = 11$.

An apparent descending aneuploid series along with presumed morphological and palynological specialization in the species toward the end of the series led Lewis to derive "Group 3" ($x = 11$–9), found in the United States and Mexico, from the stem of "Group 2," and "Group 5" ($x = 7, 8$) from the stem of "Group 3." At first glance, the eastern North American "Group 4" might be assumed to be closely related to "Group 5" since the base chromosome number of $x = 6$ (as counted by Lewis) in "Group 4" suggests the next step of the descending aneuploid sequence, but the seemingly unspecialized gross morphology, seeds, and comparatively large chromosomes observed in "Group 4" contradict such a position. In 1965, Lewis used pollen structure to link "Group 4" to "Group 3," and I infer support for this from Hayden.

In 1986 Terrell, Lewis, Robinson, & Nowicke reevaluated species relationships within *Houstonia,* using mostly characters from seed morphology, chromosome numbers, and pollen (with special attention to ora). They set up a dozen "species-groups," seven of which consist of only one or two species. The others correspond roughly to Lewis's groups 1–5, although there were several differences in membership, and the authors of the 1986 paper did not formally connect the new groups with the old. They did conclude that the new groups, except for the intermediate "*H. nigricans* group," fall into two "basic series." To paraphrase their summary, one series (not a formal nomenclatural series) has a haploid chromosome number of $n = 13$ or more (vs. $n = 11$ or less), ellipsoid or sublenticular noncrateriform (vs. crateriform) seeds, and colporate pollen with the nexine merely thin in the equatorial portion of the aperture (vs. grains colporate or the ora with thickened margins). They deferred making taxonomic changes until more data were gathered.

Examining 116 collections from the *Hedyotis purpurea* and *H. caerulea* "groups," Lewis & Terrell came across frequent intraspecific euploid variation in ploidy level but very little intraspecific aneuploidy. In two species the polyploids were separated geographically from the diploids and appeared to be colonizers—no marked geographic separation between the ploidy levels was detected in the remaining species. The authors could not distinguish individuals with different ploidy levels morphologically, which led them to attribute multiplication of chromosome sets to autoploidy rather than alloploidy, even though meiosis was mostly normal. Variability in chromosome number seemed to be connected with heterostyly and a perennial habit.

Divergent generic concepts have contributed to the profusion of names of species and infraspecific taxa recorded as occurring in the range of the Generic Flora. Beyond the problem of species and their varieties appearing under multiple generic names, botanists have achieved so little agreement concerning ranks, definitions, and names of taxa in our area that the most recent revision covering our species (by Standley, 1918) is obsolete, and subsequent sources disconcertingly contradictory. Therefore, a complete list of the species in the Southeast is currently impossible. The summary that follows rests heavily on the work of Fosberg, Lewis, and Terrell. (It is based entirely on literature—I have conducted no comparative study at the species level.) Full synonymy and consideration of questionable species lie beyond the scope of the present effort.

Subgenus OLDENLANDIA (L.) Fosb. (not accepted here as validly published by Torrey & Gray) includes in our area *Hedyotis Boscii* DC., $n = 18$; *H. callitrichoides* (Griseb.) Lewis, $n = 11$, also in Africa, probably as an introduction from the New World tropics; *H. corymbosa*, $n = 9, 18, 27$; *H. Salzmanii* (DC.) Steudel (*Oldenlandia thesiifolia* (St.-Hil.) K. Schum., introduced from South America; see Fosberg & Terrell), $n = 15$; and *H. uniflora* (including *H. fasciculata* Bertol. or not), $n = 18, 36$.

Subgenus HOUSTONIA (L.) A. Gray (Man. ed. 1. 180. 1848, see Brizicky) (subg. *Edrisia* (Raf.) Lewis[3]) corresponds to *Houstonia*, if recognized at the generic level, and as discussed above, has been broken down into informal subgroups.

"Group 3" in subg. *Houstonia* is represented by *H. nigricans* (Lam.) Fosb. (*Houstonia angustifolia* Michx.; see Fosberg, 1954, and Long & Lakela), $n = 9$ (10).

Subgenus HOUSTONIA, Group 4, is the *Hedyotis* or *Houstonia purpurea* "group" revised by Terrell (1959), who remarked on a high percentage of intergradation and geographic variation involving every species. Terrell suspected hybridization and introgression to have played significant roles in producing the pattern of variation; pairs of species seemed to interbreed at some places but not at others. In connection with the probable hybridization, it is of interest to note that Lewis (1962) encountered almost uniformly normal meiosis in his cytological survey of the genus in North America, and Fosberg (1943b, p. 15) described hybridization as "little evident" among Hawaiian species, despite "tremendous evolutionary activity." Most species of the *H. purpurea* group have polyploid races in addition to diploids (Lewis & Terrell). Terrell took a

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[3] Upon publishing subgenera in *Houstonia*, Rafinesque (Ann. Gén. Sci. Phys. **5:** 225 (13 in reprint). 1820) automatically created subg. *Houstonia*, which he called *Houstonia* subg. *Edrisia*. By ICBN Article 57.3, the combination in *Hedyotis* formed by merging the original subg. *Houstonia* and Rafinesque's other subgenera into one subgenus must be called by the generic name, not subg. *Edrisia* (Raf.) Lewis (Am. Jour. Bot. **49:** 858. 1962).

relatively narrow view in recognizing four species as opposed to Fosberg's (1954) placement of the entire complex in *H. purpurea* (L.) Torrey & Gray. Whether or not most components of the complex should be treated as varieties of *H. purpurea* or as distinct species, our representatives can be listed as follows: *Hedyotis purpurea* (including or not *Houstonia montana* Small; cf. Yelton; Terrell, 1978; Kral), $n = 6, 12$; *H. longifolia* (Gaertner) Hooker (including or not *Hedyotis Nuttalliana* Fosb. = *Houstonia tenuifolia* Nutt.; see especially Smith; the latter accepted as a species by Terrell in 1959), $n = 6, 12$; *H. canadensis*, $n = 6, 12$; and *H. ouachitana* E. B. Smith (here presumed to belong to "Group 4").

"Group 5" is represented by *Hedyotis australis* Lewis & Moore (*Houstonia micrantha* (Shinners) Terrell; see Terrell, 1975a; Lewis & Moore), $n = 16$; *H. caerulea* (L.) Hooker (including or not *Hedyotis crassifolia* Raf. = *Houstonia pusilla* Schoepf and *Houstonia patens* Ell., according to Lewis & Moore, $n = 8, 9, 16, 24$ (but see Löve & Löve for reservations); *H. Michauxii* Fosb. (*Houstonia serpyllifolia* Michx.), $n = 16, 24$; *H. procumbens* (J. F. Gmelin) Fosb., $n = 14$ (see Gaddy & Rayner); and *H. rosea* Raf., $n = 7$ (see J. E. Moore; Taylor & Taylor; Waterfall).

Seeds of *Hedyotis corymbosa* have been the subject of a series of studies (see Corbineau & Côme for an entry to the literature). While the physiological results are outside the scope of the present paper, a few salient ecological discoveries deserve mention. The seeds are dimorphic in that for germination some are "dormant" and require stratification while others do not. Artificial selection led to two lines of plants, one of which produces seeds showing no need for stratification. The other produces a mix of the two types of seeds, with the percentage of "dormant" seeds increasing as the season progresses. All demand warm temperatures and must be activated by exposure to light, although (at least in those not requiring stratification) the effects of light are variable, with a number of parameters. "Dormant" seeds are strongly inhibited from germination at a concentration of oxygen as high as that in the atmosphere, except after a sufficient period of stratification.

The citation of a lectotype for *Hedyotis* still requires choosing between alternatives. Of three species comprising the genus in Linnaeus's *Species Plantarum, H. herbacea* can be eliminated from consideration first. Although it dates back, along with *H. Auricularia* and *H. fruticosa,* to the year Linnaeus first published *Hedyotis,* it is missing from one of the two generic treatments appearing that year (in 1747a but not 1747b). For this reason and also since authors (see Bremekamp, 1939, 1952) have removed it to *Oldenlandia* (see ICBN T.4.e), since it was least known to Linnaeus, and since two different lectotype species have already been proposed, it is unsuitable as a choice. Ruling out *H. herbacea* has never provoked disagreement—the problem lies in settling on one member of the remaining pair.

As background for discussing the conflict, it is worthwhile to note that Linnaeus's description of *Hedyotis* is repeated essentially verbatim in all Linnaean publications cited in the present context, including the nomenclaturally decisive fifth edition of the *Genera Plantarum.*

The best choice for lectotype does not shine forth from recognition of Linnaeus's frequent practice of basing generic descriptions on single species. Both potential lectotype species were well known to Linnaeus from literature and specimens when he wrote the generic description, and examination of the works he cited reveals neither species as focal. (The only source I have not examined is "Marlow. obs.," cited more extensively by Dale and probably the "Marloe" discussed by Jackson.)

Nor is a single species revealed as central by Bremekamp's (1939, 1952) selection of *Hedyotis fruticosa* as lectotype, chiefly on the grounds that it, but not *H. Auricularia,* agrees with the generic description in having dehiscent fruits. (He pulled *H. Auricularia* out of *Hedyotis* as type species of his new genus *Exallage* in 1952.) Dehiscence, however, could not have entered the generic description via *H. fruticosa,* about which Linnaeus (1747a, p. 26, no. 63) admitted, "De fructu nulla nobis certitudo."

Fruits of *Hedyotis Auricularia* were described (although with no mention of dehiscence) in works Linnaeus cited (e.g., Burman). Bremekamp (1939) himself suggested quite plausibly that Linnaeus's failure to register fruits of *H. Auricularia* as indehiscent could have resulted from misinterpretation of them as immature, assuming their presence on the original specimens.

That *Hedyotis Auricularia* deviates from the generic description in this possibly minor character does not show the description to rest on *H. fruticosa*: the information in the generic description that is at odds with *H. Auricularia* did not originate with *H. fruticosa,* and Bremekamp did not show *H. fruticosa* to match the generic description better. Bremekamp's case, then, is based mostly on an error and is incomplete. As explained below, I reject his supplementary contention that Blume rendered *H. Auricularia* "illegitimate" as lectotype in 1826 by placing what Bremekamp regarded as a synonym under the generic name *Metabolos* Blume. Bullock and Terrell (1975b) accepted Bremekamp's lectotypification.

The 1983 International Code of Botanical Nomenclature (Art. 8.1) rules that the first lectotype chosen can be unseated only if demonstrated to be "in serious conflict with the protologue." If it is agreed that *Hedyotis Auricularia* has not been thus exposed, it cannot be displaced (even if it was placed in *Metabolos* under a different name), having been cited twice as typifying the genus before Bremekamp's opposing choice. Chamisso & Schlechtendal designated *H. Auricularia* "typus" in 1829 (accepted by Fosberg, 1943b; also see Wight & Walker-Arnott), although it can be objected that the early use of "typus" is not equivalent to the modern designation of a lectotype. That, however, may be a moot objection, since Hitchcock & Green selected *H. Auricularia* as "standard species" a century later but still ahead of Bremekamp.

In the interest of future investigations, it may be useful to stress that the large number of species of *Hedyotis* in the broadly stated type locality for both potential lectotypes, Sri Lanka, intensifies the hazard of working with incorrectly identified specimens. Types are presumably in the Hermann herbarium at BM (see Trimen). Several specimens of *Hedyotis,* including one labeled *H. Auricularia* by Linnaeus and another labeled *H. fruticosa,* are in the Linnean Herbarium. The latter disagrees with the *foliis lanceolatis* Linnaeus attributed to *H. fruticosa* in the *Species Plantarum,* for it has broad, mostly ovate leaf blades. (According to Stearn (p. 94), Linnaeus applied "lanceolatus" to blades "oblong, but gradually tapering towards each extremity and terminating in a point, the greatest width being at the middle, not below" (also see p. 91, *fig. 6*).)

Preparations from species of *Hedyotis* sensu lato serve as folk remedies around the world. *Oldenlandia affinis* (Roemer & Schultes) DC. (*Hedyotis affinis* Roemer & Schultes), which is given to hasten childbirth in Africa, contains the oxytocic phenolic amine serotonin and two oxytocic proteins. Practical modern usage is hampered by the toxicity of serotonin and at least one of the proteins, and both compounds are ineffective when administered orally to laboratory animals (Gran, 1973a, b, d). Topical uses for oldenlandias are common and could, at least in some cases, as exemplified by *Hedyotis diffusa* Willd., be related to the presence of antiinflammatory iridoids.

The red dye "Indian madder" or "chay-root" from the commercially cultivated *Oldenlandia umbellata* L. colors turbans and other products in India. Extracts from this species are also used in treating tuberculosis. Roots of *Hedyotis corymbosa* yield the green (after chemical treatment) dye gerancine, and bark from roots of *H. herbacea,* as well as leaves from *H. scandens* Roxb., likewise color fabrics. Capsules from *H. scandens* have been used to blacken teeth.

Leaves of *Hedyotis Auricularia, H. scandens,* and *H. nitida* Wight & Arnott are eaten in Asia. *Hedyotis fruticosa* is a minor source of wooden rods. For further information on *Hedyotis* as a medicine and on its other uses, see Datta & Sen, Lin *et al.,* Morton, Sastri *et al.,* Simmonds, and Usher.

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3. **Pentodon** Hochstetter in Krauss, Flora **27:** 552. 1844.

Hygrophilous, prostrate or feebly erect, fleshy, glabrate herbs, usually extensively branched, frequently pseudodichotomously so, often tufted with numerous basal branches; branches more or less quadrangular. Raphide bundles conspicuous on surfaces of most organs when dry. Leaves opposite, nearly sessile or on short, winged petioles, the blades (obovate to) lanceolate or ovate, penninerved, usually minutely scabrous adaxially and marginally, rounded to more often acute or acuminate at the apex, the base usually acute to cuneate or sometimes rounded; stipular sheaths continuous with the flanges on the petioles, membranaceous, interpetiolar, usually fimbriate, occasionally entire, sometimes cuspidate in the center. Inflorescences mostly terminal, sometimes axillary, usually between a pair of pseudodichotomous branches, fundamentally dichasial or monochasial, sometimes with only 1 or 2 flowers, lax with long axes, sometimes compound and sometimes paniculate with straight main or branch axes; bracts and bracteoles mostly distinctly reduced [or foliose]. Flowers pedicellate, pentamerous, small and inconspicuous, perfect, homostylous [or heterostylous in *P. laurentioides* and *P. pentandrus* var. *minor,* or "pseudoheterostylous" in some African members of *P. pentandrus* var. *pentandrus* having the anthers in fairly uniform position in the throat of the corolla but the styles varying in length]. Calyx lobes connate basally into a short tube topped with lanceolate or deltoid teeth ¼–¾ the length of the corolla. Corolla nearly cylindrical but slightly [to broadly] flared, white [or reddish or blue], pubescent or (reportedly) glabrous in the throat, the lobes usually about ¼–⅓ the length of the corolla. Stamens inserted near the throat of the corolla tube [or low in the tube in heterostylous flowers], uniform in length and included [or exserted in short-styled flowers]; anthers dorsifixed, elliptic-oblong; filaments shorter than anthers; pollen grains prolate or subspheroidal, tricolporate, reticulate. Ovaries bilocular, containing numerous ovules on apically bilobed, peltate placentae inserted on the septum; styles long enough to bear slightly exserted [or included] stigmas, at least sometimes markedly thickened at the level of the anthers beneath the stigmatic lobes, the thickening covered with pollen and, in conjunction with a pilose ring at the same level, occluding the throat of the tube; stigmatic lobes 2, linear. Capsules bilocular, crowned with persistent calyx tube and teeth, thin walled and papery, obconical or obturbinate, somewhat compressed contrary to the septum, bearing 5 longitudinal keels corresponding to the midlines of the adherent sepals, dehiscing loculicidally across the summit. Seeds numerous, minute, angular, brown, fairly isodiametric, on the surface reticulate from outlines of testa cells, these with irregular thickenings in the lateral walls. Type species: *P. decumbens* Hochst. = *P. pentandrus* (Schum. & Thonn.) Vatke *fide* Bremekamp (1952); this the sole original species. (Name from Greek, *pente,* five, and *-odon,* toothed, presumably in reference to the five toothlike calyx lobes.)

Probably consisting of only two species, *Pentodon laurentioides* Chiov., endemic to Somalia, and *P. pentandrus,* $2n = 18$, distributed in the Old World across much of tropical Africa and on the southern Arabian Peninsula, Madagascar, the Seychelles, and the Cape Verde Islands. The latter, or possibly a third species, *P. Halei* (Torrey & Gray) Gray (*Hedyotis Halei* Torrey & Gray, *Oldenlandia Halei* (Torrey & Gray) Chapman) is scattered across much of Florida and occurs in southern Georgia, Louisiana, Texas, the West Indies (at least Cuba, the Bahamas, and Guadeloupe), and according to Verdcourt (1976), Nicaragua and Brazil. (I have seen no trustworthy documentation of *Pentodon* from either Mississippi or Alabama.)

Opinion is divided as to whether *Pentodon Halei* is conspecific with *P. pentandrus.* Standley (1918) held the latter to differ from *P. Halei* in having pubescence within the corolla, longer peduncles relative to the leaves, racemose (vs. cymose) inflorescences, and more slender (vs. "clavate") pedicels longer relative to the capsules. This list probably exaggerates the differences—corollas from *P. Halei* that I examined are distinctly pubescent within, and Bremekamp (1952, p. 180) found the distinctions to break down so far as to be "of little importance," if the range of variation in African specimens is considered. He attributed differences in the inflorescence characters largely to differences in the vigor of the plants, which he assumed to be reduced in the marginal North American climate. Noting that the American material has small, elliptic leaves and shorter inflorescences than most African specimens, Verdcourt (1976, p. 263) agreed that *P. Halei* "cannot be specifically distinct" from *P. pentandrus* and agreed further with Bremekamp in suspecting introduction from Africa as lying behind the New World populations of *Pentodon.* Its widely scattered stations speak in favor of an appreciable ability to disperse. As Verdcourt has already noted, better data on the distribution of modifications to the style, as described below, could shed some light on the relationships among the widely separated populations.

Pentodon appears to be most closely related to *Hedyotis* (especially subg. Oldenlandia), in which it has been included, and from which it differs by the pentamery (vs. tetramery) of its flowers and the distinctive thickenings on the lateral walls of testa cells. Additional features that help to characterize *Pentodon* are its apically bilobed placentae; thin, papery pericarps; and seeds not producing mucilage upon moistening. (This paragraph is based largely on Bremekamp, 1952, and Lewis, 1965a, and verified for *Pentodon* through herbarium specimens.)

Pentodon laurentioides and *P. pentandrus* var. *minor* are heterostylous (for an illustration of the two floral morphs in var. *minor,* see Verdcourt, 1976).

The other members of the genus show two curious variations of the breeding system that call for further research. In the simpler case, the two flowers of *P. pentandrus* from our area that I have been able to examine internally (*Duncan 21650,* Georgia, A, and *Thomas et al. 72765 & 474,* Louisiana, GH) have had the style swollen apically and coated with pollen at the level of the anthers just below the stigmatic lobes. The swelling was so positioned that, in conjunction with the pilose ring borne on the tube, it would partly block entrance to the corolla tube. Except for a thickened stylar apex (with stigmas missing) illustrated in Godfrey & Wooten, I have seen no other indication of the thickening or of adherent pollen for either African or American specimens. The functional role of this condition, if any, will be best elucidated by field observations.

The second curiosity comes from Bremekamp (1952; also see Verdcourt, 1976), who described two floral morphs in African plants of *P. pentandrus* var. *pentandrus.* The styles on different individuals are either of two lengths, included or exserted, but the plants are not heterostylous in the conventional sense of the term, since all flowers have included stamens. Bremekamp indicated that the two morphs were geographically separated, although only on a local scale; both are widespread in Africa.

This raises the question of the condition(s) in American populations. By using bright transmitted light, I have consistently seen the anthers to occupy about the same level in the corolla throats in all examinable flowers from our area in the Harvard herbaria; all of the stigmas that I saw projected slightly beyond the anthers. Moreover, the relative positions of stamens and stigmas in the flower from the Bahamas illustrated by Correll & Correll are the same as I observed on the mainland specimens; this seems also to be true of the flowers shown by Small and by Godfrey & Wooten, although the long style is depicted in each as detached, making its exact position relative to the stamens indiscernible. Still, because the sampling so far is scanty, and because short, included styles could be overlooked in an examination by transmitted light, it would be premature to rule out the presence of such styles in the United States.

Pentodon pentandrus flowers in our area from May into October along shores and in periodically flooded spots, swampy woods, and other low, wet sites.

An incidental note potentially useful in the field, pointed out by Dr. Robert Kral (pers. comm.), is that in habit and overall appearance, *Pentodon* looks deceptively like *Lindernia crustacea* (L.) F. Mueller, an introduced scrophulariaceous weed in Florida.

Economic uses for this genus are negligible.

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FOURNET, J. Flore illustrée des phanérogames de Guadeloupe et de Martinique. 1654 pp. Paris. 1978. [*Pentodon,* 1160, 1161; illustration copied from HALLÉ and based on an African specimen, this probably also true of mention of exserted anthers in addition to included ones.]

Hallé, N. Rubiacées. Pt. 1. Fl. Gabon **12:** 1–278. 1966. [*Pentodon,* 105, 106; detailed illustrations, 77, 107.]

Schwartz, O. Flora des tropischen Arabien. Mitt. Inst. Allg. Bot. Hamburg **10:** 1–393. 1939. [*Pentodon,* 261.]

Wood, J. M., & M. S. Evans. Natal plants. Vol. 1. 83 pp. *100 pls.* Durban. 1898. [*Oldenlandia macrophylla* (*P. pentandrus*), 31, *pl. 36,* stamens slightly exserted.]

Tribe Cinchoneae DC. Ann. Mus. Hist. Nat. Paris **9:** 217. 1807, "Cinchonacées, Cinchonaceae."

4. **Exostema** (Persoon) L. C. Richard ex Humboldt et Bonpland, Plantae Aequinoctiales **1:** 131. 1808 [1807].

Vegetatively glabrous to less often hispidulous or hirsute shrubs or small trees, the branches symmetrical, sometimes supported by surrounding vegetation. Leaves opposite, petiolate [or nearly sessile]; stipules interpetiolar [or reportedly intrapetiolar], broadly deltoid to drawn out into attenuate apices, marginally ciliate, keeled when young [sometimes bilobed]. Flowers borne singly on short pedicels in axils of upper leaves [or terminal; in cymes, thyrses, or panicles in some species], pentamerous [or tetramerous], actinomorphic or nearly so, fragrant. Calyx teeth broadly deltoid [to subulate], much shorter than corolla tube. Corolla with slender cylindrical tube [less than 1 cm to] several cm long (ca. 2–5 cm in our species) [20 cm or more in *E. longiflorum* Roemer & Schultes], white, yellowish, or pinkish [red or purplish], said to change from white to darker hues in some species including ours, the 5 [4] linear-ligulate lobes about as long as the tube or a little [or much] shorter, twisted-imbricate in bud. Stamens exserted [rarely included], epipetalous near base of tube [or reportedly inserted on receptacle], the linear, basifixed anthers long (10 mm or more in our species). Style filiform, much exserted [or infrequently included], thickened apically beneath a pair of stubby stigmatic lobes [or stigma reportedly unlobed]. Capsule ellipsoid, truncate apically, crowned with persistent calyx teeth [or teeth deciduous], dark colored, rugulate, septidical (and sometimes splitting loculicidally to varying degrees); placentae large, flat, detached from septum of dry and dehisced capsule. Seeds numerous, wafer thin, surrounded by a narrow marginal wing, vertically imbricate; endosperm abundant; embryo with radicle longer than the elliptic cotyledons. Lectotype species: *E. caribaeum* (Jacq.) Roemer & Schultes.[4] (Name from Greek, *exo,* out, and *stema,* stamen, in reference to the exserted stamens.)—Princewood.

A genus of some 35 or more species in tropical and subtropical America, mostly in the West Indies, but also with a poorly studied group of roughly

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[4] Britton & Millspaugh's choice of *Exostema parviflorum* A. Rich. as lectotype (in Bahama Fl. 409. 1920) cannot be followed. This species is ruled out by ICBN (1983) Article 7.10, since this was not a member of the group to which Persoon applied the basionym *Cinchona* subg. *Exostema* Persoon (Syn. Pl. **1:** 196. 1805; cited by Richard on p. 135). (See Brizicky for comments on Persoon's infrageneric taxa.) *Exostema caribaeum* is here designated as lectotype—Persoon included it, and it is the most-widespread and best-known species.

seven species on the mainland in southern Florida (see below), Mexico, Central America, and (chiefly western) South America as far south as Peru (four species?) and southern Brazil (one species; see Angely).

Exostema caribaeum ranges along the full length of the Florida Keys, is unusual on the southern tip of mainland Florida (Tomlinson), occurs throughout much of the West Indies, Mexico, and Central America, and has been reported from scattered localities along the northern coast of South America (probably present in Colombia, but doubtfully so in Venezuela and "Guiana").

Features that help with recognition of *Exostema caribaeum* are elliptic leaves pointed at both ends; solitary, axillary flowers; short, stubby calyx teeth (less than 1 mm long); fragrant, white (or pinkish or yellowish) corollas to ca. 8 cm long, including the long, nearly linear lobes, and with slender, cylindrical tubes; long (1 cm or more), basifixed anthers conspicuously exserted; and ellipsoid, apically truncate capsules containing numerous elliptic, waferlike seeds to about 5 mm long completely surrounded by a narrow wing.

Exostema is our only member of the tribe Cinchoneae (woody plants with bilocular capsules containing numerous vertically or nearly vertically arranged, imbricate seeds having pitted testa cell walls). The genus was once included in *Cinchona* L., from which it differs in its exserted stamens and its imbricate (vs. valvate) corolla lobes. Koek-Noorman & Hogeweg found *Exostema* to differ further from *Cinchona* in having fiber tracheids in the wood, rather than fibers transitional between fiber tracheids and libriform fibers, although broadened sampling is needed to bolster the strength of this character. Additional features that help to separate *Exostema* from other members of the Cinchoneae are uniform calyx lobes, five or sometimes four corolla lobes, and slender, round, symmetrical corolla tubes. Koek-Noorman cited personal communication with C. Bremekamp in noting that the relationships of *Exostema* are unclear.

Taxonomic study of *Exostema* is both outdated and fragmentary. The most recent revision of the entire genus dates back to De Candolle, who divided it into three sections that have been ignored by more recent authors. Most of the species are covered in Standley's treatment in the *North American Flora* (1918), a picture that can be rounded out by an examination of some of his later floristic studies in the New World (1926, 1930, 1936, 1938; 1975, with L. O. Williams).

During the eighteenth century, medicinal interest in *Cinchona,* the original source of quinine as a medicine for malaria, extended to numerous species of *Exostema.* I know of no modern study aimed at relating the alleged curative properties of *Exostema* to bona fide pharmacologic effects or to its chemistry. *Exostema caribaeum* and undoubtedly other species yield a hard, strong, heavy wood that polishes well and is used for turning, cabinet work, and applications requiring durability. Because it burns readily, it has been used for torches. Species of *Exostema* with showy flowers are sometimes cultivated in the West Indies.

REFERENCES:

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Long & Lakela; Sargent; Soukup; Standley (1918, 1926, 1930, 1931, 1936, 1938); Standley & Williams; and Tomlinson.

Borhidi, A., & O. Muniz. New plants in Cuba II. Acta Bot. Acad. Sci. Hungar. **18:** 29–48. 1973. [*Exostema caribaeum* var. *pubescens,* var. nov., 44.]

——— & M. F. Zequeira. Studies in Rondeletieae (Rubiaceae) II. A new genus: *Suberanthus.* Acta Bot. Acad. Sci. Hungar. **27:** 313–316. 1981. [*Exostema neriifolium* is type species.]

Britten, J. An overlooked *Cinchona.* Jour. Bot. London **53:** 137, 138. 1915. [Also see Morgan, Warner, and Kentish. Includes no biological information or uses; concerned with history in literature and synonymy; makes combination *Exostema sanctae-luciae* with four "cinchonas" as synonyms.]

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Wright, W. Description of the Jesuits bark tree of Jamaica and the Caribbees. Philos. Trans. Roy. Soc. London **67**: 504–506. *pl. 10.* 1778. [*Cinchona jamaicensis, Cinchona caribaea* (*Exostema caribaea*).]

Tribe Naucleeae J. D. Hooker, Fl. Nigrit. 377. 1849.

5. **Cephalanthus** Linnaeus, Sp. Pl. **1:** 95. 1753; Gen. Pl. ed. 5. 42. 1754.

Deciduous (or somewhat evergreen in tropical Florida), sympodially branched shrubs (or infrequently small trees) of wet soil. Leaves opposite or in whorls of 3 (or 4), elliptic to ovate or lanceolate, usually acuminate and often cuspidate apically, the bases variable; stipules usually with 1 deltoid or ovate lobe between bases of adjacent petioles, sometimes bifid, or occasionally with 2 separate lobes between pairs of petioles, the lobe(s) with adaxial and frequently marginal colleters; foliage and twigs (especially abaxial surfaces) glabrous to densely pubescent, the indument sometimes storied and sometimes strigose; buds often multiple in leaf axils. Flowers fragrant, usually tetramerous, protandrous, tightly clustered into distinctly globose heads on long peduncles, the heads terminal or axillary, sometimes solitary, more often in racemose (or infrequently paniculate) clusters at ends of branches. Calyx much shorter than corolla, the tube topped with short, blunt teeth persistent in fruit. Corolla white or nearly so, with a narrow, cylindrical or slightly flared tube several times longer than the oblong to deltoid or ovate, imbricate, usually internally bearded lobes, these alternating with exposed glands (colleters?) in the bud and sometimes after expansion. Anthers sagittate, borne at throat of corolla tube on short, epipetalous filaments. Style filiform, about twice the length of the corolla, expanded apically into a scarcely (or not perceptibly) bifid or 4-lobed knob (*fide* Tomlinson); ovary bilocular, containing a pendulous ovule in each locule. Fruits dry, indehiscent, crowded on spherical head, each with 1 or 2 seeds, cuneiform, the halves often separating along the septum, intermixed with long, narrow bractlets, these as long as the fruits and expanded apically into pubescent knobs. Seed matching shape of locule, with a conspicuous corky caruncle (aril). LECTOTYPE SPECIES: *C. occidentalis* L.; see Haviland, Jour. Linn. Soc. Bot. **33:** 2, 3, 37. 1897; Britton & Brown, Illus. Fl. No. U. S. & Canada. ed. 2. **3:** 255. 1913; Merrill, Jour. Wash. Acad. Sci. **5:** 532. 1915. (Name from Greek, *kephale,* head, and *anthos,* flower, in reference to the spherical floral heads.)—BUTTON BUSH.

A genus of six species as circumscribed in Ridsdale's revision: *Cephalanthus natalensis* Oliver (South Africa), *C. tetrandra* (Roxb.) Rids. & Bakh. (India to Taiwan), *C. angustifolius* Lour. (southeastern Asia), *C. glabratus* (Sprengel) K. Schum. (South America), *C. salicifolius* Humb. & Bonpl. (Texas, Mexico, Central America), and our *C. occidentalis* L. (In the revision preceding Ridsdale's, Haviland recognized seven species; Ridsdale transferred two of these to *Ixora* L., changed the name of one, and added one.)

Cephalanthus occidentalis, $2n = 44$, ranges across North America virtually throughout the area defined by New Brunswick (or possibly Prince Edward Island, according to Scoggan), Cuba, Texas, southeastern Nebraska, southern Minnesota, southern Ontario, and southern Quebec. The species is absent or nearly so from the Florida Keys. A spottier distribution farther west excludes the Rocky Mountains but includes New Mexico, Arizona, Utah, California, and northern Mexico. Standley & Williams noted it in Guatemala and Honduras.

Cephalanthus occidentalis is almost exclusively an inhabitant of freshwater shores and low, wet places. It usually grows in full sun but tolerates some shading. The stands can be dense and extensive.

Distinguishing *Cephalanthus* from other shrubs in the Generic Flora area is not difficult; the restriction to wet sites is a useful character in itself. The pointed leaves are opposite or whorled and are associated with interpetiolar stipules that bear adaxial and often marginal colleters. The small, tubular, fragrant, white or nearly white flowers with long, exserted styles are packed into globose heads, a shape that remains unaltered as the fruits mature. Individual fruits are indehiscent (the halves often separate but do not open) and cuneiform; they generally contain a conspicuously caruncular seed in each locule.

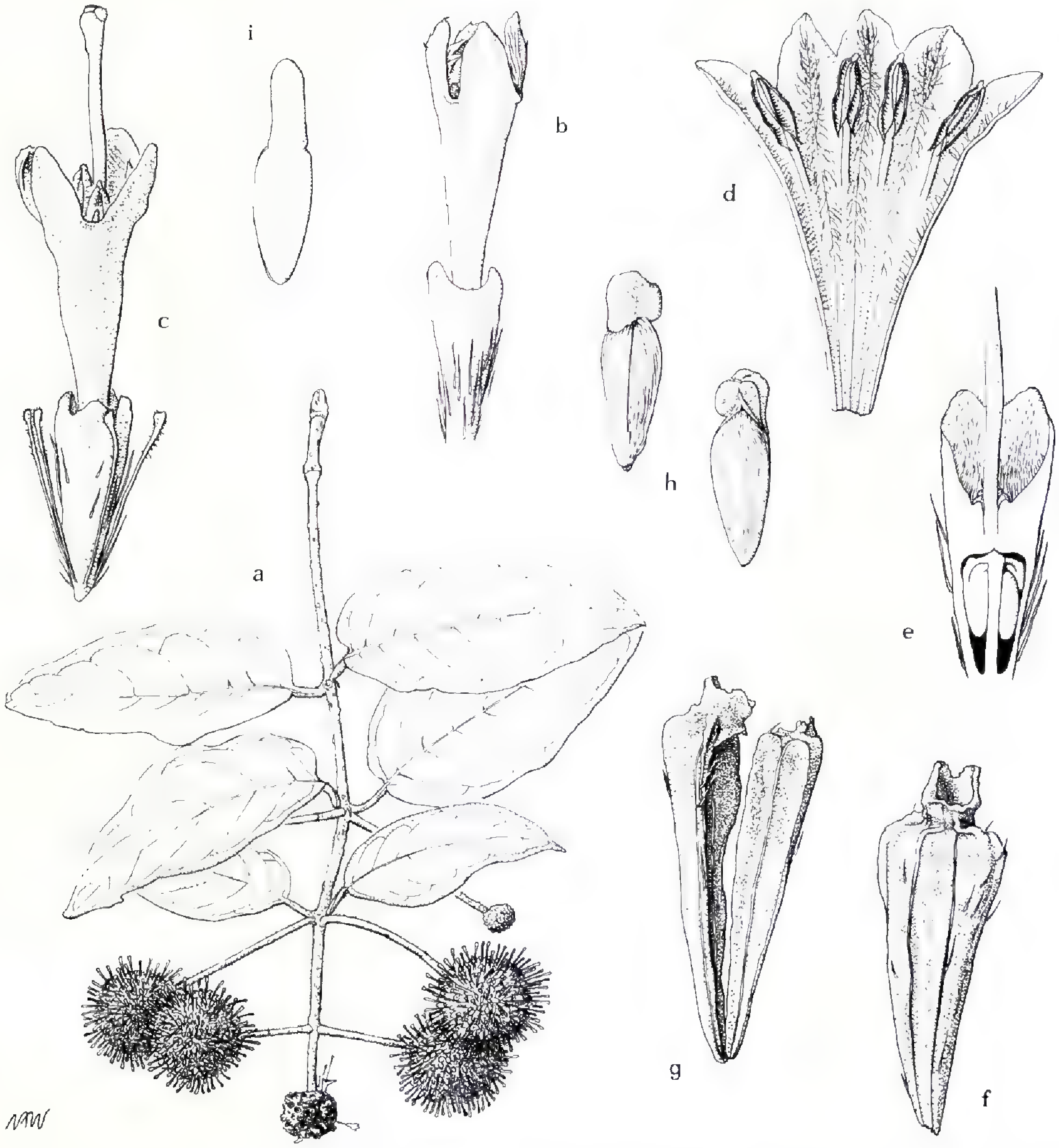

FIGURE 1. **Cephalanthus.** a–i, *C. occidentalis:* a, pendent flowering branchlet, × ½; b, flower at anthesis, style not yet expanded—note squamule between 2 corolla lobes, × 6; c, flower with mature style, the pollen shed—note bractlets at base of ovary, squamule between 2 corolla lobes, × 6; d, corolla laid open to show adnate staminal filaments, × 6; e, ovary in longitudinal section, 1 ovule (at left) in section, × 10; f, mature fruit, × 6; g, fruit splitting into 2 indehiscent 1-seeded parts, × 6; h, seed, abaxial side at left, adaxial side at right—note corky caruncle, × 6; i, embryo, oriented as in seed, × 12.

Western populations that have narrow leaves on short petioles have been set apart as *Cephalanthus occidentalis* var. *californicus* Bentham (*C. occidentalis* subsp. *californicus* (Bentham) E. Murray), another segregate that Ridsdale placed in synonymy. Fernald recognized plants with lanceolate leaves attenuate at both ends and only 1–3 cm broad as forma *lanceolatus.* Different individuals of *C. occidentalis* range from being more or less glabrous to thickly pubescent on twigs and abaxial leaf surfaces, a condition that has led some authors (e.g., Steyermark, 1963) to recognize *C. occidentalis* var. *pubescens* Raf., which is found primarily in the southern United States but has been reported from as far north as Quebec. Neither Haviland nor Ridsdale recognized the pubescent taxon at any rank, and Wells & Sharp rejected it with the observation that the two putative varieties grow together in Tennessee. My examination of herbarium specimens at the Missouri Botanical Garden inclines me to agree with these authors.

Curious threadlike structures (called bracteoles by Haviland and Tomlinson, illustrated in FIGURE 1 and in Tomlinson) are borne at the base of each flower. These are roughly as long as the ovary and are expanded apically into pubescent knobs that appear to plug the spaces between the fruits protectively.

The flowers within each head mature simultaneously and are protandrous, the pollen being released in the bud. Some grains catch in the hairs inside the corolla, and others are carried out of the tube on the apical region of the strongly exserted style. Whether all pollen delivery takes place from the style is not clear. Some wind pollination is suspected. (For more on pollination, see Robertson and Tomlinson.)

Ants may possibly play some role(s) in the life cycle of *Cephalanthus occidentalis.* "Squamules" readily interpretable as nectaries (colleters?) are conspicuous in the sinuses between unexpanded corolla lobes in the bud (see FIGURE 1b, c), and the seeds are capped with large, corky caruncles (arils). It is not inconceivable that the adaxial colleters on the stipules, too, provide nourishment for ants.

In their revisions, written in the last century, both Schumann and Haviland placed *Cephalanthus* in the tribe Naucleeae, where Haviland regarded it as closely related to the African and Asian genus *Adina* Salisb. *Cephalanthus* differs from *Adina* in having only one ovule in each locule of the ovary, indehiscent fruits, and wingless seeds. In 1976 Ridsdale revised *Cephalanthus* and isolated it as the monotypic Cephalantheae Ridsdale.[5]

Ridsdale defended his isolation of *Cephalanthus* by arguing that the tribe Naucleeae is in part artificially held together by too much emphasis on the conspicuous clustering of flowers into heads. He thought *Cephalanthus* possibly to be most closely related to *Mitragyna* Korth. and *Uncaria* Schreber, two genera he transferred from the Naucleeae to the Cinchoneae. *Cephalanthus* differs from these two in its indehiscent fruits and its single seed per locule.

In their survey of alkaloids in the Naucleeae *sensu lato,* Phillipson, Hemingway, & Ridsdale found *Cephalanthus,* along with *Uncaria* and *Mitragyna,* to deviate from the Naucleeae *sensu stricto* in producing "significant quantities" of nonquaternary nonglycosidic alkaloids of the heteroyohimbine and oxindole types. Aware of the same set of alkaloids in *Cephalanthus,* Kisakurek and colleagues agreed that the data support maintaining all three genera apart from the Naucleeae. Further, Koek-Noorman interpreted the wood structure of *C. occidentalis* and *C. salicifolius* as anomalous in the tribe, and Bremekamp

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[5] He attributed the authorship to Kunth in HBK., where Cephalantheae appeared, as Ridsdale acknowledged, as a "sectio." Although "Cephalantheae" has been used repeatedly as a name for subgroups of the Rubiaceae (see Darwin, Pfeiffer), Ridsdale appears to have been the first to call it a tribe.

(1966) disfavored a place for *Cephalanthus* in his narrowly conceived Naucleeae.

Cephalanthus is of minimal consequence in human affairs. The plants are amply supplied with alkaloids and, not surprisingly, are bioactive. They are blamed for killing livestock, but Sperry and colleagues noted that losses are negligible in Texas, probably on account of unpalatable constituents. *Cephalanthus occidentalis* has long been used in folk medicine by American Indians, among others, against such complaints as sore eyes, arthritis, toothache, fevers, and diabetes, and it has found use as a laxative. Sometimes *C. occidentalis* is grown ornamentally. According to Fernald, *C. angustifolius* Hort. (non Lour.) may be *C. occidentalis* f. *lanceolatus* Fern. The fruits serve as food for water birds, and the sweet-smelling flowers are valued by beekeepers as sources of nectar.

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6. **Randia** Linnaeus, Sp. Pl. **2:** 1192. 1753; Gen. Pl. ed. 5. 74. 1754.

Spiny [or unarmed] shrubs or small trees bearing opposite branches and short shoots. Spines axillary, paired, sharp, stiff, usually inserted at ca. 45-degree angle, generally shorter than leaves. Bark on twigs breaking up into conspicuous untidy scales or taking the form of longitudinal flanges separated by long fissures. Plants glabrous to strigillose [or more heavily pubescent] on twigs and stipules. Leaves sessile or on short petioles, opposite or fascicled on short shoots, small (not often longer than 3 cm), (infrequently) ovate to (frequently) oblanceolate or obovate [sometimes trilobed], mostly rounded and mucronate apically, the margins usually revolute when dry. Stipules with a single variably shaped (usually deltoid and apiculate) lobe centered between adjacent petiole bases, often split or shredded by growth of twig and/or by weathering. Plants typically dioecious, the flowers subsessile in leaf axils, solitary or occasionally clustered on short shoots among leaves, mostly pentamerous, imperfect, with the nonfunctional organs reduced (or possibly flowers sometimes perfect, *fide* Tomlinson) [or flowers perfect]. Calyx lobes variable in size and shape, deltoid to obovate [or foliose to suppressed], coalescent basally into a short tube. Corolla white [or yellowish], cylindrical [flared or campanulate], the imbricate-contorted lobes spreading and roughly as long as the tube, thickly pubescent in and near the throat [or internally glabrous]. Stamens on very short filaments in the corolla throat [or included or exserted]. Ovary inferior, usually bilocular; style expanded and cleft apically into a pair of thick, exserted lobes [or undivided]. Berries globose to ellipsoid, crowned with the persistent calyx, variably reported as white or greenish to purple when ripe, the pulp dark toward the inside. Seeds 1 or few, discoid. LECTOTYPE SPECIES: *R. mitis* L. (see Britton, Fl. Bermuda, 361. 1918), this regarded by most modern authors as a synonym of *R. aculeata* L., the only other species of *Randia* in the *Species Plantarum*. (Named for Isaac Rand, ?–1743, British apothecary and botanist, director of the Chelsea Physic Garden; for biographical notes see Trimen & Thiselton-Dyer.)—INDIGO BERRY.

A rather vaguely defined genus usually estimated to have 200–300 species and with a pantropical distribution (see below). *Randia aculeata,* the only species indigenous to the area of the Generic Flora, occurs in South Florida at the northern edge of its range, which extends to Mexico, Central America, northern South America, and the West Indies. Texan populations are interpretable as belonging to *R. aculeata* (for commentary see Vines, who tentatively favored this stance), although Correll & Johnston and F. B. Jones referred them to *R. rhagocarpa* Standley.

In our area *Randia aculeata* inhabits hammocks, shores (sometimes associated with mangroves), oceanside dunes, pinelands, and thickets. The soil is sometimes marly and is sometimes dry. As described by Tomlinson, the flowers, chiefly borne April–June, are for the most part functionally imperfect by abortion, although possibly some perfect ones may form. In 1966 Bremekamp reported staminate flowers in some Gardenieae to have abortive styles that act to hold pollen. The extent of involvement, if any, of the abortive styles in *R. aculeata* in the pollination system is a question worthy of new observations.

Randia aculeata is recognized and differs from other genera of Rubiaceae treated in this paper, except *Catesbaea* (see treatment of this genus for comparison), in being a shrub or small tree armed with paired axillary spines, each of which diverges from the stem at roughly 45 degrees. Further, our *Randia* has small, frequently apiculate leaves most often broadest above the middle and usually fascicled on short shoots. The small flowers are solitary or clustered on the short shoots. They have white, tubular corollas, and the thick stigmatic lobes protrude from the pistillate flowers. The few-seeded, globose to ellipsoid berries are conspicuously topped by calyx remnants.

Defining *Randia* from a global perspective is hard to accomplish. At present the generic boundaries remain unsettled, especially in the Old World. Authors disagree severely in their generic circumscriptions and synonymy. In a treatment fundamental to taxonomic accounts that followed, Bentham & Hooker conceived of *Randia* as polymorphic, pantropical, and made up of about 90 species in six sections. They named a new genus allied to *Randia, Basanacantha* J. D. Hooker, which they thought to differ in being dioecious (an invalid distinction), and in having glumaceous stipules, terminal flowers, membranaceous leaves, and other distinctive characters. Schumann held nearly the same concept of *Randia* but added a seventh section.

Critical of Schumann's treatment, Fagerlind regretted that *Randia* had become a "refuse dump" for Gardenieae of uncertain position. Emphasizing branching relationships and using diverse additional characters, he pruned *Randia* back to Schumann's sect. *Eurandia* (sect. RANDIA), emended this, added *Basanacantha,* and limited *Randia* to American species. Even if Fagerlind's work has not been particularly influential, the merger of *Basanacantha* with *Randia* has been supported by a number of later authors (see especially Standley, 1919), and it is more or less in harmony with a tendency among recent authors to transfer Old World species from *Randia* to other genera.

Concentrating on West African species, Keay dismissed Fagerlind's taxonomic conclusions about *Randia* as "not altogether satisfactory," stressed the need (that persists) for a full revision, and recognized as distinct 21 genera, "all of which have at one time or another been included, wholly or partly, in *Randia* or *Gardenia.*" Keay listed new or resurrected generic placements for 126 species previously included in *Randia.* More recently, Hepper & Keay attributed no species to *Randia* in the *Flora of West Tropical Africa.* Tirvengadum, after considering "practically all taxa described under *Randia,*" likewise confined the genus to America and characterized it as having [paraphrased] unilocular ovaries with parietal placentae, a nonwaxy bluish pericarp, imperfect flowers, pollen grains remaining in tetrads, and distinct testa cells, and as lacking serial bud formation. (In contrast with Tirvengadum, American floristic authors tend to describe the ovary as generally bilocular.) Yamazaki sorted the Asian species out among five other genera, leaving none in *Randia.* However, it must be emphasized that acceptance of such exclusive boundaries is not unanimous.

Authors working on floras in the New World (Standley; Standley & Williams; Steyermark; Dwyer) have regarded *Randia* as pantropical but have avoided assertions about its limits. They have not adopted infrageneric categories, except that Williams and Standley & Williams recognized subgenus BASANACANTHA (J. D. Hooker) L. O. Williams, which they distinguished from subg. RANDIA by the former's longer corollas, larger fruits, more often imperfect flowers, and terminal quartets of spines (vs. spines paired and scattered). Like Keay, they stressed the need for revisionary work, not only in terms of delimiting the genus, but also of redefining our *R. aculeata,* which they perceived as too inclusive.

Randia aculeata has been used as a folk remedy for dysentery, and the fruit has been the source of a blue dye. Fruits from at least one extraregional species have served as food for humans. *Randia formosa* (Jacq.) K. Schum. is cultivated as an ornamental in tropical regions, and it yields an essential oil used in making perfume (see Prance & Da Silva for an illustrated account of this species).

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7. **Casasia** A. Richard in Sagra, Hist. Fis. Cuba. ed. 2. **11:** 9. 1850.

Dioecious shrubs or small trees with thick, glabrous twigs covered with light-colored flaking bark. Leaves clustered toward branch tips, glabrous except for axillary tufts of trichomes abaxially, petiolate, obovate or oblanceolate, truncate or emarginate to obtuse or rounded at the apex, cuneate to caudate at the base; stipules with the single lobe centered between adjacent petioles, oblong to deltoid or ovate, acute or acuminate and sometimes apiculate apically, frequently denticulate along the margins, the adaxial side with colleters. Flowers fragrant, on tapered pedicels, tending to blacken upon drying, imperfect with the nonfunctional organs (gynoecium or stamens) developing and with staminate and carpellate flowers superficially fairly similar. Staminate flowers in terminal, compound, monochasial or partly dichasial inflorescences; bracts scalelike, highly irregular in shape. Carpellate flowers solitary and terminal, often overtopped and thereby left in lateral position. Calyx made up of a cup-shaped tube topped with 5 finger-shaped to filiform [to deltoid] lobes about as long as to twice as long as the tube, the lobes frequently hooked or curled at the tips when dry. Corolla much longer than calyx, white [or yellow], salverform, with 5 lanceolate or narrowly deltoid lobes as long (or nearly as long) as the slender corolla tube, imbricate-contorted in bud, often hispid-serrulate along apical margin. Stamens inserted in throat of corolla on very short filaments; anthers linear. Ovary unilocular, with 2 (or 3) intrusive, parietal placentae; style rising to throat of corolla tube, expanded apically and divided into 2 (or 3) lobes. Fruit ovoid or ellipsoid, roughly the size of a hen's egg or more nearly globose, tapered at base, spotted on the surface, crowned with the thickened calyx tube, the sclerified endocarp covered by a tough exo- and mesocarp, the large internal cavity filled with the fleshy placentae in which are embedded numerous black (dry), compressed seeds stacked horizontally or obliquely in the fleshy matrix and having pebbled testae. TYPE SPECIES: *C. calophylla* A. Richard, the only species known when the genus was established. (Named for Sr. D. Luis de las Casas, Captain General of Cuba.)—SEVEN-YEAR-APPLE.

A genus of perhaps 11 species in Florida, the West Indies, and Mexico: *Casasia Acunae* Fernandez & Borhidi (Cuba); *C. calophylla* A. Rich. (Cuba); *C. chiapensis* Miranda (Chiapas, Mexico); *C. clusiifolia* (Jacq.) Urban (Bermuda, Bahamas, Florida, Cuba); *C. domingensis* Urban (Hispaniola); *C. Ekmanii* Urban (Hispaniola); *C. haitiensis* Urban & Ekman (Hispaniola); *C. jacquinioides* (Griseb.) Standley (Cuba; *C. parviflora* Britton, synonymy *fide* Standley); *C. longipes* Urban (Jamaica; *C. piricarpa* Urban, synonymy *fide* Adams); *C. nigrescens* (Griseb.) C. Wright ex Urban (Cuba); and *C. Samuelssonii* Urban & Ekman (Hispaniola). (It should be noted that this list comes from an uncritical examination of the literature and from the Gray Herbarium Card Index. The only herbarium materials that I have studied, except for the survey of stipules mentioned below and extralimital specimens of *C. clusiifolia,* originated in the area of the Generic Flora.) Our *C. clusiifolia* (*Randia clusiifolia* (Jacq.) Chapman, *Genipa clusiifolia* Jacq.) is by far the most widespread species, occurring in our area mostly in the Florida Keys, but also as far north along the coast as Lee County, Florida.

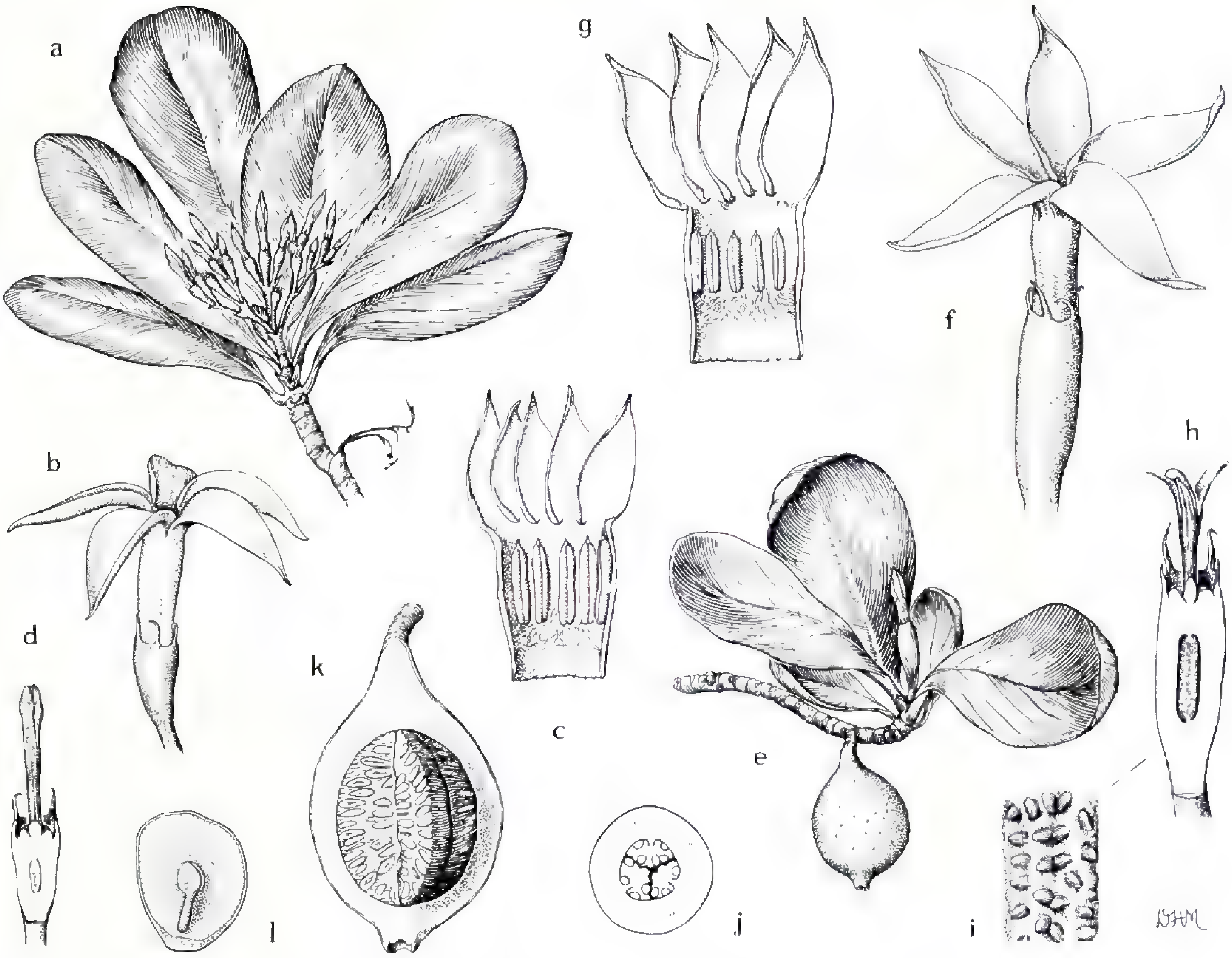

FIGURE 2. **Casasia.** a–l, *C. clusiifolia:* a, branch from staminate plant, showing partially cymose inflorescence, × ¼; b, staminate flower, × 1; c, opened corolla of staminate flower, showing functional stamens adnate to corolla, × 1; d, gynoecium from staminate flower, the ovary in longitudinal section to show rudimentary development of ovary and ovules, × 1; e, branchlet from carpellate plant with single floral bud and fruit, × ¼; f, carpellate flower, × 1; g, opened corolla of carpellate flower with nonfunctional stamens, × 1; h, tricarpellate gynoecium, ovary in longitudinal section to show 1 of 3 placentae, × 1; i, view from axis of portion of spongy placenta showing partially embedded ovules, × 5; j, semidiagrammatic cross section of tricarpellate ovary with 3 parietal placentae, × 2; k, longitudinal section of bicarpellate fruit, 1 placenta sectioned to show embedded seeds, × ½; l, longitudinal section of seed with embryo embedded in abundant endosperm, × 2.

Casasia clusiifolia tolerates high salinity and lives in coastal scrub and hammocks in our area. Flowers form throughout the year, but mostly during spring and summer. In Florida Tuskes observed that the moth *Aellopos tantalus* uses this species as a larval food plant, evidently along with at least *Annona glabra* L. Almost every plant that he examined showed signs of the moth.

As a whole, the genus *Casasia* is made up of small trees or shrubs with terminal cymose inflorescences (or solitary carpellate flowers), conspicuous white or yellow flowers that blacken upon drying, cupular calyces with subulate to deltoid lobes, salverform corollas with the lobes twisted in bud, stamens on short filaments in the corolla throat, included or nearly included anthers, included stigmas, intrusive parietal placentae bearing numerous embedded ovules, large berries with tough pericarps containing numerous more or less horizontal seeds in a fleshy matrix, corneous endosperm, and foliaceous cotyledons. Additional useful characters for our species are its usually obovate or oblanceolate, coriaceous leaves clustered toward the tips of thick twigs, staminate flowers in compound monochasia, solitary carpellate flowers, and large, mottled fruits crowned with a much-thickened calyx cup. The parietal placentae filling the ovary make it appear bi- or sometimes trilocular. Most of the published illustrations show either staminate inflorescences or the fruit, seldom the solitary carpellate flowers.

Probably the most closely related genus is *Genipa* L., which throughout the literature is held to differ from *Casasia* in having lateral (vs. terminal or mostly terminal) inflorescences. Urban (1908) further separated *Genipa* by its internally sericeous (vs. glabrous) calyx limb, this entire or with obtuse lobes (vs. lobes filiform to acute), pubescent corolla, exserted anthers and style, and thick (vs. linear) stigmas. A modern reevaluation of these differences is desirable. Despite indications to the contrary in the literature, herbarium material at the Missouri Botanical Garden showed no difference between *Casasia* and *Genipa* in the position of the stipules. One lobe of the interpetiolar stipules is centered between adjacent petiole bases in both, as it is in most Rubiaceae.

The genus needs a full revision. Schumann's treatment in the *Natürlichen Pflanzenfamilien* is based on only one (or perhaps two) species. The principal accounts are those by Standley (*North American Flora,* 1918), Fernandez Zequeira & Borhidi, and Urban (1908, 1927). In addition, Miranda's surprising report of the only continental species should not be overlooked.

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Under subfamily references see ADAMS; ALAIN; BARKER & DARDEAU; CORRELL & CORRELL; LONG & LAKELA; SCHUMANN; STANDLEY (1918); and TOMLINSON.

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8. **Hamelia** Jacquin, Enum. Syst. Pl. Carib. 2. 1760.

Shrubs with raphide bundles often conspicuous in several organs, pilose to puberulent throughout (except sometimes becoming glabrate with age). Leaves opposite or ternate, petiolate, (oblanceolate to) elliptic (to ovate-lanceolate), with several pairs of pinnate nerves, usually acute or acuminate at both ends;

stipular lobes single between adjacent petioles, narrowly deltoid to subulate. Inflorescence terminal, roughly pyramidal or somewhat flat topped, usually consisting of long, uncrowded cincinni (or occasionally dichasia) in cymose clusters, these not infrequently in thyrsiform arrangements and often with multiple orders of branching. Flowers pentamerous. Calyx lobes low, deltoid, inconspicuous. Corolla red or orange, slender and nearly cylindrical but constricted near the base, the lobes deltoid, only a small fraction of the length of the tube. Stamens inserted on the corolla tube near its base; anthers linear and very long (over half the length of the corolla tube and somewhat longer than the filaments), partly exserted (or sometimes included?), sagittate at base. Style filiform, expanded and papillose in the upper ⅕ of its length at the mid-level of the anthers. Ovary topped with a conical disc around the base of the style, usually 5-loculate, each locule containing numerous anatropous ovules on axile placentae. Fruit a berry, red before becoming black, ellipsoid, conspicuously crowned with a disc (this sometimes taking the form of a beak) and the persistent calyx. Seeds numerous, small, longer than broad, irregularly shaped, usually angular, coarsely reticulate. LECTOTYPE SPECIES: *Hamelia erecta* Jacq. (= *H. patens* Jacq., the only other species included in the protologue; see Wernham, London Jour. Bot. **49:** 206. 1911; Britton & Millspaugh, Bahama Fl. 411. 1920; and Elias, Mem. New York Bot. Gard. **26:** 112. 1976 for lectotypification and for choice of epithets when the two species are merged). (Named for Henri Louis Duhamel du Monceau, botanist, 1700–1782.)—FIREBUSH.

A genus of about 16 woody species in two sections distributed in tropical and subtropical America and concentrated in Mexico and Central America. A representative of section HAMELIA, *Hamelia patens*, $2n = 24$, is the only species indigenous to the continental United States. The range of *H. patens* var. *patens* extends from Lake County, Florida, southward through the West Indies, much of Mexico, Central America, and (mostly western) South America to northern Argentina and Chile. A second variety, *H. patens* var. *glabra* Oersted, is limited to Central America and northern South America.

In Florida *Hamelia patens* var. *patens* most frequently grows in coastal hammocks, although it sometimes occurs inland and has weedy tendencies, turning up in sunny, disturbed places. In tropical America it is common, a pioneer in clearings and a weed, and is cultivated ornamentally. It is also cultivated in the Old World, no doubt escaping there as well. Flowering takes place throughout the year in our area. Bawa & Beach found the flowers to be monomorphic, and they found selfing to yield reduced fruit set, with fruits aborting.

Hamelias are recognized as shrubs or small trees with often secund, red to yellow, frequently angular, tubular flowers with imbricate aestivation and long, linear anthers. The typically five-locular ovary is topped with a persistent, often beaklike disc. The berries contain numerous flattened seeds. *Hamelia patens* var. *patens* is easily separated from all other Rubiaceae in our area by its long, narrow, tubular, orange or red flowers with an inconspicuous calyx and short corolla lobes.

Schumann placed *Hamelia* in his large tribe Gardenieae within subfam.

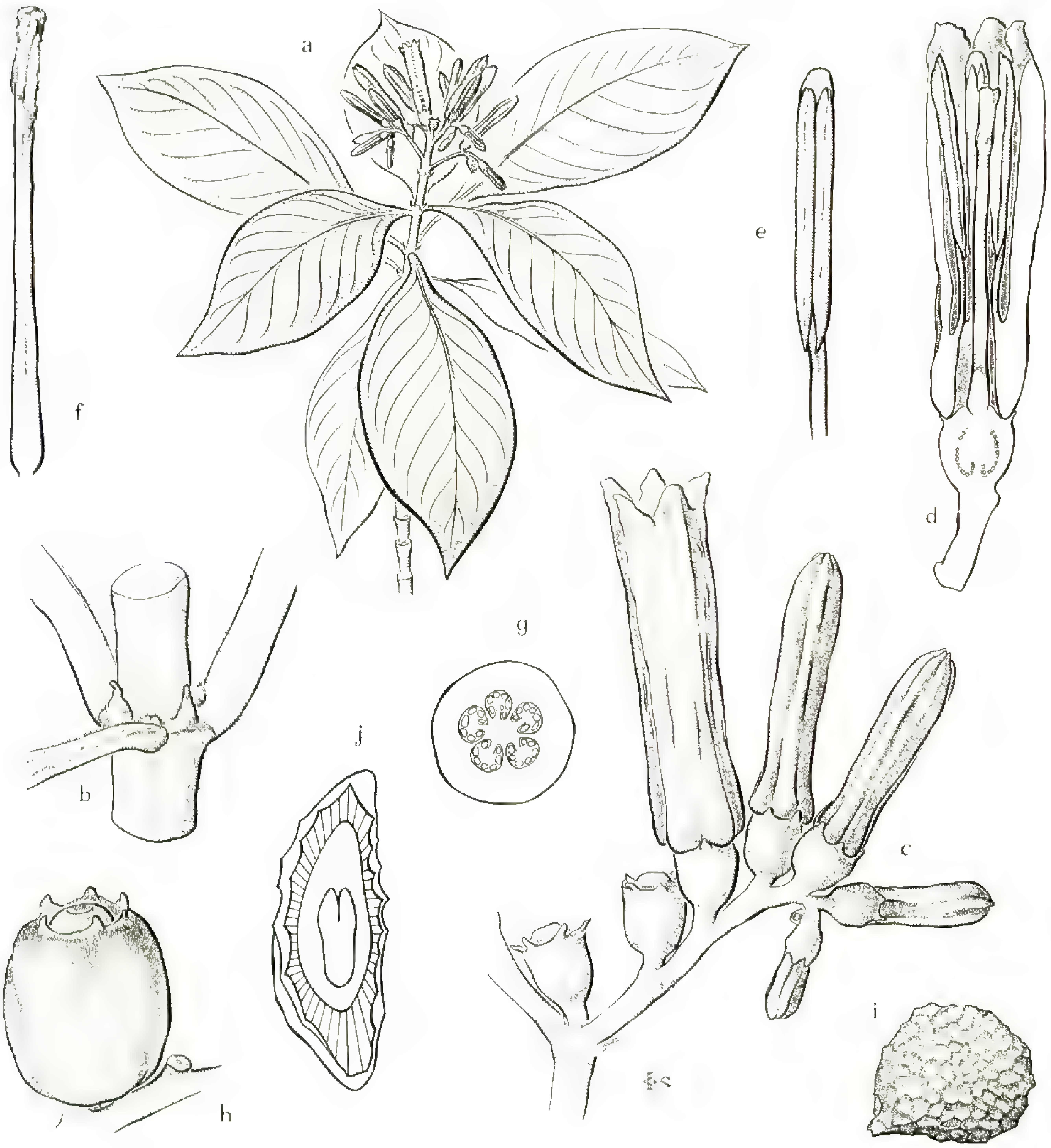

FIGURE 3. **Hamelia.** a–j, *H. patens:* a, flowering shoot—note ternate leaf arrangement, × ½; b, node with bases of petioles of 3 leaves and interpetiolar stipules, 2 axillary buds visible, × 3; c, portion of inflorescence, × 2; d, flower in longitudinal section—note epipetalous stamens, large anthers, and axile placentation, × 3; e, adaxial side of anther and portion of filament, × 4; f, style with stigmas, × 4; g, diagrammatic cross section of ovary, showing axile placentae with numerous ovules, × 6; h, fruit, a berry, × 3; i, seed, × 25; j, seed in longitudinal section, seed coats unshaded and hatched, endosperm stippled, embryo unshaded, × 50.

Cinchonoideae, a subfamilial and tribal position not generally accepted by subsequent authors. Stressing the presence or absence of raphides in distinguishing the Rubioideae from the Cinchonoideae, Bremekamp (1966), Verdcourt (1958), and Elias positioned *Hamelia* in the Rubioideae, where they all acknowledged, however, that it is anomalous in having imbricate, rather than valvate, aestivation.

At the tribal level, Bremekamp (1966) paired *Hamelia* with *Hoffmannia* Sw.

as the tribe Hamelieae, which Elias adopted in his revision of *Hamelia,* as did Standley & Williams. According to Elias, *Hamelia* and *Hoffmannia* are linked by their woody habit, raphides, imbricate aestivation, ovarian discs, two- to five-locular ovaries, numerous ovules per locule, and baccate fruits. Except for multilocular ovaries, these features are fairly generalized in the Rubiaceae; however, Elias also noted without elaboration similarities in their pollen and seeds. He distinguished *Hamelia* from *Hoffmannia* by the former's occupying lower altitudes and by its having terminal (vs. axillary), usually monopodial, more often paniculate inflorescences generally containing more flowers, usually unribbed and secund corolla tubes, pentamerous (vs. usually tetramerous) flowers, most often 5 (4) locules (vs. usually (4) 3 or 2 locules) in the ovary, stamens inserted lower in the tube, and sagittate anthers. With only a small number of chromosome counts in hand so far, *Hamelia* appears to have $2n = 24$, while only $2n = 48$ is known in *Hoffmannia.*

Steyermark (1974) accepted the tribe Hamelieae but differed from Bremekamp and Elias by including the genus *Bertiera* Aublet, which—unlike *Hoffmannia* and *Hamelia*—has contorted aestivation and lacks raphides. Dwyer, too, associated *Hamelia* and *Hoffmannia* in the Hamelieae but with *Xerococcus* Oersted, which stands apart in having valvate aestivation.

Hamelia has been revised twice in this century. Wernham recognized 28 species in 1911; Elias accepted 12 of these in 1976, changing the name of one, which was a later homonym. Most of the remainder fell into synonymy, a large cluster under the two varieties of *H. patens.* Elias added three species discovered since Wernham's study, bringing the total number in his revision to 16, sorted into two sections of eight species each.

The pollen of *Hamelia patens* is tricolporate, with circular ora and with an areolate, tegillate sexine (Anand & Bhandari).

Beyond being ornamental, *Hamelia patens* has edible berries used in Mexico for preparing a fermented beverage (Standley). Having a high tannin content, the bark has been used in tanning leather (Morton, Standley). As Morton documented, this species has multiple applications in folk remedies, mostly to counter dysentery and to treat skin wounds and irritations.

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9. **Catesbaea** Linnaeus, Sp. Pl. **1:** 109. 1753; Gen. Pl. ed. 5. 48. 1754.

Spiny shrubs [small trees or scandent shrubs] with puberulous branches often inserted at oblique angles. Leaves opposite or fascicled on short-shoots, glabrous, sessile or on short petioles, small (mostly under 1 cm long in our species) [sometimes virtually absent by reduction]. Spines stiff, sharp, frequently longer than leaves, paired, generally arising at oblique angles. Stipular lobes initially solitary between adjacent petiole bases, quickly cleft into 2 lobes, disappearing during expansion of twig. Flowers borne singly among leaves, on short pedicels, small and inconspicuous [or large and showy], tetramerous. Calyx lobes persistent, subulate, longer than ovary. Corolla white, the tube narrowing toward base, the valvate and deltoid lobes much shorter than tube. Stamens inserted at base of corolla tube, rising to level of lobes. Ovary bilocular, with ovules on faces of septum [or on placentae arising from septum]; stigma bifid. Berries globose, white (or black), containing a small number of compressed seeds with rugose surfaces. Type species: *C. spinosa* L., this the only species in the generic protologue. (Named for Mark Catesby, 1683–1749, British naturalist, known in part for his *The natural history of Carolina, Florida, and the Bahama Islands.*)

A genus of approximately 15 species in the West Indies, one of them reaching the Florida Keys. Most are known from only a single island each, although *Catesbaea spinosa* L., $2n = 24$, *C. melanocarpa* Urban, and *C. parviflora* Sw. occur on a number of islands. Cuba has the greatest number of species—about seven endemics, in addition to two more widespread species. There are about six endemics on Hispaniola. On all other islands where it occurs, *Catesbaea* is limited to one or two species. *Catesbaea parviflora,* the most broadly distributed species, grows on the Florida Keys, the Bahamas, Cuba, Jamaica, Puerto Rico, Antigua, the Cayman Islands, and undoubtedly other islands. In Florida *C. parviflora* is encountered in dry, open areas. Its habitats include pine woods, edges of hammocks, and sand dunes.

With its conspicuous paired thorns and small, clustered leaves widest above the middle, *Catesbaea* is easily recognized among shrubs in our area, although it might be confused with *Randia*. *Catesbaea* usually has tetramerous flowers (vs. pentamerous ones in *Randia*), valvate (vs. contorted) aestivation, and stamens inserted basally in the corolla (vs. in the throat in *Randia* and *Hoffmannia*). As Proctor pointed out, our species of *Catesbaea* has smaller fruits than our species of *Randia* (4 mm vs. 8–12 mm in diameter). Additional distinguishing features of *Catesbaea* include bilocular ovaries (vs. five-locular in *Hamelia*), perfect flowers (vs. imperfect ones in *Bertiera* and *Randia aculeata*), and solitary, axillary flowers.

Verdcourt diverged from Schumann in placing *Catesbaea* outside of the Gardenieae in the segregate tribe Catesbaeeae J. D. Hooker, which he regarded as close to the Gardenieae. According to him, distinguishing features of the Catesbaeeae are valvate aestivation (vs. contorted or imbricate in the Gardenieae), usually spiny branches, and fleshy fruits containing rugose seeds adhering in a mass.

Catesbaea is in need of revision. The only comprehensive treatment is Standley's (1918). Taxonomy of the genus rests on this, coupled with regional floristic works.

Catesbaea spinosa, which has large, showy flowers, is cultivated as an ornamental shrub.

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THE GENERA OF ALYSSEAE (CRUCIFERAE; BRASSICACEAE) IN THE SOUTHEASTERN UNITED STATES[1,2]

IHSAN A. AL-SHEHBAZ[3]

Tribe **Alysseae** A. P. de Candolle, Syst. Nat. **2:** 147, 280. 1821, "Alyssineae."

Annual, biennial, or perennial herbs [sometimes subshrubs, shrubs, or even trees]; usually with stellate, dendritic, cruciform, or furcate trichomes, rarely glabrous or with simple trichomes only. Inflorescences ebracteate [or bracteate], corymbose racemes, usually elongated in fruit. Sepals erect to spreading, strongly saccate at base or not saccate. Petals present or absent, undifferentiated or strongly differentiated into blade and claw. Nectar glands distinct or connate. Stamens usually 6, often tetradynamous; filaments with or without wings, teeth, or appendages. Fruits usually less than 3 times as long as wide, dehiscent [or rarely indehiscent], inflated or most commonly flattened parallel to the septum (latiseptate), sessile or long stipitate; valves usually 1-nerved, glabrous or with 1 or more types of trichome; septum present or absent; styles long to obsolete; stigmas entire to 2-lobed. Seeds 1 to numerous, usually biseriately arranged in each locule, mucilaginous or not when wet, broadly winged to wingless; funicles

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I am most indebted to Carroll Wood for his continuous support and advice during the preparation of this paper, and especially for his critical review of the manuscript. I am grateful to Reed C. Rollins for allowing me to study his manuscripts on the genera *Draba* and *Lesquerella* for his forthcoming book on the Cruciferae of North America. I am variously indebted to Norton G. Miller, George K. Rogers, R. Dale Thomas, and Kathryn Rollins, as well as to Barbara Nimblett, who typed the manuscript. I am grateful to Elizabeth B. Schmidt and Stephen A. Spongberg for their editorial advice.

Some of the illustrations (Figures 1d, j, k; 2f, i, j) were made by Karen Stoutsenberger (KS) under earlier grants. Carroll Wood prepared the material and supervised the illustrations. The remaining illustrations were drawn by me (IAS). The fruits and seeds are from herbarium specimens in the Gray Herbarium and Arnold Arboretum.

[2] For an account of the family and its tribes, see Al-Shehbaz, The tribes of Cruciferae (Brassicaceae) in the southeastern United States. Jour. Arnold Arb. **65:** 343–373. 1984.

[3] Arnold Arboretum, Harvard University, 22 Divinity Avenue, Cambridge, Massachusetts 02138.

Journal of the Arnold Arboretum **68:** 185–240. April, 1987.

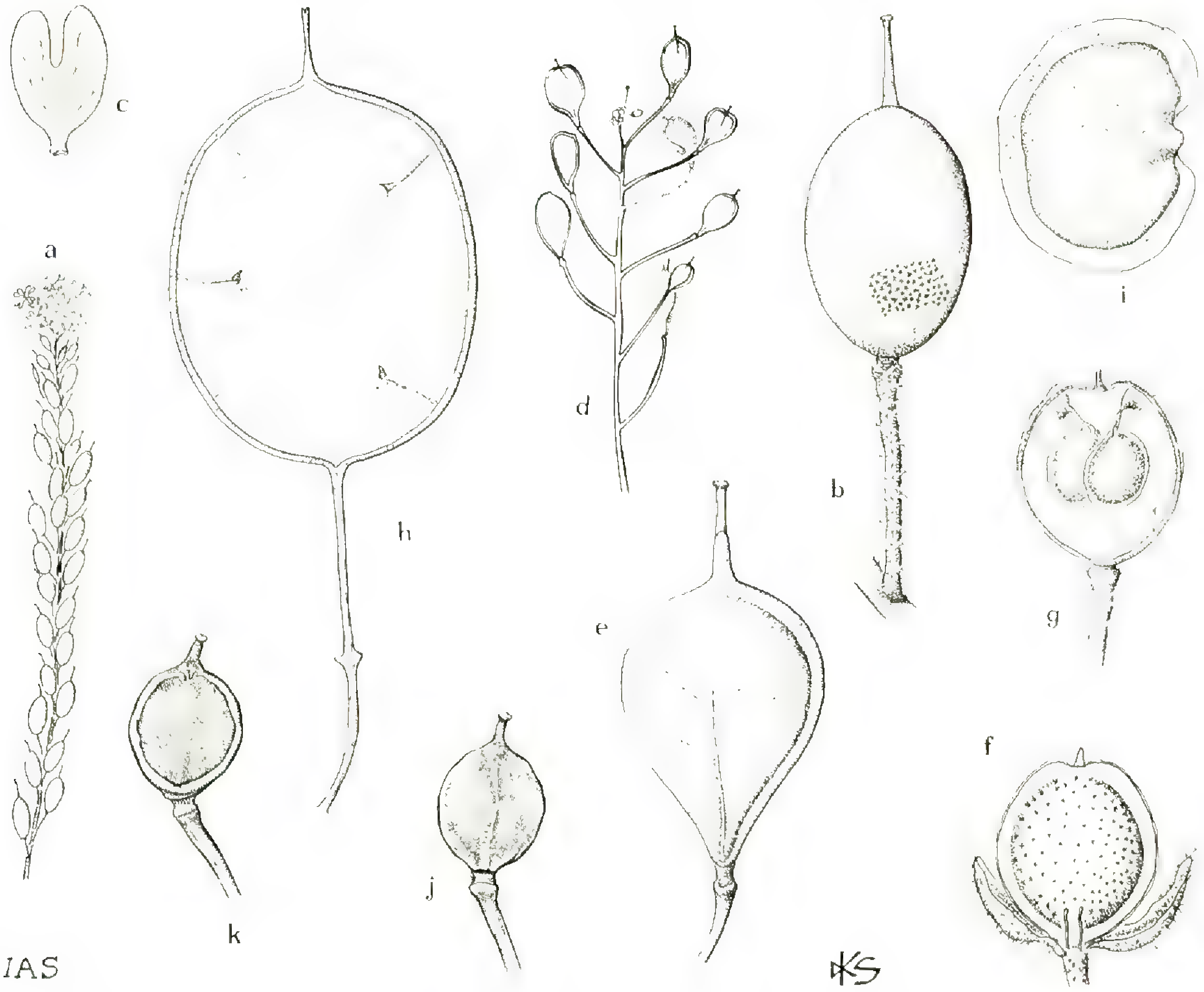

FIGURE 1. Selected representatives of tribe Alysseae. a–c, *Berteroa incana:* a, portion of plant with flowers and fruits, × ½; b, fruit with rectangular portion of valve showing trichomes, × 5; c, petal, × 5. d, e, *Camelina microcarpa:* d, portion of infructescence, × 1; e, fruit, × 5—note beaklike apex of valve. f, g, *Alyssum Alyssoides:* f, fruit with 1 persistent sepal removed, × 5—note filiform nectar glands; g, fruit with 1 valve and all sepals removed, × 5—note subapical placentae. h, i, *Lunaria annua:* h, septum and replum, × 1—note gynophore and adnation of funicles to septum; i, seed, × 3. j, k, *Lobularia maritima:* j, fruit, × 6; k, replum and septum, × 6.

free or adnate to the septum, apically or laterally attached to the replum; cotyledons accumbent. (Including Camelineae DC., Drabeae O. E. Schulz, Lunarieae O. E. Schulz.) TYPE GENUS: *Alyssum* L.

A poorly defined tribe with some 40 genera (15 monotypic) and about 650 species (excluding *Lesquerella* S. Watson) distributed primarily in the Irano-Turanian (ca. 210 species) and Mediterranean (ca. 110 species) regions. The majority of species belong to two genera: *Draba* L. (350) and *Alyssum* (170). Except for *Draba,* the Alysseae are poorly represented in Siberia, eastern Asia, and North America and are absent in the Southern Hemisphere and in the arctic and Himalayan regions. The tribe is represented in the southeastern United States by seven genera and 20 species, of which 13 are indigenous.

The limits of the Alysseae adopted here closely follow Janchen's classification, which unites the tribes Lunarieae, Drabeae, and Alysseae of Schulz. Janchen followed Von Hayek in treating the first two as subtribes of the last. Both *Selenia* Nutt. and *Armoracia* Gaertner, Meyer, & Scherb., which were placed by Schulz in the Lunarieae and the Drabeae, respectively, will be treated in the Arabideae DC., where their nearest relatives are usually placed. The South African *Schlechtera* Bolus, treated in the Lunarieae by Schulz, has diplecolobal embryos (with cotyledons twice transversely folded) and should therefore be included with its allies of the Heliophileae DC. *Lesquerella* was placed by Schulz in the Drabeae, but as is clearly shown below, it should be placed with its nearest generic relatives in the Lepidieae. However, it is treated here in the Alysseae, as shown in the outline adopted by Al-Shehbaz (1984).

Schulz separated the Lunarieae from the Alysseae mainly on the basis of simple vs. branched or stellate trichomes. Both *Ricotia* L. and *Peltaria* Jacq. (including *Leptoplax* O. E. Schulz), which he placed in the former tribe, have members with simple or branched trichomes, as do numerous other genera of the Cruciferae. Therefore, the type of pubescence alone cannot be used as the basis for tribal delimitation. Similarly, the cellular pattern of the fruit septum, considered by Schulz to be the main difference between the Alysseae and the Drabeae, is an unreliable feature and should not be overemphasized. Many authors (e.g., De Candolle, 1821, 1824; Von Hayek; Janchen) placed the core genera *Draba, Alyssum,* and *Lunaria* L., as well as their immediate relatives, in the tribe Alysseae, a disposition I presently support. It is clear, however, that the tribal classification of the Cruciferae is inadequate, and further studies may alter the boundaries of the Alysseae. Knights & Berrie found that data from sterols support the placement of *Lunaria* but not *Draba* in the Alysseae.

Chromosome numbers are known for some 275 species (ca. 43 percent of the tribe) and 28 genera (excluding *Lesquerella*). Nearly 80 percent of the species surveyed have chromosome numbers based on eight, and only about seven percent have numbers based on seven (author's compilation). About 50 percent of the species are diploid, and nearly 38 percent are exclusively polyploid. Polyploidy occurs in nearly 60 percent of the species of *Draba.* Aneuploidy and polyploidy probably played important roles in the evolution of *Lobularia* Desv. and *Hormathophylla* Cullen & T. R. Dudley.

The Alysseae are almost exclusively herbaceous; only a few species in three genera are woody. Some species of *Alyssum* and *Hormathophylla,* particularly those growing in the eastern Pyrenees, southern France, and eastern Spain, are subshrubs or shrubs to 50 cm high. *Farsetia* Turra has the most diversified habit of any genus of the Cruciferae. It includes several annual and perennial herbs, as well as subshrubs, shrubs, and even small trees. *Farsetia somalensis* (Pax) Gilg & C. Benedict (Somalia, Kenya, and Ethiopia) is a large shrub or small tree with hard wood and glossy, gray to red-brown bark, while *F. undulicarpa* Jonsell (Kenya and Tanzania) is a shrub to 2 m high (Jonsell, 1986).

The majority of the Alysseae have rather small seeds dispersed either by strong winds in open habitats or by rain wash. Wind dispersal is common in many genera with broadly winged seeds (e.g., *Farsetia, Fibigia* Medicus, *Lunaria*). It is restricted, however, to a few genera with samaroid (*Neotchihatchewia* Rauschert, *Peltaria*) or inflated (*Physoptychis* Boiss.) indehiscent fruits. Seeds that produce abundant mucilage when wet may be dispersed by adhering to animals. The fruits of two species of *Clypeola* L. (*C. lappacea* Boiss. and *C. aspera* (Grauer) Turrill) and of the monotypic *Asperuginoides* Rauschert (formerly *Buchingera* Boiss. & Hohen.; see Rauschert) are covered with glochidiate trichomes or deflexed barbellate spines and are dispersed by clinging to the fur of mammals.

Genera of the Alysseae in the southeastern United States are either noxious weeds or have members with weedy tendencies. Except for a few species of *Camelina* Crantz that are cultivated for their seed oils in parts of the Soviet Union and Europe, the tribe has no food value. Several species of *Alyssum, Aurinia* (L.) Desv. (golden-tuft alyssum), *Draba*, and *Lunaria* (honesty or money plant) are ornamentals cultivated on a limited scale. On the other hand, *Lobularia maritima* (L.) Desv. (sweet alyssum) is probably the most widely cultivated ornamental of the family Cruciferae.

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KEY TO THE GENERA OF ALYSSEAE IN THE SOUTHEASTERN UNITED STATES[4]

A. Fruits more than 1 cm wide, gynophores 1–5 cm long, funicles completely adnate to the septum; trichomes simple or lacking. .... 20. *Lunaria.*

A. Fruits less than 1 cm wide, gynophores absent or to 3 mm long, funicles free from the septum or adnate only at base; trichomes branched, sometimes mixed with simple ones.

  B. All trichomes uniformly bifurcate, medifixed, sessile, appressed. .... 22. *Lobularia.*

  B. Trichomes furcate, branched, or stellate, sometimes mixed with simple ones, stalked or sessile, usually appressed when stellate.

    C. Fruits inflated, not compressed, pyriform or globose to subdidymous.

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[4] The genera are numbered as in the treatment of the tribes of the Cruciferae in the southeastern United States (Jour. Arnold Arb. **65:** 343–373. 1984). Genera 1 and 2 (Thelypodieae) appeared in *ibid.* **66:** 95–111. 1985; genera 3–13 (Brassiceae) in *ibid.* 279–351; and genera 14–19 (Lepidieae) in *ibid.* **67:** 265–311. 1986.

D. Fruits pyriform, keeled at the replum, the valves acuminate, ending abruptly in a stylelike beak, the septum nerveless; seeds usually oblong, cotyledons incumbent. .... 26. *Camelina.*

D. Fruits globose to subdidymous, not keeled, the valves rounded or obtuse at apex, the septum (when present) with a midnerve extending from its center to the base of style; seeds nearly orbicular, cotyledons accumbent. .... 25. *Lesquerella.*

C. Fruits not inflated, compressed parallel to the septum, orbicular to oblong or lanceolate to linear.

E. Seeds 1 per locule, borne on an apical placenta, copiously mucilaginous when wet. .... 21. *Alyssum.*

E. Seeds 2 to many per locule, borne on 2 parietal placentae, not or only slightly mucilaginous when wet.

F. Cauline leaves strongly auriculate; fruits with bulbous-based trichomes, septum with a midnerve extending from its center to the base of style. .... 25. *Lesquerella.*

F. Cauline leaves usually not auriculate; fruits without bulbous-based trichomes, septum nerveless.

G. Petals deeply 2-lobed; filaments of lateral stamens appendaged; seeds winged or margined. .... 23. *Berteroa.*

G. Petals entire or sometimes emarginate, if 2-lobed (*Draba verna*) then plants scapose; filaments unappendaged; seeds neither winged nor margined. .... 24. *Draba.*

20. **Lunaria** Linnaeus, Sp. Pl. **2:** 653. 1753; Gen. Pl. ed. 5. 294. 1754.

Annual(?), biennial [or perennial] herbs with simple trichomes. Stems erect, branching above. Basal and lower cauline leaves opposite or rarely alternate, long petiolate, large, ovate-cordate, undivided, coarsely dentate [or spinulose-dentate]; upper leaves alternate, sessile or subsessile [or distinctly petiolate]. Inflorescences corymbose racemes or panicles, greatly elongated in fruit; lowermost branches bracteate; flowers ebracteate, large, showy. Sepals erect, cucullate; outer pair linear, not saccate at base; inner pair broadly oblong-elliptic, strongly saccate. Petals violet or purple, rarely lavender or white, obovate, long clawed, usually twice as long as the sepals or longer. Lateral nectar glands large, annular, 2-lobed on the outer side, 3-lobed on the inner [sometimes divided into inner and outer semiannular halves]; median glands absent. Stamens 6, tetradynamous; filaments linear, free, the bases terete or flattened, erect (median pairs) or strongly curved (lateral pair); anthers large, linear or oblong, obtuse. Ovary stipitate, 4- to 8-ovulate, glabrous or ciliate; style filiform; stigma 2-lobed, the lobes decurrent [or not], opposite the replum. Fruits dehiscent, very large (2–9 × 1–3.5 cm), strongly flattened parallel to the septum, usually pendulous, oblong to suborbicular [or lanceolate-elliptic], obtuse [or acute] at both ends; valves glabrous, flat, papery, finely or obscurely net veined, without a midnerve; styles long [or short], usually flattened near the base; replum ciliate or glabrous; septum persistent, shining, membranaceous, nerveless, very broad, with narrowly linear epidermal cells perpendicular to the long axis of fruit; funicles long, almost completely adnate to the septum; gynophores slender, 1–5 cm long [rarely obsolete or to 1 mm]. Seeds few, large, biseriately arranged in each locule, reniform or rarely suborbicular, flattened, slightly biconvex, minutely reticulate, brown, uniformly broad winged all around except at the wingless area of hilum, nonmucilaginous when wet; cotyledons accumbent, large. Base chromosome number 15. LECTOTYPE SPECIES: *L. annua* L.; see Britton & Brown, Illus. Fl. No. U. S. & Canada, ed. 2. **2:** 190. 1913; see also Green and Maire for a later lectotypification (based on *L. rediviva* L.) that contradicts article 8 of ICBN. (Name from Latin, *luna,* moon, which the large, persistent, silvery septum of the fruit superficially resembles.)—HONESTY, MONEY PLANT, SATIN FLOWER, MOONWORT.

A genus of three species native to southern, central, and eastern Europe. Two species are grown as ornamentals, and these sometimes escape from cultivation. The third, *Lunaria Telekiana* Jáv., is a narrow endemic of northeastern Albania. It differs from the other species in having very short (to ca. 1 mm) gynophores, densely ciliate valve margins, and lateral sepals with longer (to ca. 2.5 mm) saccate bases. Both *L. annua* (*L. biennis* Moench, *L. inodora* Lam.), honesty, bolbonac, silver-dollar, penny flower, money plant, $2n = 30$, and *L. rediviva* (*L. odorata* Lam., *L. alpina* Berg.), money plant, $2n = 30$, are grown in North America. *Lunaria annua* has been reported as an escape from cultivation, but apparently not a naturalized one, in many states (including Arkansas and Georgia). It is easily distinguished by its biennial habit, oblong to suborbicular fruits with both apex and base obtuse, and subsessile or sessile upper cauline leaves. In the perennial *L. rediviva* the upper cauline leaves are petiolate and the fruits are usually elliptic-lanceolate with both apex and base acute. Of the two subspecies of *L. annua,* only the biennial subsp. *annua* is present in our area. Subspecies *pachyrrhiza* (Borbás) Hayek, a perennial with fusiform tubers, is distributed in Romania, the Balkan peninsula, and southern Italy.

Lunaria is most closely related to the eastern Mediterranean *Ricotia* (nine species), from which it differs in its coarser habit (stems to 16 dm high), undivided leaves, and stipitate fruits (1–)1.5–3.5 cm wide with a well-developed septum. Species of *Ricotia* are smaller plants to 4 dm high having pinnate or trifoliolate (very rarely undivided) leaves and sessile fruits 0.5–1(–1.5) cm wide with a very delicate septum that is sometimes lacking. Both genera were maintained in the Alysseae by De Candolle (1821, 1824), Bentham & Hooker, Von Hayek, and Janchen, but the last two placed them in subtribe Lunariinae Hayek. In Schulz's classification *Lunaria* and *Ricotia,* along with six other genera, are placed in the tribe Lunarieae, which was distinguished from the Alysseae only by the presence of simple instead of branched trichomes. Both types of trichome, however, are found in several genera of the Cruciferae, notably *Arabis* L., *Draba,* and *Sisymbrium* L. Dvořák (1971) suggested that the Lunarieae *sensu* Schulz, particularly *Lunaria,* represent an evolutionary line derived from an ancestor not very different from *Macropodium pterospermum* Schmidt Petrop. of the Thelypodieae Prantl. The Lunarieae are a heterogeneous assemblage in which some genera (e.g., *Selenia* Nutt. and *Thysanocarpus* W. J. Hooker) are clearly unrelated to *Lunaria.* Von Hayek's derivation of *Lunaria* from *Ricotia* needs careful evaluation, but it is evident that the two are more closely related to each other than to other genera of the Cruciferae.

The erect sepals, long claws of the petals, and flattened bases of the median staminal filaments of *Lunaria* form a long tube that makes the abundant nectar usually accessible to insects with proboscises longer than 1 cm. The butterflies *Vanessa* (Nymphalidae) and *Pieris* (Pieridae), the bees *Bombus* (Bombidae) and *Andrena* (Andrenidae), and the honeybee *Apis mellifera* (Apidae) are among the most common visitors of *Lunaria* flowers (Knuth). Self-pollination can be brought about effectively by small pollen-collecting insects because of the close proximity of the stigma to the median anthers. Insects with short proboscises can reach the nectar by poking holes through the base of the calyx.

Most chromosome counts for *Lunaria annua* and *L. rediviva* indicate $2n = 30$, but Dvořák & Dadáková and Polatschek reported $2n = 28$ for these species. The last author suggested that *Lunaria* is based on $x = 7$, while Dvořák (1971) speculated that the genus evolved through allopolyploidy from unknown ancestors with $x = 7$ and 8. The karyotype of *Lunaria* consists of small chromosomes, of which two (at least in *L. rediviva*) are believed to be B chromosomes (Manton). Failure to observe this pair may have led to deviant counts. Diploid and tetraploid counts based on $x = 15$ have been found in *L. rediviva* (Jankun).

Lunaria is unusual in the Cruciferae for its high concentrations of unique or very rare secondary compounds. It is rich in alkaloids, of which some are known only in this genus and at least six (lunarine, lunaridine, lunariamine, numismine, tetrahydrolunarine, and tetrahydrolunaridine) have been characterized. Isopropyl, 2-butyl, and 5-methylthiopentyl glucosinolates have been found in *L. annua,* and the last compound occurs in *L. rediviva* (Kjaer). The green parts of plants of the former species also contain 3-methylthiopropylglucosinolate (Cole). It has been suggested that the high concentrations of alkaloids in *Lunaria* may have evolved as an escape from crucifer-adapted pathogens or herbivores. The seed extract of *Lunaria* is the first reported source of *m*-carboxy–substituted aromatic amino acids among higher plants (Olesen Larsen). The unhydrolyzed seed extract of *L. annua* contains four amino acids and γ-glutamyl derivatives not discovered previously in nature.

Lunaria annua is an excellent source of long-chain monounsaturated acids, which constitute 90 percent of the total fatty-acid content. The seed oil is a potential source of erucic acid (42 percent) and contains 21 to 25 percent nervonic acid. The content of the latter acid is the highest reported for any seed oil (Wilson *et al.,* Mukherjee & Kiewitt).

Because the funicles are adnate to the septum, the seeds of *Lunaria* usually remain attached to the septum after the valves fall off. They are eventually detached as a result of the vibration of the septum and may glide away from the plant because of the presence of a broad wing. However, they sometimes adhere to the valves and can be carried away with them.

Lunaria annua has an absolute requirement of cold treatment (vernalization) for flowering. Stem elongation in rosette plants can be induced by the application of the gibberellic acids GA3 and GA7. However, the gibberellin treatment fails to induce flowering in nonvernalized plants (Zeevaart). Likewise, sprouts developed on callus or on petioles grown in sterile cultures do not flower unless vernalized (Pierik, 1967). Annual plants of *L. annua,* which is otherwise a biennial, have been obtained recently (Wellensiek, 1973).

Both *Lunaria annua* and *L. rediviva* are grown for their attractive flowers and particularly for their infructescences, which are used in dry bouquets after the removal of valves and seeds. Crisp stated that the seeds are occasionally used as condiments and the roots are eaten as a salad or cooked as a vegetable. The seeds of *L. annua* contain high levels of long-chain fatty acids, but the species has not been used as a source of industrial oils. Although both species may escape from cultivation, neither is a successful weed in the New World.

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21. **Alyssum** Linnaeus, Sp. Pl. **2:** 650. 1753; Gen. Pl. ed. 5. 293. 1754.

Annual [biennial or perennial] herbs [rarely subshrubs]. Stems erect to decumbent, usually branched at base [sometimes with sterile shoots and winter rosettes]. Indumentum of appressed, stellate trichomes with few [or many] branched [or unbranched] rays [or sometimes of lepidote trichomes]; simple or furcate trichomes present [or absent]. Leaves undivided, entire, attenuate, neither swollen nor persistent at base. Inflorescence an ebracteate, corymbose raceme [or panicle], elongated [or not] in fruit; fruiting pedicels divaricate [ascending, or reflexed]. Sepals equal [or unequal], free [or sometimes appearing connate because of interlocking trichomes at adjacent margins of sepals], persistent [or caducous], [inflated] or not, equal, not saccate at base, pubescent on outside, glabrous [or pubescent] on inside. Petals yellow [white, or rarely pink or lavender], obovate [or spatulate], emarginate [or entire], gradually [or abruptly] narrowed into claws, glabrous or sparsely [to densely] pubescent on outside; claws without [or rarely with] a basal appendage. Nectar glands 4, 1 on each side of the lateral stamens, filiform [globose, or triangular], median glands always absent. Stamens 6, somewhat tetradynamous; filaments wingless [or unilaterally or bilaterally winged], toothless and unappendaged [or variously toothed and/or appendaged], free [or rarely connate]; anthers small, introrse, acute or obtuse at apex. Ovary sessile, 2 [1 or 4–8]-ovulate; placentation apical [or rarely parietal]; stigmas capitate. Fruits dehiscent [rarely indehiscent], orbicular [oblong, elliptic, ovate, obovate, or obcordate], almost always flattened parallel to the septum, inflated in the middle [or throughout, or not inflated], emarginate or truncate [acute, or retuse] at apex, entire [rarely crenulate or undulate] at margin, pubescent [or glabrous]; valves nerveless; styles persistent, pubescent [or glabrous]. Seeds compressed, narrowly [to broadly] winged [or wingless], mucilaginous [or not] when wet; cotyledons accumbent [or incumbent]. Base chromosome number 8. (Including *Gamosepalum* Hausskn.

non Schlechter, *Meniocus* Desv., *Moenchia* Roth, *Odontarrhena* C. A. Meyer, *Psilonema* C. A. Meyer, *Ptilotrichum* C. A. Meyer, *Triplopetalum* E. J. Nyárády.) LECTOTYPE SPECIES: *A. montanum* L.; see Britton & Brown, Illus. Fl. No. U. S. & Canada, ed. 2. **2:** 154. 1913. (Name from Greek, *a,* not or privative, and *lyssa,* rabies or madness; the name was used for plants reputed in ancient times as a remedy for hydrophobia, as a cure for madness, and as a calmative for anger.)—MADWORT.

A well-defined, taxonomically difficult genus of at least 170 (probably to 190) species primarily centered in Turkey (90 species, 50 endemic), with a rich representation in the Balkan peninsula (45 species, 20 endemic) and in the Caucasus and adjacent parts of the Middle East (63 species, 25 endemic). The genus is poorly developed in central and eastern Asia (seven species endemic) and in North Africa and the Iberian peninsula (eight endemic). With the exception of *Alyssum americanum* Greene (Alaska and Yukon Territory, Canada), which may be conspecific with the Siberian *A. obovatum* (C. A. Meyer) Turcz. (Dudley, 1964b), the genus is almost exclusively Eurasian and is mostly confined south of the 50th parallel. The great majority of taxa are narrowly endemic, and only about ten species are widely distributed weeds. *Alyssum* is represented in North America by one indigenous and six naturalized species, and in the southeastern United States by one weedy species.

Alyssum is divided into at least six or seven well-marked sections previously recognized as distinct genera. Section PSILONEMA (C. A. Meyer) J. D. Hooker (*Psilonema, Alyssum* subg. *Tetratrichia* Gay) (annuals; filaments slender, edentate, unappendaged, wingless; fruits dehiscent, valves equally inflated; seeds 2 per locule, winged or wingless, mucilaginous when wet), containing five species indigenous to southwestern Asia and the Mediterranean region, is represented in our area by a single species. *Alyssum Alyssoides* (L.) L. (*Clypeola Alyssoides* L., *C. campestris* L., *A. calycinum* L., *A. campestre* (L.) L., *Psilonema Alyssoides* (L.) C. A. Meyer), pale alyssum, $2n = 32$, a native of northern Africa and western Europe eastward to India, is naturalized in Canada, the United States, and Argentina. It grows on disturbed gravelly or sandy banks, waste grounds, and dry hillsides, in meadows, and along roadsides. It is rare in the Southeastern States and occurs in Cumberland County, Tennessee (R. Simmers, pers. comm.), Marion County, Arkansas (Smith), and Lincoln Parish, Louisiana (Logan). According to MacRoberts, the record from Louisiana needs verification.

Of the two varieties recognized by Dudley (1965a) in *Alyssum Alyssoides,* only var. *Alyssoides* is naturalized in the New World. The other, var. *depressum* (Schur) T. R. Dudley, is endemic to the Balkan peninsula. The species is distinguished from the other alyssums in North America by its persistent sepals; the compressed margin and inflated center of its fruits; its filiform, persistent nectar glands; and its unappendaged, toothless, and wingless staminal filaments. It may be confused with *A. desertorum* Stapf, but this has dentate filaments, deciduous sepals, and glabrous fruits.

Section ALYSSUM (annuals, biennials, or perennials; filaments winged, appendaged, or toothed; fruits dehiscent; seeds 2 per locule, winged or wingless, mucilaginous when wet), contains more than 70 species and is represented in North America by the Eurasian *A. desertorum, A. minus* (L.) Rothm. var. *micranthum* (C. A. Meyer) T. R. Dudley, *A. strigosum* Banks & Solander, and *A. Szowitsianum* Fischer & Meyer. These are naturalized in Manitoba and Alberta southward into the Mountain and Pacific states and Nebraska.

Section Odontarrhena (C. A. Meyer) W. D. Koch (perennials; filaments winged, dentate, or appendaged; fruits dehiscent or indehiscent, 1-seeded; seeds winged or wingless, rarely mucilaginous when wet) contains more than 70 species, of which only the native *Alyssum americanum* (= *A. obovatum*?) and the European *A. murale* Waldst. & Kit. grow in North America. The latter is an occasional escape from cultivation and is known from a few localities in Colorado, Michigan, and Québec.

The remaining sections of *Alyssum* (sects. Meniocus (Desv.) J. D. Hooker (seven species), Gamosepalum (Hausskn.) T. R. Dudley (ten species), and Tetradenia (Spach) T. R. Dudley (three species)) are not represented in North America. Krasnoborov has recently proposed the monotypic sect. Stevenioides, which resembles sects. Psilonema and Odontarrhena in its edentate staminal filaments and uniovulate locules, respectively.

Both *Aurinia saxatilis* (L.) Desv. (*Alyssum saxatile* L.), golden-tuft alyssum, basket-of-gold, gold-dust, rock madwort, and *Au. petraea* (P. Ard.) Schur (*A. petraeum* P. Ard.) are occasional escapes from cultivation in the United States, and the former has been reported from Mississippi (Jones). Although *Aurinia* Desv. has been treated as a section of *Alyssum* by numerous authors (e.g., Busch, Schulz, Ball & Dudley, Maire, Markgraf), Dudley (1964c) recognized it as a genus remotely related to *Alyssum* and most closely allied to *Berteroa* DC. or possibly to *Alyssoides* Miller. Dudley separated *Aurinia* from *Alyssum* mainly on the basis of leaf characters. *Aurinia* was said to have repand-sinuate or dentate rosette leaves 2–10 cm long, deeply grooved petioles with swollen and persistent bases, and cauline leaves about half (or less) the size of the rosette ones. On the other hand, *Alyssum* has entire rosette leaves 0.5–2 cm long, flat petioles neither swollen nor persistent at the base, and cauline leaves subequal in size to the basal ones. These alleged differences, however, are inconsistent within each of the two genera. For example, the basal leaves of *Au. corymbosa* Griseb. and *Au. halimifolia* (Boiss.) Cullen & T. R. Dudley are usually entire and have petioles neither swollen nor persistent, while several species of *Alyssum* (e.g., *A. aizoides* Boiss.) have persistent and swollen petiole bases, and many others (e.g., *A. argenteum* All. and *A. Bertolonii* Desv.) have deeply grooved petioles. The other differences listed by Dudley, particularly the shape of floral buds and the lobing of immature stigmas, are not sharply defined and are therefore unreliable. All species of *Aurinia* have spreading sepals, while all except a few species of *Alyssum* (e.g., *A. spinosum* L.) have erect ones. *Aurinia* consists of closely related species that are difficult to separate from *Alyssum* on the basis of fruit and floral characters alone. The differences in leaf characters between these genera may not justify the recognition of *Aurinia* as an independent genus remotely related to *Alyssum.* The lack of reliable differences between these genera has led to the reduction of the former to a section of the latter, as was done by numerous authors including Ball & Dudley.

Alyssum is easily distinguished from other members of the Alysseae by its nonsaccate sepals, entire or inconspicuously lobed stigmas, appressed stellate trichomes occasionally mixed with furcate (but never medifixed and bifid) ones, and usually dehiscent and latiseptate fruits without barbulate trichomes. The genus is often confused with *Lobularia,* but this always has bifid, medifixed, appressed trichomes.

Very high rates of selfing have been observed in several species of *Alyssum* (Persson). Cleistogamy is often associated with damp weather. Günthart suggested that the basal wings, teeth, or appendages of staminal filaments guide the proboscis of a visiting insect to the nectar glands. Dudley (1963) and Bergdolt, on the other hand, claimed that these staminal structures are not involved in pollination, and the latter maintained that they are vestiges of ancestral petaloid structures from which the filaments evolved. It is highly unlikely, however, that these floral structures, which are present in all except five species of *Alyssum* and in several other genera of the Alysseae, do not participate in pollination and do not have adaptive value. It should be noted that the distinctions between certain sections of *Alyssum* and between certain genera of the Alysseae rely primarily on the presence vs. absence of the staminal appendages or teeth (Dudley, 1964b; Dudley & Cullen).

Chromosome numbers are known for about 90 species of *Alyssum,* and all except a few are based on eight. Species with deviating base numbers (e.g., *A. hirsutum* Bieb., $2n = 46$) most likely evolved through aneuploidy from ancestors with $x = 8$. Section TETRADENIA *sensu* Dudley (1964b) is the most cytologically heterogeneous of all sections of *Alyssum.* On the basis of chromosome numbers, morphology, and geographic distributions, Küpfer has transferred its three species, *A. spinosum* ($2n = 16, 32$), *A. cochleatum* Cosson & Durand ($2n = 22$), and *A. Lapeyrousianum* Jordan ($2n = 30$), to *Hormathophylla.* Diploid and tetraploid counts based on eight are known for *A. obovatum* from Siberia (Goldblatt, 1981, 1984, 1985). Recent counts of $2n = 30$ for *A. americanum* from Alaska (Dawe & Murray) may support its recognition as a distinct species, instead of its reduction to a synonym of *A. obovatum,* as was suggested by Dudley (1964b). At least 50 species are diploid, 20 are polyploid, and 20 have both diploid and polyploid populations. Polyploidy played an important role in the evolution of *Alyssum,* as is evidenced by its occurrence in about 45 percent of the species for which counts are known. Dudley (1963), however, found polyploidy in only two of the 21 species he compiled and suggested that it was insignificant in the evolution of the genus.

Persson studied the karyotypes of several species of *Alyssum* and noted that members of sect. ALYSSUM have rod-shaped chromosomes, while *A. Alyssoides* has elliptic ones. He suggested that *A. siculum* Jordan ($2n = 48$) is an intersectional allopolyploid hybrid, the parental species of which are *A. Alyssoides* and *A. minus* ($2n = 16$). Interspecific hybridization is apparently very rare in the genus.

Little is known about the chemistry of *Alyssum*; only eight species have been surveyed for fatty-acid composition, and eight others for glucosinolates. The limited data indicate that linolenic acid is the primary seed-oil constituent (39–66 percent), that oleic and linoleic acids are secondary (9–24 percent each), and that erucic acid is lacking (Kumar & Tsunoda). Methionine-derived glucosinolates, particularly 5-methylthiopentyl, 5-methylsulfinylpentyl, 3-methylsulfinylpropyl, and 3-butenyl glucosinolates, are the dominant compounds (Hasapis *et al.,* Kjaer). The distribution of seed glucosinolates and fatty acids does not support the maintenance of *Aurinia* as a genus distinct from *Alyssum,* but that of seed sterols apparently does (Knights & Berrie).

Vaughan & Whitehouse indicated that seed-coat anatomy supports the sectional classification of *Alyssum.* They found that in *Aurinia* (treated as a section) the epidermal cells have no central columns, the subepidermis is present, and the palisade cells have thickened radial and inner tangential walls. In *Alyssum* the epidermis contains large and hollow central columns, the subepidermis is lacking, and the palisade cells either have only the inner tangential walls thickened or have all walls evenly thickened. However, they surveyed only five percent of the species of *Alyssum,* and it is not known whether their observations hold for the rest of the genus. According to Metcalfe & Chalk, the stems of *A. spinosum* are composed of alternating concentric rings of small, unlignified, spirally thickened vessels and large, lignified ones with horizontal bordered pits. It appears that the vascular cambium periodically produces the "juvenile" form of xylem.

Most species of *Alyssum* have dehiscent fruits with small, usually mucilaginous, and often winged seeds. The seeds are dispersed either by wind or (when wet) by adhering to animals and equipment. In sect. ODONTARRHENA subsect. *Samarifera* T. R. Dudley (nine species; Turkey, northern Syria, and Lesbos Island, Greece) the fruits are modified into indehiscent, thin-walled, one-seeded samaras borne on slender, brittle, usually deflexed pedicels and are therefore dispersed by wind. The evolution of this type of dispersal was accompanied by an increase of fruit size.

Several species of *Alyssum* (e.g., *A. Szowitsianum*) have conical infructescences, the lowermost pedicels of which are two to three times longer than the upper ones. The pedicels are closely appressed to the rachis, but soon after their exposure to rain, they spread horizontally, displaying the concave valves upward. The impact of raindrops eventually leads to the detachment of the valves and the release of mucilaginous seeds. The anatomical basis for this hygrochastic movement of the fruiting pedicels was studied by Zohary & Fahn. They showed that the adaxial side of the swollen bases of the pedicels consists of thick-walled fibers with transversely arranged pores, while the abaxial side has thin-walled fibers with diagonally arranged pores. Due to water absorption by the thick-walled fibers, the bases of the pedicels swell further and consequently spread in a purely mechanical way.

Species of *Alyssum* occupy diverse habitats, but the majority are distributed in arid or semiarid areas. More than 50 percent of the species, particularly members of sects. ALYSSUM and GAMOSEPALUM, occur primarily on calcareous soils. Those of the latter section often grow on soft calcareous substrates, especially chalks, and rarely on gypsum. Most species of sect. ODONTARRHENA are endemic to serpentine and other ultrabasic substrates, and at least 46 (66 percent) are hyperaccumulators of nickel. Nickel levels in these species are often higher than 1000 μg/g of dry weight. The physiology of tolerance and hyperaccumulation of nickel is directly related to the presence of high levels of malic and malonic acids. Nickel is accumulated in the cell vacuoles, and its presence in the mitochondria is believed to block the citric-acid cycle by deactivating malic acid dehydrogenase. This deactivation leads to the buildup of malic acid in the vacuoles, enabling them to absorb more nickel (Brooks *et al.*, 1981a). Seeds of the hyperaccumulators of the *A. serpyllifolium* Desv. complex (Iberian peninsula) can germinate on soils with nickel concentrations up to 12,000 μg/g, while those of the nonaccumulators can only germinate at concentrations below 60 μg/g. These physiological differences support the treatment of each of the three subspecies of *A. serpyllifolium* as a distinct species.

Except for a few weedy species, the genus has little economic importance. *Alyssum murale,* silver alyssum, is cultivated as an ornamental in parts of Europe and North America. The ancients used an infusion prepared from the flowers and leaves of some species as a sedative for anger and a cure for rabies.

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22. **Lobularia** Desvaux, Jour. Bot. II. **3:** 162. 1815, nom. cons.[5]

Annual or perennial canescent herbs [rarely subshrubs], densely to sparsely covered with a uniform indumentum of sessile, appressed, bifid, medifixed trichomes. Stems erect to prostrate, branched from the base or above. Leaves entire, short petiolate, linear, oblong, lanceolate, or spatulate, always attenuate at base. Inflorescences terminal, usually ebracteate (or the lowermost flowers subtended by leaflike bracts), densely flowered, corymbose racemes, usually greatly elongated in fruit. Sepals oblong or ovate, obtuse, always spreading, equal, not saccate at base, densely pubescent. Petals white or rarely pink or purple, clawed, suborbicular to spatulate or obovate, entire, about twice as long as the sepals. Nectar glands 8, filiform to subclavate; median glands 4, 1 outside each median stamen; lateral glands smaller, 1 on each side of lateral stamens. Stamens 6, tetradynamous; filaments free, strongly dilated at base, toothless, neither appendaged nor winged; anthers ovate. Ovary pubescent, 2- [to 12-]ovulate; ovules on subapical [or parietal] placentae. Fruits dehiscent,

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[5] The year of publication has been wrongly given in all floras as 1814. According to Stafleu & Cowan's Taxonomic Literature (Regnum Veg. **94:** 634. 1976), the year of publication of the above page of Desvaux's Journal was 1815. *Lobularia* is conserved, and the earlier generic names *Aduseton* and *Konig* of Adanson (Fam. Pl. **2:** 420. 1763) are rejected because the last name was not Latinized and *Aduseton* was spelled in two ways by Adanson, who added further confusion in his prefatory errata (p. 23) by transposing these names.

flattened parallel to the septum, sessile or short stipitate, elliptic, ovate, orbicular, [oblong, or obovate]; valves obscurely nerved, glabrous or pubescent; styles persistent, short; stigmas capitate. Seeds 1 [2–6] per locule, narrowly [to broadly] winged, compressed, minutely reticulate, mucilaginous when wet; cotyledons accumbent. Base chromosome numbers 11, 12. (Including *Konig* Adanson, *Aduseton* Adanson, *Koniga* R. Br., *Glyce* Lindley.) TYPE SPECIES: *Clypeola maritima* L. = *L. maritima* (L.) Desv. (Name from Latin *lobulus,* a little lobe, referring to the small fruit, but some authors (e.g., Fernald) maintain that the name probably refers to the 2-lobed (bifid) trichomes.)—SWEET ALYSSUM.

A genus of four species distributed primarily in the Mediterranean region and the Macaronesian archipelago (Azores, and the Salvage, Canary, and Cape Verde islands). One species, *Lobularia maritima* (L.) Desv. (*Clypeola maritima* L., *Alyssum maritimum* (L.) Lam., *Koniga maritima* (L.) R. Br., *A. minimum* L.), sweet alyssum or alison, $2n = 24$, is an ornamental widely cultivated throughout the world, an escape from cultivation, and a naturalized weed in the southeastern United States. It grows in waste places and lawns and on cultivated grounds in the Carolinas, Florida, Tennessee, Mississippi, and Louisiana. *Lobularia maritima* is an annual or perennial herb under cultivation, but in its native habitat in the Mediterranean region, Madeira, and the Canary Islands, where it occupies sea cliffs or sandy areas at sea level, it is always a perennial with a woody base and is sometimes a subshrub.

Earlier authors (e.g., De Candolle (1821, 1824), Bentham & Hooker, Baillon) treated *Lobularia* as a subordinate (often as a section) of the closely related *Alyssum.* There are, however, several morphological differences that support its treatment as a distinct genus. *Lobularia* has bifid trichomes, eight nectaries characteristically arranged (see above), spreading sepals, and toothless and unappendaged staminal filaments. *Alyssum* always has stellate trichomes, a different arrangement of the nectaries, toothed or appendaged filaments (except in five species of sect. PSILONEMA), and erect sepals (except in a few species). Two other genera of the Alysseae, *Farsetia* and *Bornmuellera* Hausskn., have trichomes similar to those of *Lobularia,* but they are easily separated by their dentate staminal filaments and strongly 2-lobed stigmas, respectively.

The identification of species of *Lobularia* relies heavily on the number of seeds per locule and on habit. Fragmentary specimens that lack mature fruits are often difficult to identify. As in several other genera of the Cruciferae, woody habit may have evolved in connection with insular isolation. All of the five taxa occurring in the Macaronesian archipelago are suffruticose perennials and under favorable conditions often become subshrubs. Annual habit, which is considered by Borgen (1984) to be derived in the genus, is found in two desert species, *L. arabica* (Boiss.) Muschler (Egypt, Israel) and *L. libyca* (Viv.) Meisner (Canary Islands, southern Spain, all of North Africa, Israel, and southern Iran). *Lobularia libyca,* the most widely distributed species in the genus, has the largest fruits, with up to six seeds per locule. *Lobularia maritima,* on the other hand, has the smallest fruits, with only one seed per locule. The fourth species, *L. intermedia* Webb & Berth., is intermediate between *L. maritima* and *L. libyca* in fruit size and in the number of seeds per locule. It is highly polymorphic, particularly in leaf morphology, fruit shape, and seed number. It was subdivided into several poorly defined varieties, the identities of which need critical evaluation. *Lobularia spathulata* (J. Schmidt) O. E. Schulz (Cape Verde Islands), *L. marginata* Webb & Berth. (high crests of the Anti Atlas Mountains, Morocco, and of Lanzarote and Fuerteventura, Canary Islands), and *L. palmensis* Webb ex Christ (eastern Canary Islands) are separated from *L. intermedia* on the basis of minor characters. They can be hybridized easily with each other and with *L. intermedia,* and the first generation hybrids show pollen fertility higher than 80 percent (Borgen, 1984). Therefore, they should be recognized as infraspecific taxa of *L. intermedia.*

Consistent counts of $2n = 24$ were reported for *Lobularia maritima* from many Mediterranean countries. However, Borgen (1984) also recorded $2n = 22$ and observed meiotic irregularities such as univalent and multivalent formations, chromosomal bridges, and lagging chromosomes. On the basis of these meiotic irregularities, particularly the frequent occurrence of univalents, Borgen (1984) suggested that *L. maritima* is probably an allopolyploid, but he did not indicate what its ancestral species were. He considered *L. maritima* to be the most primitive member of the genus despite its 1-seeded fruits that are the smallest in *Lobularia.* This species and the *L. intermedia* complex are self-incompatible, large-flowered, suffruticose perennials, whereas *L. libyca* and *L. arabica* are autogamous, small-flowered annuals. Uniform counts of $2n = 22$ have been reported for members of the *L. intermedia* complex, as well as for *L. libyca* (Borgen, 1970, 1974, 1984; Larsen). The count of $n = 6$ for *L. libyca* by Negodi may be an error. Snogerup and Borgen (1984) reported $2n = 46$ and $2n = 42$, respectively, for *L. arabica.*

Seed-coat anatomy of *Lobularia maritima* differs from that of *Alyssum* in the cell-wall thickening of the palisade layer. In *Lobularia* the cells are thin walled, while in *Alyssum* they are either evenly thickened throughout or the radial and/or inner tangential walls are thickened (Vaughan & Whitehouse).

Only *Lobularia maritima* has been surveyed for seed glucosinolates and fatty acids. High concentrations of 3-butenylglucosinolate, smaller amounts of 6-methylthiohexyl and 4-pentenyl glucosinolates, and traces of allyl, benzyl, and 2-phenylethyl glucosinolates were identified (Hasapis *et al.*). Kjaer & Gmelin found 5-methylsulfinylpentylglucosinolate to be the major component of the species. Although the fatty-acid composition of *L. maritima* resembles that of *Alyssum* in lacking erucic acid, it is markedly different in its high concentrations (42 percent) of eicosenoic acid and small amounts (10 percent) of linolenic acid. *Alyssum* contains only traces (0.4 percent or less) of the former acid and 36–66 percent of the latter (Kumar & Tsunoda). These observations, however, are based on an incomplete sampling of both genera.

Lobularia maritima growing in its natural habitats is highly variable in habit, leaf succulence, and resistance to salinity. Seashore populations are low-growing, bushy plants with broad, thick leaves and are resistant to salinity; inland ones are taller and generally erect plants with thin, linear leaves and are intolerant of salinity (Catarino *et al.*). Leaf succulence can be induced experimentally by prolonged treatment with 0.2 *M* sodium chloride. Such treatment increases the cell volume, nucleus size, and DNA content (often accompanied by endopolyploidy) in both palisade and spongy parenchyma (Capesius & Loeben).

Earlier literature indicates that *Lobularia maritima* was used as an astringent, an antiscorbutic, a diuretic, and a febrifuge. The species is the most widely cultivated of any ornamental crucifer. It is grown as a border plant and has sweet-smelling, white or purple flowers. It is also a naturalized weed in many parts of the world.

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23. **Berteroa** A. P. de Candolle, Syst. Nat. **2:** 290. 1821.

Annual or perennial herbs, densely pubescent with stellate trichomes mixed with fewer simple or bifid ones. Basal leaves petiolate, entire or occasionally repand or sinuate; upper cauline leaves sessile, entire. Inflorescences ebracteate, densely flowered, corymbose racemes, greatly elongated in fruit; fruiting pedicels erect-ascending [or divaricate], straight or curved. Sepals ascending to spreading, oblong, not saccate at base, densely pubescent, with or without a subapical tuft of simple trichomes. Petals white [or yellow], attenuate into a clawlike base, deeply emarginate, the sinus extending to nearly half the length of blade. Lateral nectar glands 4, 1 on each side of each lateral stamen; median glands absent. Stamens 6, tetradynamous; lateral filaments with a basal, adaxial appendage; median filaments dilated at base, neither appendaged nor winged;

anthers oblong, slightly exserted. Fruits sessile, 1–3 times as long as broad, elliptic, oblong, ovate [or orbicular], compressed parallel to the septum; valves with obscure midvein, inflated [or not], densely pubescent with appressed stellate trichomes [or glabrous]; styles persistent; stigmas capitate, obscurely 2-lobed, wider than the style. Seeds 2–6 per locule, compressed, suborbicular to obovate, margined [or conspicuously winged], nonmucilaginous when wet; cotyledons accumbent. Base chromosome number 8. (Including *Myopteron* Sprengel.) LECTOTYPE SPECIES: *Alyssum incanum* L. = *B. incana* (L.) DC.; see Britton & Brown, Illus. Fl. No. U. S. & Canada, ed. 2. **2:** 153. 1913. (Name honoring Carlo Giuseppe Bertero, Oct. 14, 1789–April 9, 1831, Italian physician and botanist of Piedmont, who traveled in the West Indies (1816–1821), settled in Chile in 1827, and died in a shipwreck in the southern Pacific.)—HOARY ALYSSUM.

A genus of five species centered in the Balkan peninsula and distributed from central Europe eastward into Turkey and the Caucasus. A few authors expand the limits of the genus to include *Berteroa spathulata* (Stephan ex Willd.) C. A. Meyer (central Asia and western Siberia), *B. Potaninii* Maxim. (Mongolia), and *B. macrocarpa* Ikonn.-Galitz. (Mongolia and central Asia). However, these are morphologically different and geographically disjunct from the remaining species of *Berteroa.* They have been transferred recently to a new segregate, *Galitzkya* V. Bocz., which differs from *Berteroa* in its subscapose habit, unappendaged filaments, and uniform pubescence.

Berteroa is represented in North America by two naturalized weeds, one of which is sporadic in the southeastern United States. *Berteroa incana* (L.) DC. (*Alyssum incanum* L., *Farsetia incana* (L.) R. Br., *Draba cheiranthifolia* Lam.), hoary alyssum, $2n = 16$, usually grows on dry sandy or gravelly soils in meadows, pastures, waste places, and fields, as well as along roadsides, railroad tracks, streams, and riverbanks. It was probably introduced into North America with either grass or clover seeds or in ballast (Martindale). Although *B. incana* was recorded from Tennessee as early as 1901 (Gattinger), it has been reported only recently from Arkansas, Kentucky, and Virginia. It is most abundant in the northeastern United States and is noxious in Minnesota and Michigan.

Berteroa mutabilis (Vent.) DC. is sporadically distributed in the United States and is naturalized in parts of Massachusetts, New York, and Kansas. Brooks's record of *B. obliqua* (Sibth. & Sm.) DC. from the Catskill region, New York, is based on a misidentified plant (*True 78*, NYS!) of *B. incana.* The former grows only as a native in Italy and the Balkan peninsula. The remaining species of the genus, *B. Gintlii* Rohlena and *B. orbiculata* DC., are endemic to Yugoslavia and the Balkan peninsula, respectively.

Although some earlier authors (e.g., Bentham & Hooker, Baillon) reduced *Berteroa* to a section of *Alyssum,* the two genera are not closely related. Von Hayek suggested that *Berteroa* is directly derived from *Fibigia,* while Schulz placed it between *Lobularia* and *Lepidotrichum* Velen. & Bornm. (= *Aurinia*). Obviously, the relationships between these and several other genera of the Alysseae have not been fully established. *Berteroa* is distinguished by its deeply bifid petals, appendaged lateral staminal filaments, mixed indumentum of stellate and bifid trichomes, and two to six seeds in each locule.

Very little is known about the floral biology of the genus. Knuth indicated that *Berteroa incana* is protogynous. Autogamy occurs as a result of contact between the median anthers and the stigma. In Europe the species is pollinated by several species of flies, particularly of the genera *Eristalis, Rhingia, Syritta,* and *Syrphus,* as well as by species of the butterfly genus *Vanessa* and the bee *Halictus.* Bateman listed one species of *Berteroa* (without name) as self-incompatible.

Chromosome numbers are known for all species except *Berteroa Gintlii.* The genus is uniformly based on $x = 8$, and all species are diploid. No interspecific hybridization has been reported.

The seeds of *Berteroa incana* contain very high concentrations (89 percent) of C_{18} fatty acids, of which linolenic acid is the major constituent (48 percent), and no traces of erucic acid (Appelqvist). Goering and colleagues considered the species to be agronomically acceptable and a good source of drying oils. The seedlings have large and small amounts of benzyl and isopropyl glucosinolates, respectively (Cole), while the seeds contain 5-methylsulfinylpentyl, 5-methylthiopentyl, 4-pentenyl, and 2-hydroxy-4-pentenyl glucosinolates (Daxenbichler *et al.,* Kjaer). The remaining species of *Berteroa* have not been surveyed for fatty acids or glucosinolates.

Seed-coat anatomy of *Berteroa incana* is indistinguishable from that of *B. obliqua.* The epidermis in both has large columns with markedly flattened tops and hollow centers, while the palisade layer has isodiametric cells with strongly thickened radial and inner tangential walls (Vaughan & Whitehouse).

Except for the weedy *Berteroa incana* and *B. mutabilis,* the genus has very little economic importance. The leaves of *Berteroa* are said to be eaten as a salad (Crisp).

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24. **Draba** Linnaeus, Sp. Pl. **2:** 642. 1753; Gen. Pl. ed. 5. 291. 1754.

Annual, biennial, or most commonly perennial herbs, usually with much-branched caudices. Stems simple or branched, scapose or foliose. Trichomes simple, furcate, cruciform [malpighiaceous, pectinate, stellate, or dendritically branched], usually more than one kind present. Basal leaves petiolate or rarely sessile, entire or toothed to laciniate [rarely pinnately lobed], usually forming distinct rosettes in the perennials but rarely so in the annuals. Cauline leaves (when present) sessile [or petiolate], cuneate [or amplexicaul]. Inflorescences ebracteate [or bracteate], few- to many-flowered, corymbose racemes, slightly to greatly elongated in fruit; fruiting pedicels ascending to divaricate [or erect]. Sepals erect to spreading, oblong to elliptic or ovate, not saccate or only slightly so at base, usually membranaceous at margin, caducous [or persistent], glabrous or pubescent. Petals present, reduced or absent in some autogamous annuals, white [yellow, rarely lilac, violet, orange, or red], obovate to spatulate [orbicular or linear], obscurely to distinctly clawed, the apex obtuse or rounded to truncate, or shallowly to deeply emarginate, or bifid. Nectar glands tooth- or ringlike, usually subtending the bases of filaments, median glands sometimes absent. Stamens 6 [very rarely 4], usually tetradynamous; filaments free, unappendaged, linear, slender or sometimes dilated at base; anthers oblong to ovate, polliniferous [or pollen aborted or absent in agamospermous taxa]. Ovary glabrous or pubescent, [2-] to 80-ovulate. Fruits dehiscent, ovate, lanceolate, elliptic, oblong, linear [or orbicular], sessile, flat or spirally twisted, flattened parallel to the septum, sometimes slightly inflated; valves glabrous or pubescent, usually with a distinct midnerve and with obscurely to prominently anastomosing lateral nerves; septum membranaceous, complete, usually not veined; styles persistent, long to short or obsolete; stigmas capitate, entire or 2-lobed. Seeds [1–] 3–40 per locule, ovate to ellipsoid [or orbicular], usually flattened, light to dark brown, reticulate, nonmucilaginous when wet, wingless [or very rarely broadly winged], weakly to strongly biseriately arranged in each locule, pendulous on slender funicles; cotyledons accumbent. Base chromosome numbers 6–12. (Including *Abdra* Greene, *Aizodraba* Fourr., *Dolichostylis* Turcz., *Drabella* Fourr., *Drabella* Nábělek, *Erophila* DC., *Holargidium* Turcz., *Leptonema* W. J. Hooker, *Nesodraba* Greene, *Odontocyclus* Turcz., *Pseudobraya* Korsh., *Stenonema* W. J. Hooker, *Thylacodraba* O. E. Schulz, *Tomostima* Raf.) LECTOTYPE SPECIES: *D. incana* L.; see M. L. Green, Bull. Misc. Inf. Kew **1925:** 51. 1925. Britton & Brown (Illus. Fl. No. U. S. & Canada, ed. 2. **2:** 148. 1913) chose *D. verna* L. as the lectotype species of *Draba.* This species, however, is the conserved type of *Erophila.* (Name from Greek *drabe,* acrid, used by Dioscorides to describe the taste of the leaves of certain cruciferous plants thought by some authors to have been hoary cress, *Cardaria Draba* (L.) Desv.) —WHITLOW GRASS.

A natural genus and the largest of the Cruciferae, with some 350 species distributed primarily in the Northern Hemisphere, particularly in the arctic and subarctic regions, as well as in the alpine and mountainous portions of the temperate regions. There are about 65 species in South America distributed at higher elevations from Colombia and Venezuela southward along the Andes into Patagonia. *Draba* is poorly represented in Mexico and Central America (11 species, six endemic; Rollins, 1984) and in Africa (five species, two endemic; Atlas Mountains of Morocco and Algeria) and is absent in Australia. More than 100 species are found in North America and Greenland, and the ranges of about 20 of these extend into the arctic and subarctic regions of Europe and/or Asia. The genus is well developed in the Himalayan and Irano-Turanian regions (ca. 50 and 40 species, respectively), as well as in China and Japan (ca. 35 species), Siberia and central Asia (ca. 30 species), central and northern Europe (ca. 35 species), and the Mediterranean area (18 species). *Draba* is represented in the southeastern United States by seven species, one of which is naturalized.

The sectional classification of *Draba* is controversial. Schulz (1927, 1936), who treated the genus on a worldwide basis, recognized 17 sections, while Tolmachev (1939) assigned the 91 species occurring in the U.S.S.R. to 29 series without recognizing sections. Although some of the infrageneric groups recognized by these authors represent natural assemblages of closely related species, the boundaries between the majority of them are artificially drawn and clearly unsatisfactory. Fernald (1934), who was the first to point out weaknesses in Schulz's (1927) sectional classification, indicated that his keys to the sections and to the species are misleading and impractical. It is beyond the scope of this flora to present a comprehensive sectional treatment for *Draba.* The genus is poorly represented in our area, and I prefer not to recognize any sections here.

Draba brachycarpa Nutt. (*Abdra brachycarpa* (Nutt.) Greene), $2n = 16, 24$, is the most widely distributed species in the Southeast. It grows on open clay soil in lawns, pastures, fields, disturbed areas, waste grounds, and cedar glades, on limestone rubble, and along roadsides in all of the Southeastern States. It appears to have restricted distribution in portions of the Florida Panhandle (Leon, Gadsden, Liberty, and Jackson counties) and in northern Louisiana. Its range extends west into Texas, north into Kansas, and east into Missouri, Illinois, Ohio, and Virginia. It is adventive in some of the Mountain and Pacific states. *Draba brachycarpa* is easily distinguished from the other annual drabas in our area by its glabrous, elliptic to oblong-lanceolate fruits 2–6 mm long, and by its cruciform, sessile trichomes. Diploid and triploid populations based on $x = 8$ have been found in Arkansas (Smith, 1969) and Texas (Rollins & Rüdenberg), respectively.

Draba aprica Beadle (*D. brachycarpa* var. *fastigiata* Nutt. ex Torrey & Gray) is a very close relative of *D. brachycarpa.* It grows on granite outcrops and in shallow sandy soils over siliceous rock. It is locally common in open knolls, woods, and alluvial areas near streams in South Carolina (Lancaster County), Georgia (Piedmont; Towns, Richmond, Oglethorpe, Cobb, and De Kalb counties), Arkansas (Drew, Faulkner, Cleburne, Washington, Montgomery, and Polk counties), eastern Oklahoma (McCurtain and Cherokee counties), and southeastern Missouri (Madison and Iron counties). Hitchcock suggested that *D. aprica* should be regarded as a variety of *D. brachycarpa,* but Fernald (1934) and Rollins (1961) clearly demonstrated that they are sufficiently different to be treated as distinct species. They do not hybridize in areas of sympatry, and according to Kral, *D. brachycarpa* flowers early and is usually in full fruit when plants of *D. aprica* start to bloom. Both species are white-flowered annuals with cruciform trichomes and small fruits to 6 mm long. *Draba aprica* differs from *D. brachycarpa* in its pubescent fruits, stalked trichomes, larger seeds (1–1.2 mm instead of 0.5–0.8 mm long), and corymbiform lateral branches of the infructescence (FIGURE 2g, j).

Draba ramosissima Desv. (*Alyssum dentatum* Nutt., *D. dentata* (Nutt.) W. J. Hooker & Arnott, *D. ramosissima* var. *glabrifolia* E. L. Braun), $2n = 16$, is a mat-forming perennial with much-branched, long caudices covered with remnants of old leaves and terminated by rosettes of laciniate to subpectinate leaves. It differs from its relatives with spirally twisted fruits in its paniculate infructescences with strongly divergent branches and in its styles 1–3 mm long. *Draba ramosissima* grows primarily on open shale banks, dolomitic bluffs, and limestone cliffs in North Carolina (Madison and Buncombe counties), Tennessee (Blount and Cocke counties), Kentucky, West Virginia, Virginia, and Maryland. Gattinger reported it from Polk County, Tennessee, but subsequent botanists have not confirmed this record. Plants with glabrous to sparsely pubescent stems and leaves were recognized by Fernald (1934, 1950) as var. *glabrifolia.* As shown by both Nye (1961, 1969a) and Reed, however, trichome

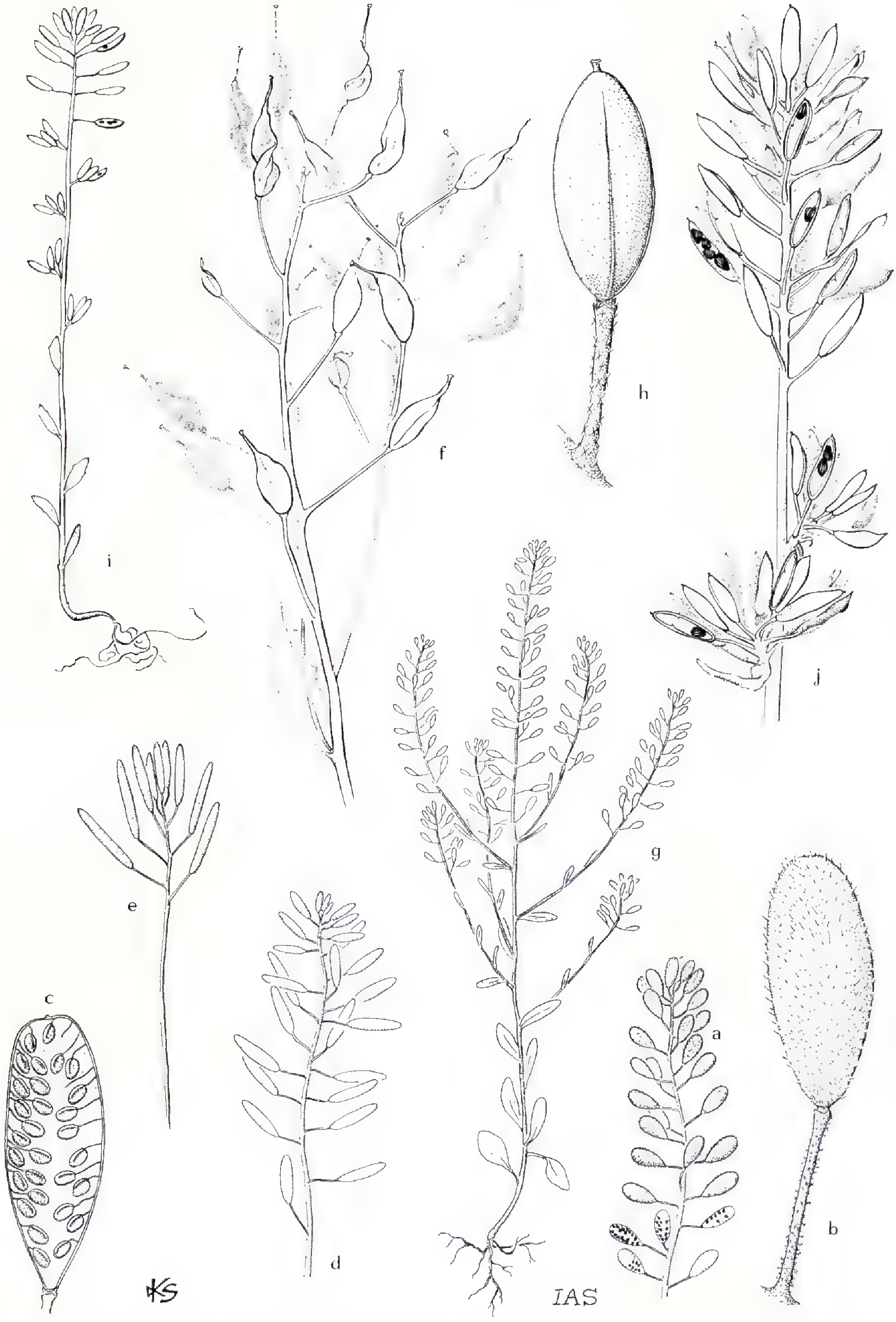

FIGURE 2. Selected species of *Draba*. a–c, *D. platycarpa:* a, infructescence, × ¾; b, fruit, × 5; c, fruit with 1 valve removed, × 5. d, *D. cuneifolia*, infructescence, × ¾. e, *D. reptans*, infructescence, × ¾. f, *D. ramosissima*, infructescence, × 2. g, h, *D. brachycarpa:* g, fruiting plant, × 1; h, fruit, × 12. i, j, *D. aprica:* i, fruiting plant, × 1; j, infructescence, × 2.

density is highly variable in the species, and both glabrous and pubescent forms are found within a given population. Schulz (1927) placed *D. ramosissima* in sect. PHYLLODRABA O. E. Schulz and assigned its nearest relative, *D. arabisans* Michx. (Maine to Newfoundland and westward to Minnesota and Ontario) to sect. LEUCODRABA DC. He separated these sections mainly on the basis of the many-leaved stems and yellow flowers in the former vs. the few-leaved stems and white flowers in the latter. Neither set of characters, however, was carefully observed or evaluated in either of the species or in the sections to which they were assigned.

The remaining species of *Draba* indigenous to the Southeastern States are very closely related. They were placed by Schulz (1927) in sect. TOMOSTIMA (Raf.) O. E. Schulz, which also included the South American *D. araboides* Wedd. and *D. australis* R. Br. All are subscapose annuals with subsessile basal leaves, obsolete styles, and heteromorphic flowers (some with broad, white petals, others apetalous and cleistogamous). *Draba reptans* (Lam.) Fern. (*Arabis reptans* Lam., *D. caroliniana* Walter, *D. micrantha* Nutt., *D. coloradensis* Rydb., *D. reptans* var. *stellifera* (O. E. Schulz) C. L. Hitchc.; see Hitchcock and Fernald (1934) for 15 additional synonyms), $2n = 16, 30, 32$, grows in open sandy areas, rock crevices, pastures, prairies, and disturbed sites, as well as along roadsides and railroad tracks. It is distributed from Massachusetts southward into North Carolina (Lincoln County), South Carolina (Darlington County), Georgia (Kenesau Mtn.), Tennessee (Nashville Basin), Alabama (Lee and Montgomery counties), Arkansas (Washington and Sebastian counties), and westward into the Pacific States, as well as in Manitoba, Ontario, and Saskatchewan. *Draba reptans* is easily distinguished from its nearest relatives by its entire or subentire leaves with simple or sometimes forked trichomes on the upper surface and stellate ones on the lower, and by its subumbellate infructescences with glabrous rachises and pedicels. Smith (1965) reported $2n = 16$ from plants of Kansas, but Löve & Löve found tetraploid populations ($2n = 32$) in Manitoba, and Mulligan (1966) counted $n = 15$ in plants from Saskatchewan and South Dakota.

Draba cuneifolia Nutt. ex Torrey & Gray is a variable and widely distributed species in which Hartman and colleagues recognized three varieties. Variety *cuneifolia* (*D. Helleri* Small, *D. ammophila* Heller, *D. cuneifolia* var. *leiocarpa* O. E. Schulz, *D. cuneifolia* var. *Helleri* (Small) O. E. Schulz, *D. cuneifolia* var. *foliosa* Mohlenbrock & Voigt), $2n = 32$, is widely distributed in northern and southern Arkansas, southeastern Kansas, Missouri, Oklahoma, the Southwestern States, central and western Colorado, western Utah, southern Nevada, and adjacent southeastern California. It is sporadic and probably introduced in North Carolina (New Hanover County), Florida (Duval, St. Johns, and Jackson counties), Alabama (Sumter County), Tennessee (Decatur County), Mississippi (Oktebbeha County), Louisiana (Grant, Rapides, and Caddo parishes), and Ohio. It is indigenous but apparently uncommon in Chihuahua, Coahuila, Baja California, and Zacatecas, Mexico. Mohr stated that *D. cuneifolia* is found in Georgia, but I have not seen any specimens from this state, and Hartman and colleagues did not list it from there. The species grows on limestone ledges, rocky slopes, and disturbed sandy soils in prairie pastures, lawns, grassy plains, fallow fields, cedar glades, and waste places. The other varieties of *D. cuneifolia,* var. *integrifolia* S. Watson and var. *sonorae* (Greene) S. B. Parish, do not occur in our area and are primarily distributed in the southern parts of California, Nevada, Arizona, and Texas and in adjacent northern Mexico. They differ from var. *cuneifolia* in their fruits with stellate instead of simple trichomes. Variety *cuneifolia* sometimes has glabrous fruits.

Draba platycarpa Torrey & Gray (*D. cuneifolia* var. *platycarpa* (Torrey & Gray) S. Watson, *D. viperensis* St. John), $2n$ = ca. 16, 32, differs from *D. cuneifolia* in its obovate to broadly elliptic, rounded fruits 2.5–3.7 mm wide and in its scapes pubescent with a mixture of long, simple trichomes and short, branched ones. The latter species has oblong to lanceolate or narrowly elliptic, acute fruits 1.8–2.8 mm wide and scapes with short, branched trichomes only. *Draba platycarpa* is sporadic in Louisiana (Lincoln Parish), Arkansas (Hempstead and Garland counties), and Oklahoma but is widespread in Texas and central and southern Arizona. It is disjunct and probably introduced in Idaho, Oregon, and Washington. Several authors (e.g., Watson, Hitchcock) reduced *D. platycarpa* to a variety of *D. cuneifolia,* but Hartman and colleagues have clearly shown that they should be treated as closely related species. They are morphologically distinct, and their profiles of flavonoid glucosides and volatile components are very different. They do not hybridize in areas of sympatry, and despite the numerous attempts to make artificial crosses between the two species, no hybrids were obtained (Hartman *et al.*). Diploid and tetraploid populations of *D. platycarpa* were found in Texas in Tarrant (Hartman *et al.*) and Kinney (Rollins & Rüdenberg) counties, respectively.

Draba verna L. (*Erophila verna* (L.) Chev., *E. vulgaris* DC.; see Schulz (1927) for more than 200 additional synonyms listed as species, varieties, or forms), whitlow grass, whitlow wort, $2n = 14, 16, 24, 30, 32, 34, 36, 38, 40, 52, 54, 58, 60, 64$, is a Eurasian plant naturalized throughout the New World. It has been reported from all of the Southeastern States except Louisiana and Florida. It is one of the earliest annuals to bloom in late winter and early spring (the generic name *Erophila,* under which *D. verna* is often placed, is derived from Greek *er,* spring, and *phileo,* to love, referring to its early appearance in spring). The species grows in lawns, fields, waste places, pastures, cedar glades, and open rangeland, on grassy hillsides, and along roadsides. It was well established in North America as early as the first half of the eighteenth century (Benson).

Draba verna is a highly variable and taxonomically difficult complex in which numerous extremes have been recognized as species, subspecies, or varieties. It consists of self-pollinating, morphologically distinct, uniform, local populations with different chromosome numbers. Crosses between such populations often produce hybrids that are sterile because of meiotic abnormalities. Autogamy played a major role in the formation and stabilization of a very large number of easily separable populations. Nearly 200 such populations were recognized by the nineteenth-century French botanist Alex Jordan as distinct "species," sometimes called "Jordanons." Schulz (1927) reduced these to eight species and some 60 varieties, but subsequent workers (e.g., Winge, 1940) questioned the taxonomic status of most of them. There is no correlation between the morphological, cytological, genetic, geographic, and ecological data on this complex, which is best recognized as a single polymorphic species with several subspecies. No attempt is made here to determine the subspecies of *D. verna* naturalized in the Southeastern United States.

Draba is a well-defined genus easily recognized by its latiseptate (flattened parallel to the septum), ovate to orbicular or oblong to linear fruits, usually wingless seeds biseriately arranged in each locule, unappendaged staminal filaments, accumbent cotyledons, and usually branched trichomes. The limits of the genus have not been altered during the past two centuries, and only one of its segregates is controversial. *Erophila,* which is united with *Draba* by North American botanists and retained as an independent genus by those elsewhere, differs from *Draba* only in its bifid instead of entire to deeply emarginate petals. The two are indistinguishable in every other morphological character. In my opinion this difference is not important; certain genera of the Cruciferae (e.g., *Megacarpaea* DC. and *Alyssoides*) have species with either entire or bifid petals. Petal apex (bifid vs. entire) may be controlled by a few genes or by a single pleiotropic gene and could therefore be insignificant for generic delimitations within the Cruciferae.

Perhaps the major taxonomic complexity in *Draba,* other than its sectional classification, lies in its species limits. Rollins (1966) suggested that apomixis together with polyploidy and interspecific hybridization are responsible for this complexity. Many species have been described on the basis of minor differences in characters of which the variation was poorly understood. For example, presence vs. absence of trichomes on fruits is insignificant in certain complexes, and numerous species (e.g., *D. reptans* and *D. cuneifolia*) have plants with either glabrous or pubescent fruits within the same population. On the other hand, the type of trichome (simple, furcate, cruciform, stellate, or dendritic) is very important in separating species.

Self-compatibility is apparently very common in *Draba,* and only a few species are self-incompatible (Bateman; Mulligan, 1976; Mulligan & Findlay). Protogyny occurs in a few species such as *D. aizoides* L. and *D. alpina* L. (Al-Shehbaz, 1977; Kay & Harrison), while autogamy is widespread in the genus. Species such as *D. reptans, D. cuneifolia,* and *D. aprica* produce heteromorphic flowers: some have sizeable petals, others have reduced ones, and still others are apetalous and cleistogamous (Fernald, 1934). They apparently produce apetalous flowers toward the end of the growing season (Kral), but *D. tenerrima* O. E. Schulz (Kashmir, Pakistan) is always apetalous and has only four stamens. Agamospermy occurs in the North American *D. densifolia* Nutt. ex Torrey & Gray, *D. Paysonii* Macbr., *D. ventosa* A. Gray, *D. exunguiculata* (O. E. Schulz) C. L. Hitchc., *D. Grayana* (Rydb.) C. L. Hitchc., *D. oligosperma* W. J. Hooker, and *D. streptobrachia* R. A. Price (Mulligan, 1976; Mulligan & Findlay; Price, 1979, 1980). In these species pollen fertility is zero or nearly so and the anthers do not dehisce. Some apomicts are triploids with highly irregular meiosis, but all produce abundant viable seeds without the need for pollen stimulation of seed production. Earlier claims of apomixis in *D. verna* (see Lotsy) were based on misinterpreted observations.

Chromosome numbers are known for some 115 species, the majority of which (nearly 60 percent) are polyploid; only a few (about 5 percent) have diploid and polyploid populations. Although base chromosome numbers in *Draba* range from six to 12, those of nearly 85 percent of the species are based on eight. Mulligan (1966) suggested that the North American species probably evolved through aneuploidy at the polyploid level. The lowest chromosome number in the genus ($2n = 12$) is found in *D. Olgae* Regel & Schmalh. (central Asia), while the highest counts ($2n = 128, 144$) are found in the North American *D. corymbosa* R. Br. ex DC. (including *D. macrocarpa* J. M. F. Adams and *D. Bellii* T. Holm), which consists of 16- and 18-ploid populations based on $x = 8$ (Böcher, 1966; Mulligan, 1974a). As shown above, *D. verna* is the most cytologically complex species in the genus. It contains many chromosomal races ranging from diploid to octoploid, as well as intermediate aneuploid derivatives.

Böcher (1966) indicated that the majority of the alpine species are diploid while the arctic ones are polyploid. He speculated that the mountains south of the arctic areas are probably the centers of origin and that *Draba* may be polyphyletic. He observed that polyvalent formations are very rare in drabas with high ploidy levels and suggested that allopolyploidy may have played an important evolutionary role at the hexaploid and decaploid levels.

Despite claims by many authors (e.g., Ekman (1932b), Schulz (1927), Weingerl) that interspecific hybridization is widespread in *Draba,* very little experimental work supports this. Fernald (1934) suggested that most of the alleged interspecific hybrids represent variations within poorly circumscribed, polymorphic species, while Knaben seriously questioned the validity of several hybrids listed by Ekman (1932b). There are strong sterility barriers between pairs of many closely related species. Mulligan (1974b, 1975, 1976) showed that artificial hybridization between many sexual species produces offspring with zero or very low pollen fertility and with aborted fruits. He concluded that interspecific hybridization is very rare in nature. Some members of the *D. nivalis* Liljeblad group produce sterile natural interspecific hybrids. Viable seeds were obtained from a few successful artificial crosses, but the second-generation hybrids did not reach maturity (Mulligan, 1975).

The chemistry of *Draba* is poorly studied, and only a few species have been surveyed for secondary constituents. Isopropyl, 2-butyl, allyl, 3-butenyl, and benzyl glucosinolates are found in four unrelated species (Kjaer; Rodman & Chew; Hartman *et al.*). The fatty-acid content of only six species has been determined (Jart).

Roots of certain rock-dwelling, perennial species of *Draba* have peculiar secondary growth characterized by the formation of armed periderm, abundant soft tissue, and secondary xylem structurally resembling the primary. These anatomical specializations, which are believed to be adaptations to rocky habitats, are also found in genera outside the Cruciferae (Pirogov).

Many species of *Draba* are cultivated as rock-garden or wall plants (Irving). Very few are weeds or show weedy tendencies. The fruiting stalks and seeds of *D. nemorosa* L. are used in China and Japan as diuretics and are prescribed to treat coughs, dropsy, nausea, and pleurisy (Perry; Kung & Huang). *Draba verna* (whitlow grass) was believed to cure whitlow, inflammation around the nails.

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25. **Lesquerella** S. Watson, Proc. Am. Acad. Arts Sci. **23:** 249. 1888.

Annual, biennial, or perennial herbs, usually densely pubescent with stellate [or lepidote] trichomes, sometimes pubescent with a mixture of simple, bifurcate, and dendritic ones. Stellate trichomes with few [to numerous] rays; rays smooth or tuberculate, simple or once [or twice] forked; webbing absent [or present only between the bases of rays, or progressively developed to their tips]. Stems decumbent to erect, several to numerous or rarely solitary, usually arising laterally from the basal rosette. Basal leaves petiolate, entire or dentate to sinuate or lyrately to pinnately lobed. Cauline leaves petiolate or sessile, usually cuneate at base, sometimes auriculate or amplexicaul, entire to dentate [rarely sinuate or incised]. Inflorescences ebracteate, few- to many-flowered, corymbose racemes; infructescences lax [or congested]; fruiting pedicels persistent, ascending to horizontal [or reflexed], straight or curved [sometimes sigmoid]. Sepals pubescent, narrowly oblong or elliptic to broadly ovate [occasionally linear or obovate], ascending to spreading [or erect], almost always deciduous, green or yellowish; lateral pair usually saccate, median pair not saccate, often thickened and somewhat cucullate at apex. Petals yellow to orange, sometimes white or lavender and with [or without] a yellow center [or purple veins], glabrous, broadly obovate [to narrowly spatulate], undifferentiated or slightly differentiated into claw and blade, obtuse or retuse to emarginate at apex. Nectar glands usually forming a ring [or a hexagon] subtending the bases of median filaments and surrounding those of lateral stamens. Stamens 6, tetradynamous; filaments linear, unappendaged, not dilated or sometimes strongly dilated at base; anthers linear [to oblong or ovate], usually sagittate at base. Fruits globose to subdidymous, sometimes obovoid to subpyriform [or ovoid to oblong], inflated or rarely strongly flattened parallel [or at right angles] to the septum, sessile or stipitate; valves glabrous or variously pubescent on the exterior or on both outer and inner surfaces, obscurely or rarely strongly nerved, thick or sometimes papery or membranaceous, rounded [or rarely strongly keeled] on the back; replum glabrous or pubescent; septum complete or occasionally with a central perforation, rarely reduced to a narrow band around the inner margin of replum, usually with a conspicuous nerve extending from the base of style to about or slightly beyond the middle, translucent or opaque; styles slender, persistent, glabrous or pubescent; stigmas capitate, entire or slightly 2-lobed, often much greater in diameter than the tip of style; ovules 2–14[–20] per locule; base of funicles usually adnate to septum. Seeds reticulate, orbicular or suborbicular, rarely hemispherical [or oblong to oval], flattened or rarely plump, with or without a narrow margin or wing, nonmucilaginous [or copiously mucilaginous] when wet; cotyledons accumbent [or rarely obliquely accumbent], longer [or equaling to shorter] than the radicle. Base chromosome numbers 5–10. LECTOTYPE SPECIES: *L. occidentalis* (S. Watson) S. Watson; see Payson, Ann. Missouri Bot. Gard. **8:** 133. 1922. The arbitrary designation of *L. Lescurii* (A. Gray) S. Watson as the lectotype species of the genus by Britton & Brown should be rejected because it is in conflict with Watson's original description of *Lesquerella.* For further discussion on the subject, see Payson and Rollins & Shaw (1973). (Name honoring Charles Leo Lesquereux, Nov. 18, 1806–Oct. 25, 1889, a distinguished Swiss-born, American paleobotanist and bryologist.)—BLADDERPOD.

A well-defined genus of some 90 species, the majority of which (83 species and 27 infraspecific taxa) occur in North America, particularly in the southwestern United States and adjacent Mexico, the Rocky Mountains, and the intermontane basin of the western United States. The remainder (probably up to 12 species; Rollins & Shaw, 1973) are found in South America from Bolivia southward. One species, *Lesquerella arctica* (Wormsk. ex Hornem.) S. Watson, is widely distributed from the coasts of Greenland across the Canadian Arctic and Alaska into Siberia. The genus is represented in the southeastern United States by seven species, of which five are endemic.

The sectional classification of *Lesquerella,* as proposed by Watson and Payson, does not reflect the natural groupings of species. The former recognized two sections: sect. ALYSMUS S. Watson (five species; plants not canescent, filaments dilated at base, cauline leaves usually auriculate) and sect. LESQUERELLA (28 species; plants canescent, filaments slender at base, cauline leaves not auriculate). Payson, on the other hand, redefined sect. ALYSMUS to include only one species, *L. Lescurii,* with latiseptate fruits (flattened parallel to the septum). He placed in sect. ENANTIOCARPA Payson three species said to have angustiseptate fruits (flattened at right angles to the septum) and retained in sect. LESQUERELLA (as sect. *Eulesquerella*) the remaining 48 species, with inflated, globose or ovoid fruits. On the basis of chromosome numbers, fatty-acid content, cross-fertility, and several morphological features, *L. Lescurii* is very closely related to several species with globose fruits. Therefore, sect. ALYSMUS is clearly artificial. One of the three species assigned by Payson to sect. ENANTIOCARPA is a *Draba,* while the other two are definitely unrelated (Rollins & Shaw, 1973). Slightly angustiseptate fruits probably evolved independently a few times within *Lesquerella,* and alone they can be unreliable indicators of relationships. As indicated by Rollins & Shaw (1973), the sectional classification of *Lesquerella* was not based on well-founded facts. It is impractical to place a few species in one or two sections and to retain the bulk of a genus in a highly heterogeneous one.

Lesquerella gracilis (W. J. Hooker) S. Watson (*Vesicaria gracilis* W. J. Hooker, *Alyssum gracile* (W. J. Hooker) Kuntze, *V. polyantha* Schlecht., *L. polyantha* (Schlecht.) Small), cloth-of-gold, $2n = 12$, is represented in the Southeastern States by subsp. *gracilis.* It grows on sandy loam or alkaline soil in prairies, pastures, and old fields, as well as along roadsides and grassy banks, in Arkansas (Howard and Little River counties), eastern Mississippi (Chickasaw, Lee, and Lowndes counties), southern Oklahoma, and east-central Texas. It is weedy and has been introduced in Tennessee in Shelby and Davidson counties (Rogers & Bowers) and in Missouri and Illinois. The subspecies is distinguished by its stipitate, glabrous, globose or ellipsoid fruits 3–6 mm long; cuneate, sessile or short-petiolate cauline leaves; 4–10(–14) ovules per locule; stellate trichomes with 4–7 bilaterally oriented rays; and straight, usually divaricate fruiting pedicels.

The records of *Lesquerella gracilis* subsp. *Nuttallii* (Torrey & Gray) Rollins & E. Shaw from Arkansas by Small (1913) (as *L. Nuttallii* Torrey & Gray and *L. repanda* (Nutt.) S. Watson) and by Payson (as *L. gracilis* var. *repanda* (Nutt.) Payson) were shown by Rollins & Shaw (1973) to be based on plants from Texas and Oklahoma, respectively. Subspecies *Nuttallii* differs from subsp. *gracilis* in its obpyriform to narrowly obovoid fruits (4.5–)5.5–9 mm long with a truncate base, instead of globose or ellipsoid fruits 3–6 mm long with a rounded base. Small (1913, p. 471) also indicated that *L. angustifolia* (Nutt.) S. Watson occurs "on prairies, near the Red River, Arkansas," but the record was from Red River County, Texas.

Lesquerella globosa (Desv.) S. Watson (*Vesicaria globosa* Desv., *V. Shortii* Torrey & Gray, *Alyssum globosum* (Desv.) Kuntze, *A. Shortii* (Torrey & Gray) Kuntze), $2n = 14$, has no close relatives in the genus and is clearly unrelated to any of the six species occurring in the Southeast. It is distributed in central Tennessee (Maury, Davidson, Cheatham, and Montgomery counties), north-central Kentucky, and Indiana (Posey County). The species was said to occur in Benton and Franklin counties, Arkansas (Smith), but I have not seen any material from this state, and neither Rollins & Shaw (1973) nor Kral has indicated that it is found there. It is most common on open rocky areas, limestone ledges, and cliffs along rivers but also grows in cedar glades and pastures and on open talus slopes. *Lesquerella globosa* has numerous small, globose, pubescent fruits (1–)2–2.8 mm long with a conspicuously wrinkled septum (FIGURE 3b); usually one subhemispherical seed per locule; straight fruiting pedicels; sessile or short-petiolate cauline leaves; and stellate trichomes with three to six usually forked rays.

The five remaining species of *Lesquerella* are endemic to the Southeastern States. All are annuals with a mixture of simple and branched (but never stellate) trichomes, auriculate cauline leaves, and staminal filaments with strongly dilated bases. They are diploids ($2n = 16$) that produce fully fertile offspring when hybridized (see below) in any combination. Furthermore, they contain high concentrations of densipolic acid, a unique seed fatty acid. The morphological, geographic, cytological, chemical, and interfertility data clearly support the derivation of the five species from a common ancestor.

Lesquerella lyrata Rollins, $2n = 16$, is a narrow endemic that grows in open pastures, old fields, cedar glades, and bottom lands, on limestone hills, and along roadsides in Franklin and Colbert counties, Alabama (Webb & Kral). Although it is locally common in a few localities, it is an endangered species. *Lesquerella lyrata* is readily distinguished from the other auriculate-leaved species by its yellow flowers and its glabrous, depressed-globose fruits with an opaque, complete septum and thick, leathery valves.

Lesquerella densipila Rollins, $2n = 16$, occurs in open alluvial sites, fallow fields, pastures, river bottoms, roadbanks, and cedar glades. It is abundant in the Central Basin of Tennessee, particularly near the West Fork of Stones

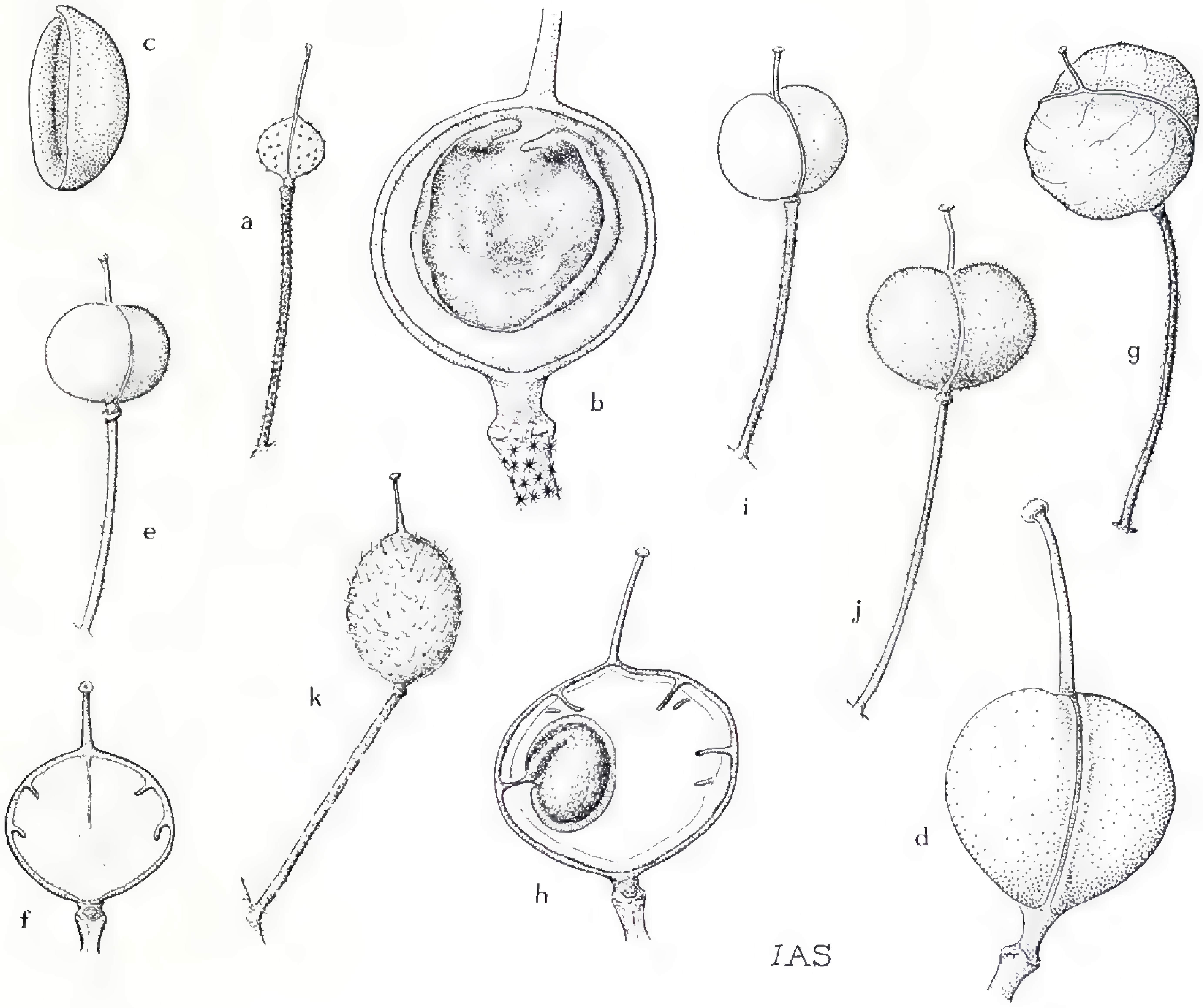

FIGURE 3. Fruits of *Lesquerella*. a–c, *L. globosa:* a, fruit, × 3; b, septum and replum, × 12—note wrinkled septum and position of seed; c, hemispherical seed, × 12. d, *L. gracilis,* fruit, × 5. e, f, *L. densipila:* e, fruit, × 3½; f, replum and septum, × 5—note midvein. g, h, *L. perforata:* g, fruit, × 2½; h, septum and replum, × 5—note central perforation. i, *L. lyrata,* fruit, × 3. j, *L. stonensis,* fruit, × 2½. k, *L. Lescurii,* fruit, × 3.

River, the Duck River, and the upper Harpeth River (Rutherford, Bedford, Williamson, Marshall, Maury, and Davidson counties). It also occurs, probably as a recent introduction, in northern Alabama (Franklin, Lawrence, Morgan, and Marshall counties). *Lesquerella densipila* is a very close relative of *L. lyrata,* from which it can be distinguished by its dense indumentum of short, simple or branched trichomes on the styles and the outer valve surfaces. According to Rollins (1955), *L. lyrata* is morphologically and geographically intermediate between *L. densipila* and *L. auriculata* (Engelm. & Gray) S. Watson (central Texas and south-central Oklahoma) and may well be the evolutionary link between the latter species and the auriculate-leaved members endemic to Tennessee.

On the basis of fruit morphology, earlier authors considered *Lesquerella Lescurii* (A. Gray) S. Watson (*Vesicaria Lescurii* A. Gray, *Alyssum Lescurii* (A. Gray) A. Gray), $2n = 16$, to be anomalous in the genus, and Payson placed it in a monotypic section. As shown above, however, the species is very closely related to and readily hybridizes with the auriculate-leaved lesquerellas of the Southeast. It is most closely related to and was probably derived from *L. densipila. Lesquerella Lescurii* is readily distinguished from all other species of the genus by its fruits that are strongly flattened parallel to the septum and its valves that are pubescent with a mixture of long, simple, bulbous-based trichomes and short, branched ones. It grows in open areas of river-bottom pastures, fields, and flood plains, as well as on thin soil over limestone in cedar glades and on hill slopes, in north-central Tennessee (Summer, Wilson, Rutherford, Davidson, Williamson, Cheatham, Montgomery, Dickson, and Stewart counties), particularly along the Cumberland River and several tributaries of the Harpeth River. Rollins (1981) listed *L. Lescurii* as having weedy tendencies. It is adventive and has been recorded only recently from Alabama (Limestone County) and Kentucky (Trigg County), by Kral and Chester, respectively.

A narrow endemic of central Tennessee, *Lesquerella stonensis* Rollins, $2n = 16$, grows in pastures, flood plains, and fields and on knoll tops, as well as on roadsides and stream banks along the East Fork of the Stones River (Rutherford County). According to Kral, it is locally abundant in some years and almost absent in others, with its present range restricted to a few fields along the Stones River.

Lesquerella perforata Rollins, $2n = 16$, is the nearest relative and perhaps a direct descendant of *L. stonensis.* It is also a narrow endemic of Tennessee and is presently known only within a radius of six miles around Lebanon (Wilson County), where it grows in open fields, pastures, floodplains, and limestone glades. Both species are easily distinguished from the other auriculate-leaved lesquerellas by their perforated septa (FIGURE 3h) and their white petals with yellow claws. *Lesquerella stonensis* has densely hirsute, depressed-globose to subdidymous fruits, hirsute styles, and glabrous inner-valve surfaces, while *L. perforata* has glabrous to sparsely hirsute, pyriform to obovoid fruits, glabrous styles, and densely pubescent inner-valve surfaces.

In no other genus of Cruciferae has natural interspecific hybridization been so well documented as in *Lesquerella.* In a series of papers, Rollins (1954, 1957) and Rollins & Solbrig (1973) demonstrated that species pairs involving *L. Lescurii, L. densipila,* and *L. stonensis* hybridize in all three combinations in parts of Tennessee where their ranges come together. Hybrid populations of *L. densipila* × *L. stonensis* (*L.* × *maxima* Rollins, *L. densipila* var. *maxima* Rollins) were found in Rutherford and Davidson counties along the Stones River downstream from the junction of its East and West forks, where *L. stonensis* and *L. densipila,* respectively, grow. Those hybrids were more similar to the former than to the latter species. The hybrid *L. Lescurii* × *L. densipila* occupied a stretch of more than 40 miles downstream along the Harpeth River between its junctions with Arrington Creek and the Cumberland River in Williamson, Davidson, and Cheatham counties. The third hybrid combination, *L. stonensis* × *L. Lescurii,* was found only once (in a vacant lot in the town of La Vergne, Rutherford County) and was not directly associated with any river system, unlike the other hybrid combinations.

The establishment, persistence, and population size of hybrids or their parental species in a given area are influenced by spring flooding of rivers, agricultural practices, and factors controlling seed germination. For example, the hybrid *Lesquerella Lescurii* × *L. densipila,* which was estimated in 1955 to occupy approximately 600 acres around the junction of Arrington Creek and the Harpeth River (Rollins, 1957), was reduced to less than 10 plants in 1966 because of the conversion of that area into pasture land (Rollins & Solbrig, 1973). Man's agricultural activities in the Central Basin of Tennessee have played a major role in bringing the ranges of the auriculate-leaved species of *Lesquerella* into contact and consequent hybridization. These species are largely allopatric and presumably evolved and persisted in isolation from each other until a few decades ago. Very high degrees of interspecific fertility exist among *L. Lescurii, L. densipila, L. stonensis, L. perforata,* and *L. lyrata.* Artificial hybrids between any pair of these show very low levels of meiotic irregularities that are not significantly different from those observed within each parental species (Rollins, 1957; Rollins & Solbrig, 1973). The artificial first- and second-generation hybrids have very high pollen quality, and their seeds germinate at levels as high as 86 percent.

Many authors (e.g., Maguire & Holmgren; Mulligan; Payson; Rollins, 1939a, 1950, 1983; Rollins & Shaw, 1973) have emphasized the very close relationship between *Lesquerella* and *Physaria* (Nutt.) A. Gray (22 species; Alberta, the Pacific and Mountain states, Arizona, and New Mexico). It is generally agreed that *Physaria* is derived from *Lesquerella.* The line separating them is artificially drawn, and there is a continuous morphological gradation from one to the other. Both genera, however, should be maintained. Similar situations exist between pairs of related genera throughout the Cruciferae, and it is not practical to merge the larger *Lesquerella* with the smaller and earlier-published *Physaria* (Rollins, 1950; Rollins & Shaw, 1973). *Physaria* differs from *Lesquerella* in its highly inflated, always didymous fruits either markedly constricted at the replum or strongly flattened contrary to the septum (angustiseptate). In general, the fruits of *Lesquerella* are not inflated, not didymous, and not constricted at the replum. There are, however, some exceptions. In *L. inflata* Rollins & Shaw and *L. perforata* the fruits are inflated, while in *L. hemiphysaria* Maguire and *L. stonensis* they are subdidymous. Angustiseptate fruits are found in unrelated species of *Lesquerella* and are well developed in *L. carinata* Rollins, *L. Paysonii* Rollins, and *L. lasiocarpa* (W. J. Hooker) A. Gray var. *Berlandieri* (A. Gray) Payson. *Physaria oregona* S. Watson, *P. Geyeri* (W. J. Hooker) A. Gray, and *P. alpestris* Suksd. have slightly inflated fruits. They were transferred to *Lesquerella* by Mulligan but, as shown by Rollins & Shaw (1973), should be retained in *Physaria.*

Lesquerella is also related to *Synthlipsis* A. Gray (three species; Texas and northern Mexico), and *L. lasiocarpa* var. *Berlandieri* was suggested as the possible link between the two genera (Rollins, 1955; Rollins & Shaw, 1973). The Old World genera *Alyssoides* (= *Vesicaria* Adanson) (four species; southern France, Balkan peninsula, Turkey) and *Alyssum* were also said to be closely related to *Lesquerella* (Rollins, 1950; Rollins & Shaw, 1973). Both *Alyssum* and *Alyssoides* have stellate trichomes indistinguishable from those of *Lesquerella,* but they differ in their winged or appendiculate staminal filaments, their pollen morphology, their winged seeds, and their lack of a nerve in the septum. In my opinion, *Lesquerella* should be associated only loosely with *Alyssum* and *Alyssoides.*

The tribal disposition of *Lesquerella* is problematic. Schulz placed the genus in the tribe Drabeae and assigned its nearest relative, *Physaria,* to the tribe Lepidieae. He defined the latter tribe mainly on the basis of its angustiseptate fruits. As delimited by Rollins & Shaw (1973), however, *Lesquerella* contains several species (see above) with such fruits. According to Schulz's key to the tribes, various species of *Lesquerella* will be identified in the Alysseae, the Drabeae, and the Lepidieae. Angustiseptate fruits evolved independently in at least four tribes of the Cruciferae (Al-Shehbaz, 1986). Angustiseptate and latiseptate fruits are found in *Lesquerella, Graellsia* Boiss., *Smelowskia* C. A. Meyer, and *Nerisyrenia* Greene. Therefore, the type of flattening of fruits is not always useful for assigning genera to tribes. Rather, problematic genera such as *Lesquerella* should be placed in the tribe containing what seem to be their nearest relatives.

On the basis of pollen morphology, *Lesquerella* should be associated with *Physaria, Synthlipsis, Nerisyrenia,* and *Dimorphocarpa* Rollins. All these New World genera have 5- to 10-colpate pollen grains not found elsewhere in the Cruciferae (Rollins, 1979; Rollins & Banerjee, 1979; Rollins & Shaw, 1973). The last genus is closely related to *Dithyrea* Harvey, which has 4-colpate pollen. Because all of these genera have angustiseptate fruits and are traditionally assigned to the Lepidieae, there is no major obstacle to placing *Lesquerella* with them. Von Hayek's grouping of these genera in one tribe was more natural than Schulz's, but he assigned them, along with several unrelated genera, to the tribe Schizopetaleae Prantl, which was considered to have a polyphyletic origin from tribe Thelypodieae Prantl. In this paper I have placed *Lesquerella* in the Alysseae, following the modified tribal classification adopted earlier (Al-Shehbaz, 1984). It is obvious, however, that the genus is more appropriately placed with its nearest relatives in the Lepidieae.

Although individual flowers are not showy in *Lesquerella,* they are densely grouped in compact inflorescences that can be quite attractive. These are visited by various species of flies, butterflies, and solitary bees, but the most common pollinator in the Southeast is the introduced honey bee (*Apis mellifera*). Self-incompatibility is widespread in *Lesquerella* and occurs in all of the auriculate-leaved species growing in our area (Rollins, 1957; Rollins & Solbrig, 1973; Sampson).

Chromosome numbers have been reported for at least 52 species, the majority of which are diploid with $n = 5$ to 10. Polyploidy did not play a major role in the evolution of *Lesquerella,* and only ten species have both diploid and polyploid populations. Three species, *L. mendocina* (Phil.) Kurtz (South America), *L. arctica,* and *L. peninsularis* Wiggins (Baja California) are polyploid, with $2n = 50$, 60, and ca. 40 or 48, respectively. Diploid, tetraploid, and hexaploid populations are found in *L. Engelmannii* (A. Gray) S. Watson ($x = 6$) and *L. ludoviciana* (Nutt.) S. Watson ($x = 5$). Complex aneuploid series occur in both *L. argyraea* (A. Gray) S. Watson and *L. ovalifolia* Rydb. subsp. *ovalifolia* (Clark; Rollins & Shaw, 1973). Except for *L. grandiflora* (W. J. Hooker) A. Gray ($2n = 18$) and *L. lasiocarpa* ($2n = 14$), the remaining auriculate-leaved species have $2n = 16$. The uniformity in chromosome numbers and in the presence of densipolic acid (see below) support the placement of these auriculate-leaved species in a position somewhat remote from *L. grandiflora* and *L. lasiocarpa.*

Seeds of the auriculate-leaved species of *Lesquerella* endemic to the Southeast (*L. densipila, L. Lescurii, L. lyrata, L. perforata,* and *L. stonensis*) contain high concentrations of densipolic acid (C_{18}) and lack lesquerolic acid (C_{20}). Those of sixteen other species (including *L. grandiflora* and *L. lasiocarpa*) are rich in lesquerolic acid (45–72 percent of the total fatty-acid content). In *L. auriculata,* which is believed to be the link between the auriculate-leaved species of the Southeastern States and the rest of the genus, small amounts of densipolic (two percent) and lesquerolic (ten percent) acids were found, in addition to high concentrations (32 percent) of auricolic acid. The last is lacking in our auriculate-leaved species and is only a minor constituent in many other species of *Lesquerella* (Appelqvist). It is a higher homologue of densipolic acid, while lesquerolic acid is a higher homologue of ricinoleic acid, a trace acid present throughout the genus.

Five glucosinolates were found in 13 species (Daxenbichler *et al.,* 1961, 1962). 6-Methylthiohexylglucosinolate occurs in all of the auriculate-leaved species (*Lesquerella auriculata* was not analyzed) and in *L. Engelmannii.* Other compounds were 4-methylthiobutyl, 3-methylthiopropyl, isopropyl, and 2-butyl glucosinolates.

Trichome diversity in *Lesquerella* is probably greater than that in any other genus of Cruciferae. Rollins & Banerjee (1975, 1976) studied the trichomes of 69 species of *Lesquerella* and observed well-marked trends of specialization. From the dendritic type (stalked, with unequal branches forming an irregular pattern), which is presumably primitive, stellate trichomes evolved by the reduction of irregularities in branching and by the disposition of the rays in one plane. Further specialization from stellate trichomes with few, simple rays proceeded in two directions. The first trend, found in many species, is a progressive increase in the branching of rays. As a result, two- or four-forked rays either without thickened bases (*L. macrocarpa* A. Nelson) or with massively thickened and fused bases (*L. Hitchcockii* Munz, *L. rubicundula* Rollins, and *L. thamnophila* Rollins & Shaw) probably evolved. In the second trend, found in at least ten species, the increase in the number of simple rays is correlated with a centrifugal increase of webbing between the rays. The two representative extremes of this trend are *L. Douglasii* S. Watson (with about 13 rays webbed only between their bases) and the highly specialized *L. mexicana* Rollins (with ca. 50 rays webbed to their tips and forming peltate scales).

The trichomes of the Cruciferae are unicellular, and those of *Lesquerella* have calcium carbonate deposited as calcite on the interior of the cell wall (Lanning, 1961). Rollins & Shaw (1973) indicated that there is a broad correlation between the density of trichomes and the availability of moisture. Species growing in arid areas and at high elevations have the densest trichome covering, while those of mesic areas have a sparse indumentum. Ancíbor showed that the fully developed trichome remains alive and has a very conspicuous nucleus and a dense cytoplasm. She suggested that trichomes may have a water-absorbing function, but Rollins & Shaw (1973) indicated that they probably reduce water loss from plants of arid areas by reflecting light rays, by forming a layer that slows down air movement, and by establishing a moisture gradient between the epidermis and the open air.

Lesquerella has little if any economic value. Several species analyzed for fatty-acid content show very high concentrations of hydroxy acids, which are valuable in industry. Tough plastics and reinforced elastomers have been produced from the oils of *L. Palmeri* S. Watson. Hinman (1984, 1986) suggested that *L. Fendleri* (A. Gray) S. Watson has superior qualities and can compete with castor bean (*Ricinus communis* L.) in its industrial oils. It has no allergenic or toxic properties, is capable of growing on sandy or calcareous soils of semiarid areas, tolerates cold and drought, and can be harvested by combine. No species of the genus, however, is a crop, and the agronomic values of most have not been evaluated.

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26. **Camelina** Crantz, Stirp. Austriac. **1:** 17. 1762.

Spring or winter annual or biennial herbs, with furcate-stellate and[/or] simple trichomes, sometimes glabrescent; stems simple or branched at base, often branched above. Basal leaves petiolate or subsessile, usually not in a rosette, entire to sinuate. Cauline leaves sessile, sagittate or amplexicaul, oblong to linear or lanceolate, entire or dentate, gradually decreasing in size upward. Inflorescences ebracteate, corymbose racemes, greatly elongated in fruit; fruiting pedicels horizontal to ascending [or appressed to rachis]; rachis of infructescence straight [or flexuous], glabrous [or pubescent]. Sepals oblong, erect, equal, not saccate at base, usually membranaceous at margin, villous in bud, often glabrescent. Petals yellow to white, clawed, spatulate, attenuate at base, longer than sepals. Nectar glands 4, 1 on each side of lateral stamens, median glands absent. Stamens 6, usually in 3 different lengths; filaments linear, free, unappendaged, slightly dilated at base; anthers oblong to ovate. Fruits usually dehiscent, obovate or narrowly to broadly pyriform [or linear], somewhat flattened parallel to the septum, short stipitate, strongly keeled and narrowly winged at the replum, rounded [truncate or notched] at apex, ending abruptly in a stylelike beak; valves thick, slightly to strongly convex, obscurely to prominently reticulate, the midvein evident in the lower half or along the entire length of the valve, glabrous [or pubescent], glossy on inside, the acuminate apex extending 0.5–1.5 mm into the beak area; beaks longer to shorter than styles; styles filiform, persistent; stigmas capitate; replum covered by the connate margins of valves, becoming visible after fruit dehiscence. Seeds 4–12 per locule, reticulate, oblong, copiously mucilaginous when wet, biseriately [or uniseriately] arranged in each locule; cotyledons incumbent or rarely accumbent. Base chromosome numbers 6, 7, 10, 13. (Including *Dorella* Bubani, non Weber-van Bosse, *Linostrophum* Schrank.) TYPE SPECIES: *Myagrum sativum* L. = *Camelina sativa* (L.) Crantz. (Name of obscure origin, possibly derived from Greek *chamai,* dwarf or on the ground, and *linon,* flax, perhaps referring to the stunting or suppressing influence of *Camelina* on the growth of flax.) —FALSE FLAX, GOLD-OF-PLEASURE, FLAXWEED.

A well-marked genus of six or seven species centered in Turkey and adjacent parts of southwestern Asia and southeastern Europe. *Camelina* is represented in North America by four naturalized species, of which two occur in the southeastern United States.

Of the two sections recognized in *Camelina* by De Candolle (1821, 1824), sect. CAMELINA (as sect. *Chamaelinum* DC.) is now retained in the genus, while sect. PSEUDOLINUM DC. has been transferred to *Rorippa* Scop. Boissier's sectional classification, which was accepted by Schulz and neglected by many subsequent authors, is more practical than any other infrageneric classification of *Camelina.* The monotypic sect. ERYSIMASTRUM Boiss. (fruits linear-cylindrical, seeds uniseriate) includes *C. anomala* Boiss. & Hausskn. of southern Turkey and the Bekaa valley, Lebanon. Section CAMELINA (fruits obovate to pyriform, seeds biseriate) contains the remaining species of the genus. On the basis of seed size and other characters of continuous nature, Mirek (1981) recognized two series in *Camelina.* It is doubtful, however, that these improve the taxonomy of the genus.

Camelina microcarpa Andrz. ex DC. (*C. sativa* subsp. *microcarpa* (Andrz.) E. Schmid), false flax, $2n = 40$, which is naturalized throughout North America, grows in grainfields, meadows, waste places, and disturbed habitats, as well as along roadsides, in North and South Carolina, Georgia, Tennessee, Arkansas, and Louisiana. It is likely to be found in the remaining states of the Southeast. It is distinguished by its mixed simple and furcate-stellate trichomes on the lower part of the stem, fruits 2.5–5 mm long, petals to 4.2 mm long, and seeds 0.9–1.5 mm long.

Most of the earlier reports of *Camelina sativa* (L.) Crantz (*Myagrum sativum* L., *Alyssum sativum* (L.) Scop., *C. sativa* var. *glabrata* DC., *C. glabrata* (DC.) K. Fritsch), false flax, flaxweed, gold-of-pleasure, Dutch-flax (Small), $2n = 40$, from North and South Carolina, Tennessee, Arkansas, and Louisiana are doubtful and may well represent misidentifications of plants of *C. microcarpa. Camelina sativa* is less common in North America than *C. microcarpa* and may be only a waif in the southeastern United States. It is distinguished from *C. microcarpa* by its glabrous or sparsely stellate-furcate stems rarely with simple trichomes, its longer fruits 7–9 mm long, and its shorter infructescences with fewer fruits.

Camelina Rumelica Velen., which has only recently been recorded in the United States (McGregor, 1984), is easily confused with *C. microcarpa* because of similarities in fruit shape and size, seed length, and lack of trichomes on the infructescence. It differs in its petals 5–9 mm long, in having only simple trichomes with some usually 2–3.5 mm long, and in its fruits more widely spaced in the lower than the upper part of the infructescence. The species is naturalized in Oklahoma, Texas, Kansas, Colorado, Nevada, and Oregon.

Camelina has obovate-pyriform (very rarely linear) fruits, thick valves abruptly acuminate into a stylelike beak (FIGURE 1e), and connate valve margins that make the replum invisible until dehiscence. The genus is related to *Chrysochamela* Boiss. (three species; Turkey and Syria) but certainly not to *Neslia* Desv., *Capsella* Medicus, or *Cochlearia* L., as has been suggested by several earlier workers.

The tribal disposition of *Camelina* is controversial, and there is little or no agreement among the several classifications consulted. The genus was placed in the Camelineae DC. (De Candolle, 1821, 1824; Bentham & Hooker), the Lepidieae DC. (Von Hayek, Janchen), and the Sisymbrieae DC. (Schulz). Although the placement of *Camelina* in the Alysseae is only a minor improvement, it is obvious that the boundaries of the Alysseae defined above are not natural and that this tribal disposition of the genus is not final.

Camelina is taxonomically troublesome, and only three species, *C. anomala, C. laxa* C. A. Meyer (Turkey, Iran, the Caucasus), and *C. hispida* Boiss. (Syria, Turkey, Iran) are distinct. The last is variable and contains three varieties (Hedge). The remaining species are weeds, and the boundaries between some of them are artificially drawn. Forms intermediate between *C. Rumelica* and *C. microcarpa* and between the latter and *C. sativa* have been found. *Camelina*

Alyssum (Miller) Thell., a weed of flax (*Linum usitatissimum* L.) fields in Europe said to be naturalized in the Dakotas and southern Canada, is completely interfertile with *C. sativa.* Their hybrids produce a very large array of intermediates found in nature (Tedin, 1925; Sinskaja & Beztuzheva). There is continuous variation in every character said to distinguish the two species. The nomenclature of the weedy camelinas can be quite misleading, and the number of species recognized has varied from seven (Vasil'chenko) to five (Meikle), four with several subspecies and varieties (Smejkal; Mirek, 1981; see both for extensive synonymy), and two (one of which has four subspecies) (Markgraf). In my opinion, *C. Rumelica, C. microcarpa,* and *C. sativa* are sufficiently distinct to merit specific status, but *C. Alyssum* should be treated as a subspecies of the last (as *C. sativa* subsp. *Alyssum* (Miller) E. Schmid). Interspecific hybridization has probably been responsible for blurring species boundaries, which otherwise are sharply defined in areas of allopatry. The pattern of continuous variation between species has been interpreted as a series of evolutionary differentiations from *C. microcarpa* to *C. sativa* and from the latter to *C. Alyssum* (Zinger). Both man's selection of flax (see below) and natural hybridization probably played major roles in creating the taxonomic complexity of the weedy camelinas.

Although most chromosome counts for *Camelina sativa* (including subsp. *Alyssum*) and *C. microcarpa* agree on $2n = 40$, counts of $2n = 26$ and $2n = 16$ and 32 have been reported for these species, respectively. Manton suggested that the base chromosome number for *Camelina* is eight and that all species are pentaploid, while others have believed that they are tetraploids based on ten. Stebbins, on the other hand, suggested that they may well be ancient allotetraploids, the ancestral species of which are unknown. Diploid counts of $2n = 12$ and $2n = 14$ are reported for *C. Rumelica* and *C. hispida,* respectively (Brooks; Goldblatt, 1984), but other counts ($2n = 24$, 26, and 40) are also recorded for the former.

The chemistry of *Camelina* is poorly understood. The scant data indicate that both *C. sativa* and *C. microcarpa* contain 10-methylsulfinyldecylglucosinolate (Kjaer *et al.*). These species and *C. Rumelica* have uniform fatty-acid composition characterized by high concentrations (33–38 percent) of linolenic acid, by lower and nearly equal amounts (9–19 percent) of oleic, linoleic, and eicosenoic acids, and by negligible amounts (1–3 percent) of erucic acid (Kumar & Tsunoda).

The mode of origin of *Camelina* species as weeds of flax fields was studied by Zinger, Sinskaja & Beztuzheva, and Tedin (1925) and was reviewed by Hjelmqvist, Stebbins, and Barrett. According to these authors, certain forms of *C. sativa* (variously recognized as varieties, subspecies, or species) originated under selection pressures (climatic, phytosociological, agricultural—e.g., threshing and winnowing) operating in the cultivation of flax. Whether flax is grown for fiber or for seed oils, it is "mimicked" by plants of *C. sativa* in growth habit, branching pattern, internode length, leaf width, stem diameter and pubescence, flowering time, fruit dehiscence, and winnowing properties of the seeds. *Camelina sativa* subsp. *Alyssum* (listed in the literature as a distinct species or as a subordinate of *C. sativa* under the epithets *Alyssum, macrocarpa,* *foetida, dentata,* and *linicola*) scarcely grows outside flax fields, and it has evolved winnowing characteristics so similar to those of flax that their seeds remain mixed and are therefore resown the following season. Other aspects of *Camelina-Linum* relationships have been discussed by Stebbins and Barrett.

It has been shown that competition between *Camelina* and flax reduces the yield of the latter and produces in it smaller leaves, thinner stems, reduced branching, and smaller infructescences (Balschun & Jacob, 1961, 1972; Kranz & Jacob). Grümmer & Beyer demonstrated that the decline in productivity of flax is caused by allelopathic effects of leaf phenolic compounds (e.g., vanillic, p-hydroxybenzoic, and ferulic acids) washed from *Camelina* by rain. Others (e.g., Lovett and various co-workers) indicated that in the presence of certain free-living, nitrogen-fixing bacteria, aqueous washings of foliage of *C. sativa* (presumably containing toxic degradation products of isothiocyanates) stimulate the early growth of flax but inhibit its later growth and may cause marked ultrastructural changes in its root tips.

Species of *Camelina* accompanied the spread of agriculture in prehistoric times. Subfossil remains (as carbonized seeds) date back to the Neolithic and the Iron Age. *Camelina sativa* was cultivated for its stem fibers and edible oils by the Romans as early as 600 B.C. Despite the drastic decline in its cultivation, it is still grown in parts of Europe and the Soviet Union for the same purposes. The seeds contain 34–42 percent oil and about 33 percent protein. The seed oil has been used as an illuminant and for making soap, while the seed cake is fed to cattle.

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THE BUXACEAE IN THE SOUTHEASTERN UNITED STATES[1]

R. B. CHANNELL[2] AND C. E. WOOD, JR.[3]

BUXACEAE Dumortier, Comment. Bot. 54. 1822, nom. cons.

(BOXWOOD FAMILY)

Monoecious [or dioecious, rarely perfect-flowered] evergreen shrubs, subshrubs, or rhizomatous herbs [rarely trees], with entire or dentate, alternate or opposite, exstipulate leaves, the hypogynous flowers actinomorphic, borne in usually dense racemes, spikes, or heads, the staminate above the carpellate, the latter rarely solitary, both usually subtended by 1 to several bracts and bracteoles. Perianth of 4 [or 6] imbricate tepals in 2 pairs [or in whorls]. Androecium of 4 [or 6] stamens opposite the tepals, sometimes surrounding a central nectary [or a rudimentary gynoecium], the distinct filaments often thickened and bearing large anthers. Gynoecium [2- or] 3-carpellate with [as many or] twice as many locules, each with [2 or] 1 (respectively) pendulous anatropous ovules, the carpels connate below, distinct above, grading at length into linear-subulate style branches stigmatic along the inner surface, often becoming divergent, divaricate or recurved in fruit. Fruit [a loculicidal capsule forcibly ejecting the seeds (*Buxus*) or] apparently indehiscent but capsular, baccate [or drupaceous], regularly failing to dehisce, disarticulating below, falling entire and freeing the enclosed seeds from the base or by degeneration of fruit pulp. Seeds dark brown or black, shining, sometimes conspicuously carunculate; endosperm fleshy. (Buxacées Loiseleur, Man. Pl. Us. Indig. **2:** 495. 1819, nom. inval.) TYPE GENUS: *Buxus* L.

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This treatment was originally prepared by Channell. Channell's student, H. C. Robbins, later studied the genus *Pachysandra* under his supervision and produced the thesis quoted in the references. Channell and Wood have updated the text and references. The illustration of *Pachysandra procumbens* was prepared by Dorothy H. Marsh, with Channell's dissections and supervision, from plants grown at the Arnold Arboretum and fruits collected by Elsie Quarterman in Tennessee in May, 1957 (GH). We are indebted to Barbara Nimblett for her help with the references and the manuscript.

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An apparently ancient group, to judge from the diversity of the constituents (including about 70 species of *Buxus,* seven or eight of *Notobuxus* Oliver, 11 of *Sarcococca* Lindley, and four of *Pachysandra* Michaux) and the widespread intercontinental distribution, especially in the Old World tropics. The family has been treated as a tribe of the Euphorbiaceae (Bentham; Bentham & Hooker), or a "series" (Buxeae) of the Celastraceae (Baillon, 1875), or assigned variously to the Celastrales (Scholz), the Euphorbiales (Takhtajan, 1959, 1969; Cronquist, 1968, 1981), the Hamamelidales (Takhtajan, 1954, 1980; Hutchinson, 1969, 1973), the Pittosporales (Thorne, 1976, 1983), and a separate order Buxales in Dahlgren's (1983) Rosiflorae. Airy Shaw (in Willis) thought the Buxaceae to be related to the Euphorbiaceae and perhaps the Celastraceae.

The pollen of *Pachysandra* and *Sarcococca* is similar. The spheroidal grains are radially symmetrical. In *Pachysandra* they are polyforate, with more than 12 apertures or foramina. They have a pattern characteristic of *Croton* L. and other Euphorbiaceae, with well-defined, regularly arranged triangular excrescences of the sexine that form reticulate polygons. The pollen of *Sarcococca Conzattii* (Standley) I. M. Johnston (*S. guatemalensis* I. M. Johnston) is quite different from that of the Asiatic species and that of *Pachysandra* (see Gray & Sohma), strengthening Sealy's (1986) exclusion of this species from *Sarcococca.*

The pollen of *Buxus* evidently in no way resembles that of either *Pachysandra* or *Sarcococca,* being similar, however, to that of *Styloceras* Juss. (Stylocerataceae), a genus comprising four species of glabrous trees of western tropical South America and related to Buxaceae but differing, according to Airy Shaw (in Willis), in the naked staminate flowers with many more or less sessile anthers borne on a solitary bract, and in the locules of the ovary that are completely divided by secondary longitudinal septa (but cf. *Pachysandra procumbens*). The staminate flowers of *Styloceras* appear to be simple androphylls, as in *Didymeles,* a genus of two arborescent Madagascan endemics and the basis for the Didymeleaceae, the fruits of which are large, one-seeded drupes (cf. the berries of *P. terminalis*), the flowers evidently primitively simple, and the genus possibly having some relationship to the Buxaceae through the Stylocerataceae.

It is of interest in passing that the distribution of the Buxaceae, the Stylocerataceae, and the Didymeleaceae together includes the major continental land masses of the world, suggesting that comparative knowledge of the alliances may contribute to a refined appreciation of phytogeography and a better understanding of the efficacy of isolation in phylogeny.

The family is notable for the alkaloids that occur in its members. Gibbs noted, "steroid alkaloids in bewildering numbers occur in: *Buxus, Pachysandra, Sarcococca*" (p. 1217) and "the *steroid alkaloids* of the Buxaceae certainly define that family" (p. 1221).

The Buxaceae are economically important for various ornamentals used in horticulture, principally *Buxus* (various species, especially *B. sempervirens* L. and *B. microphylla* Sieb. & Zucc., selections, and cultivars, including those variously known as English, Japanese, Korean, Chinese, and 'California' box or boxwood), and to a lesser extent representatives of four or five (see Bailey *et al.* and Sealy, 1949) species of *Sarcococca* (including *S. ruscifolia* Stapf, sweet box, and *S. saligna* (D. Don) (Müll.-Arg., willow-leaf box) and *Pachysandra* *terminalis* Sieb. & Zucc., Japanese spurge or Japanese pachysandra, widely used as a ground cover. The firm, close-grained wood of certain members of *Buxus* (especially *B. sempervirens*) is used for turning and engraving. Other products also find use in commerce.

A useful liquid wax, difficult to synthesize commercially, is obtained from the seeds of *Simmondsia chinensis* (Link) Schneider (*S. californica* Nutt.), the jojoba or goatnut. Contrary to the connotation of the original epithet, this long-lived, low shrub (under cultivation attaining a height of three feet when staked) is indigenous to large areas of the Sonoran Desert of California, Arizona, and northern Mexico. Although long assigned to the Buxaceae (Müller; Pax, 1890; Hutchinson, 1967; Scholz), it constitutes a separate family taxonomically, the Simmondsiaceae.[4] The seeds contain up to 25 percent liquid, unsaturated wax, which can be solidified by hydrogenation, used in the manufacture of extreme-high-pressure lubricants, especially for transmissions in heavy-duty vehicles. It is a suitable substitute in uses calling for spermaceti (sperm-whale "oil," itself technically a wax), carnauba wax, and beeswax, and it is currently also used in a number of cosmetics. Resistant to pests and diseases, jojoba thrives without irrigation in areas where rainfall is less than 24 cm annually, with mature plants producing up to 12 pounds dry weight of seeds during the period. It has elicited considerable interest as a potential agricultural crop, not only in desert regions of the North American Southwest, but in arid regions of Argentina, Chile, Israel, Africa, and Australia.

The monogeneric Simmondsiaceae have flowers with (4) 5 (6) tepals, numerous (8–12) stamens, unique pollen, and a solitary ovule in each of the three locules (cf. *Pachysandra*); usually a single large seed with a large embryo and little or no endosperm; and anomalous wood structure with several concentric rings of vascular strands, besides other distinctive anatomical features. In pollen and anatomy *Simmondsia* has much in common with some members of the Centrospermae, although an actual relationship with them is difficult to envision, according to Airy Shaw (in Willis), who suggested that the most probable affinity of *Simmondsia* is with the Monimiaceae (*sensu stricto*), from which it differs in the syncarpous gynoecium and fruit and the scanty or absent endosperm. However, Wettstein (1924, 1935), Takhtajan (1969), Cronquist (1981), Thorne (1983), and Dahlgren all have associated *Simmondsia* with the Euphorbiales. Scogin (see references to Simmondsiaceae) found that in taxa from a wide array of families examined for cross-reactivity with *Simmondsia* antiserum, a reaction was detected only with three species of Euphorbiaceae. It

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[4] The name Simmondsiaceae is usually attributed to Van Tieghem (Ann. Sci. Nat. VIII. **5:** 289–338. 1897, the section on *Simmondsia* repeated almost verbatim in Jour. Bot. Morot **12:** 103–112. 1898), but nowhere did he use the Latin form. He always referred to the family as "Simmondsiacées." (And in none of his papers do we find anything but the French vernacular form for family names, and frequently for generic ones, e.g., "le genre Simmondsie.") Not being in Latin, these names are invalidly published. Insofar as we have been able to determine, the name Simmondsiaceae should be cited as Takhtajan ex Dostál, Botanická Nomenklatura, 217. 1957. Airy Shaw's citation (in Willis) attributing the name to (Pax) Van Tieghem is certainly incorrect, for nowhere did Van Tieghem either use the correct form of the family name or mention Pax.

seems clear that the relationships of *Simmondsia,* whatever they may be, are not with the Buxaceae as formerly thought.

Because of the economic interest of *Simmondsia,* a selected series of references to this genus is included here following those for the Buxaceae.

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1. **Pachysandra** Michaux, Fl. Bor.-Am. **2:** 177, 178. *pl. 45.* 1803.

Evergreen or semi-evergreen, erect, decumbent, or prostrate, sympodial [shrubs, subshrubs, or] perennial herbs, usually with [woody or] fleshy rhizomes, fibrous roots, and simple, alternate, exstipulate, petiolate leaves with glabrous, glabrescent, or pubescent, variously toothed, subdentate to nearly entire blades with prominently 3-nerved pinnate venation. Inflorescences spicate, basal [or axillary or terminal], the distal portions occupied by 5–40 pedicellate, subsessile, or sessile carpellate flowers. Staminate flowers subtended by a single ciliate-pubescent bract, and with a perianth of 4 decussate, imbricate, ciliate tepals sometimes with accompanying bracteoles, and (2 or) 4 (or 6) distinct stamens with long-exserted, thickened or compressed clavate filaments, each surmounted by a linear-oblong, rotund to sagittate, dorsifixed, longitudinally dehiscent, introrse anther, the connective sometimes prolonged as an appendage; pollen spheroidal, polyforate, with polygonal ornamentation. Carpellate flowers inserted on the inflorescence axis below the staminate flowers, subtended by 7–13 distinct imbricate herbaceous bracts, with 4 or more acute tepals; ovary [2- or] 3-carpellate, the carpels connate below, each with 2 locules separated by a false partition, each locule then containing a single pendent ovule; the styles [2 or] 3, subulate to linear, erect or spreading at anthesis, becoming recurved in fruit; stigma linear or linear-lanceolate, papillose, usually sulcate, covering the inner surface of the style branches. Fruit capsular [or baccate], indehiscent but becoming detached basally and falling entire. Seeds trigonal, with [or sometimes without] a micropylar caruncle, the smooth, glossy testa finally hard and dry, dark brown or black, the endosperm whitish and oily, the embryo straight, the cotyledons considerably broader than the radicle. Type species: *P. procumbens* Michaux. (Name from Greek *pachys,* thick, and *andros,* of a man, alluding to the thick filaments of the stamens.)

The genus includes four species: *Pachysandra procumbens,* Allegheny spurge or Allegheny-Mountain spurge, indigenous to the southeastern United States, and three indigenous to eastern Asia. *Pachysandra terminalis* Sieb. & Zucc. (China and Japan) and *P. axillaris* Franchet (Yunnan, China), as their epithets connote, are well marked and, together with *P. procumbens,* easily distinguished by the disposition of the inflorescences; *P. stylosa* Dunn (China) is characterized by its long, prominent styles, recurved in fruit. Treated by Robbins (1962) on the basis of herbarium material as comprising six taxonomic varieties, the last species deserves reexamination on the basis of more and better material. Cheng has recently (1980) treated *P. stylosa* as a variety of *P. axillaris.*

The geographic distribution of the genus, with a single species endemic to the eastern United States disjunct from the four of eastern Asia, exemplifies the well-known affinities of the floras of the two regions pointed out by Asa Gray in 1840 and elaborated by him in 1846. Fossil evidence of the occurrence of *Pachysandra* in the western United States might be thought to lend credence to the belief that the genus was a member of the northern temperate "Arcto-Tertiary" flora, but Leopold & Macgintie pointed out that *Pachysandra* "appears to have had ancestral types at middle latitudes in America well before the 'Arcto-Tertiary' flora came into being." They further suggested that the "Pachysandra-Sarcococca group may well have had a New World origin." The center of morphological and taxonomic diversity, however, is clearly in eastern Asia.

Gray & Sohma have shown that *Sarcococca* and *Pachysandra* have distinctive and related pollen structure. Although the pollen morphology of the two genera merges when they are viewed as a whole, some types are distinctive—for example, the pollen of *P. procumbens* has a sculpture pattern and a pore frequency that set it off from that of other species of *Pachysandra* and *Sarcococca.* Muller noted that *Pachysandra*-type pollen is known from the Campanian of Canada and from the Campanian-Danian interval of Germany. Later Cretaceous records of the group come from deposits of Maestrichtian age in Wyoming (Leopold & Macgintie), California, Montana, and Canada (see Muller). In the eastern United States pollen of the *P. procumbens* type is known from the middle Eocene and from the Miocene (Leopold & Macgintie). "Most of the available western records of the group appear to be related to Old World species."

Believed to have survived the geologic changes of the past few million years in the limestone plateau country of central Kentucky, Tennessee, and adjoining states, *Pachysandra procumbens* is now of local occurrence, for the most part in rich woods of moist ravines near streams.

Braun considered *Pachysandra procumbens* to be a characteristic herbaceous plant of the Western Mesophytic Forest Region, an area having as its eastern boundary the western escarpment of the Cumberland and Allegheny plateaus and as its western boundary the loess bluffs of the Mississippi River. She remarked that, although commonly thought to be rare, it is an abundant plant of mesophytic woods in the region.

Pachysandra procumbens is of some floristic, phytogeographical, and wildflower interest. A strongly rhizomatous herb of rich woods, it displays sympodial growth, the shoots bearing approximate, mottled, strongly dentate, pubescent leaves, urticaceous in superficial appearance, and abscising as simultaneously replaced by new growth from scaly basal buds in spring. (As might be expected, anomalous flowers with two or four styles instead of three, and five stamens instead of four, have been described.) Old reports of the occurrence of the plant in West Virginia and New Jersey, as well as at Memphis, Tennessee, are probably erroneous but are of considerable interest if verified. The species has been reported from central Kentucky, central and eastern Tennessee, western North Carolina, western Georgia, Alabama, Mississippi, the Marianna Caverns in Jackson County, Florida, and the Tunica Hills of

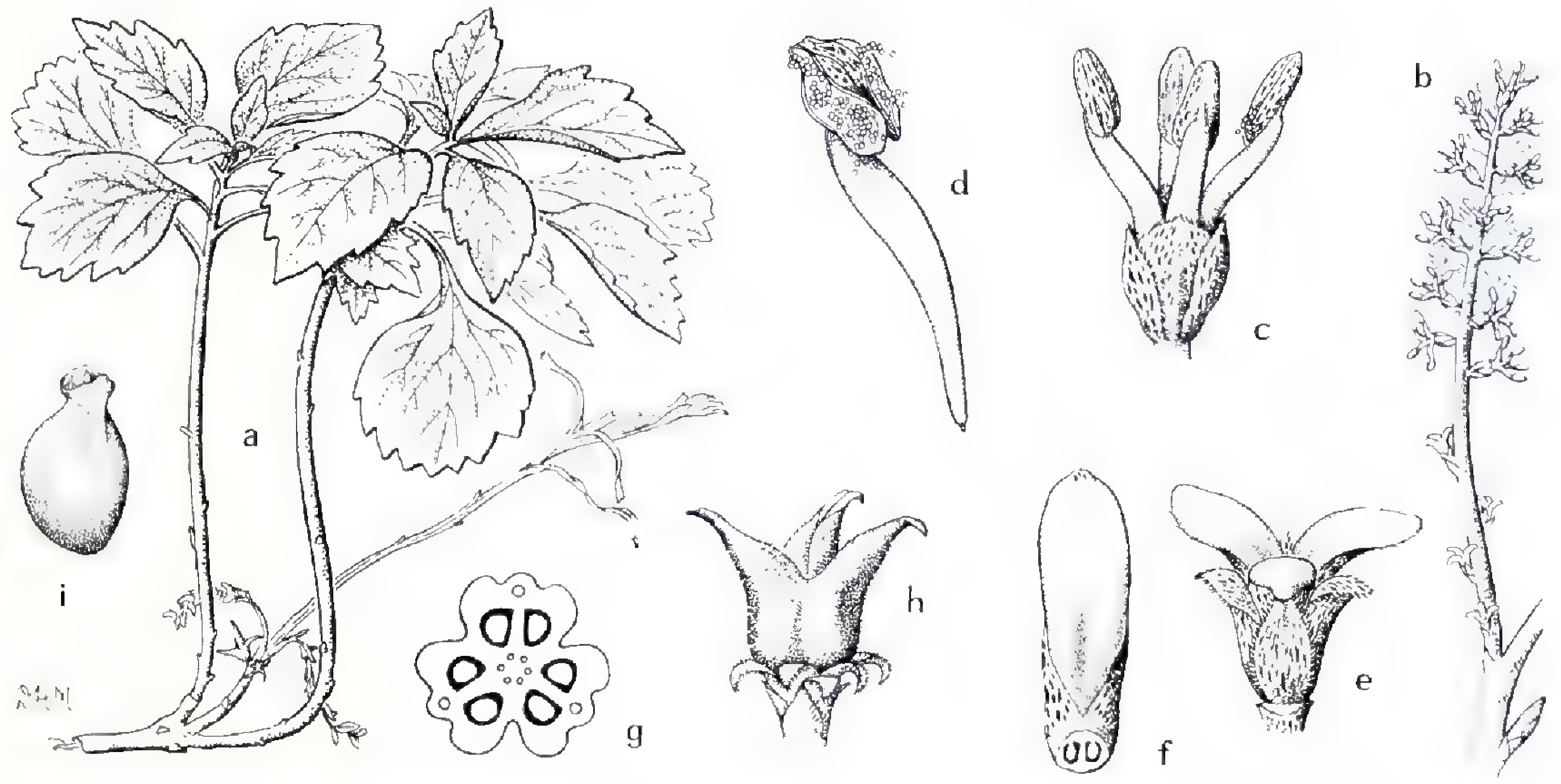

FIGURE 1. **Pachysandra.** a–h, *P. procumbens:* a, portion of plant with fruit, × ¼; b, inflorescence, carpellate flowers below the staminate, × ½; c, staminate flower, × 2; d, stamen, × 4; e, carpellate flower, × 2; f, carpel, the lower portion in longitudinal section to show the single ovule suspended in each of the 2 locules, × 4; g, semidiagrammatic cross section of young ovary to show 6 locules, each with a single ovule, × 6; h, mature fruit, × 1; i, seed, × 3.

Louisiana. Its distribution outlines the dissected portion of the Highland Rim Province surrounding the Central Basin of Tennessee, but it is not known to occur on outlying portions of the Rim isolated within the Basin.

Robbins (1962) has reported results of investigations of embryology and life history in *Pachysandra procumbens.* Microspore mother cells undergo the first meiotic division, giving rise to two dyad nuclei without cytokinesis. The second division, followed by simultaneous furrowing, results in a tetrahedral arrangement of the pollen tetrad. Excrescences of the sexine, arranged as reticulate polygons, develop after the microspores are released from the mother-cell wall. (See J. Gray and J. Gray & Sohma for illustrations of pollen.)

The ovary is divided into six locules by three true and three false partitions. Early in development the ovary is three-locular, each locule enclosing two ovules. Later it becomes six-locular by formation between the ovules of secondary partitions that are thinner than the original septa (see FIGURE 1). Differentiation of the ovules and the appearance of the archesporial cells occur in late June of the year prior to anthesis, which happens as early as February of the following year.

The anatropous ovule has two integuments. The archesporial cell, differentiating from a hypodermal cell of the nucellus, divides, forming a primary parietal cell and a primary sporogenous cell, the latter, pushed into the nucellus, functioning as the megaspore mother cell. The primary sporogenous cell is separated from the nucellar epidermis by several layers of cells, a characteristic of crassinucellate ovules.

Megagametophyte (embryo sac) development follows the Polygonum or normal course, being of the monosporic, eight-nucleate type. Pollen tubes make their way between the stigmatic papillae down through the tissues lining the stylar canal, passing between the cells rather than penetrating them. Before fertilization a protuberance (obturator) develops by proliferation of placental cells immediately dorsal to the ovule. Growing downward, it meets the outer integument, which has grown over and enclosed the ovule, and continues to develop until it forms a hood over the nucellus, possibly functioning in the penetration of the pollen tube into the ovule. Proliferation of the outer integument in the micropylar region results in the formation of a prominent caruncle, a conspicuous feature of the mature seed. All of the nucellar tissue, except the epidermis and groups of cells at the chalazal and micropylar ends of the seed, disappears with development of the cellular-type endosperm, which constitutes the bulk of the seed.

The trigonal, black, shining, carunculate seeds are shed in July and August, remain dormant through the following fall and winter, and germinate in late March and early April in close proximity to the parent plants, beneath leaf litter, usually in direct contact with moist mineral soil. Rupture of the seed coat occurs as the rapidly growing primary root emerges through the caruncle. Eventually the seed coat is shed, the cotyledons and epicotyl still enclosed within the surrounding fleshy endosperm. The cotyledons and epicotyl eventually emerge, with only remnants of the endosperm then being evident.

The cotyledons, which persist for as long as a year, have thick, glossy, green blades and short petioles, the latter undergoing elongation as development proceeds. Within six weeks of germination, the minute epicotyl develops into a short aerial stem bearing three to five small foliage leaves. Growth is slow, the shoot attaining a height of only five inches by the end of the first year. Secondary aerial shoots develop from the base of the initial shoot at the point of attachment of the cotyledons. The rapid growth of these shoots results in the establishment of lateral branches that soon overtop the primary axis. Protuberances that develop along with the lateral aerial branches are evidently the source of the rhizomes and adventitious roots. Eventually the seedling develops a sympodially branched rhizome system. The flowering of seedlings was not observed, although their development was followed for three years.

Established clones of *Pachysandra procumbens* have a well-developed sympodial system of rhizomes terminated by decumbent aerial shoots surmounted by a cluster of approximate leaves, diminishing in size distally and mottled pale green (if not silver) on dark green in late fall and winter. Upon excavation clones with as many as 38 aerial shoots were found to be interconnected by underground rhizomes. Each aerial shoot dies as the result of abscission, which occurs in spring as a new vegetative bud gives rise to a replacement shoot. A lateral vegetative bud, already established at the base of the old shoot stub, now rapidly develops into a new aerial shoot. This process, repeated successively year after year, results in the prominent and characteristic sympodium, one actual analysis of which estimated the age at 34 years! "Dichotomous" branching of the axis occurs when two lateral buds of a single segment develop into leafy shoots. Indeed, the typical circular growth habit of well-established clones of considerable age is attributable to the repetition of such branching.

It seems plausible, therefore, that an entire "population" may in fact represent a single clone, having developed from one plant by repeated sympodial growth and dichotomous branching, followed by subsequent fragmentation or degeneration of older portions of the rhizome system.

By early May or June of the year prior to the spring in which a given aerial shoot abscises, not only is a lateral shoot bud developed but so also are one to three flower buds. These occupy a lateral position, well below the point of shoot abscission. Anthesis occurs as early as mid-February in the vicinity of Nashville, Tennessee, but usually during the last week of March and early April. Either the staminate or the carpellate flowers may open first. In some instances the staminate flowers will have fallen before the carpellate ones open. There appears to be no single, regular, progressive order of events with respect to the details of flowering—probably the differential effect of short-term environmental influences upon the preformed flower parts. The conspicuous white staminal filaments elongate rapidly, well overtopping the sepals. The originally erect style branches diverge, curve outward, and expose the inner stigmatic surface, which is covered with minute papillae.

The whitish pollen grains are exposed by longitudinal splitting and slight recurving of the anther walls. A heavy "rain" of pollen onto the carpellate flowers below commonly occurs, with a glistening appearance of the stigmatic surface presumably indicating receptivity. Soon after anthesis the anthers fall, carrying with them adherent pollen and thus possibly providing a second opportunity for pollination.

During anthesis the staminate flowers emit a rather penetrating odor faintly resembling that of carnations or, to some people, the essence of ammonia or of an amine. It has been described as being pleasantly fragrant at the outset, later becoming sharp and penetrating. Insects, including beetles and bees, have been reported to visit the staminate flowers but never the carpellate ones. Red spiders (mites) covered with pollen have been observed on and in both types of flowers. There is no question but that the staminate flowers are structurally equipped to attract insects and are effective in doing so. In addition to the attractant features of the conspicuous white filaments and the abundant whitish pollen, the existence of a central nectary in the staminate flowers would appear to be especially significant. Evidence that self-pollination occurs is unquestionable. That insects provide a medium for cross-pollination seems not only possible but probable.

The plant is hardy well to the north of its native range and is sometimes grown as an ornamental novelty in partial shade, where it spreads slowly. Isolated clones in cultivation—indeed, those in nature—behave as though they may be genetically self-sterile, apparently never setting seeds. That fruits are seldom seen in nature is believed to reflect actual absence, as opposed to faulty, casual, or cursory observation.

In the self-pollination experiments of Robbins (1962), 50 plants, collected from five different populations, were used. These bore a total of 288 carpellate flowers, representing a potential of 1368 seeds (on the basis of six seeds per fruit). Of the 228 flowers self pollinated, only 104 set fruit, with a potential of

624 seeds. However, only 17 seeds were actually produced, and these by only three plants. Ten fruits contained only one seed each, two contained two seeds each, and only one contained three.

The crossing experiments made use of 43 plants with a total of 191 carpellate flowers, representing a potential of 191 fruits and 1146 seeds. Only 57 (30 percent) of the flowers set fruit, and only six of these produced seeds, the total number of seeds being 12.

Of the 423 carpellate flowers on 40 plants used in the initial apomixis test in which pollen was withheld, 87 (21 percent) set fruit, but none produced seeds. In a "replication" of the experiment the following spring, 98 carpellate flowers on 28 plants were observed. None of these produced fruits. In a third replication 95 carpellate flowers on 13 plants were observed, but again no fruits were set. In all experiments 248 fruits out of a potential of 1991 were produced. The total number of seeds produced was only 29, these being recovered from only nine fruits.

The experiments indicate that the species is both self- and cross-compatible. The possibility of apomixis being involved, although unlikely, cannot be ruled out entirely on the basis of the negative results obtained. The general paucity of fruits in nature tends to mitigate against apomixis, however. Pollination could be shown to be a stimulus to apomictic development, for in most pseudogamous species the embryo begins development autonomously, but the endosperm will not develop unless it is fertilized.

The overall results of these experiments further emphasize previous observations that development of fruits in *Pachysandra procumbens* is sporadic and that seed production is generally rare. This implies that the species may indeed have a very low degree of sexual fertility. Vegetative propagation has assumed a major role, with reproduction involving seeds occurring only rarely. As previously pointed out, the possibility exists that an entire population occupying the slopes of a ravine could represent a single clone, having originated vegetatively from a single plant.

The combination of rhizomatous habit, morphological constancy, restricted habitat, and low sexual fertility indicates that *Pachysandra procumbens* is a nonaggressive if not "senile" species with a very low evolutionary potential. Like other persistent perennials of low sexual capacity inhabiting ecologically closed communities, *P. procumbens* no doubt benefits from either a sustained low or a sporadic incidence of sexual output. Whether or not genetic self-incompatibility operates between and among clones is not known, although the crossing results suggest the existence of such a possibility.

Of the species of *Pachysandra, P. terminalis* is clearly the most important economically, being widely used in horticulture as an ornamental ground cover since its introduction into the United States in the 1800's. It is known in the trade by the somewhat contrived name Japanese spurge. Its glossy evergreen leaves, low, creeping growth habit, and tolerance of shade make it an attractive subject for ground-cover use. It is propagated vegetatively. It is unique in having terminal inflorescences and two-carpellate, white, baccate fruits (cf. *Didymeles*), described as about the size of a 'Delaware' grape, the pulp decidedly sweet. Other distinctive characters include the elevated veins of the adaxial surface of the leaf blades, the comparatively small stigmatic area occupying only the distal one-third of the style branches, the presence of a coriaceous bract and two bracteoles subtending each staminate flower, and the somewhat elongated pedicel of the carpellate flowers.

Although *Pachysandra terminalis* in cultivation is subject to attack by various insect pests and fungus diseases, it is in general resistant to them. Dodge (1944a) reported that canker blight or leaf-spot disease of the plant is due to the fungus *Volutella pachysandricola.* He also noted susceptibility to fungi of the genera *Phyelosticta* and *Glocosporum* and to attack by the scale insect *Chionaspis evonymi.*

While the leaves of Chinese plants of *Pachysandra terminalis* are reportedly somewhat smaller than those of the Japanese ones, no taxonomic significance has yet been attached to the difference. Variegated selections with ivory-white areas confined to the leaf margins have been described and are extant in the horticultural trade.

Pachysandra stylosa Dunn var. *glaberrima* Hand.-Mazz. also finds limited use in ornamental horticulture, mainly as a ground-cover subject, being similar in gross aspect to the preceding.

Horticultural use of *Pachysandra axillaris* and the varieties of *P. stylosa* is rarely, if ever, encountered, although individuals of these species are occasionally grown for exhibition in botanical gardens. These plants for the most part present a more nearly woody, even shrubby habit of growth and have thicker, more coriaceous leaves than do the other two. It would appear that they deserve greater attention horticulturally.

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THE ZANNICHELLIACEAE IN THE SOUTHEASTERN UNITED STATES[1]

Robert R. Haynes[2] and Lauritz B. Holm-Nielsen[3]

ZANNICHELLIACEAE Dumortier, Anal. Fam. Pl. 59, 61. 1829, "Zanichelliaceae," nom. cons.

A small family of annual [or perennial], glabrous, monoecious, aquatic herbs, growing entirely submersed in fresh or brackish waters, rooting at the lower nodes. Roots unbranched, 1–7 at a node, nonseptate. Stems slender, dimorphic, the lower often stoloniferous, the upper erect and leafy, without teeth along internodes; turions and tubers absent. Leaves alternate, opposite, or pseudowhorled, scalelike, without vascular tissue or foliaceous, linear, 1- [or rarely 3-] veined, subterete, sessile, with basal sheaths, the sheath adnate to or free from the blade, the infravaginal scales membranaceous. Inflorescences axillary, with 2 [to several] imperfect flowers. Staminate flowers short-pedicellate, perianth absent [rarely minute and 3-lobed], androecium consisting of 1 stamen, the connective extended into a blunt appendage, the anthers (2–)4(–8)[–12]-loculate, dehiscing by longitudinal slits; pollen inaperturate, globose, often in a gelatinous matrix. Carpellate flowers short-pedicellate, often enclosed in a membranaceous, spathelike envelope; perianth absent [or a small cuplike sheath; or segments 3, separate]; carpels (1–)4 or 5(–8), separate, short-stipitate, 1-loculate; ovule solitary, bitegmic, pendulous, anatropous, placentation apical; style short [long], stigma enlarged, ± funnel shaped [feathery or peltate]. Fruit drupaceous, with a membranaceous exocarp, fleshy mesocarp, and stony endocarp. Seed solitary; embryo curved; endosperm helobial in development, absent in mature seed. (Zannichelliaceae *sensu stricto,* excluding genera that

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The illustration was drawn by Karen Stoutsenberger at the Arnold Arboretum under Haynes's direction from material he collected in Alabama.

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are better placed in the Potamogetonaceae, Cymodoceaceae, and Posidoniaceae.) TYPE GENUS: *Zannichellia* L.

Four genera and ten to twelve species; represented in the southeastern United States by one species of *Zannichellia,* a nearly cosmopolitan genus consisting of four or five species. *Zannichellia* differs from *Pseudalthenia* Nakai, *Althenia* Thouars, and *Lepilaena* Drumm. ex Harvey in lacking a creeping rhizome, in having mostly four- or five-carpellate flowers (rarely fewer than four-carpellate), and in having warty fruits. Tomlinson & Posluszny indicated that no clear lines of evolution are recognizable in the family.

Pseudalthenia Aschersoniana (Graebner) Den Hartog (*Vleisia Aschersoniana* (Graebner) Tomlinson & Posluszny) is an endemic of the Cape Southwest region of South Africa, where it grows in vleis (depressions in which water collects during the wet season). The species is unique in the family in having leaves with a submarginal vascular strand and transverse strands continuous with the midvein. The staminate flower lacks a perianth, is eight-sporangiate, and has a pair of vestigial appendages on the connective. The carpellate flower is always unicarpellate and produces a papillate fruit, with the papillae not arranged in lines.

Althenia, with two species in northern Africa, the west-central Mediterranean region, and the Atlantic coasts of Morocco, Spain, Portugal, and France, is characterized by peltate stigmas and styles about 3 mm long.

Lepilaena consists of three species endemic to Australia and a fourth occurring in New Zealand and Australia. Diagnostic features of the genus include two- or twelve-sporangiate staminate flowers and carpellate flowers with short styles and funnel-shaped or feathery stigmas.

Cronquist placed the Zannichelliaceae in the Najadales, whereas Dahlgren, Dahlgren & Clifford, and Thorne (1976, 1983) put the family in the Zosterales. The Zannichelliaceae as here interpreted have been combined variously with members of the Potamogetonaceae, Najadaceae, Zosteraceae, and Cymodoceaceae under the names Zannichelliaceae (Taylor), Zosteraceae (Fernald), Najadaceae (Gleason & Cronquist), and Potamogetonaceae (Ascherson & Graebner). Miki considered *Najas* L. to be closely related to the Zannichelliaceae, especially *Althenia,* less so to *Zannichellia.*

Pollen is mostly dispersed as single grains but is occasionally contained in a gelatinous matrix (as in *Zannichellia palustris*). The grains are spherical, nonaperturate or rarely monosulcoidate, binucleate, and sparsely and unevenly verrucate. Adjacent verrucae are often in contact. The endexine, according to Pettitt & Jermy (see generic references), is very indistinct, and the intine is thin.

The family is known to have secondary compounds, including flavonoid bisulphates, flavones (Gornall *et al.*), and apiose (Van Beusekom).

Cytological data are incomplete for the family, but the reported chromosome numbers include $2n = 12, 24, 28, 32$, and 36 ($x = 6$ or 8).

The Zannichelliaceae are all aquatic herbs and grow clonally in shallow, generally brackish coastal waters or in inland freshwater lakes.

The roots are all adventitious and unbranched; they arise from nodes of the creeping and sympodially branched rhizomes or from those of the erect and richly branched leafy stems. The leaves are linear, sheathing at the base, and with rounded, pointed, truncate, or toothed apices. Pairs of inconspicuous, filiform squamules (nonvasculated scales) occur laterally at the nodes.

The unbranched roots have a thin-walled epidermis of large cells and conspicuous root-hairs that arise from short trichoblasts. The outer cortex is compacted into an exodermis of one or two layers of narrow, slightly lignified, thick-walled cells, while the inner part is lacunose, the endodermis uniseriate and thin walled, and the stele narrow, surrounding a metaxylem lacuna.

The stems are nearly without mechanical tissue, and the epidermis, cortex, endodermis, and stele resemble those of the roots. Vascular bundles supporting lateral organs diverge directly from the stele, and there is no cortical vascular system.

The leaf blade is glabrous, with the epidermis uniform, thin walled, and chlorophyllous. The epidermis mostly lacks stomata, although they do occur in the apices of leaf blades of certain species of *Zannichellia.* The mesophyll is lacunose either throughout or only on each side of the midvein. The vascular system is reduced to a single median vascular bundle surrounded by a uniseriate endodermis. The leaf blades have submarginal fibers.

The plants are monoecious, with complex, terminal, sympodial inflorescences of reduced, specialized flowers subtended by reduced bractlike leaves. Each inflorescence usually has one staminate flower terminating the first-order meristem and one to several carpellate flowers terminal on branches of higher orders.

The staminate flowers are short-pedicellate, reduced to one stamen, and with or without a short, three-lobed, scalelike perianth. The anther consists of one or more bisporangiate units, sometimes with a short connective appendage; dehiscence is longitudinal. The tapetum is of the periplasmodial type, microsporogenesis is of the successive type, and the pollen grains are three-celled at dispersal.

The carpellate flowers are short-pedicellate and have one to eight separate, short-stalked, slightly asymmetric carpels. The carpels are surrounded by a biseriate perianth that consists of a closed tubelike structure in *Zannichellia* and *Pseudalthenia,* and of three separate segments in *Althenia* and *Lepilaena,* with the segments opposite the carpels. The styles are more or less elongate and are terminated by enlarged peltate or funnel-shaped stigmas that have more or less lacerate margins or are occasionally feather shaped. Each of the stipitate carpels contains a solitary, pendulous, anatropous, bitegmic ovule. The embryo sac is of the Allium type, with embryo formation of the caryophyllad type. Endosperm is of the helobial type but is absent in the mature seed.

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1. **Zannichellia** Linnaeus, Sp. Pl. **2:** 969. 1753; Gen. Pl. ed. 5. 416. 1754.

Annual or rarely perennial, monoecious plants of fresh or brackish waters. Roots single or in pairs at the nodes. Leaves in pseudowhorls of 3 but usually also alternate and opposite on same plant, entire, stipulate, mostly less than 1 mm wide, 1 veined. Inflorescence usually consisting of 2 flowers, 1 staminate and 1 carpellate. Flowers without a perianth. Staminate flowers with a single usually 4-loculate [2–8-loculate] stamen, the connective prolonged into a blunt appendage. Carpellate flowers with (1–)4 or 5(–8) carpels surrounded basally by a membranaceous envelope, the style less than 1 mm long, the stigma asymmetrically funnel shaped. Fruit endocarp often coarsely papillose. TYPE SPECIES: *Z. palustris* L., the only species of the genus in *Species Plantarum.* (Named after Gian Girolamo Zannichelli, 1662–1729, a Venetian apothecary and botanist.)—HORNED PONDWEED.

A nearly cosmopolitan genus of perhaps five species, represented in the southeastern United States only by *Zannichellia palustris* L. The genus has been variously interpreted as consisting of one highly variable species (e.g., Dandy) or as many as five species (e.g., Holm-Nielsen & Haynes; Van Vierssen, 1982a). We recognize the genus to comprise at least one near-cosmopolitan species (*Z. palustris*) and four others of restricted distribution, of which three (*Z. major* Boenn., *Z. pedunculata* Reichb., and *Z. peltata* Bertol.) are in northern Europe and one (*Z. andina* Holm-Nielsen & Haynes) is in the high Andes of South America.

Zannichellia has an unusual pollination system in which the anther of the staminate flower arches over the funnel-shaped stigmas of the carpellate flower. Pollen transfer is entirely underwater: it is released from the anther in a gelatinous mass and falls directly into the stigma. Such a system limits outcrossing but is valuable for a submersed annual aquatic since pollination is essentially assured.

Reported chromosome numbers for *Zannichellia* are $n = 12$, $2n = 24$, 28,

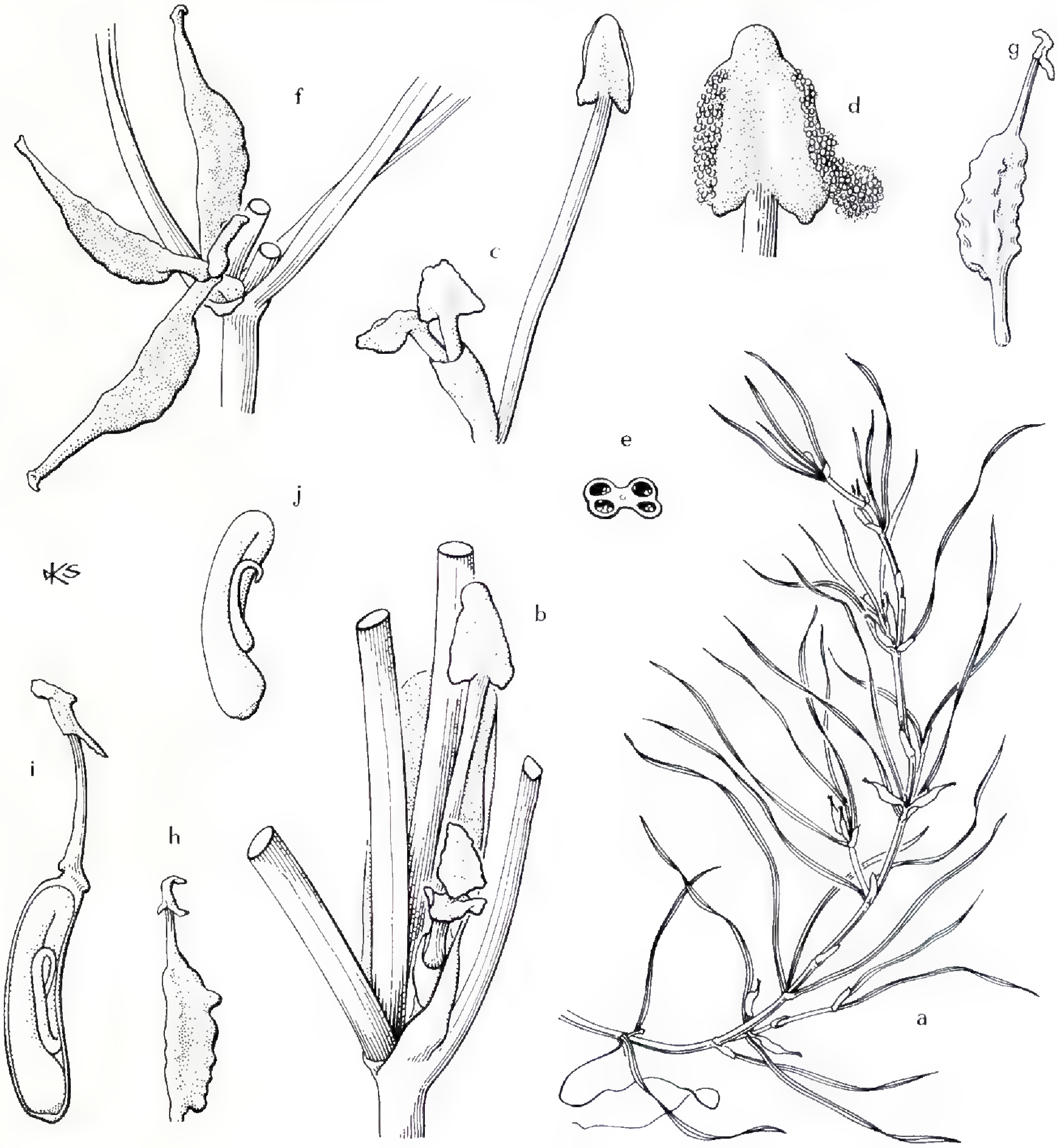

FIGURE 1. **Zannichellia.** a–j, *Z. palustris:* a, branch of plant with fruit, × 1; b, node with staminate and carpellate flowers, base of leaf (to right), portion of stem, and base of 2 branches, × 12; c, staminate flower (a single stamen) and carpellate flower with 2 carpels, × 12—note expanded stigmas; d, anther shedding pollen, × 25; e, cross section of anther before dehiscence, showing 4 locules, a few pollen grains indicated diagrammatically, the vascular bundle dotted, × 25; f, nearly mature fruits of a 4-carpellate flower, 1 carpel undeveloped, × 6; g, h, endocarps of 2 fruits, with tip of style still covered by outer part of pericarp, × 6; i, fruit, the ovary in longitudinal section to show embryo, × 12; j, embryo, × 12.

32, 36 for *Z. palustris* (Bolkhovskikh *et al.*), $2n = 36$ for *Z. pedunculata* and $2n = 12, 36$ for *Z. peltata* (Van Vierssen & Van Wijk).

Daghlian did not report the Zannichelliaceae in the fossil record, although Katz and colleagues listed three species from the Quaternary in the Soviet Union. Miller reported *Zannichellia* from lateglacial deposits in western New

York, and Pierce & Tiffney have reports from the postglacial Holocene in Connecticut.

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GEORGE RALPH COOLEY

May 29, 1896–September 27, 1986

We record with regret the death of George R. Cooley, a friend of botany and botanists and a generous supporter of the Generic Flora of the Southeastern United States during its initial years.

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A CLADISTIC ANALYSIS OF CONIFERS: PRELIMINARY RESULTS

JEFFREY A. HART[1]

A data matrix of 123 binary and multistate characters of 63 genera of conifers was constructed based on an extensive literature review and study of herbarium and living specimens. Subsequent cladistic analysis of this matrix strongly supports the monophyly of conifers; there is no reason to exclude the taxads. *Sciadopitys* should be considered as constituting a separate family, the Sciadopityaceae, which appears to be the sister group of the Cupressaceae-Taxodiaceae lineage. The Taxodiaceae and Cupressaceae together form a monophyletic group. The Cupressaceae form a monophyletic group within this lineage and can be divided into two groups, one of northern and the other of southern taxa. Within the Southern Hemisphere group, there are monophyletic groupings with separate Gondwanaland distributions. The remaining Taxodiaceae appear to be paraphyletic. The Taxaceae and Cephalotaxaceae also come out as sister taxa. The Pinaceae appear to be the sister group of the other living conifers. The placement of Araucariaceae and Podocarpaceae in relationship to the other living conifers is problematic.

Conifers have long been of interest to morphologists, anatomists, paleobotanists, and foresters. A cosmopolitan group, conifers include 60 to 63 genera and 500 to 600 species. Known from the fossil record from as far back as the Permian, conifers dominated the forest vegetation in the Mesozoic Era. They are the largest and most diverse group of living gymnosperms. To date, the monophyly of the conifers and the phylogenetic relationships of the families and genera have not been determined.

Most modern textbooks follow Pilger (1926) in dividing the group directly into seven families (Taxaceae Sprengel, Podocarpaceae Endl., Araucariaceae Strasburger, Cephalotaxaceae Neger, Pinaceae Lindley, Taxodiaceae Neger, and Cupressaceae S. F. Gray), but other classifications have also been proposed. Buchholz (1933) divided the Coniferae into two suborders: the Pinineae (in-

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cluding Pinaceae, Cupressaceae, Taxodiaceae, and Araucariaceae), with obvious cones, and the Taxineae (including Podocarpaceae, Taxaceae, and Cephalotaxaceae), without obvious cones. Sahni (1920) and Florin (1948b, 1951) elevated the Taxaceae to the Taxales, equal to all other conifers in ordinal rank. Keng (1973, 1975) has recently recognized eight families, elevating *Phyllocladus* Rich. (Podocarpaceae) to family rank. For a more complete review, see the excellent summaries by Florin (1955) and Turrill (1959).

The phylogenetic and evolutionary relationships among these families and genera have been widely debated. The lack of precise, explicit methodologies for assessing phylogenetic relationships has resulted in a diversity of views about conifer relationships. Historically, schemes of evolutionary relationships have been based primarily on assertions as to the usefulness of individual plant characters as phylogenetic markers.

With the introduction of cladistic theory as developed by Hennig (1950, 1966) and his followers, there has been a renewed interest in the study of higher-level taxonomic relationships in systematic biology. The purposes of this paper are to review the kinds of evidence used historically in assessing phylogenetic relationships among conifers; to construct a comprehensive character data matrix both to serve in the analysis and to provide the basis for further studies; to utilize cladistic methodology in the study of phylogenetic relationships of coniferous genera; to compare these results with previously held notions of relationships; and to suggest new areas of research needed to test my hypotheses of relationships among coniferous genera.

HISTORICAL CONCEPTS OF CONIFER SYSTEMATICS AND PHYLOGENY

The history of conifer studies shows somewhat closer relationship to the history of zoological systematics (at least in some groups) than to that of angiosperm systematics. The reasons for the similarity are precisely those that make conifers well suited for a cladistic analysis. First, gymnosperms, including conifers, have a clear fossil record compared to angiosperms (Florin, 1951; Stewart, 1983). Their remains are well preserved and have yielded a great deal of information. The relative antiquity of gymnosperms was realized very early. Brongniart (1849) recognized three principal plant groups—cryptogams, gymnosperms, and angiosperms—thought to follow one another in time and in a progression from "lower" to "higher" forms. Second, early anatomical and developmental studies of vegetative and reproductive structures have proved useful in elucidating relationships among conifers. Anatomical studies have also been employed in demonstrating relationships to other fossil and living groups of gymnosperms (Strasburger, 1872, 1878, 1879; Bertrand, 1879; Coulter, 1909; Buchholz, 1918, 1920, 1933, 1939, 1941; Jeffrey, 1926; Phillips, 1941; Greguss, 1955). Third, the small number of coniferous taxa, together with their economic and horticultural importance, has permitted botanists (e.g., Chamberlain, 1935; Sporne, 1965) to stress comparative biology more than species identification based on external morphology. Since the quantity is small, however, it is surprising that so few systematic revisions (for example, Shaw, 1914; De Laubenfels, 1969; Liu, 1971; and Liu & Su, 1983) have been completed.

Evolutionary hypotheses concerning conifers have been characterized by attempts to link extant groups in evolutionary time, very different relative importances attributed to characters, preconceived notions of the nature of evolution or evolutionary trends, and ideas regarding correlation of characters. The result has been confusion in determining phylogenetic relationships and classification.

Linking Extant Groups in Evolutionary Time

A common problem, not unique to phylogenetic studies on conifers, has been the tendency to link extant groups in evolutionary time, an apparent holdover from the ancient *scala naturae* or "great chain of being" theme (Lovejoy, 1936). Living taxa, instead of characters, are viewed as either advanced or primitive. There are numerous examples in the systematics of both gymnosperms and conifers. For example, Eichler (1889) considered the Taxaceae advanced, while Penhallow (1907) considered them primitive. Other families and genera—Abietinae (= Pinaceae) (Jeffrey, 1917), Podocarpaceae (Sporne, 1965), and *Phyllocladus* (Core, 1955; Keng, 1973, 1975)—have been chosen as the most "primitive." Similarly, some groups such as the Taxodiaceae are considered relicts, while others such as the Cupressaceae are considered progressive (De Laubenfels, 1965). A few early morphologists saw the fallacy of lining up living taxa in this manner. Coulter (1909, p. 92) correctly remarked that "living forms . . . do not represent a series, but the ends of many series."

Specialization of Research

Gymnosperm biologists have often specialized in particular aspects of the plant body or life cycle. While many interesting studies have resulted from this approach, an unfortunate outcome has been systematic and phylogenetic speculation based on limited subsets of characters. Chamberlain (1935, p. 230) aptly stated that, "The grouping into families and the sequence of families and genera will depend upon each investigator. If he is an anatomist, anatomy will determine the grouping and sequence. . . . If the gametophytes are emphasized, there will be still another arrangement."

Examples of single-character analyses in conifer studies are common. The most frequently emphasized set of characters has involved the ovulate cone. For example, Čelakovský (*fide* Florin, 1955) assumed that the Pinaceae, Taxodiaceae, Cupressaceae, and Araucariaceae constitute a phylogenetic series based on increasing fusion of the bract and scale. The principal classification followed today is that of Pilger (1926); it is based primarily on the structure of the ovulate cone (although vegetative characters were also used).

The excessive attention paid to the ovulate cone structure is evident in the debate about the status of conifers without "evident" cones. Pilger's (1903) monograph on the Taxaceae included the conifers without (evident) cones; he later (1926) divided this group into the Taxaceae *sensu stricto,* the Cephalotaxaceae, and the Podocarpaceae. Sahni (1920) proposed an independent order, the Taxales, of equivalent rank with the Ginkgoales, the Cordianthales, and the Coniferales. Florin (1948b) also concluded that the taxads should be segregated from the rest of Pilger's families; he therefore placed them in the separate order Taxales. He maintained that the taxads are distinct from the conifers and traced their more immediate ancestry not to the Cordaitales but to the Devonian Psilophytales. His principal evidence was that both living and fossil members of the Taxales and the Psilophytales have a solitary ovule that is a direct continuation of the axis (uniaxial). Thus, the uniovulate strobilus of the Taxaceae was considered primitive rather than derived. Florin (1951) maintained that in the Podocarpaceae, in contrast, the uniovulate strobili are independently derived from taxa with multiovulate strobili. Others are reluctant to accept Florin's separation of the taxads from the rest of the conifers, at least at the ordinal rank. Chamberlain (1935) and Takhtajan (1953) have suggested that the uniovulate, uniaxial strobilus of taxads is derived from the multiovulate, biaxial cone. The argument becomes dangerously circular when the very character whose evolution is being discussed has been used as the principal line of evidence in forming the groups under discussion.

Other subsets of characters have been used to a lesser extent as the basis of phylogenetic and systematic speculation. Saxton (1913) and Moseley (1943) produced classifications based entirely on characters of the gametophyte and the embryo. Thomson and Sifton (1926) thought the Pinaceae to be the most highly evolved of conifers on the basis of the arrangement and structure of resin canals. Flory (1936) proposed a phylogeny using chromosome numbers. Praeger and colleagues (1976), relying on antigenic distances, suggested relationships among genera of Pinaceae.

Finally, as an extension of this approach, relationships of entire families of conifers are occasionally suggested based on characters found only in a few taxa. For example, the peltate, perisporangiate microsporophyll is often attributed to all Taxaceae (Stewart, 1983), although it is found only in *Taxus* L. and *Pseudotaxus* Cheng.

PRECONCEIVED NOTIONS OF HOW EVOLUTION WORKS

Interpretations of the evolution of conifers have been influenced by general notions of evolution. Florin (1951) made use of Zimmerman's (1930) telome theory to explain various aspects of the evolution of the ovulate cone of conifers. Jeffrey's (1917) three canons of comparative anatomy include the doctrine of conservative organs, which considered the leaf, reproductive axis, root, first annual ring of the stem, seedlings, and sporangia as "conservative." This idea was apparently borrowed from zoological embryology, in which it was thought that ancestral features, such as gill slits, are apt to persist in the earlier stages. Ideas about complexity have also influenced perceptions of relationships. Penhallow (1907) claimed that resin canals are more advanced than resin cells since they are more complex. Other preconceived theories can lead to just the opposite results. Jeffrey (1905) believed that resin canals disappear and are replaced by resin cells.

Another of Jeffrey's (1917) canons of comparative anatomy was the doctrine of reversion, in which wounding induces ancestral traits. The presence of resin canals after wounding was thus seen to be a reversion to a more primitive condition. Čelakovský (1890) also argued that teratological structures and wound tissues indicate evolutionary direction. Guédès and Dupuy (1974) observed hypertrophied, leaflike segments of ovulate cone scales and interpreted the ovules to be dorsal appendages ("leaves") of scale components. Chamberlain (1935) thought that the occasional abnormal occurrence of bisporangiate cones represent the ancestral state.

Botanists have long ranked characters according to preconceived notions of adaptive significance. Adaptive characters have generally been considered less useful at higher (less inclusive) taxonomic categories than at lower (more inclusive) ones (Stevens, 1980). Saxton (1913) thought that the stability of plant parts or organs is proportional to their distance from the surface of the plant and their proximity to, or connection with, the reproductive structures. Thus the external characters of the vegetative organs, such as shape and position of leaves—characters most susceptible to adaptive change—are less important than those of the reproductive structures (e.g., micro- and megagametophytes), embryology, and the internal anatomy of vegetative structures (such as the vascular system). Lawson (1907) similarly thought that various reproductive structures of conifers that are buried deep within the tissues of the sporophyte are less likely to be modified by external factors and more likely to preserve ancestral characters. Coulter (1909, p. 86) believed that gymnosperm leaves respond to "conditions of living" and so largely ignored them in his taxonomic studies. Holgar Erdtman (1963) emphasized the taxonomic importance of constituents excreted into dead conifer heartwood as metabolic end products since he believed they were not subject to external influence.

Correlation of Characters

The notion of correlation of characters has been common in conifer studies. Gaussen (1944, 1950) believed that the most recent species of a group are generally more evolved in all characters than were their ancestors. Stevens (1980) aptly pointed out that character states may occur in any combination: all primitive, all derived, or mixed.

A somewhat more reasonable class of correlations comprises functional ones. Sporne (1965) noted that the loss of the pollination drop is correlated with the loss of pollen wings. Coulter (1909) suggested that the position of the archegonium is related to the position of the pollen tube that reaches the embryo sac before the archegonial initials are evident.

Given such diverse views on how to classify organisms, the importance attributed to certain characters by some botanists, and how evolution is thought to proceed, it is little wonder that attempts at reconstructing phylogenetic relationships have been stuck in a morass of confusion, contradiction, uncertainty, and appeal to authority.

CLADISTIC THEORY

Several excellent discussions of cladistic methods now exist (e.g., Hennig, 1966; Hecht & Edwards, 1977; Wiley, 1981; Bremer, 1983). In a cladistic analysis, certain conditions are sought: the group being studied must be monophyletic, characters selected must be homologous (inherited from a common ancestor), there must be a known outgroup, and character states must be designated as either primitive or derived (Arnold, 1981). Hull (1967) and others have pointed out that there is not necessarily a precise order or progression in cladistic analysis. A systematist may work at several levels of analysis simultaneously.

Initially, a group being studied may not be known to be monophyletic. In this situation, a group may be selected based on previous taxonomic judgments or phenetic similarity.

Characters are recognized by similarity of structure in different organisms. Recently there has been considerable discussion about characters and homology (Sattler, 1984; Stevens, 1984; Tomlinson, 1984). During the first stages of phylogenetic reconstruction, it is not known if the characters are homologous in the cladistic sense (i.e., equivalent to apomorphies—see Patterson, 1982; Stevens, 1984). Homologies should, however, meet several criteria, including location, similarity, and connection of intermediate forms (Remane, 1952). Patterson (1982) recommended three tests of homology: similarity (topographic, ontogenetic, compositional), congruence (with other hypothesized homologies), and conjunction (two homologues cannot coexist in the same organism). Of these, the criterion of similarity is the first and thus the most important—the tests of congruence and conjunction can be applied only after an initial determination of the similarity of characters (Stevens, 1984).

Distinguishing between primitive and derived characters is one of the critical problems in phylogenetic reconstruction. Recently, attention has been devoted to the criteria by which this distinction is made (e.g., Crisci & Stuessy, 1980; Stevens, 1980; Watrous & Wheeler, 1981; Maddison *et al.*, 1984). Outgroup analysis based on parsimony is considered to be the most defensible criterion (Stevens, 1980). Wiley (1981, p. 139) defined the outgroup rule as follows: "Given two characters that are homologous and found within a single monophyletic group . . . the character found only within the monophyletic group is the apomorphic character." The underlying methodological principle of the outgroup rule is parsimony. The simplest hypothesis—the one that minimizes the number of parallelisms and convergences (homoplasy)—is preferred (Stevens, 1980; Farris *et al.*, 1982). This means that the preferred tree is congruent with the majority of apparent apomorphies. The use of parsimony does not mean that homoplasy is rare or uninteresting; it only seeks to minimize it.

MATERIALS AND METHODS

This study was based on a literature survey, an examination of herbarium specimens, and observations of living plants. The 63 genera of conifers used in the analysis were selected from the treatments of Dallimore and colleagues

(1966), Quinn (1970), and Silba (1984). I chose a set of characters using three criteria: a reasonable argument of similarity could be made supporting the homology of the different states of the character; character-state transformations could be determined on the basis of outgroup analysis; and character states could provide discrimination of families and genera (see Appendix, Table) (Rodman *et al.,* 1984). Characters or character states unique to individual genera (autapomorphies) were not included in the analysis. Morphological and anatomical information from all aspects of the life cycle, as well as chemical and chromosomal data, was utilized to avoid favoring certain subsets of characters.

A number of characters were not used for a variety of reasons, one of the most common being insufficient sampling. Quantitative characters showing apparently continuous variation or considerable overlap between possible states were avoided as much as possible (Almeida & Bisby, 1984; Hart, 1985). Characters showing considerable overlap between taxa were excluded. On some occasions when derived character states were rare and when the character was not recorded in many taxa, I assumed the primitive condition for missing characters (e.g., characters 75 and 76).

Different classifications of characters are often found in the literature. Thus Ueno's (1960) classification of pollen (character 61) based on extensive sampling using light microscopy differs somewhat from Reyre's (1968; character 62) system based on a more limited sampling using scanning electron microscopy. In this situation I have used Reyre's system but have included Ueno's in the Table for purposes of comparison.

Binary as well as multistate coding was used. The number 0 (primitive or plesiomorphic) was assigned to the character state found in one or all of the outgroups. With multistate coding, both unordered and ordered coding were used (Appendix, Table), depending upon whether or not there was justification for a transformation series. For example, leaves tetragonal in cross section (character 28) are found in the fossil conifer outgroups, and a variety of shapes are found among modern conifers (De Laubenfels, 1953); *a priori,* it is not possible to determine a transformation series of bifacially flattened, scalelike, or needlelike leaves. In certain situations it was possible to justify a transformation series. Thus, the presence of specialized winter bud scales (character 37) can be interpreted as having had intermediate steps in evolution.

The PAUP program used in the analysis allows for the coding of missing data ("9" in Table), treating them as equivalent to "all possible states." The missing states are filled in by the program according to what would be the most parsimonious character states, had they not been missing, and the tree length is then computed. Variable character states were also coded as "missing" (9).

A data matrix including 63 genera and 123 characters was assembled. Since current programs such as Swofford's PAUP cannot guarantee parsimony with such a large data matrix, the information was broken up into several smaller units. The first was a family-level analysis using eight representative genera: *Taxus* (Taxaceae), *Cephalotaxus* Sieb. & Zucc. ex Endl. (Cephalotaxaceae), *Araucaria* Juss. (Araucariaceae), *Podocarpus* L'Hér. ex Pers. (Podocarpaceae),

Data matrix for character states of conifers and outgroup gymnosperms listed in Appendix.*

	5 10 15 20 25 30 35 40 45 50 55 60
Ginkgo	01000000900000000000000000081000008009000200000109800081000000
Cordaitales	00000990990000090000090099080090000009999299999009811190900000
Lebachiaceae	00099999099000090000090099100090000000999099999010100000900900
Amenotaxus	10000000101110000000010000110100000041000000000011110101120120
Austrotaxus	90000000100100000000000000110900000041000000000111190101920190
Pseudotaxus	00000000000110000001010000110101000041000000000111011101920190
Taxus	00000000000110000001010000110901000041000000000111011101120120
Torreya	10000000101110000001010000110100000041000000000111010101120120
Cephalotaxus	10000000111110000001010010110100000021000000000111100101120129
Agathis	00001900000000010000000001010900000041000200000911000101010133
Araucaria	00001900000000010000000009111000000001000200000910000101010133
Acmopyle	00000000100100000000000000130000000029000000001100000001000000
Dacrycarpus	00000000100100000000000000120000000010000000001100000001000000
Dacrydium	00000000100100000000000000190000000010000000001100000001000000
Decussocarpus	00000000100100000000000000110000000030000900001119000001000000
Falcatifolium	00000000100100000000000000130000000020000000001100000001000000
Halocarpus	00000000000100000000000000120000000000000000001100000001000000
Lagarostrobos	00000000000100000000000000120000000000000000001100000001000000
Lepidothamnus	00000000000100000000010000120000000000000000001100000001000000
Microcachrys	00000000000100000000000000120200000020000000001100000001000000
Microstrobus	00000000101100000000110000120000000020000000000100000001000000
Parasitaxus	00000000100100000000000000120000000000000000001100000001000000
Phyllocladus	01000000000100000000000000180000000021000000001111000001000000
Podocarpus	00000000100100000000000000110000000041000000001111000001000000
Prumnopitys	00000000100100000000000000110000000031000000001111000001000000
Saxegothaea	10000000110100000001900010110000000021000000001110000001010000
Abies	00010101111100000001110010110002001049001110000011000021000000
Cathaya	01010100111101001911101000110002001041111110000011000001000090
Cedrus	01010100111100000111111010101001000040101110001011000001000000
Keteleeria	00010101111100001101110000110002001049001110000011100021000000
Larix	01010110111190001011111010111001000140101110000011000001110020
Picea	00010100081190001011111110190001000049191110001011000001000000
Pinus	01010100081100001019901900142000009049111910000011200001000000
Pseudolarix	01010101111100000001110000111001000141001110000011100021000000
Pseudotsuga	00010110111111001011111010110002001041101110000011000011010020
Tsuga	00010100111100000001111000110001000049001110000011000021000010
Athrotaxis	00000000110100000000000000190000000012000000000100000001030122
Cryptomeria	00000000111100000001010000100000000010000000100011200101031122
Cunninghamia	00000000119100000001010000110000000010000000100010200101031122
Glyptostrobus	01100000119100000001010000190000000020000000101010000101031122
Metasequoia	11100000119100001001009000110100000020000900101011100101031122
Sciadopitys	00001000000100000000000000150000000021000000001010300001020119
Sequoia	00000000119100000101009000190000000020000000100010000101031122
Sequoiadendron	00000000119100000001009000120000000020000000900010000101031122
Taiwania	00000000110100000000010000120000000010000000100010200101031122
Taxodium	01100000111100000001010000190000000020000000100011100101131122
Actinostrobus	00000000100100000000000000120300000000000900900011010101030121
Austrocedrus	00000000100100000000000000120200110001000090900010010101030121
Callitris	00000000100100000000000000120300000000000900100010010101030121
Calocedrus	00000000111100000001100000120200100000000900110010010101030121
Chamaecyparis	00000000199100000001090000120200100000000909110010010101030121
Cupressus	00000000191100000001190000120200900000000901110010010101030121
Diselma	00000000199100000001110000120200000000000900900110010001030121
Fitzroya	00000000119100000009190000120310000000000900900110010101030121
Fokienia	00000000119100000001000000120200100000000900900010010101030121
Juniperus	00000000111100000001100000190900000099000901110919010101030121
Libocedrus	00000000100100000009000000120200110000000900900010010101030121
Microbiota	00000000119100000001090000120200000000000900990010010101030121
Neocallitropsis	00000000100100000000000000110200000000000900900010010101030121
Papuacedrus	00000000100100000000000000120200110000000900910010010101030121
Pilgerodendron	00000000109100000000090000120210000002000900900010010101030121
Platycladus	00000000119100000001010000120200000000000900910010010101030121
Tetraclinis	00000000100100000000000000120200100000000900910010010101030121
Thuja	00000000119100100001010000120200100000000900910010010101030121
Thujopsis	00000000119100100001019000120200100000000900910010010101030121
Widdringtonia	00000000100100000000000000120200000000000900100010010101030121

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*Plesiomorphic condition shown by 0, apomorphic states by 1-4, unknown and variable states by 9, character state not applicable by 8.

Data matrix for character states of conifers and outgroup gymnosperms listed in Appendix (*continued*)

	65 70 75 80 85 90 95 100 105 110 115 120
Ginkgo	0000000000000000000000000000000000088888888888880081000810000
Cordaitales	0000909900099909099000999899999998000000000980008119089998 9
Lebachiaceae	0000999900099909099000999899999999001000000090000800908099 89
Amenotaxus	90110100000000010000000020100000000011888888888888012001110008
Austrotaxus	9019010000000001000000002010000000001188888888800000200101000 8
Pseudotaxus	10190100000000010000000020100000000011888888888000002001010 0?8
Taxus	1011010000000001000000002010000000001188888888800000200101001 8
Torreya	1011010000000001000000004010000000011188888888880000120011100 08
Cephalotaxus	1011000900000010000000020100000000010290000000000000291001000 8
Agathis	101102001100009011001001010011110000021000000000000000900000 08
Araucaria	001102001100009011001001010011110000021000000000000000900009 08
Acmopyle	000002000000000900010000201010000009102000010100100010000100 98
Dacrycarpus	002002000000001000100002010100000010020000101001000000000100 08
Dacrydium	000002000000000000100002010100000010020000110100000100001000 8
Decussocarpus	000002000000000900010000201010000001902000010100000000000100 98
Falcatifolium	000002000000000900010000201010000009002000010010000010000100?8
Halocarpus	000002000000000000100002010100000090020000100000000200101000 8
Lagarostrobos	000002000000001000100002010100000000020000110100000100001000 8
Lepidothamnus	000002000000000000100002010100000000020000110100000200001000 8
Microcachrys	002000000000101000100002010100000010020000100100000000000100 18
Microstrobus	002001000000100000110002010100000090080000020000000200001009 8
Parasitaxus	009009000000000900010000201010000009002000010100000000000100 98
Phyllocladus	000000000000000000100002010100000001080000020110000200101009 8
Podocarpus	000002000000000000100002010100000011020000101000000000000100 98
Prumnopitys	000002000000000000100002010100000091020000101000000000000100 08
Saxegothaea	000002010100000000100002010100000000102000011011000000000100 08
Abies	0100001010010001000000031110000000010201000000000110011000111 0
Cathaya	0000001010010001000000031110000000110200000000000000110000110
Cedrus	0000001010010001000000031110000000110200000000000110011000111 0
Keteleeria	0000001010010001000000031110000000110201000000000100110001110
Larix	1010001010110001000000031110000000010200000000000090011000011 0
Picea	0000001000010001000000031110000000010201000000000000011000011 0
Pinus	0000001000010001000000031110000000110200000000000000011000010 0
Pseudolarix	0000001010010001000000031110000000010200000000000110011000111 0
Pseudotsuga	0110001010110001000000031110000000010200000000000000011000011 0
Tsuga	0090001019010001000000031110000000110201000000000000011000111 0
Athrotaxis	0011010100000010000100040100000000000210000000000000110000011
Cryptomeria	0011910100000010000100030100000000100210000000000000110000011
Cunninghamia	0011010100000010000110030100000000100210000000000000110000011
Glyptostrobus	0011010100000010000100030100000000100210000000000000110000111
Metasequoia	0011010100000010000100030100000000100210100000000000110000011
Sciadopitys	0011010000000000000000020100000000100210000000000000110000002
Sequoia	0011010100000010000101150200000000100210100000000000110000111
Sequoiadendron	0011010100000000000101130100000000100210100000000000110000001
Taiwania	0011010100000010000100030100000000100210000000000000110000011
Taxodium	0011910100000010000100030100000000110210100000000002110000111
Actinostrobus	0011110100000110000101040200000011110210010000000002110009091
Austrocedrus	0011010100000010000109030100000000100210010000000002110009011
Callitris	0011110100000110000101040200000011110210010000000002110009091
Calocedrus	0011010100000010000100030100000000100210000000000002110009091
Chamaecyparis	0011110100000010000100030100000000100210100000000002110009011
Cupressus	0011110100000010000100030100000000110210100000000002110009191
Diselma	0011010100000010000109030100000009100210010000000002110009091
Fitzroya	0011110100000010000109040100000001100210010000000002110009011
Fokienia	0011110100000010000109030100000000100210900000000002110009011
Juniperus	0011110100000010000100030100000000190210100000000002010019091
Libocedrus	0011010100000010000109030100000000100210010000000002110009091
Microbiota	0011010100000010000109030100000000100210000000000002010019091
Neocallitropsis	0011010100000010000109030100000000100210010000000002110009091
Papuacedrus	0011010100000010000109030100000000100210010000000002010009091
Pilgerodendron	0011010100000010000109030100000000100210010000000002110009011
Platycladus	0011010100000010000100030100000000100210000000000002010019011
Tetraclinis	0011110100000010000100030100000000100210010000000002110009191
Thuja	0011010100000010000100030100000000000210000000000002110009011
Thujopsis	0011010100000010000100030100000000000210000000000002110009011
Widdringtonia	0011110100000010000101040200000011110210010000000002110009001

Pinus L. (Pinaceae), *Taxodium* Rich. (Taxodiaceae), *Cupressus* L. (Cupressaceae), and *Sciadopitys* Sieb. & Zucc. *Sciadopitys* was added to the list since it does not seem to share obvious synapomorphies with the Taxodiaceae, with which it is normally associated. In this analysis the characters chosen for the representative genera were consistent (with minor exceptions) within the family but varied across the families. This analysis was conducted using the branch-and-bound algorithm (Hendy & Penny, 1982). Next, a series of analyses of the separate families, such as Pinaceae, Podocarpaceae, and Taxaceae, or pairs of families, such as Taxodiaceae and Cupressaceae, was run. These analyses were conducted using the local-branch-swapping algorithm.

The selection of outgroups requires some discussion. The Lebachiaceae, *Cordaites* Unger, *Ginkgo* L., and other gymnosperms were chosen as outgroups (see FIGURE 1). For many characters, only the living gymnosperms—*Ginkgo,* cycads, and the Gnetales—could be used as outgroups. Other characters were represented in the fossil record. Paleobotanists generally accept the family Lebachiaceae—which includes *Lebachia* Florin, *Ernestiodendron* Florin, and *Walchiostrobus* Florin—as the "stem" conifer group (Florin, 1951). It is, however, not certain that the "Lebachiaceae" represent a monophyletic group; C. N. Miller (pers. comm.) indicated that the family is paraphyletic and thus constitutes a series of outgroups. For some characters the various genera of "Lebachiaceae" were individually used as outgroups. On the other hand, the family Voltziaceae Florin—including *Pseudovoltzia* Florin, *Ullmannia* Göppert, and *Glyptolepis* Schimper—seems to comprise taxa intermediate between the Lebachiaceae and modern conifers (Stewart, 1983); these were not used as outgroups since they may be ingroups to conifers. The next outgroup chosen, *Cordaites,* is generally acknowledged to be represented earlier in the fossil record than *Lebachia* and its relatives and is considered to share a common ancestor with them (Florin, 1951; Taylor, 1981; Stewart, 1983; Clement-Westerhof, 1984; Mapes & Rothwell, 1984). The position of *Ginkgo* and then cycads as the next most inclusive outgroups is supported by the work of Meyen (1984), Doyle and Donoghue (1986), and Crane (1985). Occasionally it was possible to use the initial cladogram of the families of conifers to determine polarity of particular characters (Watrous & Wheeler, 1981). Thus, the presence of inverted ovules in the Pinaceae, which seem to form a basal clade or functional outgroup (FIGURE 2), and in many members of the Lebachiaceae lent credibility to the polarity of this character. In determining the polarity of the characters generally, the algorithm developed by Maddison and colleagues (1984) was followed.

RESULTS

In this section I describe the results of attempts to analyze relationships 1) of conifers to other gymnosperms, 2) among families of conifers, and 3) among the genera of conifers within the different families. A complete resolution of the cladistic relationships among the genera and families of conifers requires more data. However, several hypotheses of phylogenetic relationships can be proposed with the information available.

In the larger data sets, only the most parsimonious cladograms—those with

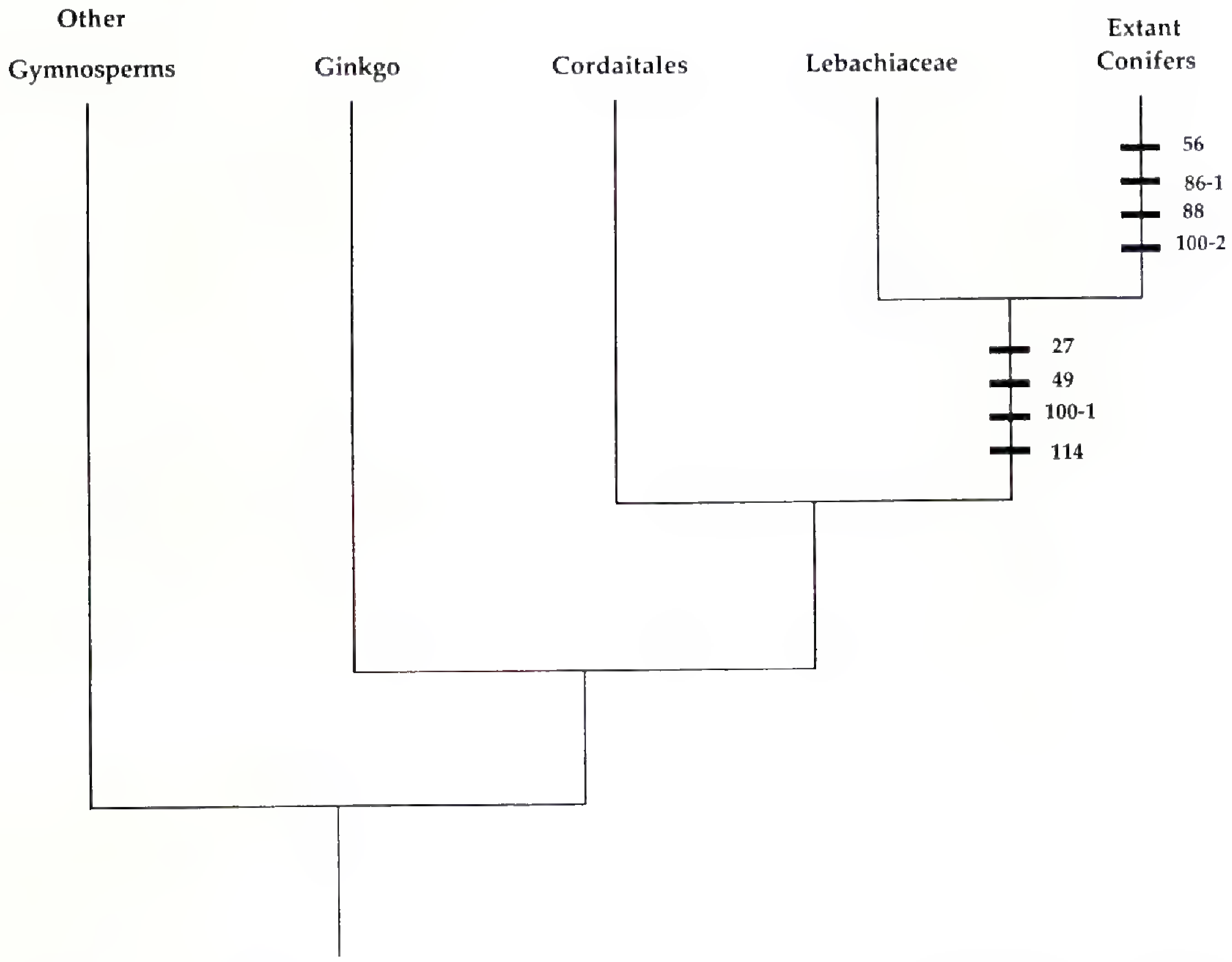

FIGURE 1. Hypothesized relationships of modern conifers to outgroups, including fossil and living gymnosperms, used as basis for polarization of character states. For some characters other taxa related to *Lebachia* used as outgroups intermediate between modern conifers and Cordaitales.

the fewest reversals, parallelisms, and convergences—are presented. The branch-and-bound algorithm, which generates the most parsimonious cladograms, can only work with smaller data sets. This algorithm was used solely in the family-level analyses and for the Taxaceae. The other data sets were analyzed using the local-branch-swapping algorithm, which unfortunately does not generate most parsimonious cladograms. A basis for comparing parsimony among cladograms is the consistency index, which is the minimum range of character-state changes in the data divided by the actual length of the tree—or the sum of character-state changes or patristic distances along all branches. Fractions close to unity indicate a tree with little homoplasy (Kluge & Farris, 1969).

MONOPHYLY OF CONIFERS AND PHYLOGENETIC RELATIONSHIPS WITH OTHER GYMNOSPERMS

A manually generated cladistic hypothesis for the monophyly of living conifers and the relationships of these conifers with fossil and living gymnosperm outgroups is presented in FIGURE 1. The distinguishing characteristics that separate extant conifers from all other extant gymnosperms and angiosperms—and hence suggest monophyly—are embryological. There are at least two characters of importance. First, the number of free nuclear divisions in embryo-

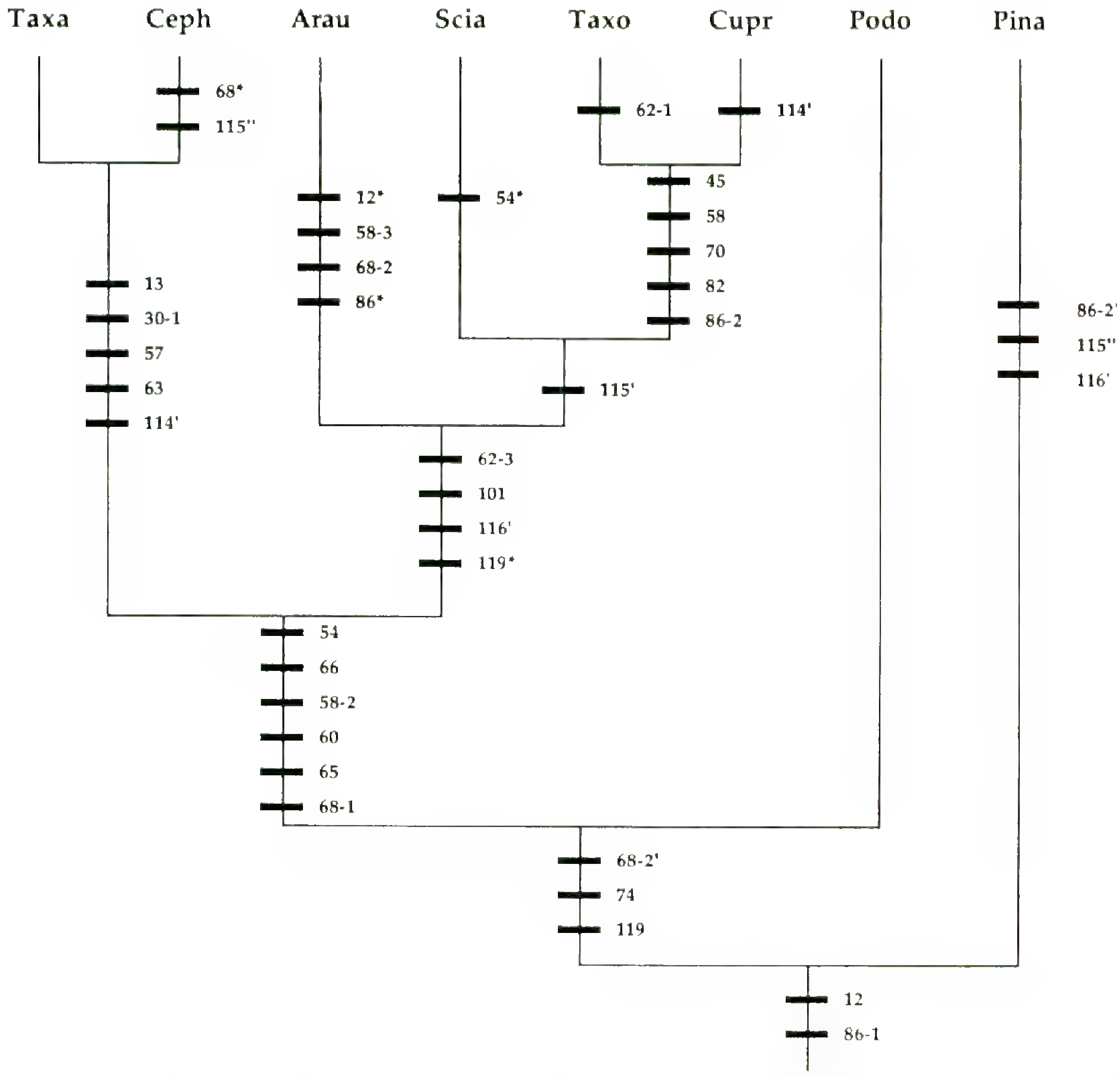

FIGURE 2. Hypothesized relationships between families of conifers, using representative genera. (Arau = *Araucaria* (Araucariaceae); Ceph = *Cephalotaxus* (Cephalotaxaceae); Cupr = *Cupressus* (Cupressaceae); Pina = *Pinus* (Pinaceae); Podo = *Podocarpus* (Podocarpaceae); Scia = *Sciadopitys*; Taxa = *Taxus* (Taxaceae); Taxo = Taxodiaceae; * = reversal; ′ = one parallelism; ″ = character evolved twice.)

genesis (character 86) is greatly reduced in living conifers (five or fewer) compared to *Ginkgo* and cycads (eight and ten, respectively). Second, the structure of the proembryo of conifers (character 88) is unique. In contrast to the proembryo of cycads and *Ginkgo,* which is characterized by an unstratified cell arrangement, that of conifers is stratified or tiered. The proembryo of *Gnetum* L. differs from them in having no free nuclear stage and no definite arrangement of cells, and in the elongation of each cell to form a suspensor (Johansen, 1950). In conifers the primary proembryo is the first cellular structure formed after the wall. It has two morphological units: an open tier and a lower primary embryonal cell group (Chowdhurry, 1962; Dogra, 1978). This is characteristic of nearly all conifers, including the Araucariaceae (Haines & Prakash, 1980) and the Taxaceae (Chen & Wang, 1984). Since these characters are not known for the Cordaitales or the Lebachiaceae, they may be placed at one of three

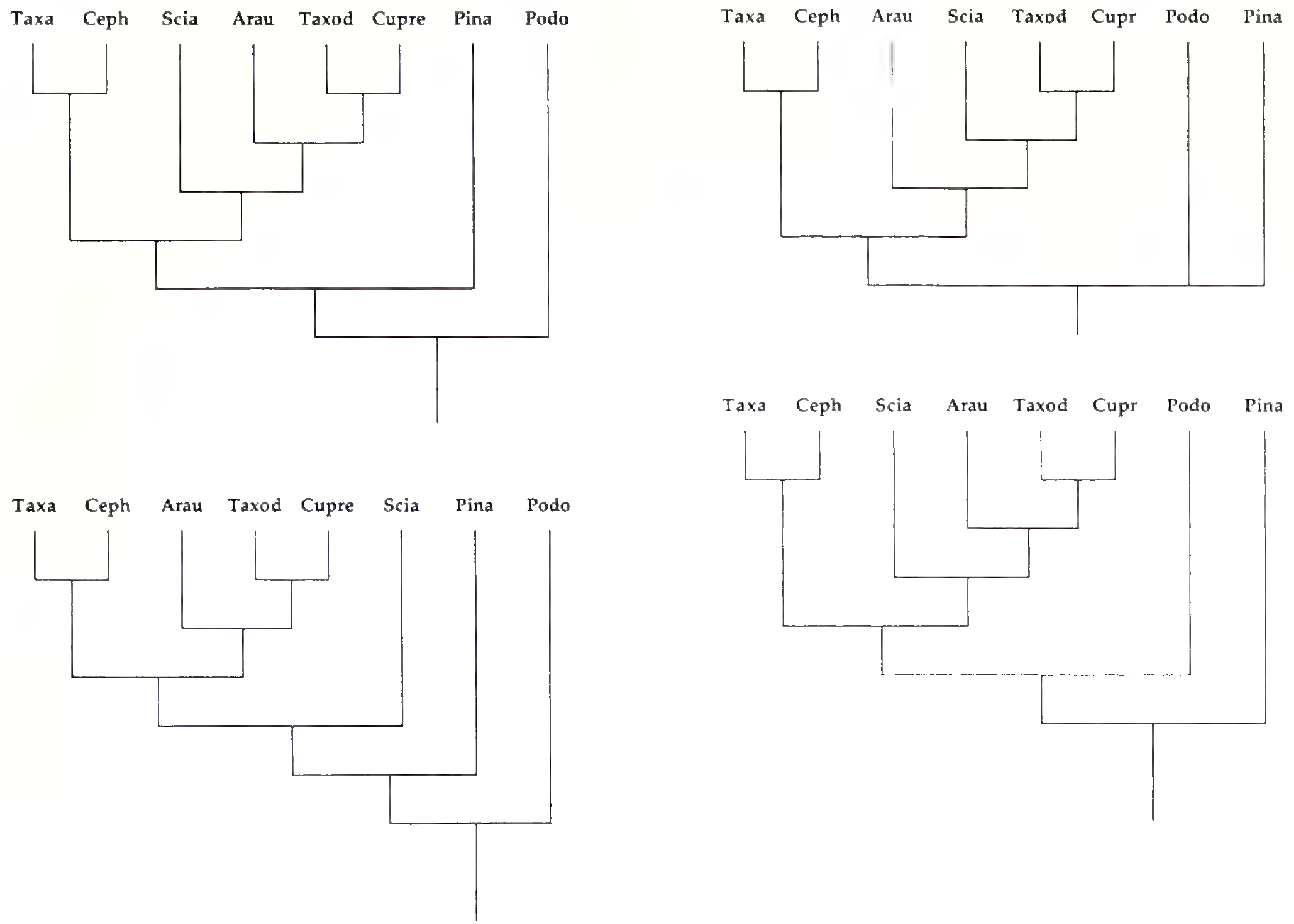

FIGURE 3. Hypothesized relationships of families, using representative genera; 4 cladograms involving 1 more step than in FIGURE 2.

nodes in the clades in FIGURE 1: extant conifers; extant conifers + Lebachiaceae; or extant conifers + Lebachiaceae + Cordaitales.

Other characters can be used to establish monophyly and outgroup relationships when fossil gymnosperms are used for comparison. Extant conifers can be distinguished from the fossil *Lebachia* by at least two characters. One is the cone scale (character 100-2), a highly modified fertile short shoot (Florin, 1951; Taylor, 1981; Stewart, 1983; Meyen, 1984; Crane, 1985). Crane (1985) stated that the ovulate fertile short shoot—or "scale"—of extant conifers differs from that of the Lebachiaceae in that the shoot apex is not differentiated and that there is no phyllotactic spiral in parts of the former. There is still considerable discussion as to exactly what it represents: for example, short shoot alone or short shoot plus sterile scale (Guédès & Dupuy, 1974; Jain, 1976). However, the exact nature of the structure does not affect my argument as long as part of the scale is a short shoot.

The second character is palynological. Pollen of modern conifers is characterized by distal germination, whereas that of the Lebachiaceae does not have a thin area on the distal surface, thus indicating proximal germination (Mapes & Rothwell, 1984). This character shows homoplasy; Millay and Taylor (1976) have shown that the shift from proximal to distal germination also occurred in the Callistophytaceae and the Cordaitales.

If *Cordaites* is considered as the outgroup to conifers (Doyle & Donoghue, 1986), a number of derived characters support monophyly of the Lebachiaceae + extant conifers. The pollen cones (character 49) of the Lebachiaceae and modern conifers are simple or uniaxial; those of *Cordaites* are compound. Conifer leaves—"microphylls" (character 27)—are rather small and usually single veined (except in the Araucariaceae and a few species of the Podocarpaceae); the leaves of the Cordaitales, *Ginkgo,* and the cycads are rather large and many veined. The Lebachiaceae (except a few species of genera such as *Ernestiodendron*) and extant conifers have bilaterally flattened ovulate short shoots (or scales); the Cordaitales have radially symmetrical fertile ovulate short shoots (Florin, 1951; Taylor, 1981; Rothwell, 1982; Stewart, 1983).

Ovule orientation (character 114) is a difficult character to employ because it is variable in some groups. The ovule is erect in *Ginkgo*, the cycads, *Ephedra* L., and *Gnetum.* The most recent interpretation for the Voltziales is that most have inverted ovules (Clement-Westerhof, 1984; Mapes & Rothwell, 1984).

Crane (1985) also suggested resin canals as a synapomorphy for *Lebachia* and extant conifers. Resin canals do occur in nearly all conifers and taxads, although in many different plant parts (i.e., xylem, roots, leaves, seed coats); this may suggest different origins (homoplasy). Mucilage canals have been described for *Ginkgo* and may be similar to resin canals in conifers. Studies of resin-duct development and resin chemistry may help our understanding of these characters.

FAMILY-LEVEL ANALYSIS

In this analysis the characters chosen for the representative genera were consistent (with minor exceptions) within the family but varied across the

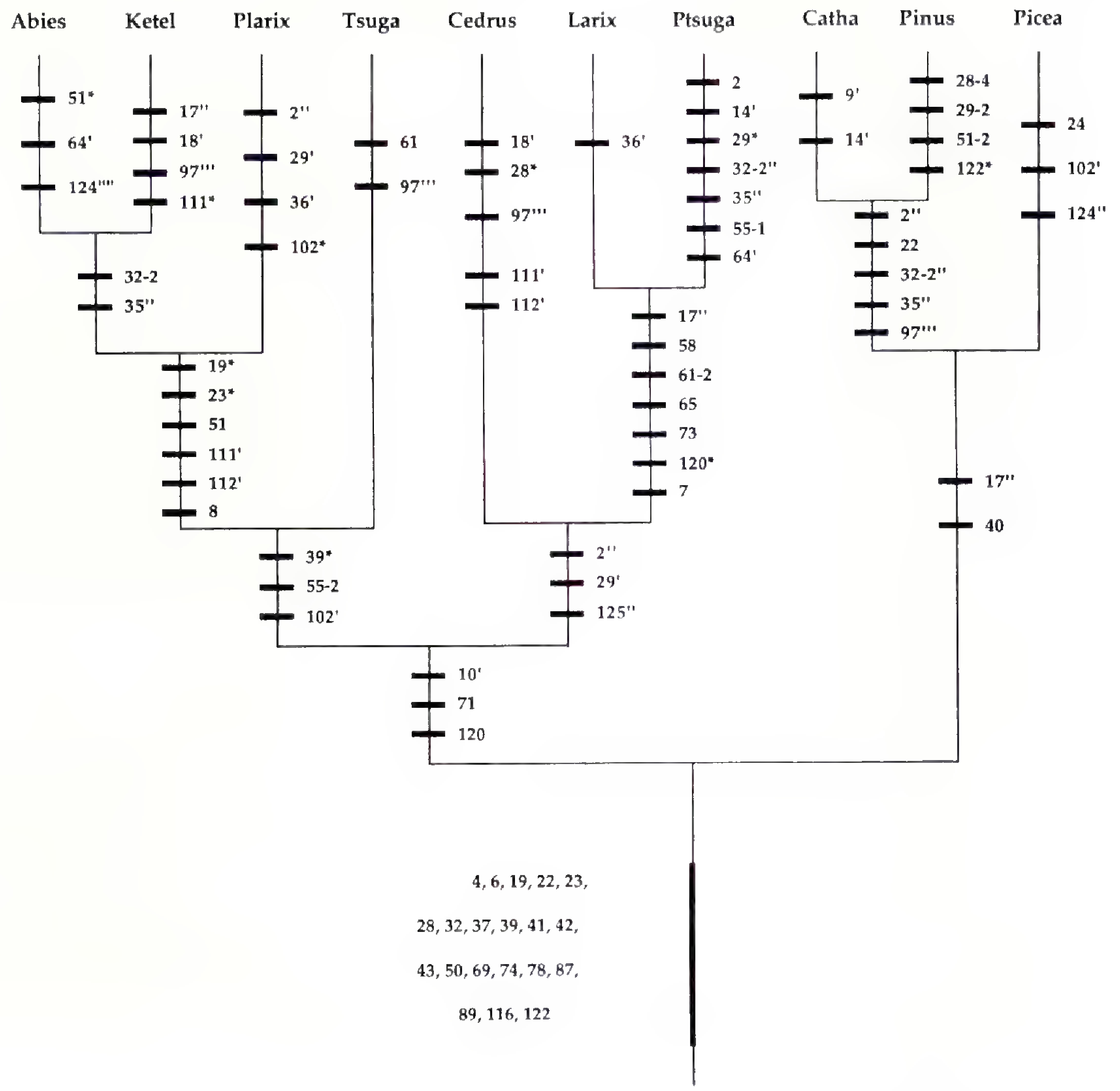

FIGURE 4. Cladistic relationships of Pinaceae. (Catha = *Cathaya*; Ketel = *Keteleeria*; Plarix = *Pseudolarix*; Ptsuga = *Pseudotsuga*; * = reversal; ′ = one parallelism; ″ = character evolved twice; ‴ = character evolved three times; ⁗ = character evolved four times.)

families. Thus the characters were the important consideration, the genera being chosen merely to represent them. FIGURE 2 shows the results of the family-level analysis, which employed 22 characters and representatives of the seven commonly recognized families of conifers (Taxaceae, Cephalotaxaceae, Araucariaceae, Podocarpaceae, Pinaceae, Cupressaceae, and Taxodiaceae), as well as *Sciadopitys* (included because it differs in so many characters from the Taxodiaceae, in which it is normally placed, that it has sometimes been put in other families—e.g., Pinaceae, Saxton, 1913; Sciadopityaceae Hayata, Hayata, 1932). The consistency index is .711.

Four additional trees, each with one extra step (consistency index of .659), were generated (see FIGURE 3). In all of these, the Taxaceae and the Cephalotaxaceae came out as sister taxa, as did the Taxodiaceae and the Cupressaceae. *Sciadopitys* is most often the outgroup to the Cupressaceae and the Taxodiaceae and is placed there in the subsequent family-level analysis. The family Pinaceae is most often the outgroup to all living families of conifers.

The placement of *Sciadopitys,* the Podocarpaceae, and the Araucariaceae is variable.

PINACEAE. Ten genera and 48 characters were used in the cladistic analysis of the Pinaceae (results shown in FIGURE 4). The consistency index is .600. Members of this family are distinguished by seven synapomorphies restricted to them: 6 phloem fibers absent), 41 (leaf transfusion-tissue tracheids all around vascular bundle), 43 (biflavonoids absent), 69 (sperm cells without cell walls), 74 (ventral-canal cells without walls (nuclei only), 78 (megaspore membrane thin at micropylar end), and 89 (proembryo four-tiered). Several other characters (e.g., resin ducts, character 19), initially scored as derived within the Pinaceae, are derived at the family level but show subsequent loss in different lineages. There were numerous other synapomorphies (e.g., character 39) showing homoplasy within conifers that are evidently derived at the family level.

PODOCARPACEAE. Fifteen genera and 24 characters were used in the analysis of the Podocarpaceae (results presented in FIGURE 5). The consistency index is .500, rather low. Only two unique synapomorphies seem to unite the Podocarpaceae: the binucleate embryonal cell of the proembryo (90), and the epimatium (105, but missing in two taxa). Additional apomorphies are found in other conifers (28-2; 119) or are only found in most Podocarpaceae (e.g., 48); the algorithm has interpreted them as being derived at the family level but subsequently lost within the family.

TAXODIACEAE-CUPRESSACEAE. Thirty-one genera and 53 characters of the Cupressaceae and the Taxodiaceae (including *Sciadopitys*) were analyzed (see FIGURES 6 and 7). The consistency index is .544. *Sciadopitys* is even more clearly separated from the Taxodiaceae-Cupressaceae than the family-level analysis indicated, with 12 synapomorphies separating them. It can be seen that the Taxodiaceae, even exclusive of *Sciadopitys,* are paraphyletic. There are several monophyletic groupings within the Taxodiaceae, including *Sequoia* Endl. and *Sequoiadendron* Buchholz; *Metasequoia* Miki, *Taxodium,* and *Glyptostrobus* Endl.; and *Taiwania* Hayata, *Cryptomeria* D. Don, and *Cunninghamia* R. Br. ex Rich.

Several synapomorphies define the Cupressaceae as a monophyletic group within the Taxodiaceae (see FIGURE 6). Within the Cupressaceae, there is division of northern and southern taxa (FIGURE 7). The analysis indicates that northern Cupressaceae are paraphyletic although there are several monophyletic groupings, including *Microbiota* Komarov and *Platycladus* Spach, *Thuja* L. and *Thujopsis* Sieb. & Zucc., *Fokienia* A. Henry & H. Thomas and *Calocedrus* Kurz, and *Juniperus* L., *Chamaecyparis* Spach, and *Cupressus.* However, it should be remembered that these hypotheses of relationships are tenuous since few characters were utilized in the analysis. The southern taxa, including the African *Tetraclinis* Masters, form a monophyletic group. This group divides into an unresolved quadrachotomy: *Diselma* J. D. Hooker, *Fitzroya* J. D. Hooker, and *Pilgerodendron* Florin; *Austrocedrus* Florin & Boutelje, *Libocedrus* Endl., and *Papuacedrus* L.; *Neocallitropsis* Florin; and *Widdringtonia* Endl., *Callitris* Vent., and *Actinostrobus* Miq.

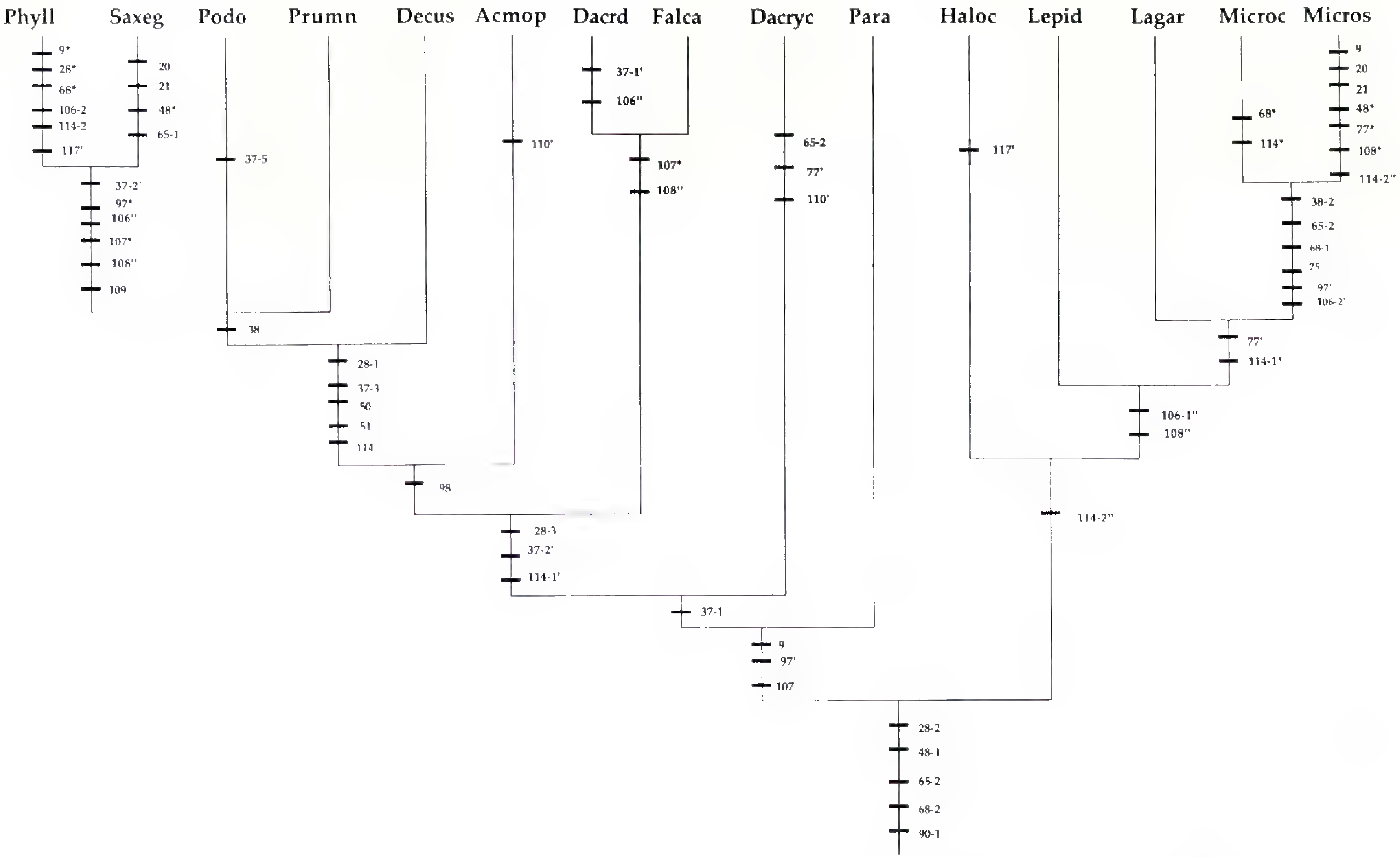

FIGURE 5. Cladistic relationships of Podocarpaceae. (Acmop = *Acmopyle*; Dacryc = *Dacrycarpus*; Dacrd = *Dacrydium*; Decus = *Decussocarpus*; Falca = *Falcatifolium*; Haloc = *Halocarpus*; Lagar = *Lagarostrobus*; Lepid = *Lepidothamnus*; Microc = *Microcachrys*; Micros = *Microstrobos*; Para = *Parasitaxus*; Phyll = *Phyllocladus*; Podo = *Podocarpus*; Prumn = *Prumnopitys*; Saxeg = *Saxegothaea*; * = reversal; ′ = one parallelism; ″ = character evolved twice.)

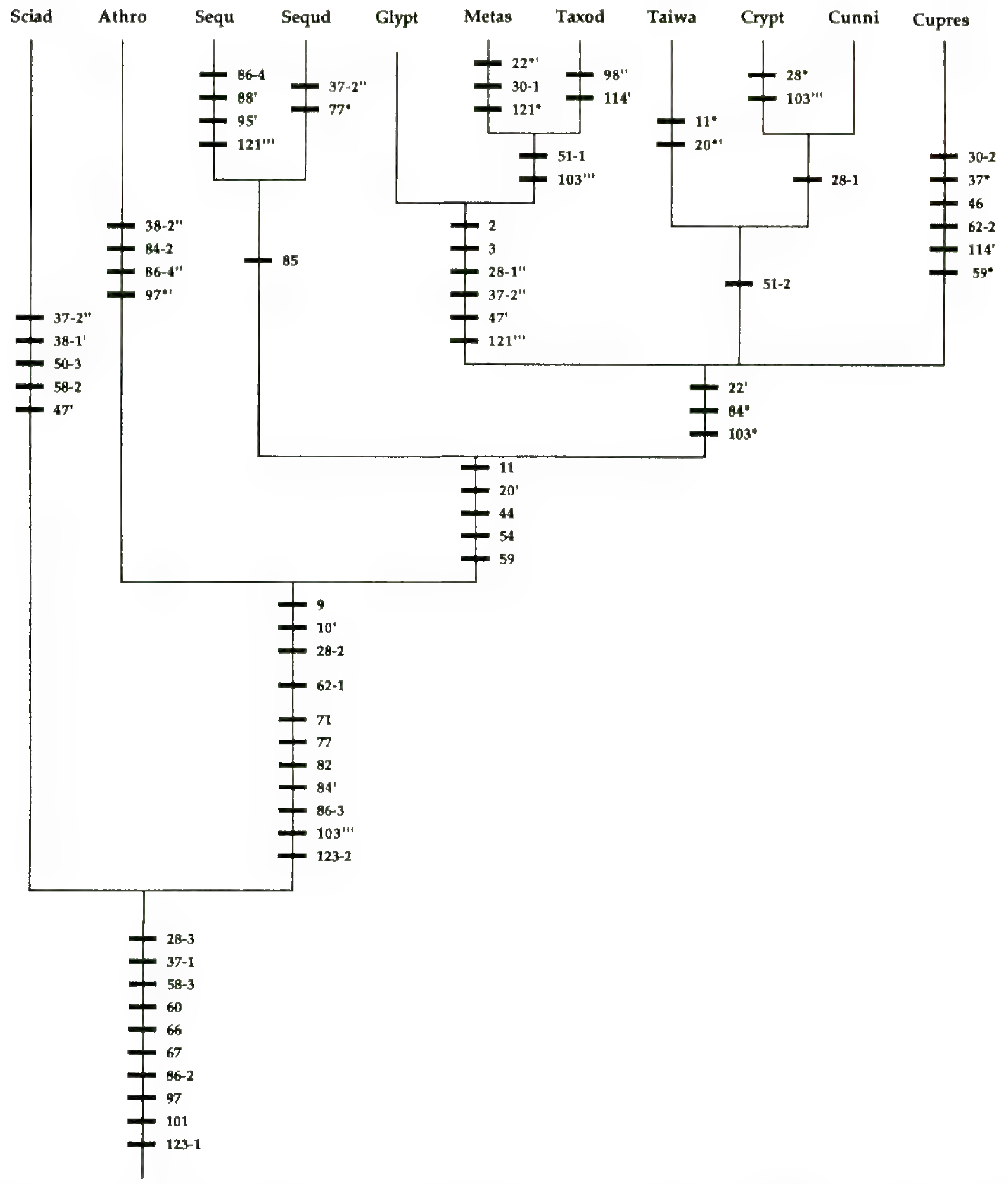

FIGURE 6. Cladistic relationships of Taxodiaceae and Cupressaceae. (Athro = *Athrotaxis*; Crypt = *Cryptomeria*; Cunni = *Cunninghamia*; Cupres = Cupressaceae; Glypt = *Glyptostrobus*; Metas = *Metasequoia*; Sciad = *Sciadopitys*; Sequ = *Sequoia*; Sequd = *Sequoiadendron*; Taiwa = *Taiwania*; Taxod = *Taxodium*; * = reversal; ′ = one parallelism; ″ = character evolved twice; ‴ = character evolved three times.)

TAXACEAE. Five genera and 16 characters were used in the analysis (see FIGURE 8); the consistency index is .857. This family can be recognized at least by the uniaxial or "simple" seed "cone" (99). Characters such as the aril (117) are also found in other families.

ARAUCARIACEAE. This family comprises only two genera (*Agathis* Salisb. and *Araucaria*) and as such does not require a phylogenetic analysis. It is defined by at least ten apomorphies (FIGURE 8).

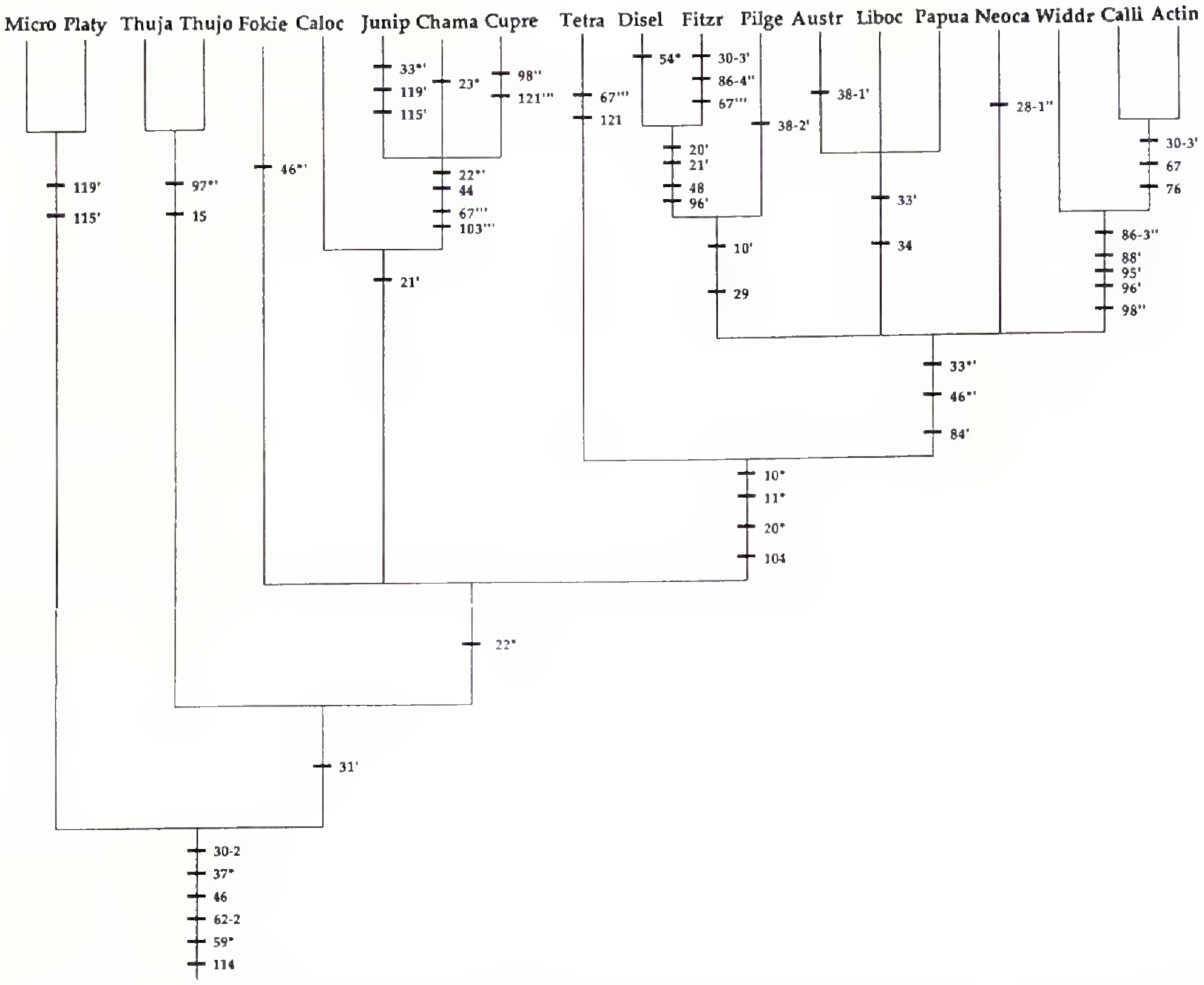

FIGURE 7. Cladistic relationships of Cupressaceae. (Actin = *Actinostrobus*; Austr = *Austrocedrus*; Calli = *Callitris*; Caloc = *Calocedrus*; Chama = *Chamaecyparis*; Cupre = *Cupressus*; Disel = *Diselma*; Fitzr = *Fitzroya*; Fokie = *Fokienia*; Junip = *Juniperus*; Liboc = *Libocedrus*; Micro = *Microbiota*; Neoca = *Neocallitropsis*; Papua = *Papuacedrus*; Pilge = *Pilgerodendron*; Platy = *Platycladus*; Tetra = *Tetraclinis*; Thujo = *Thujopsis*; Widdr = *Widdringtonia*; * = reversal; ′ = one parallelism; ″ = character evolved twice; ‴ = character evolved three times.)

DISCUSSION

This cladistic analysis of conifers provides explicit criteria for establishing phylogenetic relationships and classifications based on multiple character sets, facilitates the understanding of the evolution of characters, illustrates the distinction between character-state polarity and taxonomic polarity, is helpful in understanding evolution and biogeography of the group, demonstrates the usefulness of fossil gymnosperms as outgroups, and focuses attention to gaps in knowledge requiring further research.

CLASSIFICATION

The classification of conifers, especially with regard to their relationships with taxads and other taxa lacking "evident" cones, has been much discussed. The results of this analysis strongly support the monophyly of conifers and taxads. Traditional approaches to conifer systematics (e.g., Sinnott, 1913; Aase, 1915; Thomson, 1940; Florin, 1951; C. N. Miller, 1976, 1982, 1985) have

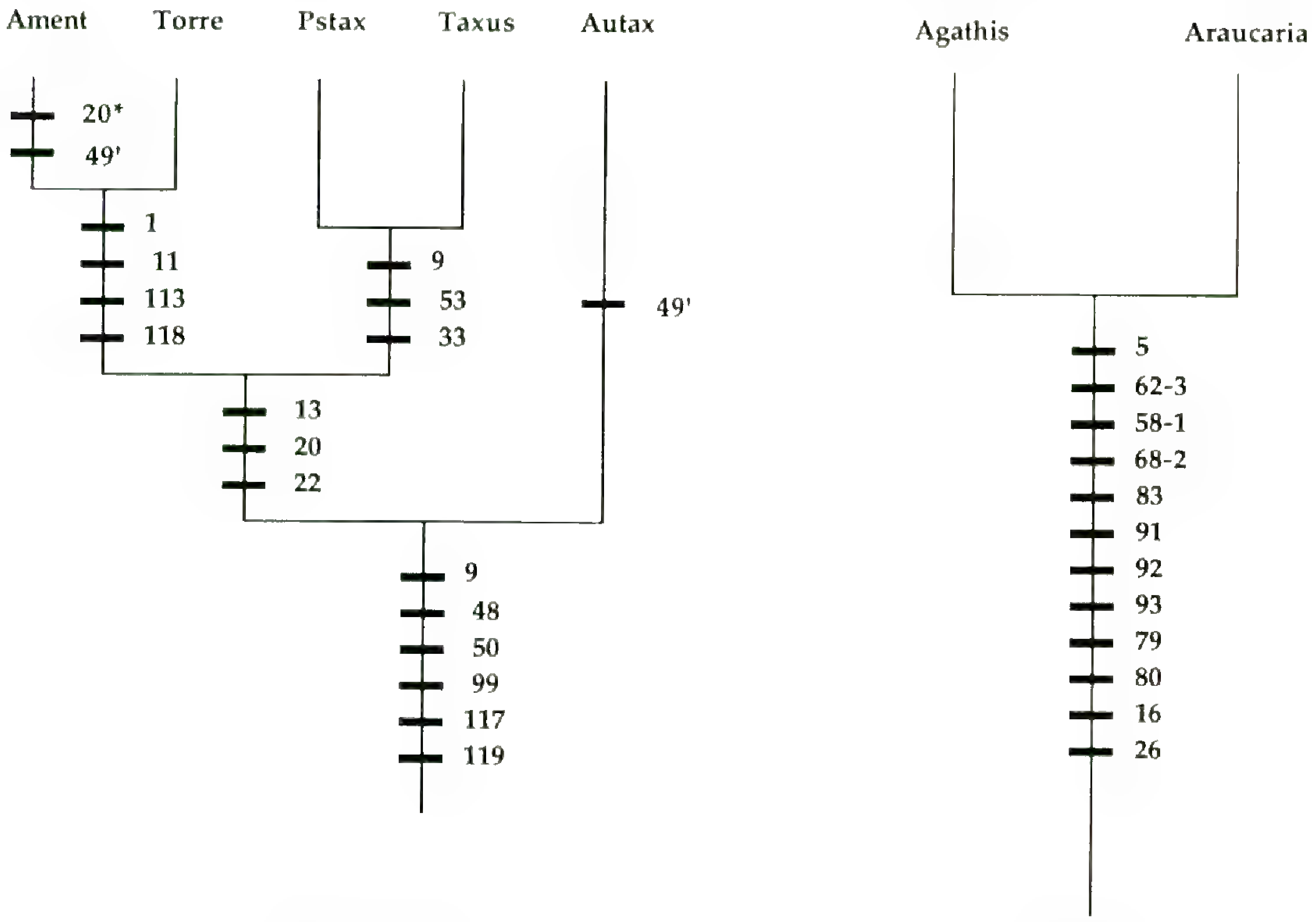

FIGURE 8. Cladistic relationships of Taxaceae (left) and Araucariaceae (right). (Ament = *Amentotaxus*; Autax = *Austrotaxus*; Pstax = *Pseudotaxus*; Torre = *Torreya*; * = reversal; ' = one parallelism.)

tended to emphasize ovulate cone structure. This study has uncovered embryological, palynological, and anatomical features that also provide bases for the recognition of conifers as a monophyletic group (see FIGURES 1, 2).

The placement of the Taxaceae has been controversial in the past (see, for example, Chamberlain, 1935; Florin, 1948b, 1951; Takhtajan, 1953; Sporne, 1965). The simple, uniaxial cone—in contrast to the biaxial one found in all other conifers—is unique to this family, and Florin (1948b, 1951) championed the separation of the Taxaceae from the rest of the conifers based on this character alone. He found a similar cone in the Jurassic *Paleotaxus jurassica* Florin and concluded that, since this structure is old and thus primitive, the Taxaceae should therefore be elevated to the rank of Taxales, coordinate with the Coniferales. In this cladistic analysis the taxads clearly fall out as a sister group to the Cephalotaxaceae, well within the rest of the conifer families (see FIGURE 2), all of which have biaxial cones. Embryologically, the Taxaceae have patterns of development similar to those of other conifers—a reduced number of divisions in embryogenesis and a tiered proembryo. In this analysis the most parsimonious explanation of the distribution of character states suggests that the uniaxial ovulate cone is derived from a compound, biaxial one. Florin's reason for elevating the Taxaceae is apparently unjustified: although uniaxial cones apparently similar to those of *Taxus* are found in the Jurassic, numerous earlier gymnosperms had biaxial cones.

A close relationship between the Taxodiaceae and the Cupressaceae has been recognized (e.g., Saxton, 1913; Eckenwalder, 1976; Stewart, 1983), although an isolated position for *Sciadopitys* (which is placed in the Taxodiaceae) has also been suggested (Velenovský, 1905; Seward, 1919; Florin, 1922; Hayata, 1932; Eckenwalder, 1976; Schlarbaum & Tsuchiya, 1985). The results from this cladistic analysis support these general conclusions since the monophyly of the Taxodiaceae (minus *Sciadopitys*) + Cupressaceae is supported by many characters (see FIGURE 6). However, the Taxodiaceae as currently recognized are not monophyletic but paraphyletic; the Cupressaceae form a monophyletic grouping *within* that family. Thus, if one chooses to recognize the Cupressaceae as presently circumscribed at the family rank, then the Taxodiaceae cannot be recognized, and many clades within the current Taxodiaceae will have to be elevated to family ranking. A possible solution is to recognize the entire Taxodiaceae-Cupressaceae clade as the Cupressaceae, which has nomenclatural priority (Eckenwalder, 1976).

The monophyly of the Pinaceae is well established (see FIGURE 4), with at least ten unique synapomorphies. Within the Pinaceae, grouping of genera is uncertain, as has been suggested by previous workers (e.g., Van Tieghem, 1869; Jeffrey, 1905; Pilger, 1926; Gaussen, 1966), who have each emphasized different characters in suggesting relationships. Van Tieghem (1869), for example, divided the family into two groups, those with short shoots and those without them. My results do not support his division of the family. In my analysis short shoots have evolved three times: in the lineage giving rise to *Pinus, Cathaya* Chun & Kuang, and *Larix* Link; in *Cedrus* Trew; and in *Pseudolarix* Gordon. Inspection of the morphology of the short shoots suggests differences between them (Thomson, 1914). Those of *Cedrus, Larix,* and *Pseudolarix* are persistent, and the leaves fall separately on an annual basis or in the second to fifth year. In *Pinus* the short shoots are deciduous as an entire unit in the second to twentieth (rarely to the forty-fifth) year, they produce a fixed number of needles in a single season, and they are axillary to a scale. In the other genera of Pinaceae, the needles are not fixed in number, and the short shoots are not deciduous or axillary to a scale. In *Cathaya* the short shoots are poorly developed. However, even acknowledging the differences between short shoots within the Pinaceae does not tell if they represent the same character or separately evolved, nonhomologous ones. Phylogenetic hypotheses can assist in answering such questions: this analysis suggests that short shoots have evolved three different times and so may not be homologous, yet that the morphological variation noted by Thomson (1914) may not be relevant in suggesting different evolutionary origins. Alternatively, if the information given by Thomson is used to record the character, short shoots may have evolved at least four times! Barnard (1926) claimed that some shoot dimorphism is common in conifers—another suggestion that short shoots are a weak phylogenetic character.

The grouping of the Pinaceae into two lineages is based on a few characters: the presence of resin ducts in the seeds (character 120) and of cleavage polyembryony (97) supports monophyly of *Abies* Miller, *Pseudolarix, Keteleeria* Carrière, *Cedrus,* and *Tsuga* Carrière; resin ducts in the secondary wood (17) and leaves with endodermis having thickened Casparian strips (39) support monophyly of *Cathaya, Pinus, Larix, Pseudotsuga* Carrière, and *Picea* Dietr.

Singh (1978) listed embryological characters of the Podocarpaceae in addition to those used in this analysis; for example, densely staining cytoplasm surrounding the archegonium (character 81). This character, however, needs further investigation to verify its use as a character state. De Laubenfels (1962) suggested that the presence of two cotyledons, each with two vascular bundles, is a feature unique to the Podocarpaceae. However, the use of this character does not stand up to cladistic reasoning. The fact that members of the outgroup comprising *Ginkgo,* the cycads, and the Gnetales have two cotyledons—and those of *Ginkgo* have two vascular bundles—might suggest that this is a primitive character within the Podocarpaceae. The morphological heterogeneity of the Podocarpaceae is underscored by the variation in chromosome numbers, which is extreme when compared to that within other conifer families (Sax & Sax, 1933; Hair & Beuzenberg, 1958; Khoshoo, 1961; Mehra, 1968). Given the high levels of homoplasy, the groupings of genera within the Podocarpaceae (FIGURE 5) must thus be very tentative, and additional research is clearly needed to confirm them.

Although the Podocarpaceae are usually considered a natural group, Keng (1973, 1974, 1975) has elevated *Phyllocladus* to family ranking, suggesting that the phylloclade of *Phyllocladus* was a very ancient structure that linked conifers with progymnosperms. For this to be the case, *Phyllocladus* would have to fall out not only as separate from the rest of the Podocarpaceae, but also as splitting off first in the family-level analysis. This is clearly not the case (see FIGURES 2 (Podocarpaceae), 5). *Phyllocladus* is not only a terminal taxon within the Podocarpaceae, but the Podocarpaceae in which it belongs split off after the basal Pinaceae (FIGURE 2; compare FIGURE 3).

How does one evaluate a cladogram? A significant quantity of homoplasy (the amount of parallelisms, convergence, and reversals in character states) seriously weakens cladistic hypotheses. One measure of homoplasy is the consistency index, which is the minimum range of character-state changes in the data divided by the actual length of the tree—or the sum of character-state or patristic changes along all branches. Fractions close to unity indicate a cladogram with little homoplasy (Kluge & Farris, 1969). In this study it varied from .500 to .857, a modestly good figure compared to that in some studies (for example, .40 in Rodman *et al.,* 1984). There may be several factors—both artificial and real—that explain the relatively low levels of homoplasy in this study. Comparing homoplasy indices among different taxonomic groups may lead to divergent values due to different sizes of data matrices. The greater the number of taxa and characters, the greater the amount of homoplasy. Thus, the consistency index for the Cupressaceae-Taxodiaceae analysis, with 31 taxa and 53 characters, was .544, while that for the Taxaceae analysis, with 5 taxa and 15 characters, was .857.

There may also be biological reasons why the homoplasy values are comparatively low in this study. In groups like conifers, in which great gaps exist between taxa due to extinction, character states may be comparatively distinctive, while in some more recent angiosperm groups characters may show nearly continuous variation, with character-state delimitation correspondingly uncertain.

Phylogenetic analyses using multiple sets of characters taken from all aspects of the plant demonstrate the value of not relying on any particular subset of characters, such as cone structure. We also see, not surprisingly, the importance of looking beyond the readily visible morphological features. Many of the phylogenetically useful characters are anatomical, embryological, palynological, or chemical. For example, apomorphies for the Pinaceae include p-type plastids, absence of biflavonoids, arrangement of transfusion-tissue tracheids, absence of phloem fibers, lack of cell walls in ventral-canal nuclei, thinning at the micropylar end of the megaspore membrane, and four-tiered proembryo. But the converse position—that gross morphological characters are not useful as phylogenetic markers—cannot be maintained. Saxton (1913) and Eckenwalder (1976) downplayed the value of decussate phyllotaxy that characterize Cupressaceae, but for different reasons. Saxton (1913) believed that external morphological characters respond to "conditions of living" and are therefore poor indicators of phylogeny. Although there is some merit in what Saxton says, a case can be made for the functional nature of just about any structure. It is best to exclude notions of adaptation and/or function from phylogenetic analysis, at least in the initial stages. This is not to say that phylogenies based on characters that seem adaptive should not be questioned.

Eckenwalder (1976) dismissed decussate phyllotaxy as not being a useful character for the Cupressaceae since it reportedly occurs elsewhere. However, there are two problems with this position. First, some of Eckenwalder's examples of decussate phyllotaxy are not really decussate, but bijugate or spiral opposite—e.g., *Metasequoia* and the Taxaceae (Morley, 1948; De Laubenfels, 1953; Greguss, 1955). Second, while perfectly decussate leaves have indeed evolved elsewhere (e.g., in the Cheirolepidiaceae Takht. (Alvin, 1982) and in *Microcachrys tetragona* J. D. Hooker), the usefulness of this character, although perhaps weakened, cannot be altogether discounted.

UNDERSTANDING THE EVOLUTION OF PARTICULAR CHARACTERS

Cladograms facilitate the understanding of the evolution of particular characters. Florin (1951) argued for a separation of conifers and taxads based on the single terminal ovule of the latter, which he claimed did not evolve by reduction from a bract and ovuliferous short-shoot system. The results of this cladistic analysis suggests, on the contrary, that the ovule structure of the taxads evolved from the biaxial cone of the conifers. Indeed, Harris (1976) suggested a possible scenario. An example is the peltate, perisporangiate microsporophyll of some Taxaceae (*Taxus, Pseudotaxus*), which has been likened to the sporangiophore of the Cordaitales (Dupler, 1919). Outgroup analysis indicates that this unique taxad microsporophyll is derived from the bisporangiate, hyposporangiate microsporophyll of other conifers.

"PRIMITIVE" CHARACTERS VS. "PRIMITIVE" TAXA

The cladistic results illustrate what to many is a contradiction: the presence of both specialized and generalized (or primitive) traits within particular taxa, or heterobathmy (Stevens, 1986). As mentioned above, much early discussion centered on which of the modern groups of conifers is the most primitive. In cladistic reasoning, living taxa are not viewed as primitive or advanced; only individual characters are advanced or primitive with respect to their condition in related taxa. Cladograms themselves simply represent the sequence of divergence of lineages. Thus the occurrence of so many derived characters in an apparently basal clade such as the Pinaceae may seem to be a contradiction, but it is not unexpected. The cladistic interpretation of the relative age of the Pinaceae is not inconsistent with the fossil record, which indicates that the group is very old (C. N. Miller, 1976, 1982; Meyen, 1984).

BIOGEOGRAPHY

The distribution of conifers—both fossil and extant—has long been of interest to biogeographers. Conifers have been divided into northern and southern "groups." Florin (1940, 1963) found that the southern conifer floras were different from the northern ones as early as the late Carboniferous and Permian periods.

Li (1953b) discussed the high diversity of extant conifers in the Pacific Basin and showed that in both Northern and Southern hemispheres, the majority of relict, endemic, or disjunct genera are concentrated in moist, mountainous regions with warm temperatures bordering the eastern and western parts of the Pacific.

In accounting for the distribution of conifers, biogeographers have drawn upon various explanations: migration and dispersal from centers of origin, extinction, and continental drift (Florin, 1963).

Seeking centers of origin was a common endeavor for conifer biogeographers, as it was for other specialists. Brown (1869) concluded that each genus had arisen out of the center in which the greatest number of species is found. Conifers were commonly believed to have originated in northern polar regions. Koch (1927) suggested a European origin for them.

In explaining the disjunct distribution patterns of conifers, biogeographers generally have suggested that long-distance dispersal has not been as frequent as in angiosperms. This is expected, given the relatively large size of most conifer seeds. However, the fleshy propagules of many conifers (e.g., Podocarpaceae, Taxaceae, *Juniperus*) are likely candidates for long-distance dispersal, since birds are known to eat them (Givnish, 1980). Land bridges and connections have been hypothesized to get conifers from one continent to another. Florin (1963) postulated that the migration of conifers has occurred in or along mountain belts during the Paleozoic, Mesozoic, and Cenozoic eras. Continental drift has often been employed to explain conifer distribution, especially in the Southern Hemisphere (Florin, 1963; Aubréville, 1973; Page & Clifford, 1981).

Whatever cause for these distribution patterns of conifers one chooses, the explanation will be influenced—if not determined—by cladistic relationships. As an example, consider some of the southern Cupressaceae (FIGURE 7). Several groups show Gondwanaland distributions: *Pilgerodendron, Fitzroya* (both South America), and *Diselma* (Tasmania); *Austrocedrus* (South America), *Libocedrus* (New Zealand, New Caledonia), and *Papuacedrus* (New Guinea); and *Callitris, Actinostrobus* (both Australia), and *Widdringtonia* (southern Africa). Of these, the first two groupings are somewhat tenuous since they are supported by few characters, but the clade of *Widdringtonia, Callitris,* and *Actinostrobus* is supported by several. A likely explanation is that the common ancestor of these genera inhabited Gondwanaland, and with subsequent continental drift these lineages became recognizable. Florin (1963) contended that the conifers divided very early into northern and southern groups. The Araucariaceae, the Podocarpaceae, *Athrotaxis* D. Don, *Paranocladus* Florin, *Walkomiella* Florin, and *Buriadia* A. C. Stewart & B. Sahni constituted the southern group, while the rest of the conifers constituted the northern one. My cladistic analysis does not support the contention that modern evolutionary distributions reflect that early distribution of two groups. It does suggest multiple Gondwanaland distributions—two in the Taxodiaceae-Cupressaceae clade and one in the Taxaceae. Many conifer groups (e.g., *Araucarites* C. Presl, *Athrotaxites* Unger, and *Podocarpus, fide* Krassilov, 1974) had both northern and southern distributions, relative to the Tethys Sea, in the Mesozoic. Extinction, perhaps due to changing climates, may also account for some of the disjunctions, especially in the Northern Hemisphere.

Role of Fossils

Many botanists (e.g., Stevens, 1980, 1984) and some zoologists (e.g., Patterson, 1982) are reluctant to use fossils in polarizing character states. Stevens (1980, p. 342) stated ". . .the imperfections of the fossil record cast doubt on this method of giving evolutionary polarity to a morphocline." However, the relevance of fossils depends upon the group being studied (Crane & Manchester, 1982). It may also depend upon the level of grouping in which a systematist is interested: for example, fossils may be of importance in assessing relationships of conifers to other gymnosperms, or among genera of conifers, but less useful for species of *Podocarpus.*

The use of fossils in phylogenetic reconstruction may be questioned somewhat differently: are fossils automatically to be considered ancestors, are they merely another organism, or are they special outgroups, to be given special consideration? The answer to the first query should be obvious. Despite repeated claims by paleontologists to have discovered *the* "ancestor" for particular groups, it is extremely doubtful that ancestors for many groups will ever be determined with any certainty.

The answer to the second will be determined by the quality and quantity of the characters shown by the fossils. Fossils may help greatly in the understanding of characters. Thus Florin (1951) was perfectly justified in discussing the evolution of cone scales in modern coniferous taxa from short shoots of fossils, because these characters are well represented in the fossil record.

Should fossil outgroups be given special status—that is, greater importance than living outgroups? Here there can be no easy solution. *A priori,* fossil outgroups cannot be given special status over living outgroups. However, it all depends on the group being studied. Well-represented fossil groups may be weighted more than isolated living outgroups, or vice versa. Fossil representatives have been crucial in the phylogenetic analysis of conifers. The use of fossil groups like the Lebachiaceae, the Cordaitales, and others puts the cladistic analysis of living conifers on a much firmer footing than if only other living gymnosperms were employed for outgroup comparison.

Fossils also tell us something of past distributions. The relictual nature of many genera of conifers is borne out in studies such as Chaney's (1951). *Sequoia,* for example, once had a far greater distribution than it does now. Florin (1940, 1963) used fossil evidence to plot former distributions of conifers on a global basis. This type of information would never be known from the study of living taxa.

Despite these manifest benefits of the fossil record, numerous characters are not readily observable from fossils. Many paleobotanists will be dependent upon the more enriched data sets available only from living plants.

NEW RESEARCH

This study has attempted to demonstrate the potential of cladistic analysis in phylogenetic reconstruction; Hennig's work (e.g., 1950, 1966) is now taking root in systematic botany. While much of the current direction in cladistics is methodological, the basis of phylogenetic hypotheses and evolutionary scenarios is careful research on the organisms—their characters and character states. This analysis was possible only because of the careful work of the classical morphologists—biologists who were greatly motivated by discovering patterns of evolution (e.g., Thomson, 1905, 1940; Coulter, 1909; Coulter & Chamberlain, 1917; Buchholz, 1918, 1920, 1933, 1939, 1941; Chamberlain, 1935). Since the purpose of this study was to bring together and critically analyze current information, future research utilizing new techniques is needed to confirm (or modify) some of the preliminary conclusions presented above.

This future work must develop in two directions. First, new and more complete information is needed. Anatomical analyses have already proven useful in elucidating phylogenetic relationships, and character analyses using new techniques should be given priority. Especially needed are more studies of reproductive biology—such as microgametophyte and megagametophyte development, embryology, and palynology—which have already contributed many characters useful in understanding the phylogeny of conifers (Thomson, 1905; Buchholz, 1941; Lurzer, 1956; J. Doyle, 1957; Ueno, 1960; Chowdhurry, 1962; Dogra, 1966, 1978; Pettitt, 1966, 1977; Singh, 1978; Haines & Prakash, 1980). In particular, studies are needed of the poorly understood tropical and south-temperate genera in the Podocarpaceae, Cupressaceae, and Araucariaceae, but many northern taxa, especially those in groups that are not economically important, also need investigation. A fresh look at characters studied decades ago, such as the megaspore membrane (Thomson, 1905), is necessary. New anatomical techniques such as ultrathin sectioning and scanning and transmission electron microscopy can contribute much to character discovery and analysis and ultimately to phylogenetic reconstruction. We can also look for important results from biochemical and molecular research (Praeger *et al.,* 1976; Praeger & Wilson, 1978; Cronin & Sarich, 1980; Sibley & Ahlquist, 1984), but the use of this approach is not without criticism with respect to inherent assumptions of the constancy of molecular evolution ("molecular clock") and to whether these kinds of data are amenable to tree construction (Farris *et al.,* 1982; Farris, 1985).

Second, once the information is collected, character states must be analyzed very carefully before they are incorporated into cladistic analyses. There is substantial character variation in any group of organisms that is not suitable for cladistic analysis due to continuous variation or incomplete surveys. As mentioned above, careful attention must be given to the recognition of character states. Polarization of character states may be impossible due to their unknown status in outgroups. After construction of a cladogram, a second stage of character evaluation may be necessary in the weighting of functionally correlated characters.

Assumptions of computer programs also need to be addressed. The underlying assumption of Swofford's PAUP program used in this analysis is unrestricted parsimony. Characters may be lost, regained, and perhaps lost again. Unlimited reversals, especially of complicated characters, may be unlikely in evolution. We might look to the next generation of computer programs to address this problem.

Third, new paleobotanical information is needed. Much of the past digging has been conducted near major research institutions in northern regions. It is not surprising that most fossil conifers—such as *Lebachia*—are northern in distribution. No doubt there are as-yet-undiscovered fossils in southern regions that will cast light on early conifer evolution. Eventually, fossil and modern taxa will be included in the same analysis.

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APPENDIX. **Character states used in the phylogenetic analysis of coniferous taxa.***

BRANCHING AND GROWTH PATTERNS. 1, Higher-order branches spiral / opposite (Morley, 1948; Dallimore *et al.*, 1966). 2, Short shoots absent / present (Barnard, 1926; Doak, 1935; Morley, 1948; Stebbins, 1948; Dallimore *et al.*, 1966). 3, Branches not annually deciduous / annually deciduous (Morley, 1948; Stebbins, 1948; Eckenwalder, 1976).

ANATOMY. 4, Sieve-element plastids starch accumulating / protein accumulating (Behnke, 1974).

STEM ANATOMY. 5, Stem tip without / with tunica corpus (Johnson, 1951; Griffith, 1952; Jackman, 1960; Pillai, 1963; Sporne, 1965; Pillai & Pillai, 1974). 6, Phloem fibers present/ absent (Esau, 1969).

WOOD ANATOMY. 7, Phloem-fiber sclereids absent / present (Lotova, 1975). 8, Phloem mucilage absent / present (Lotova, 1975). 9, Xylem parenchyma absent / present (Bailey, 1909; Phillips, 1941; Greguss, 1955; Sporne, 1965; Tegner, 1965, 1967; H. J. Miller, 1973; Chu & Sun, 1981). 10, End or transverse walls of wood parenchyma (as seen in tangential section) smooth / nodular or pitted (Peirce, 1936, 1937; Phillips, 1941; Boutelje, 1955). 11, Horizontal walls of wood parenchyma (as seen in radial section) smooth / nodular or pitted (Greguss, 1955). 12, Bordered pits of tracheids alternate, multiseriate, hexagonal in outline / uniseriate (Phillips, 1941; Florin, 1951; Greguss, 1955; Sporne, 1965; Stewart, 1983). 13, Spiral thickenings on longitudinal tracheid walls (early wood) absent / present (Compton, 1922; Phillips, 1941; Greguss, 1955, 1972; Stewart, 1983). 14, Spiral thickenings on transverse tracheid walls absent / present (Greguss, 1972; Hu & Wang, 1984). 15, Bordered pits with / without torus (Bauch *et al.*, 1972). 16, Crassulae

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*The descriptor to the left of the slash (/) indicates the primitive condition, the one to the right the derived condition. For multistate characters a slash (/) is used for ordered characters, a vertical line (|) for unordered ones.

(bars of Sanio) present / absent (Jeffrey, 1905; Gerry, 1916; Hale, 1923; Chamberlain, 1935; Phillips, 1941). 17, Resin ducts in secondary wood absent / present (Jeffrey, 1905; Chamberlain, 1935; Jain, 1975; Taylor, 1981; Hu & Wang, 1984). 18, Traumatic resin ducts absent / present (Bailey, 1909; Phillips, 1941). 19, Resin ducts in rays present / absent (Patton, 1927; Phillips, 1941; Hu & Wang, 1984). 20, Horizontal walls of wood rays smooth / thickened, nodular or with simple pits (Bannan, 1934; Phillips, 1941; Boutelje, 1955; Greguss, 1955). 21, Tangential walls of wood rays smooth / thickened, nodular (Greguss, 1955). 22, Indentations on horizontal walls of ray parenchyma absent / present (Phillips, 1941; Kaeiser, 1954; Greguss, 1955). 23, Ray tracheids absent / present (Holden, 1913; Phillips, 1941). 24, Ray tracheids smooth walled / dentate (Phillips, 1941). 25, Cross-field pits cupressoid or taxoid (round) / piciform (narrow slits) (Phillips, 1941). 26, Tracheids not resinous / resinous (Patton, 1927; Pool, 1929).

Leaves. 27, Leaves large / small. 28, Leaves falcate in profile and tetragonal in cross section / (1) linear or lanceolate and bifacially flattened | (2) scalelike | (3) bilaterally flattened | (4) needlelike | (5) double (fused?) (De Laubenfels, 1953). 29, Leaves single, spread out on branch / (1) in fascicles, spirally arranged on short shoots | (2) helically arranged on short shoots (Thomson, 1914). 30, Leaf phyllotaxy spiral / (1) spiral opposite (bijugate) | (2) decussate | (3) ternate (3-whorled) (De Laubenfels, 1953). 31, Seedling phyllotaxy whorled / opposite (De Laubenfels, 1953, 1965). 32, Leaf attachment decurrent / (1) with stalklike constrictions | (2) with shield-shaped attachment (De Laubenfels, 1953; Liu, 1971). 33, Mature foliage leaves monomorphic / dimorphic (facial and lateral leaves) (De Laubenfels, 1953). 34, Lateral margins of lateral leaves (in flattened branches with dimorphic leaves) free / fused. 35, Leaf bases distinctly decurrent / fused (De Laubenfels, 1953). 36, Leaves persistent / annually deciduous (Dallimore *et al.*, 1966). 37, Apical meristems without modified leaves / (1) shorter leaves interrupting growth / (2) scale leaves / (3) winter buds, tips free / (4) winter buds, scales overlapping (Florin, 1951; De Laubenfels, 1953). 38, Leaves amphistomatic / (1) hypostomatic | (2) epistomatic (Florin, 1951; Florin & Boutelje, 1954). 39, Leaves with endodermis (vascular sheath) not having / having thickened Casparian strips (Yao & Hu, 1982). 40, Mesophyll parenchyma smooth / plicate (Kausik & Bhattacharya, 1977; Yao & Hu, 1982; Han, 1984). 41, Tracheids of leaf transfusion tissue lateral to the vascular bundle / all around vascular bundle (mostly on abaxial side) (Griffith, 1971; Kausik, 1976; Kausik & Bhattacharya, 1977; Hu & Yao, 1981). 42, Vascular bundles of leaf 1 / (1) 2 / (2) more than 2 (Chamberlain, 1935; Kausik & Bhattacharya, 1977; Stewart, 1983).

Chemistry. 43, Biflavonoids present / absent (Hegnauer, 1962; Harborne, 1967). 44, Nootkatin absent / present (H. Erdtman, 1963; H. Erdtman & Norin, 1966). 45, Hinokinflavone absent / present (H. Erdtman, 1963; Harborne, 1967). 46, Tropolones absent / present (H. Erdtman, 1963; H. Erdtman & Norin, 1966). 47, Leaf wax estolid / nonestolid (Hegnauer, 1962).

Sex distribution. 48, Plants monoecious / dioecious (Chamberlain, 1935; Florin, 1948b; Li, 1952; Greguss, 1955; Singh, 1961; Dallimore *et al.*, 1966; Ntima, 1968; Givnish, 1980).

Microsporangiate strobilus. 49, Microsporangiate strobili compound / simple (Stewart, 1983). 50, Microsporangiate strobili terminal / axillary. 51, Microsporangiate strobili single at ends of leafy shoots / (1) grouped in clusters | (2) grouped in racemes or panicles. 52, Microsporophylls spiral / decussate (whorled). 53, Microsporophylls open (laminar), hyposporangiate / peltate, perisporangiate (Thomson, 1905; Dupler, 1919; Chamberlain, 1935; Ueno, 1960; Wilde, 1975). 54, Microsporangia 2 / more than 2 (Saxton, 1934; Chamberlain, 1935; Florin, 1951; Ueno, 1960). 55, Microsporangial dehiscence longitudinal / (1) oblique / (2) transverse (Liu, 1971).

Microgametophyte. 56, Prepollen / pollen (Mapes & Rothwell, 1984). 57, Pollen-tetrad formation simultaneous (tetrahedral) / successive (bilateral) (Ueno, 1960). 58, Pollen with shallow functional germination furrow / (1) with harmomegathus | (2) with functionless germ furrow | (3) with pore (Wodehouse, 1935; Ueno, 1960; G. Erdtman, 1965). 59, Pollen without / with papilla germination (Elliot, 1950; Takeuchi, 1953; Ueno, 1960; Ho & Sziklai, 1973). 60, Pollen grains with comfit perine absent / present (Ueno, 1960). 61, Pollen sexine tegillate / (1) rough corrugate | (2) granular | (3) roughened (Wodehouse, 1935; Ueno, 1960). 62, Pollen-sexine ultrastructure simple or absent / (1) compound / (2) double / (3) roughened (Wodehouse, 1935; Ueno, 1960; Reyre, 1968). 63, Pollen without / with annular thickenings (Ueno, 1960). 64, Pollen without / with triradiate streaks (Ueno, 1960). 65, Pollen winged (monosaccate: bilateral or bisaccate) / (1) wingless | (2) with 3 or more wings (Wodehouse, 1935; Cranwell, 1940; Buchholz & Gray, 1948; Florin, 1951; Ueno, 1960; Bharadwaj, 1963; Sporne, 1965; Millay & Taylor, 1974; Singh, 1978). 66, Pollen intine thin / thick (Ueno, 1960; Singh, 1961; Liu & Su, 1983). 67, Pollen multi- or binucleate / uninucleate at pollination (Singh & Chatterjee, 1963; Vasil & Sahni, 1964). 68, Pollen grains containing 1 or 2 / (1) 0 | (2) many prothallial cells (Chamberlain, 1935; Wodehouse, 1935; Elliot, 1950; Ueno, 1960; Sterling, 1963; Konar & Oberoi, 1969; Millay & Eggert, 1974; Singh, 1978). 69, Sperm nuclei with / without cell walls (Chamberlain, 1935; Singh, 1978). 70, Sperm cells unequal / equal (Burlingame, 1915; Ueno, 1960; Sterling, 1963; Owens & Molder, 1975; Wang, Chen, & Hu, 1979).

MEGAGAMETOPHYTE AND EMBRYO. 71, Pollination drop present / absent (J. Doyle, 1945; Dogra, 1964; Singh, 1978). 72, Pollen germination on nucellus / on scales (Dogra, 1964; Singh, 1978). 73, Micropyle symmetrical / asymmetric (J. Doyle & O'Leary, 1935a, 1935b; J. Doyle & Kane, 1943; Looby & Doyle, 1944; J. Doyle, 1945; Dogra, 1964; Singh, 1978). 74, Ventral-canal cell with distinct cell wall / with no wall, but having nuclei (Lawson, 1907; Chamberlain, 1935; Owens & Molder, 1975). 75, Alveoli open on area adjacent to central vacuole / closed by cell walls (Lawson, 1923). 76, Megagametophyte without / with layer of peripheral cells (Saxton, 1913; Maheshwari & Singh, 1967; Singh, 1978). 77, Megaspore membrane thick, double / thin (Thomson, 1905; Lawson, 1907; Quinn, 1966; Owens & Molder, 1975; Stidd & Cosentino, 1976; Singh, 1978). 78, Megaspore membrane of uniform thickness / thin at micropylar end (Thomson, 1905). 79, Megaspore membrane suberized / not suberized (Thomson, 1905). 80, Tapetum primary / secondary (Thomson, 1905; Saxton, 1913; Singh, 1978). 81, Archegonia not surrounded / surrounded by densely cytoplasmic tissue (Singh, 1978). 82, Archegonia separate / grouped together to form complexes (Lawson, 1907; Chamberlain, 1935; Maheshwari & Singh, 1967; Owens & Molder, 1975, 1980; Singh, 1978; Wang, Lee, & Chen, 1980). 83, Archegonia separated by vegetative cells / arranged in ring (Eames, 1913; Eckenwalder, 1976). 84, Archegonia apical (at micropylar end) / (1) lateral (at middle of gametophyte) | (2) lateral (at chalazal end of gametophyte) (Saxton, 1913; Moseley, 1943; Florin, 1951; Maheshwari & Singh, 1967; Konar & Oberoi, 1969; Foster & Gifford, 1974; Singh, 1978). 85, Archegonial jacket present / absent (Singh, 1978). 86, Proembryo with free nuclear divisions many / (1) 5 or 4 / (2) 3 / (3) 2 / (4) 0 (Eames, 1913; J. Doyle & Saxton, 1933; J. Doyle, 1954; Chowdhurry, 1962; Sporne, 1965; Chen & Wang, 1984). 87, Proembryo with secondary / primary type of wall formation (Dogra, 1966). 88, Proembryo nontiered / (1) with upper, suspensor, and embryonal tiers / (2) nontiered (reduced) (Moseley, 1943; Chowdhurry, 1962; Foster & Gifford, 1974; Dogra, 1978; Haines & Prakash, 1980). 89, Proembryo 3- / 4-tiered (Dogra, 1978; Singh, 1978). 90, Proembryo with embryonal cells uninucleate / binucleate (Saxton, 1913; J. Doyle & Looby, 1939; Buchholz, 1941; Elliot, 1950; Brownlie, 1953; J. Doyle, 1954; Chowdhurry, 1962; Quinn, 1964, 1966, 1970). 91, Proembryo basal / central (Haines & Prakash, 1980). 92, Proembryo with irregular shape / with spherical shape of free nuclear embryo and curved planes of upper, suspensor, and embryonal tiers of cellular phase (Haines & Prakash, 1980). 93, Proembryo with development of primary suspensor from suspensor / from upper tier (Dogra, 1978). 94, Suspensor anchorage of proembryo not within / within archegonium (Haines & Prakash, 1980). 95, Prosuspensor present / absent (Baird, 1937, 1953; Johansen, 1950). 96, Proembryo not completely filling / completely filling archegonium (Moseley, 1943). 97, Polyembryony simple / cleavage (J. Doyle, 1957; J. Doyle & Brennan, 1971, 1972; Singh, 1978).

Ovulate strobilus. 98, Cone terminal on leafy branches / axillary on short, leafy shoots (Saxton, 1913; Moseley, 1943; Florin, 1951; Dallimore *et al.,* 1966; Quinn, 1970). 99, Ovulate strobilus compound / simple (Dupler, 1920; Li, 1952; Sporne, 1965). 100, Ovulate strobilus short shoots radially symmetrical / (1) bilaterally flattened / (2) "scales" (Taylor, 1981; Mapes & Rothwell, 1984; Meyen, 1984). 101, Bract-scale complex free / fused (Sporne, 1965). 102, Cone bract not keeled / keeled (C. N. Miller, 1985). 103, Cone scales flat / peltate (Chamberlain, 1935; Li, 1953a; Sporne, 1965; Foster & Gifford, 1974). 104, Cone scales imbricate, thin / valvate, thickened (Li, 1953a). 105, Cone scales woody / modified into an epimatium (Sinnott, 1913). 106, Epimatium fully covering seeds / (1) half covering seeds / (2) lacking (Sinnott, 1913; Herzfeld, 1914; Aase, 1915; Chamberlain, 1935; Florin, 1951, 1958). 107, Epimatium not fused / fused to seed coat (Quinn, 1982). 108, Bracts not fleshy / fleshy (De Laubenfels, 1969; Quinn, 1982). 109, Bracts free / fused (De Laubenfels, 1969; Quinn, 1982). 110, Receptacle not warty / warty (De Laubenfels, 1969). 111, Cone scales persistent / deciduous (Chamberlain, 1935; Liu, 1971). 112, Cones pendulous / upright at maturity (Liu, 1971). 113, Uniaxial seeds arranged singly on primary shoots of unlimited / limited growth (Florin, 1948a, 1948b, 1954).

Ovules and seeds. 114, Ovules inverted / (1) semi-erect / (2) erect (Stebbins, 1948; Stewart, 1983; Clement-Westerhof, 1984; Mapes & Rothwell, 1984; Miller, 1985). 115, Number of ovules per cone scale: 1 / 2 or more (Clement-Westerhof, 1984). 116, Seed storage product: starch / oils (Hegnauer, 1962). 117, Seed without / with aril (Florin, 1951, 1958; Sporne, 1965; Foster & Gifford, 1974; Quinn, 1982). 118, Aril not developed by intercalary growth, not fused to seed / partly developed by intercalary growth, fused to seed coat (Florin, 1948a, 1948b). 119, Seeds winged / not winged (Taylor & Stewart, 1964; De Laubenfels, 1965; Dallimore *et al.,* 1966; Singh, 1978; Rothwell, 1982). 120, Resin ducts in seed coat absent / present (Price, pers. comm.). 121, Number of cotyledons: 2 / more than 2 (Hill & De Fraine, 1906, 1908, 1909a, 1909b; Buchholz, 1920; Butts & Buchholz, 1940; De Laubenfels, 1962). 122, Seeds maturing in 2 / 1 year(s) (Singh, 1978).

Cytology. 123, Chromosome number: 12 / (1) 10 | (2) 11 (Sax & Sax, 1933; Flory, 1936; Mehra & Khoshoo, 1956).

TAXONOMIC AND NOMENCLATURAL NOTES ON THE GENUS MIMOSA (LEGUMINOSAE)

ROSAURA GRETHER[1]

These notes result from studies concerning the revision of *Mimosa* species occurring in the state of Oaxaca, Mexico. They comprise revised synonymies, typifications, a new combination, and a new name and are based on study of type collections and field observations.

The following taxonomic and nomenclatural notes are based on a study of those species of *Mimosa* L. occurring in the state of Oaxaca, Mexico. Examination of type specimens and of additional material from Oaxaca, other parts of Mexico, and Central and South America, as well as field observations in Mexico, supports the synonymies and changes proposed here.

This paper formalizes and validates synonymies, lectotypifications, a new combination, and a new name before publication of "Leguminosas de Oaxaca," now in preparation, which will include keys, descriptions, and geographic distributions for the genus.

The following species, in alphabetical order, are known to occur in Oaxaca.

Mimosa acantholoba (Humb. & Bonpl. ex Willd.) Poiret *in* Lam. Encycl. Méth. Bot. Suppl. **1:** 83. 1810.

Acacia acantholoba Humb. & Bonpl. ex Willd. Sp. Pl. **4:** 1089. 1806. TYPE: America Meridional, *Humboldt & Bonpland 3800* (holotype, B-Willd., IDC 7440. 1391: II. 3!; isotype, P).

Mimosa eurycarpoides Robinson, Proc. Amer. Acad. Arts **36:** 472. 1901. *Neomimosa eurycarpoides* (Robinson) Britton & Rose, N. Amer. Fl. **23:** 172. 1928. TYPE: Mexico, Sinaloa, near Colomas, 21 July 1897, *Rose 1805* (holotype, US! (fragments, GH!; photo and fragments, NY!)).

Mimosa colimensis Robinson, Proc. Boston Soc. Nat. Hist. **31:** 258. 1904. *Neomimosa colimensis* (Robinson) Britton & Rose, N. Amer. Fl. **23:** 172. 1928. TYPE: Mexico, Colima, near Colima, Aug. 1897, *Palmer 128* (holotype, GH! (fragments, NY!); isotype, US!).

Neomimosa russellii Britton & Rose, N. Amer. Fl. **23:** 173. 1928. TYPE: Mexico, Sinaloa, vicinity of Rosario, 14 April 1910, *Rose, Standley, & P.G. Russell 14555* (holotype, US! (photo, MEXU!)).

The original description of *Mimosa eurycarpoides* was based on a flowering specimen (with an associated unattached fruit, probably of *Acacia farnesiana,* as indicated by Robinson (1904)). *Mimosa colimensis* was also based on flowering material; *Neomimosa russellii,* on a fruiting specimen.

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Because all the type specimens of the synonyms are incomplete, I have collected material with flowers and fruits in type localities or nearby (Sinaloa, 0.5 km NW de Rosario, *R. Grether 810,* MEXU, UAMIZ; Colima, 8.5 km SE de Colima, *R. Grether 875,* MEXU, UAMIZ) and have examined many specimens from the states of Sinaloa, Nayarit, Jalisco, Colima, Michoacán, Guerrero, and Oaxaca in the field and/or the herbarium.

Concerning the inflorescence, Robinson (1904) remarked that *Mimosa colimensis* differs somewhat from *M. eurycarpoides* in the oval form of the young heads; however, examination of the type specimens shows that both of them have subglobose young heads, although they look globose to almost globose when mature. Flower characteristics of both types are also the same: calyx campanulate, glabrous, one third to one half of corolla length; corolla five-lobed, glabrous, 2–2.5 mm long; stamens ten.

Although I could not gather flowering specimens of *Neomimosa russellii* in the type locality, remnants of flowers show the corolla to be five-lobed and glabrous, and fruits of the population growing there clearly correspond to *Mimosa acantholoba.*

Form, pubescence, and size of stipules and leaflets are essentially the same in type specimens of *Mimosa eurycarpoides, M. colimensis,* and *Neomimosa russellii,* as are the number of pinnae and leaflets.

My analysis of the original description and the microfiche of the type specimen of *Acacia acantholoba,* as well as my examination of several specimens from Nicaragua, Ecuador, and Peru, leads me to the conclusion that all these names have been used for a single widely distributed American species.

The fruits of *Mimosa acantholoba* vary in form and in the density of bristles (Grether, 1984): the valves can be elliptic to oblong and completely glabrous to setose, even in a single population.

Mimosa adenantheroides (Martens & Galeotti) Bentham, London J. Bot. **5:** 88. 1846.

Acacia adenantheroides Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles **10**(2): 312. 1843. TYPE: Mexico, Oaxaca, mountains of Sola de Vega and Yolotepec, S of Oaxaca, 1840, *Galeotti 3208* (holotype, BR (*fide* Rudd, 1984); isotype, K! (photos, MEXU!, US!)).

Acacia cylindriflora Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles **10**(2): 313. 1843. TYPE: Mexico, Oaxaca, Don Dominguillo, 1840, *Galeotti 3207* (holotype, BR (photos, MEXU!, US!)).

Mimosa remota Bentham, London J. Bot. **5:** 88. 1846. TYPE: Mexico, Oaxaca, Cordillera, 1840, *Galeotti 3240* (holotype, BR; isotype, K!).

Mimosa gomezii Britton & Rose, N. Amer. Fl. **23:** 159. 1928. TYPE: Mexico, Oaxaca, valley of Oaxaca, 20 Sept. 1894, *Nelson 1479* (holotype, US! (fragments, K!, photo and fragments, NY!); isotype, GH!).

The type specimens of *Acacia adenantheroides, A. cylindriflora,* and *Mimosa remota* are in flower, while that of *M. gomezii* has both fruits and flowers (although the spikes are very short in the latter).

I consider *Mimosa adenantheroides* to be a single variable species because all the types were collected in the state of Oaxaca and examination of numerous specimens from Oaxaca, including material collected near the type locality of *Acacia adenantheroides* (Distrito Sola de Vega, La Cumbre, 18 km SW de Sola de Vega, *M. Sousa et al. 10509,* MEXU!, UAMIZ!; Distrito de Juquila, 22 km E de Juquila, 4 km W de Yolotepec, *M. Sousa et al. 10545,* MEXU!, UAMIZ!), and from the states of Jalisco, Michoacán, México, Puebla, Morelos, Guerrero, and Chiapas, indicates much variation in populations with respect to size and number of pinnae and leaflets, length of spikes, and number of corolla lobes (four or five) and stamens (eight to ten), as well as to size of the legume and density of glandular dots and prickles at its margin.

The genus has been widely collected in Oaxaca, and no other closely related species that could be confused with *Mimosa adenantheroides* has been found.

Mimosa camporum Bentham, J. Bot. (Hooker) **2:** 130. 1840. TYPE: British Guiana, June 1839, *Schomburgk 725* (holotype, BR; isotypes, F!, G, K, M, NY!, US!, W).

Mimosa flavescens Splitg. Tijdschr. Natuurl. Gesch. Physiol. **9:** 110. 1842. TYPE: Surinam, *Splitgerber s.n.* (isotypes, K (photo, A!), W).

Mimosa aeschynomenes Bentham, Bot. Voy. Sulphur, 89. 1844. TYPE: [Nicaragua,] Realejo, 1841, *Hinds s.n.* (holotype, BM; isotype, K!).

Mimosa pusilla Bentham, Bot. Voy. Sulphur, 90. 1844. TYPE: [Nicaragua,] Realejo, 1842, *Hinds s.n.* (holotype, BM; isotype, K!).

Mimosa flaviseta Bentham, London J. Bot. **5:** 90. 1846. TYPE: Surinam, 1843, *Hostman 813* (holotype, BM; isotypes, GH!, K (photo, A!), NY!).

Mimosa martensis Britton & Rose *in* Britton & Killip, Ann. New York Acad. Sci. **35:** 152. 1936. TYPE: Colombia, Santa Marta, 1898–1899, *H. H. Smith 714* (holotype, NY!; isotype, US!).

Bentham (1875) considered *Mimosa flaviseta, M. aeschynomenes,* and *M. flavescens* as synonyms of *M. camporum* and mentioned (p. 436) *M. pusilla* as "possibly a small slender variety of *M. camporum.*"

Robinson's (1898) description of *Mimosa camporum* was based on two specimens from Mexico (*Rose 3116* (US!), from Acaponeta [Nayarit], and *3295* (F!, K!, US!), from Tepic [Nayarit], however this corresponds to *M. occidentalis* Britton & Rose, mainly in the large oval heads 2.5 cm in diameter. In fact, Britton and Rose selected *Rose 3295* as the type of *M. occidentalis,* described in N. Amer. Fl. **23:** 162. 1928.

I am here placing *Mimosa pusilla* and *M. martensis* in the synonymy of *M. camporum,* because stipule, leaflet, bracteole, flower, and fruit characters are those of *M. camporum.* Even though size and density of pubescence have been indicated as differences between *M. pusilla, M. martensis,* and *M. camporum,* examination of type specimens and other material from Mexico (states of Guerrero, Oaxaca, Veracruz, Tabasco, and Chiapas), Nicaragua (near Realejo, *Øersted 4323,* F!), Costa Rica, and Venezuela shows variation in size and density of hispidity, even in specimens from the same locality.

Mimosa ervendbergii A. Gray, Proc. Amer. Acad. Arts **5:** 178. 1862. TYPE: Mexico, Veracruz, Prov. Huasteca, near Tantoyuca, 1858, *Ervendberg 2, p.p.* (holotype, GH!; isotypes, K! (photo, MEXU!), US!).

Mimosa costaricensis Bentham, Trans. Linn. Soc. London **30:** 423. 1875. TYPE: Costa Rica, Aguacate, *Øersted 15* (lectotype, here designated, K! (photo and fragments, US!)).

Mimosa mexiquitensis Britton, N. Amer. Fl. **23:** 168. 1928. TYPE: Mexico, Chiapas, Finca Mexiquito, Sept. 1913, *Purpus 6816* (holotype, NY!; isotypes, GH!, MO!, US!).

Neomimosa donnell-smithii Britton & Rose, N. Amer. Fl. **23:** 173. 1928. *Mimosa donnell-smithii* (Britton & Rose) Standley & Steyerm. Publ. Field Mus. Nat. Hist., Bot. Ser. **23:** 163. 1944. TYPE: Guatemala, Departamento Alta Verapaz, Cubilquitz, 1902, *Von Tuerckheim 8197* (holotype, US!).

Mimosa scalpens Standley, Publ. Carnegie Inst. Wash. **461:** 58. 1935. TYPE: British Honduras, vicinity of Jacinto Hills, 4 May 1934, *Schipp 1306* (holotype, F!; isotypes, GH!, MO!, NY!).

Mimosa ervendbergii was based on a mixed collection of flowering material, as indicated by Robinson (1898); the specimen on the left correponds to this species, and the one on the right to *M. invisa* Martius. Robinson considered *M. costaricensis* to be a synonym of *M. ervendbergii,* and I have confirmed the correctness of that decision by examining the type specimens. *Øersted 15* is here selected as the lectotype of *M. costaricensis.*

Mimosa mexiquitensis also corresponds to the same species; examination of flowering and fruiting material from Chiapas, in addition to the type specimen, leads me to this conclusion.

The type of *Neomimosa donnell-smithii,* a fruiting specimen, has remnants of flowers that clearly match the same structures in *Mimosa ervendbergii* (calyx long ciliate, one third to one half of corolla length; corolla glabrous, four-lobed, stamens eight). It is interesting to note that Standley and Steyermark transferred *Neomimosa donnell-smithii* as *Mimosa donnell-smithii* in 1944; the same authors included that species in the *Flora of Guatemala* (1946), although pointing out (p. 56) that "we have seen no representation of this species." In the same publication they considered *M. scalpens* from Belize, described by Standley in 1935, to be a different species occurring in Guatemala, even though the two are, in fact, the same taxon.

The original description of *Mimosa scalpens* indicates pentamerous flowers, and that of *M. ervendbergii* tetramerous ones; however, variation in the number of corolla lobes (four or five) and stamens (eight to ten) has commonly been observed in the species. Although corolla-lobe number is a good character for many species of *Mimosa,* it varies (four or five) in several species of the genus.

Considering the characters that distinguish *Mimosa ervendbergii* (calyx lobes long-ciliate, very conspicuous in bud; corolla four- or five-lobed, glabrous; stamens eight to ten; legume articulated, stipitate, glabrous, apex rostrate, margins prickly; twigs angled, densely tomentose; stipules filiform, tomentose; leaflets puberulous above, tomentose below, with a prominent excentric nerve) and having seen all of them in the type specimens and in additional herbarium material from Mexico (states of Veracruz, Puebla, Oaxaca, Tabasco, and Chiapas), Guatemala, Nicaragua, and Costa Rica (Monte Aguacate, 11/47, *Øersted 4463,* F!, topotype of *M. costaricensis*), as well as in field observations made mainly in the states of Chiapas and Oaxaca, I conclude that all these names have been used for one taxon, the correct name of which is *M. ervendbergii* A. Gray.

Mimosa hexandra Micheli, Mém. Soc. Phys. Genève **30**(pt. 2, 7): 91. *t. 27.* 1889.

Mimosa bimucronata (DC.) Kuntze subsp. *hexandra* (Micheli) Hassler, Repert. Spec. Nov. Regni Veg. **9:** 3. 1910, and var. *intermedia* Hassler, *ibid. Mimosa bimucronata* (DC.) Kuntze var. *hexandra* (Micheli) J. F. Macbr. Contr. Gray Herb. **59:** 12. 1919. TYPE: Paraguay, bords du Mbay, près de Paraguari, Oct. 1882, *Balansa 4422* (holotype, G (photo, US!); isotypes, B (photo, US!), F!, NY!, P).

Mimosa vepres Lindman, Bih. Kongl. Svenska Vetensk.-Akad. Handl. **24**(3,7): 46. *fig. 12.* 1898. TYPE: Paraguay, Colonia Risso, 30 Oct. 1893, *Lindman A2263* (holotype, S, *fide* R. C. Barneby, pers. comm.; isotypes, GH!, US!).

Mimosa coroncoro Killip & Dugand, Caldasia **3**(11): 33. 1944. TYPE: Colombia, Departamento Atlántico, entre Palmar de Varela y Ponedera, Finca "El Paraíso," Aug. 1943, *Dugand & Jaramillo 3461* (lectotype, COL *16064*; isolectotypes, A!, COL *16065*, US!).

The original description of *Mimosa coroncoro* indicates *Dugand & Jaramillo 3461* (COL) as the type; however, Forero and Ruíz (1983) lectotypified the species because there are two specimens of that collection at COL; they selected COL *16064* as lectotype and COL *16065* as isolectotype.

I am placing *Mimosa coroncoro* in the synonymy of *M. hexandra* mainly because the corolla is three-lobed and there are six stamens, characteristics rarely encountered in the genus. The legume is also very distinctive: examination of *Dugand 3132* (US!; from Finca "El Paraíso," entre Palmar de Varela y Ponedera, Departamento Atlántico, Colombia) shows that it has a persistent margin, even though the authors of the original description indicated that this was not the case.

This is the first report of *Mimosa hexandra* in Mexico; observation of fruits in the field (Isthmus of Tehuantepec, state of Oaxaca) confirms the presence of persistent margins.

Macbride considered the species to be a variety of *Mimosa bimucronata*; however, the very distinctive, completely sessile fruit with very thick coriaceous valves, the predominantly trimerous flowers, and the fewer (six to twenty), thicker-textured leaflets (all characters observed in material from Mexico, Colombia, Venezuela, Brazil, and Paraguay) clearly distinguish *M. hexandra* from the related *M. bimucronata.*

Mimosa lacerata Rose, Contr. U. S. Natl. Herb. **5:** 141. 1897.

Acanthopteron laceratum (Rose) Britton, N. Amer. Fl. **23:** 179. 1928. TYPE: Mexico, Puebla, vicinity of Piaxtla, 24 Nov. 1894, *Nelson 2008* (lectotype, here designated, US!; isolectotype, NY!).

Mimosopsis glutinosa Britton & Rose, N. Amer. Fl. **23:** 178. 1928; not *Mimosa glutinosa* Malme, Ark. Bot. **23**(13): 51. 1931. TYPE: Mexico, Puebla, near San Luis Tultitlanapa, July 1908, *Purpus 3174* (holotype, US!; isotypes, F!, GH!, MO!).

Mimosa biuncifera Bentham var. *horrida* Miranda, Anales Inst. Biol. Univ. Nac. México **12:** 610. 1941. TYPE: Mexico, Puebla, cerro NW de Matamoros, 22 March 1941, *F. Miranda 1410* (lectotype, here designated, MEXU!).

Two syntypes of *Mimosa lacerata, Nelson 2008* (NY!, US!) and *Pringle 6247* (F!, GH!, K!, MEXU!), were originally cited; no lectotype has been chosen. I hereby select the specimen collected by Nelson because it represents the taxon more completely.

Britton (*in* Britton & Rose, 1928, p. 179) transferred the species to the monospecific genus *Acanthopteron*; he considered the "legume with marginal wings deeply irregularly cleft into flat, rigid spinous teeth" to be a generic character; however, all other characters are those of *Mimosa. Mimosa lacerata* is not the only species with lacerate margins of the legume; for example, the legumes of *M. bahamensis* Bentham also have such a margin, even though it is not closely related to *M. lacerata*. Therefore, I cannot consider *Acanthopteron* a distinct genus.

Britton and Rose (*op. cit.*) described *Mimosopsis glutinosa* based on a fruiting specimen; the type specimen has abnormal and immature fruits of *M. lacerata*. In addition, field observations in the states of Puebla and Oaxaca have demonstrated that some individuals growing in very eroded areas are depauperate, with the lacerate margin of the legume not well developed; however, such plants can always be recognized as *M. lacerata* because of other vegetative and flower characters, as well as the somewhat lacerate margin and the glandular dots of the fruit.

Miranda (1941) described *Mimosa biuncifera* var. *horrida*, pointing out that he had not found any other character besides the prickles to distinguish the plant collected in Matamoros from the typical *M. biuncifera*. Miranda did not cite specimens in the original description, but he mentioned (p. 611) "la planta de Matamoros" in the protologue and annotated the specimen *F. Miranda 1410* (MEXU!) as *M. biuncifera* var. *horrida*. Considering all aspects of the protologue and having found the specimen collected and annotated by the author, I hereby propose *Miranda 1410* as lectotype. Examination of that specimen shows tetramerous flowers with puberulous corollas, as well as the twinned, laterally compressed, very broad prickles typical of *M. lacerata*.

Fruiting material collected in Matamoros, Puebla (*Miranda 2279*, MEXU!) also corresponds to *Mimosa lacerata*. In addition, herbarium and field observations, mainly in the states of Puebla and Oaxaca, show that flowering *Mimosa lacerata* (e.g., *Miranda 1410*) has rose to purple heads and rose stamens, and it can thus be clearly distinguished from *M. biuncifera*, which has pentamerous flowers with pubescent corollas, white to slightly rose heads, and white stamens. Therefore, I consider *M. biuncifera* var. *horrida* to be conspecific with *M. lacerata*.

Mimosa lactiflua Del. ex Bentham, Trans. Linn. Soc. London **30:** 393. 1875; Martius, Fl. Brasil. **15**(2): 311. 1876, descr. ampl. TYPE: habitat in America Meridionali (an Brasilia?), ex specimine olim in Horto Monspeliensi culto, in Herb. D.C. asservato, 1836, *307b* (holotype, G-DC!).

Mimosa mixtecana Brandegee, Univ. Calif. Publ. Bot. **3:** 379. 1909. TYPE: Mexico, Puebla, vicinity of San Luis Tultitlanapa, near Oaxaca, May–July 1908, *Purpus 2673* (lectotype, here designated, US! (photo, MEXU!); isolectotypes, F!, GH!, MO!, NY!, UC (photo, MEXU!)).

Mimosa vazquezii Britton & Rose, N. Amer. Fl. **23:** 153. 1928. TYPE: Mexico, Oaxaca, Distrito de Tlacolula, Cerro de la Carbonera, Matatlán, June 1906, *Conzatti & Vázquez 1482* (holotype, US! (photo and fragments, NY!); isotype, GH!).

Concerning the occurrence of *Mimosa lactiflua* in Mexico, Bentham (1875, pp. 393, 394) stated, "Delile's specimens were from the Botanical Garden of Montpellier, supposed to be of American, perhaps Brazilian, origin. In the Berlin herbarium there is a specimen from Mexico, *Ehrenberg,* which agrees with the detailed description I had made (now inserted in the Flora Brasiliensis), except that the leaflets are under instead of over ½ in. long."

I (Grether, 1978) cited the species as occurring only in the state of Oaxaca, Mexico. Since that time, however, numerous specimens from the states of Morelos, Puebla, Guerrero, and Oaxaca have been examined that clearly correspond to *Mimosa lactiflua*. Personal communication with R. C. Barneby and a review of the holdings of different herbaria have yielded no evidence that this species occurs in Brazil. Besides, I have not seen it in material examined from Central America.

The holotype of *Mimosa lactiflua,* seen when it was on loan to NY from G-DC, is a flowering specimen characterized mainly by its glabrous, tetramerous flowers and its oblong-lanceolate to elliptic or ovate, glabrous, glaucous leaflets with prominent reticulate nerves beneath. The lectotype and isolectotypes of *M. mixtecana* (*Purpus 2673*) are flowering and fruiting specimens, also with glabrous, tetramerous flowers and glabrous, glaucous leaflets, very variable in shape and size as *M. lactiflua*. The type of *M. vazquezii* shows the same flower characters and variable, elliptic to ovate leaflets. In spite of the uncertain origin of the specimen cultivated at Montpellier, the holotype of *M. lactiflua* is a good specimen, and this is the oldest and correct name for the species.

Mimosa langlassei Micheli, Mém. Soc. Phys. Genève **34**(3): 277. *t. 22.* 1903. TYPE: Mexico, Michoacán, pied du Volcán de Jorullo, 13 April 1898, *Langlassé 99* (holotype, G; isotypes, F!, K! (photo, MEXU!)).

Mimosa conzatti Britton & Rose, N. Amer. Fl. **23:** 153. 1928. TYPE: Mexico, Oaxaca, Distrito del Centro, Cerro San Antonio, 6 Sept. 1908, *Conzatti 2239* (holotype, GH! (photo and fragments, NY!, US!); isotype, F!).

Mimosa langlassei was described from a flowering specimen, and the description of *M. conzattii* was based on a fruiting one; however, examination of material of the latter at F, GH, NY, and US shows remnants of flowers at the base of fruits; these flowers are tetramerous and the corolla lobes are puberulous, as in *M. langlassei.* Vegetative characters observed in types, and mentioned in the original descriptions of both species, clearly correspond.

Flowering and fruiting material of *Mimosa langlassei* (Michoacán, 18 km N de La Huacana, cerca del Volcán El Jorullo, *R. Grether 1117,* MEXU, UAMIZ) was collected near the type locality; the pubescent and slightly setose valves of the legume agree with the fruits of *M. conzattii,* and the flowers are tetramerous and puberulous. I also visited the type locality of *M. conzattii*; unfortunately, the area is quite disturbed, and the species is no longer growing there.

Concerning typification of *Mimosa conzattii,* there is a note on the GH, NY, and US sheets of *Conzatti 2239* saying "ex herb. Field Mus." I have studied the Field Museum specimen distributed by Conzatti as "*Acacia*"; this was annotated in 1910 by Greenman, who identified it as *M. xanti* Gray and sent fragments to B. L. Robinson (GH), who verified the identification. Britton and Rose saw only the specimen of the same number at GH and took even smaller fragments from it. These were deposited at NY by Britton and at US by Rose, and each was mounted with a photograph of the undivided GH specimen. At the suggestion of D. H. Nicolson (US), I now recognize the GH specimen as the holotype of *M. conzattii,* the specimens at NY and US as fragments of the holotype, and the specimen at F as an isotype.

Examination of additional material from Michoacán, Guerrero, Oaxaca, Puebla, and Chiapas confirms that it is a single species, *Mimosa langlassei.*

Mimosa mellii Britton & Rose, N. Amer. Fl. **23:** 155. 1928. TYPE: Mexico, Oaxaca, near Chivela, 18 Jan. 1927, *Mell 2* (holotype, US! (photos, MEXU!, UAMIZ!)).

Mimosa chiapensis Britton, N. Amer. Fl. **23:** 154. 1928. TYPE: Mexico, Chiapas, river bottom, Hacienda Monserrate, May 1925, *Purpus 10313* (holotype, NY! (photos, MEXU!, UAMIZ!); isotype, US!).

Mimosa doylei Britton & Rose, N. Amer. Fl. **23:** 155. 1928. TYPE: Mexico, Chiapas, near Los Pinos, 12 Dec. 1906, *C. B. Doyle 56* (holotype, US! (photos, MEXU!, UAMIZ!; fragments, NY!)).

Mimosa oaxacana Britton & Rose, N. Amer. Fl. **23:** 155. 1928. TYPE: Mexico, Oaxaca, between Guichocovi and Lagunas, 27 June 1895, *Nelson 2746* (holotype, US! (photos, MEXU!, UAMIZ!; fragments, NY!)).

Mimosa mellii, M. chiapensis, M. doylei, and *M. oaxacana* were all described by Britton and Rose in the same publication. Although the original descriptions show some differences (mainly in pubescence of leaflets and corolla lobes), all of them correspond to a single species.

There are several bases for this conclusion. Types of *Mimosa mellii* and *M. doylei* are fruiting specimens with remnants of flowers; fruits of both are sessile and slightly setose, and they clearly correspond to the same taxon. The type specimen of *M. doylei* has few, tetramerous flowers, like those of *M. mellii*—not pentamerous, as quoted in the original description. The type of *M. doylei* has puberulous corolla lobes and leaflets, while the type of *M. mellii* has glabrous to slightly puberulous corolla lobes and completely glabrous leaflets.

The types of *Mimosa oaxacana* and *M. chiapensis* are flowering specimens; both have tetramerous flowers, as well as puberulous corolla lobes and leaflets.

I have visited the type locality of *Mimosa mellii* and have collected a topotype of that species (Oaxaca, Chivela, *R. Grether 1363,* MEXU, UAMIZ); I have also examined other topotypes (*Mell s.n.,* Aug. 1928, US!, and Dec. 1928, NY!). The type locality of *M. oaxacana* (between Guichocovi and Lagunas) is south of Chivela in the same region. There are several collections from this area, although it is difficult to state which could be considered as a topotype. I located Hacienda Monserrate through Sousa's (1969) publication on Purpus's botanical collections in Mexico; despite a thorough search of this locality and the vicinity, I could not find *M. chiapensis* there. However, I did collect additional material southwest of the type locality (Chiapas, Municipio Cintalapa, 9.5 km NW de

Rizo de Oro, camino a Colonia Rodolfo Figueroa, cerca del límite con Oaxaca, *R. Grether 1758*, MEXU, UAMIZ). I could not locate the type locality of *M. doylei* (Los Pinos) on present or old maps, or by asking local people in Chiapas.

Field observations—as well as examination of type specimens, topotypes of *Mimosa mellii*, and additional flowering and fruiting material from Oaxaca and Chiapas—permit me to state that variation in pubescence of leaflets is probably due to the stage of leaf development: flowering specimens (May to July) generally have puberulous leaflets, although some populations show variation from puberulous to glabrate leaflets even in a single individual, and some others have leaflets always glabrous. In fruiting specimens (December to January) the leaflets are generally glabrous, although they are puberulous to glabrous in a few of them. However, the linear-oblong, strongly reticulate-nerved leaflets are constant in all flowering and fruiting material examined. The corolla lobes of *M. mellii* also vary in pubescence: in some individuals they are glabrous and in others puberulous; in some variation is from puberulous to glabrous even on a single plant. In addition, the legume varies from slightly setose to completely glabrous.

Despite the differences mentioned above, it is not possible to distinguish several species or varieties. Also, the geographic distribution of this taxon is apparently restricted to the Isthmus of Tehuantepec (Distrito de Juchitán), Oaxaca, and the adjacent region of Chiapas (Municipio de Cintalapa and Municipio de Arriaga), at altitudes between 150 and 1000 m.

I have selected *Mimosa mellii* as the name for the species, considering that its type is the best and most complete specimen (with mature fruits and remnants of flowers).

Mimosa mollis Bentham, J. Bot. (Hooker) **4:** 408. 1842. TYPE: Mexico, Puebla, Acatlán, 1834, *Andrieux 400* (holotype, K; isotypes, G (photos, F!, MEXU!), OXF (photo, MEXU!), W (photo, F!)).

Mimosa herincquiana Micheli, Mém. Soc. Phys. Genève **34**(3): 276. 1903. TYPE: Mexico, Guerrero, Cariote [Cañón] del Zopilote, 27 May 1899, *Langlassé 1040* (holotype, G; isotypes, F!, GH!, K! (photo, MEXU!), US!).

The types of *Mimosa mollis* and *M. herincquiana* are flowering specimens; the original descriptions show differences only in numbers of pinnae (four or five vs. seven or eight, respectively) and leaflets (six to ten vs. seven or eight).

Examination of photographs of types, specimens collected near the type locality of *Mimosa mollis* (Puebla, 11 km SE de Acatlán de Osorio, *M. Sousa 8210*, MEXU!), isotypes, and the topotype of *M. herincquiana* (Guerrero, Cañón del Zopilote, 36 km N de Zumpango del Río, *R. Grether 1143*, MEXU, UAMIZ), as well as additional flowering and fruiting material from Puebla, Guerrero, and Oaxaca, indicates the similarity of the two taxa, which I consider synonymous.

There are four to ten pinnae and six to twelve leaflets. The tomentose branchlets and stipules, the villous oblong to elliptic leaflets, the villous pentamerous flowers, and the tomentose, unarmed, sessile fruits are distinctive characters of the species.

Mimosa orthocarpa Spruce ex Bentham, Trans. Linn. Soc. London **30:** 437. 1875; Martius, Fl. Brasil. **15**(2): 380. 1876, descr. ampl. SYNTYPES: Brazil, "habitat prope Santarem provinciae Paraensis," *Riedel s.n.* (K); ad Lacum Quiriquiry, Prov. Pará, 1850, *Spruce 518* (K, herb. Bentham; NY neg. 1897!).

Mimosa glandulosa Bong. ex Bentham, Trans. Linn. Soc. London **30:** 437. 1875, *nomen nudum.*

Mimosa calderonii Britton & Rose, N. Amer. Fl. **23:** 167. 1928. TYPE: El Salvador, El Angel, Oct. 1923, *S. Calderón 1842* (holotype, US! (photo and fragments, NY!); isotype, GH!).

Two syntypes of *Mimosa orthocarpa, Riedel s.n.* and "*Sello*" *518* were originally cited. According to Barneby (pers. comm.), "Sello" must be an error for Spruce, considering that Sello was never on the Amazon. Bentham attributed the epithet to Spruce, and the specimen at K in Bentham's herbarium is labeled *Spruce 518.*

I have examined a photograph from B (F neg. 1350) and a specimen at NY, both labeled "*Spruce s.n.,* ad ripas fluminis das Trombétas et lacus Quiriquiry, Prov. Pará, Dec., 1849." Barneby has examined other specimens labeled *Spruce s.n.* at K (herb. Hooker), LE, and W. The specimens *Spruce s.n.* could be from the same collection as *Spruce 518,* but they have different collection dates (Dec. 1849, and 1850, respectively). According to Urban (1906), Spruce was at Quiriquiry in December, 1849. If that is so, then the date on Bentham's sheet could be an error; however, there is no doubt that the specimens *Spruce s.n.* and *Spruce 518* are conspecific.

Bentham (1875) considered *Mimosa glandulosa* to be a synonym of *M. orthocarpa,* based on the specimen named by Bongard. After examining two specimens originally named *M. glandulosa* Bong. (Santarem, Nov. 1828, *Riedel 37,* A, K, *Riedel 1560,* LE), Barneby (pers. comm.) confirmed that *M. glandulosa* Bong. ex Bentham is a *nomen nudum* and a synonym of *M. orthocarpa.*

Barneby's and my examinations of type specimens of *Mimosa orthocarpa* and *M. calderonii,* of additional material from Mexico (states of Guerrero, Oaxaca, Veracruz, Tabasco, and Chiapas), Colombia, Venezuela, and Brazil, as well as my study of original descriptions, support this synonymy.

I have not chosen a lectotype of *Mimosa orthocarpa* because I have seen a photograph only of *Spruce 518.*

Mimosa polyantha Bentham, J. Bot. (Hooker) **4:** 410. 1842. TYPE: Mexico, Puebla, Acatlán, *Andrieux 397* (holotype, K; isotype, W (photos, F!, MEXU!)).

Mimosa polyanthoides Robinson, Proc. Boston Soc. Nat. Hist. **31:** 260. 1904. TYPE: Mexico, Guerrero, on mountains above Iguala, 5 Oct. 1900, *Pringle 8408* (holotype, GH!; isotypes, K!, MEXU!, MO!, NY!, US!).

Mimosa stipitata Robinson, Proc. Boston Soc. Nat. Hist. **31:** 261. 1904. TYPE: Mexico, Guerrero, on mountains above Iguala, 5 Oct. 1900, *Pringle 8406* (holotype, GH!; isotypes, F!, K!, MEXU!, NY!, US!).

Mimosa setigera Britton & Rose, N. Amer. Fl. **23:** 160. 1928. TYPE: Mexico, Sinaloa, vicinity of Rosario, 14 April 1910, *Rose, Standley, & Russell 14553* (holotype, US!; isotypes, GH!, NY!).

The fruits of *Mimosa polyantha* were unknown to Bentham; however, Robinson (1898) described them, and he assumed material with oblong legumes abruptly acuminate at each end, hispid on the margins, and with valves having short, spreading setae to be typical, based on the specimens *Pringle 4635* (MEXU!), *Rose 1475,* and *Palmer s.n.*

I have examined topotypes of *Mimosa polyantha* (Puebla, 4 km SE de Acatlán de Osorio, *R. Grether 735,* MEXU, UAMIZ; 11 km SE de Acatlán, *Téllez 1086,* MEXU!; Acatlán, *F. Miranda 2971,* MEXU!), and the legumes correspond to Robinson's description of them.

Mimosa stipitata and *M. polyanthoides* were collected in the same place. I have visited the type locality and vicinity and have observed variation in number of pinnae and leaflets, as well as in density of setae and length of the stipe of the legume, even in the same population (Guerrero: 22 km W de Iguala, camino a Teloloapan, *R. Grether 1132,* MEXU, UAMIZ; 6 km W de Xalostoc, camino a Teloloapan, *R. Grether 1133,* MEXU, UAMIZ).

Mimosa setigera was based on a specimen with setose legumes; however, examination of material from Rosario, Sinaloa, and vicinity (Sinaloa: 16 km SE de Escuinapa, *R. Grether 1099,* MEXU, UAMIZ; between Agua Caliente and Rosario, *Rudd 2099,* MEXU!, *Rudd 3000,* MEXU!) also shows variation in valves (from setose to glabrous) and differences in the length of the legume stipe.

Differences in number of pinnae and leaflets depend on the season, because flowering specimens have immature leaves, while fruiting material has mature and old ones. Flower characters are constant for all material examined from Sonora, Sinaloa, Michoacán, Guerrero, and Oaxaca, as well as from Puebla, Morelos, and Veracruz.

Mimosa pueblensis R. Grether, *nomen novum*

Mimosopsis filipes Britton & Rose, N. Amer. Fl. **23:** 177. 1928. *Mimosa filipes* (Britton & Rose) Gentry, Brittonia **6:** 315. 1948, not Martius, Herb. Fl. Brasil. 132. 1837. TYPE: Mexico, Puebla, vicinity of San Luis Tultitlanapa, July 1908, *Purpus 3175* (holotype, US!; isotypes, GH!, MO!).

I am proposing a new name for the species because the epithet *filipes* used by Britton and Rose was not available. It had been used by Martius for a different Brazilian *Mimosa,* making the Britton and Rose name a later homonym.

Mimosa pueblensis is known only from the states of Puebla and Oaxaca, Mexico; although Britton and Rose mentioned the state of Morelos, I have not seen material from there.

The species is characterized mainly by its slender, puberulous peduncles with red glandular dots, axillary, solitary or in clusters of two to six (to ten); its deep purple buds and flowers; its deeply five- (rarely four-)lobed, glabrous to puberulous corolla; and its sessile, glabrous legume, with red glandular dots more conspicuous in young fruits, and the margin sparingly prickly or unarmed.

Britton and Rose (1928) cited *Purpus 3175* as the type of *Mimosopsis filipes*;

however, the original description was based on two specimens, *Purpus 3175* (flower) and *Purpus s.n.* (flower and fruit). Both were annotated as type, and both were collected in the same locality on the same date; there is no doubt that they are conspecific.

Mimosa rhodocarpa (Britton & Rose) R. Grether, *comb. nov.*

Mimosopsis rhodocarpa Britton & Rose, N. Amer. Fl. **23:** 175. 1928. TYPE: Mexico, Michoacán, Patamban, Jan. 1903, *Nelson 6550* (holotype, US!; isotype, GH!).

A new combination is necessary to transfer the species to the genus *Mimosa. Mimosopsis* Britton & Rose is an artificial genus: the only distinctive character is the unsegmented legume; all other vegetative and flower characters are those of *Mimosa.*

The species is distinguished by its oblong, glabrous, rather thick leaflets with ciliate margins; its five-lobed, glabrous calyx about half as long as the corolla and with a ciliate margin; its five-lobed, glabrous, purple corolla; and its sessile, reddish, puberulous to glabrous, shiny, reticulate, completely unarmed legume 3–4.5 cm by 8–10 mm. *Mimosa rhodocarpa* has the broadest fruit of all the related Mexican species.

Mimosa rhodocarpa is known from the states of Zacatecas, Jalisco, Michoacán, México, Hidalgo, Puebla, Guerrero, and Oaxaca.

Mimosa ursina Martius, Flora 21(2), Beibl. **4:** 56. 1838. TYPE: Brazil, Prov. Bahiensis, inter Conceiçâo et Arrayal da Feira de S. Anna in desertis, II–III, 1819, *Martius s.n.* (holotype, M).

Mimosa paucisperma Britton & Rose, N. Amer. Fl. **23:** 151. 1928. TYPE: Mexico, Chiapas, Jalisco Arriaga, Sept. 1923, *Purpus 9306* (holotype, UC (photo and fragments, NY!, US!)).

Barneby examined the holotype of *Mimosa ursina* at M, and he and I examined photographs and fragments (branchlets, leaves, flowers, and fruits) of the type collection of *M. paucisperma* at NY and US; the characters of the type material are in accord. In addition, the original descriptions of both species are complete, and all characters, including those of habitat (in savannas and flooded places) clearly agree.

Our review of additional material from Brazil, Honduras, El Salvador, and southern Mexico (states of Oaxaca, Tabasco, and Chiapas), including a topotype of *Mimosa paucisperma* (Chiapas, alrededores de Arriaga, salida de la carretera a Tapachula, *R. Grether 1783,* MEXU, UAMIZ), indicates that it comprises only one species.

Detailed observation of herbarium specimens and fresh material shows some flower characters not considered in the original descriptions of *Mimosa ursina* and *M. paucisperma,* including a glabrous, four-lobed corolla, four stamens, and a widened stigma.

Mimosa watsonii Robinson, Proc. Amer. Acad. Arts **36:** 473. 1901. TYPE: Guatemala, eastern portion of Vera Paz and Chiquimula, 1885, *Watson 323* (lectotype, here designated, GH!; isolectotype, US!).

Mimosa recordii Britton & Rose, N. Amer. Fl. **23:** 170. 1928. TYPE: British Honduras, Stann Creek District, Middlesex, 19 Jan. 1926, *Record s.n.* (holotype, US!; isotype, NY!).

Mimosa rekoana Britton, N. Amer. Fl. **23:** 170. 1928. TYPE: Mexico, Oaxaca, Cafetal Concordia (Cerro Espino), 20 Nov. 1917, *Reko 3610* (holotype, US! (fragments, NY!); isotype, MEXU!).

Mimosa resinifera Britton, N. Amer. Fl. **23:** 169. 1928. TYPE: Honduras, Department of Atlántida, vicinity of Tela, 14 Dec. 1927–15 March 1928, *Standley 54698* (holotype, NY!; isotypes, A!, F!, US!).

Robinson described *Mimosa watsonii* from flowering and fruiting material (*Watson 185* and *Watson 323,* respectively); I am here selecting *Watson 323* as lectotype because fruiting material is more distinctive of the species than the flowering specimen.

The species was originally characterized by its leaves with two pairs of pinnae, the lower pinnae bearing one or two pairs of leaflets and the upper ones with two or three pairs; terminal leaflets up to 5 cm long; tetramerous flowers with a four-lobed corolla and eight stamens; and 5 cm by 7–10 mm, articulate, glabrous and finely papillose pods unarmed except for a few scattered, minute, recurved spines on the tomentulose replum.

Mimosa recordii was described by Britton and Rose; *M. rekoana* and *M. resinifera* by Britton. The descriptions of these three taxa were based on flowering material and were published in *North American Flora.*

Standley and Steyermark (1946) included *Mimosa watsonii, M. resinifera,* and *M. recordii* in the *Flora of Guatemala.* The authors considered *M. rekoana* to be a synonym of *M. recordii* and described its legume, which is like that of *M. watsonii.* The amplified description of *M. resinifera* given by Standley and Steyermark also agrees with that of *M. watsonii,* even though the fruit was not described.

I have examined type specimens and additional material from Mexico (states of Guerrero, Oaxaca, Veracruz, Tabasco, and Chiapas), Guatemala, Belize, and Costa Rica. Although the presence of resinous dots on the lower surface of the leaflets was cited as a distinguishing character for *Mimosa resinifera,* these are present in the other three type specimens, as well as in all additional material examined. Other constant leaf characters include the cupular gland at the petiole base, some cylindrical glands along primary and secondary leaf rachides, and the pubescence and reticulate nerves of the leaflets. Great variation has been observed in the number of pinnae and leaflets: from two pairs of pinnae with one to three pairs of leaflets, as *Mimosa watsonii* was originally described, to two or three pinnae with two to five leaflets per pinna, to two to four pinnae with four to seven leaflets, to five or six pinnae with four to nine leaflets. The leaflets also vary from 2.5 to 12 cm in length, and from 1.5 to 6 cm in width. Intermediate combinations are frequent and make it difficult to delimit several taxa.

I have analyzed geographic distribution, altitudinal range, vegetation types where the species grows, and flowering and fruiting times but have not found it possible to delimit subspecific taxa from the accumulated data.

The flowers are arranged in large panicles of white heads and the corolla is four- (rarely 5-)lobed, glabrous, and with few or no resinous dots on the lobes in all types and additional material examined. The fruits are sessile or very slightly stipitate, with five to eleven segments, glabrous, and with resinous dots on the valves on the type specimen of *Mimosa watsonii,* as well as on additional material. Because flower and fruit characters are exactly the same for the four taxa originally described, and there are several constant leaf characters, I consider these four taxa to be a single species, *Mimosa watsonii.*

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TAXONOMIC STUDIES IN FREZIERA (THEACEAE), WITH NOTES ON REPRODUCTIVE BIOLOGY

ANNA L. WEITZMAN[1]

Three new species of *Freziera,* one each from Venezuela (from the Guayana Highland), Colombia, and Ecuador (both from the Andes), are described, illustrated, and compared to related species. The monotypic genus *Patascoya* is reduced to synonymy in *Freziera,* and the appropriate combination is made. Observations of herbarium specimens and natural populations suggest an unequal sex ratio in this dioecious genus, with carpellate plants predominating. This is the reverse of the situation in most tropical forest trees.

Freziera Willd. is a Neotropical genus of trees mostly distributed in cloud forests in northwestern South America. It is easily recognized by its alternate, distichous leaves and its axillary clusters of flowers. Most species grow at high altitudes, close to the upper limit of cloud forests. A few species grow at lower altitudes in moist coastal regions in Colombia, Panama, and Venezuela.

Species of *Freziera* are trees 5 to 15 (to 35) m tall, or rarely shrubs. The leaves of all species are alternate and distichous. Flowers are axillary and solitary or in racemose fascicles of two to seven (to 15). The pedicel of each flower is subtended by a single bract (or by two bractlike structures in some species with exclusively solitary flowers). As in most Theaceae, each flower has two bracteoles; in *Freziera* they are nearly always apical on the pedicel and often appear to be part of the calyx, since they are attached to the floral receptacle and may be quite sepaloid in appearance (FIGURES 1c, 2d). The corolla of all species of *Freziera* is urceolate and thickened above. The thickening is made up of sclereids, although in the field the corolla looks and feels quite waxy. The petals spread only at the tips, and the opening is, as far as I have observed, 1 mm or less in diameter. The stamens and stigma are well within the flowers. The pollen grains of *Freziera* are small, averaging ca. 10 μm in diameter, and copious. The fruits are berries, which are nearly always immature on herbarium specimens. Although carpellate plants usually have everything from buds to large green fruits, I did not find mature fruits (reportedly blue or black) in the field. Seeds from the largest green fruits fail to germinate, implying that they are immature.

Species of *Freziera* occur in cloud and moist coastal forests at elevations up to 3500 m, and the genus is distributed in the West Indies (Cuba, Jamaica, and the Lesser Antilles), southern Mexico, Central America, and much of South

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America (the Guayana Highland, the Venezuelan coastal cordillera, and the Andes south to central Bolivia).

Morphologically, *Freziera* has gynodioecious flowers; however, all species for which there are sufficient data are functionally dioecious. Carpellate plants have flowers with staminodia and a functional gynoecium. The flowers in staminate plants have functional stamens and usually have what appears to be a functional gynoecium but nearly always fall off soon after anthesis. Only three collections of one species (*F. chrysophylla* Bonpl.) have so far been observed to be hermaphroditic. These specimens have flowers with nearly 100 percent viable pollen (tested with cotton blue in lactophenol) on the same branch as fruits. The flowers may be truly hermaphroditic, or the flower type may have changed as the branch matured.

In herbaria there are far more specimens of *Freziera* representing carpellate plants than staminate ones. Of 448 collections of about 29 species, 303 (67.6%) are carpellate, 102 (22.8%) are staminate, and 43 (9.6%) either are sterile or have buds too young for determination if anthers would develop or not. In 86 specimens of *Freziera candicans* Tul., the ratio is 62:20:4 (72.1:23.3:4.6 percent), respectively, and in 49 of *Freziera canescens* Bonpl., 40:5:4 (81.6:10.2:8.2 percent). This unequal sex ratio in collections may be due to collection artifact or to unequal sex ratios in natural populations. I suspect that one reason for the preponderance of carpellate specimens may be that botanists, in trying to collect what appear to be better specimens, select those with buds, flowers, and fruits (i.e., specimens from carpellate plants), rather than ones with only buds and flowers. Since staminate and carpellate flowers are externally identical, many collectors probably do not realize the importance of separate collections of the two sexes.

There may be a truly unequal sex ratio in *Freziera.* It is usually harder to find staminate than carpellate individuals in the field; in some small populations (about eight to ten observed individuals) I was unable to find any staminate plants at all. According to Opler and Bawa (1978, and references therein), dioecy is more common in tropical ecosystems than in temperate ones (see also Bawa, 1980), and dioecious plants often have sex ratios that depart from unity. Forty-four percent of the dioecious tropical forest trees they studied had sex ratios departing significantly from unity: of ten species, eight were biased toward a greater number of staminate individuals, and only two were carpellate-dominant (both were members of the Polygonaceae, a family known for carpellate-dominant sex ratios (Opler & Bawa, 1978)). Lloyd (1973) found that when sex ratios are skewed, perennials tend to show an excess of staminate plants, the reverse of the apparent situation in *Freziera.*

Explanations advanced for carpellate-dominant sex ratios in plants include differential survival rates, differential reproductive maturation, and seral position (Opler & Bawa, 1978). Further field study of *Freziera* is necessary since my observations of individual sex ratios are anecdotal rather than quantitative. If the genus is really carpellate-dominant in natural populations, it is very unusual among tropical trees.

The three new species and one new combination proposed below result from work on a monograph of the entire genus.

Freziera carinata A. Weitzman, sp. nov. FIGURE 1.

A speciebus aliis Frezierae in ramulis alatis, foliis auriculis basalibus demum revolutibus (foliis ut videtur base abrupte attenuatis), et costis petiolis carinatis, differt.

Small tree 2–9 m tall; mature branches terete; twigs dorsoventrally flattened, with narrow paired wings decurrent from base of petiole keel and descending through 2 internodes; bark dark red-brown, papillate when young, striate and splitting with age, glabrous or occasionally very short-strigose-glabrescent; lenticels few, large, very narrowly to widely elliptic, appearing late; terminal bud conduplicate-involute, (2–)4–6.3 cm long, finely strigose. Leaves with petiole (0.1–)0.3–0.6(–1.8) cm long, erectly winged, canaliculate above, keeled below, glabrous; colleter(s) 1 to several in petiole base, linear or triangular, flattened, red to black; blade elliptic or narrowly obovate, (4.1–)9.2–14.8 by (2.1–)2.9–4.9(–6) cm, coriaceous, the base rounded, ciliolate, auriculate, with auricles becoming revolute (base then appearing attenuate), the apex acute, short-acuminate, ultimately retuse, terminating in caducous, thick, conical, black seta, the margin finely serrate, teeth (46 to) 71 to 95 (to 122) per side, with caducous, thick, conical or slightly curved, forward-pointing, black setae inserted in the sinuses (rarely—only in specimens from Cerro de la Neblina—with few thin hairs surrounding base of each seta), the surface glabrous above, densely short-strigose (rarely glabrous) below, with small papillae densely and evenly distributed above and below, and larger ones on midrib in horizontal rows above and scattered below, the midrib flat with small central ridge above, keeled below, the lateral veins (16 or) 17 to 24 (to 31) per side, flat to slightly rounded above, prominently rounded below. Inflorescence axis 0.5–2.5 mm long, with flowers 1 to 5, pedicel scars absent or 1 to 5 and contiguous; floral bract persistent, triangular, 1.1–3.1 by 0.8–1.5 mm, sclerotic, the base clasping, the apex acute to rounded, terminating in thick, conical, black seta, the margin entire, sometimes with several black setae and/or flaps, sometimes ciliolate, the outer surface sparsely to densely sericeous; pedicel erect, cylindrical, 3.1–6 by 0.7–1.1 mm, glabrous to strigose; bracteoles 2, apical on pedicel, subopposite, persistent, sepaloid, seemingly part of calyx, broadly to very broadly ovate, equal or unequal, 1.4–2.4 by 1.5–2.4 mm (lower), 1.8–3 by 1.9–2.9 mm (upper), sclerotic basally and chartaceous above, the base clasping or cordate, the apex rounded, with terminal or subterminal (on outer surface) thick, conical, black seta on lower (or rarely both) bracteole(s), the margin ciliolate, with basal conical, dark setae, the outer surface sparsely strigose or centrally glabrescent. Flowers 4.7–7 by 3.1–4.1 mm; sepals 5, broadly ovate, nearly equal, 2.2–3.8 by 2.1–3.1 mm, sclerotic basally and chartaceous above, the base cordate, the apex rounded and often splitting, the margin membranaceous, minutely ciliolate, with dark or pale basal flaps, the outer surface glabrous to minutely strigose, the inner surface glabrous; corolla urceolate, the petals 5, slightly connate basally, ovate, nearly equal, 3–5.8 by 1.5–2.5 mm, membranaceous in lower ⅓, sclerotic above, apically acute, recurved at anthesis. Staminate flowers with stamens (14 or) 15, uniseriate, free or slightly adnate basally, unequal, unordered, the filaments unequal, flat, linear, ca. 0.9 and ca. 1.4 mm

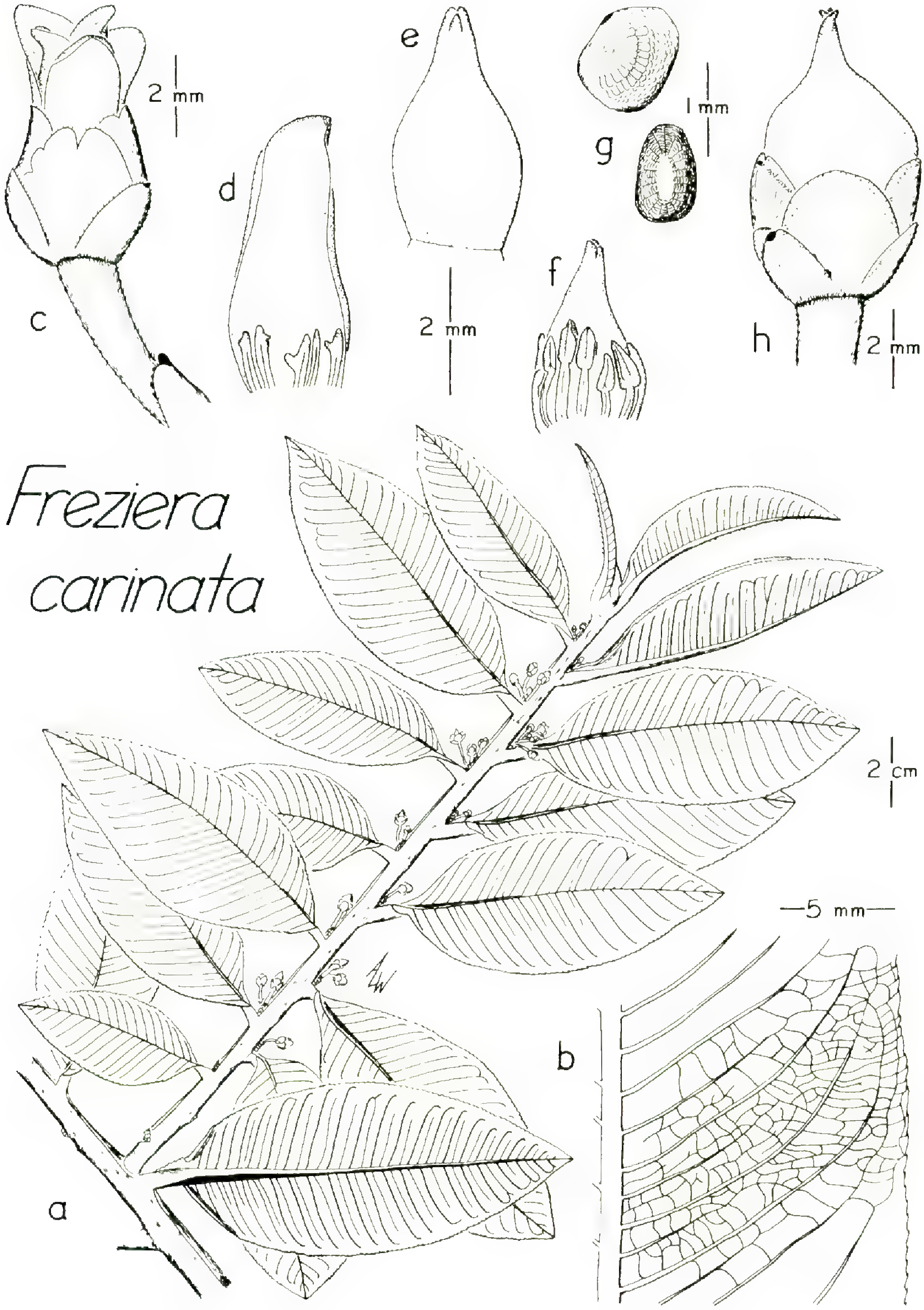

FIGURE 1. *Freziera carinata*: a, habit; b, undersurface of leaf; c, flower; d, petal of carpellate flower, stamens adnate; e, gynoecium of carpellate flower; f, ovary and stamens of staminate flower; g, seeds, side and chalazal views; h, fruit (b, f from holotype; c–e, g, h from *Maguire & Maguire 35334*).

long, the anthers linear, equal, 0.8–0.9 mm long, lightly pigmented, basally cordate, the apiculus ovate, ca. 0.1 mm long, apically rounded; gynoecium conical, 2.4–3.2 by 1.5–1.7 mm, the ovary 3-locular, with locules ca. 1.5 mm long, each containing ca. 12 ovules, the style tapering, the stigmatic lobes 3, erect, 0.25–0.35 mm long, dark, minutely papillate. Carpellate flowers with staminodes 15 (or 16), uniseriate, free, linear, flat and rarely with peripheral flaps, equal or unequal, 0.6–1.6 mm long, apically rounded; gynoecium conical, 3.2–4.9 by 1.7–2.1 mm; the ovary (2- or) 3-locular, with locules 1.3–1.8 mm long, each containing 16 to 30 ovules, the style tapering, the stigmatic lobes (2 or) 3, erect, 0.2–0.3 mm long, dark and minutely papillate. Immature fruits globose, tapering abruptly into persistent style, 6.9–7.7 by 4.9–5.7 mm, green; mature fruits unknown but reportedly blue; immature seeds (6 to) 16 to 29 per locule, reniform, 1.2–1.4 mm long, dark red, the testa reticulate.

Type. Venezuela, Edo. Bolívar, Auyan-tepuí, cumbre de la parte central occidental (división occidental del cerro), vecindad del "Drizzly Camp," sobre piedra de arenisca, a lo largo de afluente del Río Churún, 1760 m, 4 May 1964, *J. Steyermark 93366* (bud, ♂ fl[2]—holotype, GH; isotypes, NY, U (n.v.), US, VEN).

Additional specimens examined. **Venezuela.** Terr. Fed. Amazonas: Serranía Yutajé, Cerro Yutajé, Río Manapiare, 2100 m, *Maguire & Maguire 35334* (♀ fl, fr; NY (3 sheets)); Cerro de la Neblina, Río Yatúa, NW head of Cañón Grande, 2000 m, *Maguire et al. 42322* (young fr; NY); Cerro de la Neblina, limite Venezuela-Brasil, altíplano, 1800–2000 m, *Ewel 177* (bud, young fr; MY, NY); Cerro de la Neblina, Camp VII, 5.1 km NE of Pico Phelps, 1730–1850 m, *Nee 30641* (mixed coll., bud, ♂ & ♀ fl, fr; liquid-preserved material GH, duplicates yet to be distributed); Dpto. Atabapo, below Salto Los Monos on tributary of headwaters of Río Iguapo, 3°35′N, 65°23′W, 1500–1600 m, *Liesner 18515* (bud, fruit; GH); Dpto. Atabapo, gallery forest and open area on Plateau of Huachamacari, 3°50′N, 65°25′W, 1720 m, *Liesner 18073* (bud; GH). Edo. Bolívar: Disto. Cedeño, Serranía Guanay, sector NW, en las cabeceras mas orientales del Río Paraguaza, 5°55′N, 66°23′W, ca. 1700 m, *Huber 11003* (♀ bud, fl, fr; NY); Meseta de Jaua, Cerro Sarisariñama, cumbre, porción NE, interior de la Sima Mayor, 4°41′N, 64°13′W, 700 m, *Brewer-Carías s.n.* (♂ bud; VEN); Cerro Guaiquinima, cumbre, sector NE, cerca del borde, cabeceras de brazo NE del Río Carapo, 5°59′N, 63°25′W, 1490–1500 m, *Steyermark et al. 117329* (♂ bud; MO, NY, U, VEN); Auyan-tepuí, no further locality or date, *Pannier & Schwabe s.n.* (♀ bud, young fr; VEN); Auyan-tepuí, Valle Encanto, lado derecho del Salto Angel, *Foldats 7135* (bud; VEN); Auyan-tepuí, plateau, central E section of NW arm, 5°56′N, 62°34′W, 1850 m, *Prance & Huber 28302* (bud, ♀ fl, fr; GH); Chimantá Massif, SE-facing upper shoulder of Apácara-tepuí, below summit, 2000–2100 m, *Steyermark 75782* (♀ bud, fr; MO, NY, VEN (2 sheets)); Chimantá Massif, central section, along W branch of headwaters of Río Tirica above upper falls, 2090 m, *Steyermark & Wurdack 880* (bud; F, VEN (2 sheets)); Chimantá Massif, altiplanicie en los farallones superiores de Apacará-tepuí, sector N del Macizo, 5°12′N, 62°12′ W, ca. 2200 m, *Steyermark et al. 128337* (fr; GH, MO (2 sheets), VEN); Chimantá Massif, sector SE, amplia altiplanicie en la sección NE del Acopán-tepuí, en las cabeceras del Río Yunek, 5°12′N, 62°5′W, 1950 m, *Huber et al. 10118* (bud, ♂ fl; NY); Ptari-tepuí, along base of E-facing high sandstone bluffs, 2410–2450 m, *Steyermark 59937* (bud; A, F); Cerro Venamo (parte SW), cerca de los límites con la Guayana Inglesa, a lo largo del afluente W subiendo el Río Venamo, 950–1150 m, *Steyermark et al. 92345* (bud, ♀ fl, fr; GH, K, US, VEN); Cerro Roraima, no further locality, 2000 m, *Ule 8726* (bud, ♀ fl; K); Cerro Roraima, forested SW-facing quebrada

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[2] In the specimen citations below, I state flowering condition and sex for the flower stage observed; if no sex is indicated, floral material was insufficient for examination.

near Rondón Camp, 2040–2130 m, *Steyermark 58697* (bud, ♀ fl, young fr; A, F); Cerro Roraima, trail through cloud forest to summit, 5°12′N, 60°40′W, 2280–2600 m, *Luteyn & Aymard 9767* (bud, ♀ fl, fr; GH, NY, U, VEN), *9772* (CAS, GH, NY, VEN).

Freziera carinata is characterized by its winged stems and its prominently keeled petioles and midribs. The leaf blades are auriculate, but the auricles become revolute very early and the blades then appear attenuate. Specimens of *F. carinata* are unusual: the young growth of most other species dries dark or light brown or rarely green, while that of *F. carinata* usually dries orange-brown with paler orange spots. Like most species of *Freziera* for which phenology is known, *F. carinata* flowers throughout the year.

Kobuski (1941), who recognized only one species from the Guayana Highland, apparently did not see any specimens of *Freziera carinata* for his monograph of the genus. However, despite having seen only a photo and a leaf fragment of the type of *F. roraimensis* Tul. and no material of *F. guianensis* Klotzsch ex Wawra, he correctly placed the latter in synonymy under *F. roraimensis,* stating (p. 490), "*F. roraimensis* and *F. guianensis* were collected at the same locality by the same collector. There is no doubt in my mind that only one good species exists in this locality. . . ." Although the name *Freziera roraimensis* has been used by Kobuski and subsequent workers in all determinations of Guayana Highland material, that species has not been re-collected since Schomburgk found it in November 1842 in the vicinity of Mt. Roraima. All other known material from the Guayana Highland belongs to *F. carinata. Freziera carinata* has been collected on most of the larger tepuis so far visited except Duida. The two species now recognized from the Guayana Highland region can be distinguished by use of the following key:

Twigs flattened; midribs and petioles strongly keeled; twigs and leaves glabrous to minutely strigose; leaf blades elliptic or narrowly obovate, (4.1–)9.2–14.8 by (2.1–)2.9–4.9(–6) cm; flowers 4.7–7 by 3.1–4.1 mm. .... *F. carinata.*

Twigs terete; midribs and petioles rounded; twigs and leaves densely long-sericeous and short-villous, leaf blades narrowly elliptic, 8.1–9.7 by 2.6–3.6 cm; flowers 4.4–5 by 2.4–2.7 mm. .... *F. roraimensis.*

Freziera echinata A. Weitzman, sp. nov. FIGURE 2.

A speciebus aliis Frezierae in ramulis et foliis utrinque pilis erectis densis longis persistentibus praeditis, setis erectis pilis erectis cingentibus in marginibus foliis instructis, et bracteolis sepalisque dense longe sericeis extus paginis totis et intus versus apices acutes, differt.

Tree ca. 5 m tall; mature branches and twigs terete, dark red-brown, papillate, conspicuously ridged below each side of leaf base, finely striate elsewhere, very densely golden-hirsute, the hairs persistent, erect, of 2 lengths (ca. 3 and 0.5 mm), the lenticels ovate, 0.4–0.6 mm across, splitting vertically; terminal bud conduplicate-involute, 4–6 cm long, erect-hirsute. Leaves with petiole 2–3 mm long, erectly winged, canaliculate, hirsute above and below; blade narrowly ovate, 10.4–12.3 by 2.6–3.5 cm, subcoriaceous, the base unequal with sides asymmetric, truncate or rounded on long side, cuneate to truncate and revolute on short side, the apex long-acute, terminating in caducous, thick, conical,

FIGURE 2. *Freziera echinata*: a, habit; b, leaf undersurface (hairs omitted); c, leaf margin; d, flower; e, inside of outer sepal; f, stamens; g, style and stigma (from type).

black seta, the margin entire, slightly revolute, with numerous erect, articulated, conical, black setae ringed by longer erect hairs, the upper surface sparsely hirsute (densely so on midrib) and densely papillate, with hairs persistent, erect, up to 3 mm long, the lower surface densely hirsute, the midrib sunken above, prominently rounded below, the lateral veins 11 to 13 per side, inconspicuous, slightly sunken above, prominently rounded below. Inflorescence axis less than 1 mm long, with 3 to 5 flowers; floral bract persistent, ovate, 6.2–9.3 by 2.1–3.3 mm, sclerotic, keeled, the base clasping, the apex acute, terminating in thick, conical, black seta, the margins entire, the surface densely long-tomentose; pedicel erect, angled, ca. 1 by 1 mm, densely long-tomentose; bracteoles 2, persistent, sepaloid, ovate, nearly equal, 5–6.4 by 2.6–3.3 mm, sclerotic, the base clasping, the apex acute, the surface densely tomentose outside, tomentose near upper margin inside. Staminate flowers 8.5–9.6 by 5–5.5 mm; sepals 5, ovate, unequal, 6–6.8 by ca. 2.9 mm (outer), 4–5.6 by 2–2.7 mm (inner), sclerotic, the base clasping, sometimes with dark lobes or few dark basal setae, the apex acute, the margin ciliolate, the surface densely tomentose outside, tomentose on upper ⅓ (outer sepals) or glabrous (inner ones) inside; corolla urceolate, white, the petals 5, distinct, narrowly ovate, unequal, 6–7.7 by 2.2–2.5 mm (outer), 5.5–6 by 1.6–1.7 mm (inner), membranaceous in lower ¼–⅓, sclerotic above, apically acuminate; stamens 15, uniseriate, free or slightly adnate at very base, the filaments unequal, geniculate or linear, 1.1–2.2 mm long, flattened at base, cylindrical above, the anthers 1.1–1.2 mm long, connective pigmented, the apiculus 0.05–0.13 mm long, apically rounded and with terminal seta; gynoecium narrowly conical, 3.8–4.9 by ca. 1 mm, the ovary 3-locular, with locules ca. 1.1 mm long, each containing ca. 60 ovules, the style 1.8–2.1 mm long, the stigmatic lobes 3, erect, 0.4–0.7 mm long, dark, minutely papillate. Carpellate flowers and fruits unknown.

TYPE. Colombia, Dpto. Cauca, Parque Nacional Munchique, km 50–55 along road above Uribe, 2256–1875 m, 25 April 1979, *J. L. Luteyn, M. Lebrón-Luteyn, & G. Morales L. 7448* (bud, ♂ fl—holotype, NY; isotypes, AAU, CAS, COL (n.v.), GH, MO).

Freziera echinata is characterized by long, narrow leaf blades; long, erect, persistent hairs on both leaf surfaces and on the stems; and erect setae surrounded by erect hairs on the leaf margins. The flowers have densely long-sericeous bracts, bracteoles, and sepals that are conspicuously pointed at the apex. The bracteoles and outer sepals are sericeous inside, a condition unknown elsewhere in the genus. The hairs are so dense that the floral parts cannot easily be distinguished from each other. I have not seen a flower past anthesis, but the most developed buds have extremely long, narrow corollas and petals. Some floral characters are only partly known since the few flowers observed have all been at least partially eaten wherever the sclereids in the tissues are not dense, so the stamens, the base of the petals, and the ovary are usually gone.

This species, known only from the type collection, cannot be confused with any other. No other taxon has this erect pubescence on the twigs and leaves, or the extremely dense, long indumentum on the flowers. *Freziera chrysophylla,* which has similarly shaped leaves, differs from *F. echinata* in having leaves glabrous above and densely golden sericeous below, and pedicellate flowers with round, sericeous bracteoles and sepals. *Freziera tomentosa* Ruiz & Pavón, which like *F. echinata* has sessile flowers, is actually more similar to *F. chrysophylla,* with leaf blades glabrous above and densely sericeous below, but has leaf blades wider than *F. echinata* or *F. chrysophylla* and rounded, glabrous bracteoles and sepals.

Freziera minima A. Weitzman, sp. nov. FIGURE 3a–i.

A speciebus aliis Frezierae praeter F. stuebelii (Hieron.) A. Weitzman in habitus fruticoso foliis minutis crenatis, et a F. stuebelii in foliis reticulato-venosis differt.

Compact shrub 1 m tall; mature branches terete, brown, the bark conspicuously striate, splitting vertically; twigs square, slightly winged, persistently brown-sericeous, the lenticels large, round, 1–1.7 mm in diameter on older branches, splitting horizontally and vertically; terminal bud merely conduplicate, 1.5–4 mm long, short-sericeous. Leaves with petiole 0.9–3.1 mm long, with narrow, involute wings, canaliculate, sericeous above and below; blade broadly ovate, 7–12.1 by 4.9–10.6 mm, subcoriaceous, the base equal to subequal, obtuse, truncate, round, or slightly cordate, the apex acute or obtuse, ultimately retuse, terminating in caducous, thick, conical, red to black seta, the margin crenate, with teeth 9 to 16 per side, and caducous, thick, conical, short, black setae inserted in the sinuses, the surfaces glabrous, but with few caducous, short, sericeous hairs on midrib above and below, the midrib flat to prominent above, prominently rounded below, the lateral veins 5 to 7 per side, prominently rounded above and below. Flowers solitary, subtended by 2 bractlike structures, these basal on pedicel, persistent, narrowly ovate, 1.5–2.5 by 0.7–0.8 mm, sclerotic, keeled, the base clasping, the apex acute, terminating in thick, conical, black seta, the margin entire, with erect, thick, conical, black setae, the outer surface sparsely short-sericeous; pedicel erect in bud and fruit, recurved at anthesis, cylindrical, 2–2.9 by 0.7–1 mm, ridged, strigose, bracteoles 2, apical on pedicel, opposite, persistent, broadly ovate, unequal, 2.5–2.8 by 1.9–2.5 mm (larger), 2–2.1 by 1.6–1.8 mm (smaller), smaller one sometimes keeled, the base rounded, the apex obtuse to rounded, on smaller bracteole always and on larger one sometimes terminating in conical, black seta, the margin membranaceous, with caducous cilia, the outer surface sparsely strigose-glabrescent centrally. Flowers 6.7–7.7 by 3.4–4.1 mm; sepals 5, broadly ovate, nearly equal, 3–3.6 by 2.5–3.3 mm (outer), 2.9–3.3 by 2.5–3 mm (inner), sclerotic basally and chartaceous above, the base broadly cordate, the apex rounded, the margin membranaceous, with caducous cilia and dark basal setae (outer sepals) or pale basal flaps (inner sepals), the surfaces glabrous; corolla urceolate, the petals 5, distinct or slightly connate basally, ovate, nearly equal, 5.3–6.4 by 2.1–3.4 mm, membranaceous in lower ¼–⅓, sclerotic above, the apex obtuse, recurved at anthesis. Staminate flowers with stamens 18, uniseriate, slightly adnate basally, unequal, unordered, filaments flat; long stamens with the filaments linear, ca. 1.8 mm long, the anthers ovate, ca. 1.1 by 0.8 mm, the apiculus ovate, 0.1 mm long, apically rounded; short stamens with the filaments linear or geniculate, 0.9–1.1 mm long, the anthers ovate, 0.7–1 mm long, basally cordate, the apiculus ovate, 0.1–0.2 mm long, apically rounded; gynoecium narrowly conical, the ovary 3-locular, ca. 1.1 by 1.5 mm, with ovules ca. 7 per locule on 2 pendulous axile placentae, the style abruptly tapering to linear, ca. 2.2 mm long, the stigmatic lobes 3, erect, ca. 0.25 mm long, the stigmatic surface adaxial, dark, minutely papillate. Carpellate flowers with

FIGURE 3. a–i, *Freziera minima*: a, habit, from below; b, shoot apex; c, undersurface of leaf; d, flower; e, petal of staminate flower, stamens adnate; f, gynoecium of staminate flower; g, gynoecium and staminodia of carpellate flower; h, seed; i, fruit (a–e from type, g–i from *Holm-Nielsen et al. 3906*). j, *Freziera stuebelii*, undersurface of leaf (from photo of type).

staminodes 18, uniseriate, free (1 adnate to inner petal), linear, flat, equal, ca. 1.5 mm long, apically rounded; gynoecium conical, the ovary 3-locular, ca. 1.3 by 1.7 mm, with ovules 8 to 14 per locule, the style ca. 1.9 mm long, the stigmatic lobes 3, slightly flaring, ca. 0.9 mm long, dark, conspicuously papillate. Fruits ovoid, 6.8–7.5 by 5.1–5.5 mm, with narrow dark band just below stigmas, 2- or 3-locular, locules splitting out of fruit separately as mericarps; seeds 2 to 8 per locule, irregularly rounded, ca. 1.6 mm long, dark brown.

TYPE. Ecuador, Prov. Loja, Zamora-Chinchipe border, crest of E cordillera, ca. 13 km E of Loja, cloud forest and stunted crest vegetation, ca. 3°58′S, 79°10′W, 2840 m, 28 Jan. 1985, *J. L. Luteyn & E. Cotton 11288* (bud, ♂ fl—holotype, NY; isotypes, AAU, CAS, GH, MO, QCA (n.v.), U).

ADDITIONAL SPECIMEN EXAMINED. **Ecuador,** PROV. ZAMORA-CHINCHIPE, road Loja-Zamora, km 14, mountain ridges with elfin forest and open bogs, 4°S, 79°09′W, 2750–2770 m, 19–20 April 1973, *Holm-Nielsen et al. 3906* (bud, ♀ fl, fr; AAU).

Freziera minima is characterized by minute, broadly ovate, crenate leaf blades. In appearance the foliage does not resemble that of any previously known *Freziera.* Other species with leaves nearly as small are *F. microphylla* Sandw. (11.5–27.5 by 7.4–14.9 mm) and *F. suberosa* Tul. (10.7–18.6 by 7.5–10.4 mm), both of which are densely sericeous on the twigs and leaf undersurfaces and have revolute and therefore apparently entire leaf margins, quite unlike *F. minima.* Other species such as *F. euryoides* Kobuski and *F. parva* Kobuski, which have relatively small leaves and are sparsely pubescent (like *F. minima*), have leaves two to five times longer than those of *F. minima. Freziera minima* may also be closely related to the following species (see below).

Freziera stuebelii (Hieron.) A. Weitzman, comb. nov. FIGURE 3j.

Taonabo stuebelii Hieron. Bot. Jahrb. Syst. **21:** 320. 1896. TYPE: Colombia, Cerro Patascoy, 3300 m, *Stübel Colomb. 366* (holotype, B, destroyed; photos at GH, MO, negative at F (no. 9738)).

Patascoya stuebelii (Hieron.) Urban, Ber. Deutsch. Bot. Ges. **14:** 283. 1896.

Ternstroemia stuebelii (Hieron.) Kobuski, J. Arnold Arbor. **23:** 343. 1942, as *steubelii,* nomen illegit.

Freziera stuebelii was collected only by Stübel at Cerro Patascoy, Colombia. It is known only from a photograph of the holotype, which was destroyed at Berlin (no isotypes are known). Urban (1896) mentioned the likely relationship of *Patascoya* Urban to *Freziera* because they both have distichous leaves, pubescence, and relatively few stamens. The photograph of the type suggests similarity in habit, at least, to *Freziera,* and the leaves are similar to those of *F. minima,* both having very broadly ovate, crenate blades about 1 cm long and wide. Although no flowers or fruits are visible in the photograph, according to the descriptions provided by Hieronymus (1896), Urban (1896), and Melchior (1925), the flowers agree in all characters with those of *Freziera.*

When placing this species in its own genus, Urban (1896) heavily emphasized the two bractlike structures at the base of the pedicel and the position of the ovules. In both *Freziera minima* and *F. stuebelii* the solitary flowers are subtended by two bractlike structures; these are morphologically similar to the single bracts that subtend each flower in an inflorescence of other species of *Freziera.* The fact that there are two such structures in these species is not surprising since they are the equivalent of bud scales and since branches in

Freziera usually are just an extension of the inflorescence axis. In describing *Taonabo stuebelii,* Hieronymus (1896), following Szyszylowicz's (1893) keys to the Theaceae, placed the species in *Taonabo* Aublet (= *Ternstroemia* Mutis ex L.f.) because that genus has pendulous ovules with apical placentation and *Freziera* has exclusively axile placentation. I have observed pendulous placentae and ovules in several species of *Freziera.* For example, in functionally staminate flowers of *F. minima,* there are ca. seven ovules per locule that hang from two pendulous axile placentae, which may appear apical.

Compared to *Freziera minima, F. stuebelii* has leaves that are broader and more cordate at the base, with the lateral veins apparently sunken above, very prominent below, and bifurcate instead of reticulate (compare FIGURE 3c and j). Bifurcate venation is unknown in other species of *Freziera.* All other aspects of leaf morphology are apparently similar to those of *F. minima* and are present elsewhere in the genus. In all species of *Freziera* most small veins that go to the margin end in a seta, as they do in *F. stuebelii,* although in the other species the veins are reticulate.

The relatively slight differences between *Freziera* and *Patascoya* discussed above do not warrant generic status for *Patascoya.* Based on the evidence at hand, I believe that *F. stuebelii* belongs to *Freziera* and is most closely related to *F. minima.*

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STATUS OF THE NAME AESCULUS FLAVA SOLANDER (HIPPOCASTANACEAE)

FREDERICK G. MEYER[1] AND JAMES W. HARDIN[2]

The name for the yellow buckeye, *Aesculus octandra* Marshall (1785), has been in general use since publication of Robinson and Fernald's seventh edition of *Gray's New Manual of Botany* (1908). Earlier, the name *A. flava* Aiton (1789) had been in general use for this tree of the southern Appalachian Mountains of the eastern United States. More recently, it has been shown that the name *A. flava* Sol. was effectively published in 1778 and has priority as the oldest valid name for this well-known tree.

The yellow buckeye of the eastern United States, a well-known tree and a characteristic component of the mixed mesophytic forests of the southern Appalachians (Hardin, 1957), has been known as either *Aesculus flava* Aiton or *A. octandra* Marshall for nearly two centuries. Aiton's *A. flava* (1789) was used fairly consistently until publication of Robinson and Fernald's seventh edition of *Gray's New Manual of Botany* (1908), when *A. octandra* Marshall (1785) was accepted as the earlier valid name because of its priority of four years over *A. flava* Aiton. Since that time, Marshall's name has been universally accepted for this North American tree as the earliest valid epithet (Hardin, 1957). More recently, a note published in Bean's *Trees and Shrubs Hardy in the British Isles* (1970) explained that the name *A. flava,* as pointed out by B. L. Burtt, of the Royal Botanic Garden, Edinburgh, was originally published by Daniel Solander in *Catalogus Arborum et Fruticum in Horto Edinensi Crescentium* (Anonymous, 1778). Solander's name precedes *A. octandra* Marshall by seven years, and Aiton's *A. flava* by eleven. Our aim is both to include additional details to confirm Burtt's observations that *A. flava* Sol. is the older and correct name, and to alert botanists, foresters, and others who might easily have overlooked the horticultural reference in Bean (1970).

With respect to the name *Aesculus flava* Aiton, it is well known that Aiton's *Hortus Kewensis* (1789) was in preparation for some twenty years; the text was written largely by Jonas Dryander, who had succeeded Daniel Solander as librarian for Sir Joseph Banks after Solander died in 1782. Also, Dryander is known to have used manuscript material written earlier by Solander in preparing the descriptions for *Hortus Kewensis,* but without reference to the source of the information. Dryander may indeed have consulted Solander's original manuscript notes, but the wording in Aiton (1789, p. 494) on *A. flava* was

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altered: *Ae. foliolis quinis, corollae laminis cordato-subrotundis; unquibus calyce duplo longioribus.* (Compare FIGURE 1 and the description of *A. flava* below.)

The catalogue with the name *Aesculus flava* Sol. published at Edinburgh anonymously in 1778 was (*fide* Morton, 1986) issued under the direction of Dr. John Hope (1725–1786), at that time Regius Keeper of the Edinburgh Botanic Garden; however, no author's or editor's name appears on the title page of that publication. In the Edinburgh *Catalogus* five new species in the genera *Aesculus* L. (one), *Andromeda* L. (one), *Cornus* L. (two), and *Crataegus* L. (one) can be clearly attributed to Solander as the publishing author (Burtt *in* Morton, 1986). Of these, only *Aesculus flava* has been adequately typified. Following a brief Latin diagnosis for each of the names, we find the identifying letter "S" standing for Solander, the publishing author, as explained at the end of the catalogue.

In the recent edition of his *Checklist of United States Trees (Native and Naturalized)* (1979), Elbert Little rejected *Aesculus flava* Sol. with the argument (pers. comm. to Hardin, September, 1979) that the name had no publishing author. On the other hand, *Index Kewensis* (Suppl. XV, 1974) listed the name *A. flava* Sol. ex [Hope]. However, it is clear that the name *flava* was effectively and validly published in 1778 in the Edinburgh *Catalogus,* which was published anonymously, and that Solander, not Hope, was the author of the name. The name *A. flava* Sol., listed by Bean (1970), Spongberg (1975), and Kartesz and Kartesz (1980), is correct as cited, although the full bibliographic citation should be *A. flava* Sol. *in* Anonymous, Cat. Arb. Frut. Horto Edin. Cresc. 1778, 3. 1778.

HISTORICAL BACKGROUND

Matters relating to the history and typification of the name *Aesculus flava* are of concern because we have only Solander's original manuscript notes and the brief description published in the Edinburgh *Catalogus.* We are without a clue as to the source of the material seen by Solander, except that it was cultivated and growing in England. Specimens of wild material were not available to him. What was the source of the original North American material? Was it really the tree we know as yellow buckeye, or another species? There are no definitive answers for these questions. Original herbarium voucher specimens of this tree from the wild collected in this period have not been located and probably do not exist. We do know that in Solander's time material of this species was already growing in private gardens in England, and that it was offered by at least one nursery in the London area in 1774.

Aiton (1789) reported that *Aesculus flava* was in cultivation by Mr. John Greening (d. 1770) in 1764, the earliest recorded date of introduction, and that it was from North Carolina. We also have evidence that yellow buckeye was in cultivation in the Vineyard Nursery of Messrs. Lewis Kennedy and James Lee at Hammersmith, London. In their *Catalogue of Plants and Seeds,* issued in 1774, the third entry under *Aesculus* (p. 3) is "β *Flo. flavo,* Yellow Horse Chestnut." This clearly confirms that Lee was indeed growing the yellow buckeye (*A. flava*) in his nursery in 1774. It is possible that Solander, a friend of

James Lee, saw flowering specimens of *A. flava* growing in Kennedy and Lee's Vineyard Nursery at Hammersmith.

James Lee (1715–1795), nurseryman, author, and correspondent, although not a well-known figure in botanical circles, made noteworthy contributions both to horticulture and to botany (Willson, 1961).

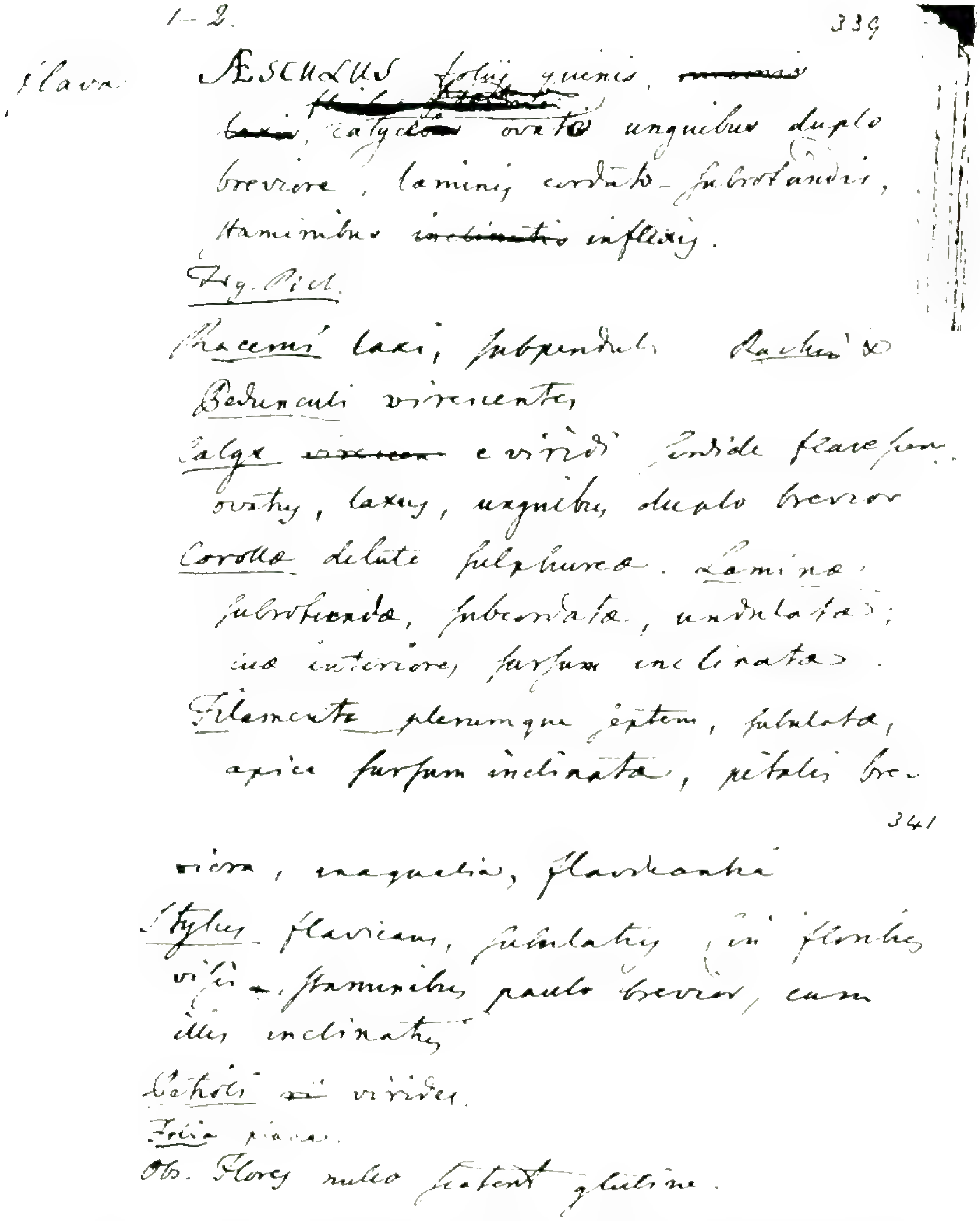
In his early years after coming to London, Lee was employed as a gardener first at Syon, near Kew, and later, by the Duke of Argyle, at Whitton, near Hounslow. About 1745 James Lee entered into a partnership with Lewis Kennedy (1721–1782) in a nursery called "The Vineyard" at Hammersmith, now the site of Olympia, the great London exhibition hall. Lee devoted the remainder of his life to his nursery and to introducing rare plants from different parts of the world. In the preface to *Hortus Kewensis*, Aiton (1789) mentioned that Lee had supplied a list of plants introduced by the Duke of Argyle at Whitton. At that time the Vineyard Nursery maintained a collector in America, one at the Cape of Good Hope, and another in South America (Loudon, 1838). The genus *Leea* Royen ex L. of the Vitaceae was named in honor of James Lee.

INTRODUCTION OF AESCULUS FLAVA FROM NORTH AMERICA

While we are unable to pinpoint the original source of *Aesculus flava* in British gardens, we know that seeds of North American plants were regularly being sent to England from about 1735 onward. John Bartram (1699–1777), of Philadelphia, sent no less than 145 shipments of seeds and plants to correspondents in England between 1735 and 1769 (Berkeley & Berkeley, 1982). Bartram also sent many shipments of plants to his English Quaker friend, Peter Collinson, of Mill Hill, near London, who in turn distributed much material to his horticultural friends and to Daniel Solander, the botanist, for identification (Earnest, 1940; Darlington, 1967).

John Bartram (Earnest, 1940; Darlington, 1967; Berkeley & Berkeley, 1982) visited Pittsburgh in the fall of 1761 and met Col. Henry Bouquet from Ohio, receiving from him plant material from the Ohio River valley. Yellow buckeye (*Aesculus flava*) and Ohio buckeye (*A. glabra* Willd.) could have been included in this material. In the fall of 1762, Bartram was on an extended trip to the interior of South Carolina (Wateree and Congaree rivers), to western North Carolina, and to southwestern Virginia (Yadkin and New rivers, Natural Bridge, Luray Caverns, Staunton, and the Shenandoah Valley). On this excursion he collected fruits of three different "horse chestnuts" from southwestern Virginia that were later identified by Solander as *A. hippocastanum* L., *A. pavia* L., and *A. media,* the last "not taken notice of by Dr. Linnaeus" (Berkeley & Berkeley, 1982, p. 349). The one called *A. hippocastanum* was undoubtedly *A. glabra,* which is interesting because *A. glabra* is unknown in that area today, so far as we know. Those called *A. pavia* and *A. media,* initially identified without flowers, were probably variations of *A. flava,* which could have been named by Solander after flowering material was available in England.

Another possible source of yellow-buckeye material from the North Carolina mountains was W. V. Turner, an Indian agent who sent plants to Sir Joseph Banks (Joseph Ewan, pers. comm. to F. G. Meyer, September, 1980).



1–2. 339

flava ÆSCULUS foliis quinis, ~~[illegible]~~ ~~laxis~~, calycibus ovatis unguibus duplo breviore, laminis cordato-ſubrotundis, ſtaminibus ~~inclinatis~~ inflexis.

Fig. Pict.

Racemi laxi, ſubpenduli. Rachis et Pedunculi virescentes.

Calyx ~~[illegible]~~ e viridi ſordide flaveſcens. ovatus, laxus, unguibus duplo brevior

Corolla dilute ſulphurea. Laminae ſubrotunda, ſubcordata, undulatae; duo interiores ſurſum inclinatae.

Filamenta plerumque ſeptem, ſubulata, apice ſurſum inclinata, petalis bre-

341

viora, inaequalia, flaveſcentia

Stylus flavicans, ſubulatus, (in floribus virginis) ſtaminibus paulo brevior, cum illis inclinatus.

Petioli [illegible] virides.

Folia quina.

Obs. Flores nullo ſcatent glutine.

FIGURE 1. Solander's original manuscript slips describing *Aesculus flava*.

TYPIFICATION OF *AESCULUS FLAVA*

A copy of Solander's original manuscript slips (nos. 339–341) with a description of *Aesculus flava* was kindly supplied by the librarian of the Department of Botany at the British Museum (Natural History). Thus, for purposes of typification, it has been possible to use Solander's original description and to publish more than 200 years later his complete manuscript notes for the first time (see FIGURE 1). This is important, since the brief protologus of *A. flava* published in the Edinburgh *Catalogus* included only the first four lines

FIGURE 2. Neotype of *Aesculus flava* Sol.

from Solander's original manuscript (our translation of Solander's protologue: "calyx ovate, half the length of the upper petal claws, blade cordate-subrotund, stamens curved") and therefore was incomplete and is inadequate for typification. These details allow a positive identification only of a buckeye—*A. flava* or *A. sylvatica* Bartram. In his complete text, however, Solander describes the yellow flowers, the relative length of calyx and upper petal claws, the extremely dimorphic petals, and the included stamens of *A. flava/sylvatica,* details that are adequate for typification. In addition, these characters definitely eliminate *A. pavia* and *A. glabra* from consideration. *Aesculus glabra* was described by Willdenow in 1809. The differences between *A. flava* and *A. sylvatica* are mainly in habit (tree vs. shrub) and in rather subtle features of pubescence and size of floral parts (Hardin, 1957).

Marshall's (1785) description of *Aesculus octandra* was only slightly more diagnostic, for he did indicate that it was a tree. His common name "New River horse chestnut" would most likely have come from John Bartram (E. Berkeley, pers. comm. to J. Hardin, February, 1982), in reference to the material brought back from his trip of 1762 to the New River in southwestern Virginia.

Unfortunately, there is no specimen of *Aesculus flava* that was collected or annotated by Solander. The earliest possibly appropriate material in the British Museum (Natural History) was collected by James Lee at the Vineyard Nursery of Messrs. Kennedy and Lee and has the number "74" (interpreted as 1774) on the herbarium label. This specimen (see FIGURE 2), although somewhat damaged after more than two centuries, contains several leaves and a short portion of a poorly preserved inflorescence with a few flowers. We consider it to be authentic *A. flava* Sol. The leaflets are somewhat narrower than normal, but well within the range of variation of the species. There are a few poorly preserved stipitate glands at the base of the calyx, which definitely identify the specimen as *A. flava* rather than *A. sylvatica.* There is no evidence of *A. sylvatica* in England prior to William Bartram's discovery and description of 1791. Bean (1970) indicates its cultivation (probably as *A. neglecta* Lindley) in Europe in 1826.

We hereby designate the James Lee specimen (BM), the earliest known documented material, as the neotype of *Aesculus flava* Sol.

DESCRIPTION OF *AESCULUS FLAVA* SOLANDER

Aesculus flava Sol. *in* Anonymous, Cat. Arb. Frut. Horto Edin. Cresc. 1778, 3. 1778. NEOTYPE: ex hort. Lee, [17]74 (BM).

Aesculus octandra Marshall, Arbust. Am. 4. 1785. TYPE: not seen.
Aesculus lutea Wangenh. Schriften Ges. Naturf. Freunde Berlin **8**: 135. 1788. TYPE: not seen.
Additional synonymy is given in Hardin (1957).

Translation of Solander's holographic description of *Aesculus flava* (FIGURE 1):

flava AESCULUS leaflets five; calyx ovate, half the length of the upper petal claws; blade cordate-subrotund; stamens incurved.
Raceme lax, subpendulous. *Rachis* and *peduncles* green.
Calyx [turning] from green to dull yellowish, ovate, open, half the length of the upper petal claws.
Corolla pale sulphur yellow. *Blade* subrotund, subcordate, undulate; the two inner ones inclined upward.
Filaments generally seven, subulate, apices inclined upward, shorter than the petals, unequal, turning yellow.
Style yellow, subulate (in flowers seen, little shorter than the stamens, with those inclined).
Petioles green.
Leaves flat.
Observation. Flowers without copious secretion.

ACKNOWLEDGMENTS

We are indebted to the Keeper and the Librarian of the Department of Botany, British Museum (Natural History) for providing critical materials, including a historic specimen and a copy of Daniel Solander's manuscript notes, which together were invaluable in the typification of *Aesculus flava* Sol. We also wish to thank Joseph Ewan and Edmund Berkeley for their interest and diligence in helping to solidify some of the historical aspects of our paper. Finally, we would like to thank B. L. Burtt, T. R. Dudley, Elizabeth McClintock, R. C. Rollins, E. E. Terrell, and R. M. Tryon for their kindness in critically reading our manuscript.

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A NEW SPECIES OF LANTANA (VERBENACEAE) FROM DOMINICA, LESSER ANTILLES

Roger W. Sanders[1]

Lantana hodgei Sanders is described from Dominica and is contrasted with *L. camara* L. and *L. urticifolia* Miller on the basis of gross morphology, scanning electron microscopy of laminar surfaces, and pollen stainability.

Studies of *Lantana* L. (Verbenaceae) for the *Flora of the Lesser Antilles,* edited by Richard A. Howard, reveal the existence of an undescribed species from the montane forests of the island of Dominica.

Lantana hodgei R. Sanders, sp. nov. Figure 1.

Differt a Lantana camara L. habitu subscandenti, trichomatibus caulium foliorumque brevioribus sparsioribus validius appressis, petiolis longioribus, laminis angustioribus circa duplo longioribus quam latioribus supra subtusque nitentibus subtus subviridi-griseis, nervis secundariis nervellisque laminarum subtus non elevatis; a L. urticifolia Miller trichomatibus laminarum remotis non nisi nervis mediis secundariis tertiariisque insidentibus angustate conicis antrorse geniculatis.

Subscandent shrub; main branches 2–3 m long, usually few, weak, trailing or sprawling, usually without prickles, often scabrous with scattered appressed hairs 0.2–0.6 mm long. Leaves with petiole 1–2.5 cm long; lamina ovate to elliptic-lanceolate, 5–13 cm long, usually 1.7–2.5 times longer than wide, nonrugose, the higher-order and often the secondary veins not impressed above or keeled below, the apex usually abruptly acuminate, the base attenuate to shortly attenuate, the margin serrate-dentate, with teeth 20 to 40 per side, 1–2 mm long, 1–3 times longer than wide, the adaxial surface dark green, lustrous, thinly strigillose, with hairs very sparse, restricted to midrib, secondary veins, and center of major areoles (1 hair per areole), to 0.4 mm long (0.8 mm on veins), often deciduous, the abaxial surface gray-green, lustrous, nearly glabrous, with hairs very sparse, restricted to midrib and secondary and tertiary veins, tapering-conical, 0.1–0.5 mm long, geniculate toward base, antrorse, strongly appressed, weak, often deciduous. Inflorescences capituliform spikes in axils of distal leaves; peduncle 2–3 cm long; receptacle fistulose; bracts (excluding single outer series) narrowly lanceolate, ca. 5 mm long, widest near proximal third, deciduous in fruit, abaxially sparsely hirsute, hairs strongly appressed. Calyx ca. 2 mm long, 2- or 3-toothed; corolla salverform, bilaterally

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4-lobed, tube 5–8 mm long (when dried), limb ca. 6 by 4–5 mm, orange to red (sometimes dull pink, according to note on *A. C. Smith 10216*). Drupes 4–5 mm across, black; pyrenes obovoid, 3–4 by 3 mm, bilocular, inflated, basally acute, distal ornamentation semicircular, shallow, oblique, not trilobed.

TYPE. Dominica, near Fresh Water Lake, common along road, steep slopes in "elfin forest," 10 March 1967, *F. R. Fosberg 48269* (holotype, US!; isotypes, F!, GH!, K [*fide* C. H. Stirton], MO!, NY!).

DISTRIBUTION AND ECOLOGY. Known only from Dominica on sunny slopes in borders and openings of montane rainforest, 450–900 m alt. Flowering and fruiting January to August, possibly year-round.

ADDITIONAL SPECIMENS EXAMINED. **Dominica:** S slope of Morne Macaque on road to Fresh Water Lake, *Ernst 1728* (US); between Laudat and Fresh Water Lake, *Hodge & Hodge 1808* (US), *A. C. Smith 10216* (A, NY, UC, US); Laudat, *Lloyd 201* (NY), *Nicolson 2102* (FTG); Springfield, *Krauss 1268* (LL); Sylvania, Morne Colla Anglais, *Cooper 5* (F, GH, NY, US), *Hodge 861* (GH), *1038* (GH), *1115* (GH).

EPITHET. The epithet honors Walter H. Hodge, whose extensive collections have helped to elucidate the nature of this species.

Two other species of *Lantana* sect. *Camara* Cham., *L. camara* L. and *L. urticifolia* Miller, occur in Dominica and the Lesser Antilles and could be confused with *L. hodgei*. The three taxa are contrasted in the following key:

1. Hairs of abaxial leaf surface sparse, restricted mostly to midrib and secondary and tertiary veins, tapering-conical, geniculate toward base with distal ⅔ parallel to lamina or vein surface.
    2. Laminas 1.2–1.6 times longer than wide; base usually truncate or cordate; adaxial surface at maturity scabrous or strigose, more or less dull, moderate green, the hairs scattered over entire surface, stout, usually persistent (at least the conical bases); abaxial surface lighter yellow-green, thinly strigose on veins, the hairs scattered to moderately abundant, stout, antrorse but with tip held above surface, the secondary and higher-order veins keeled. .... *Lantana camara.*
    2. Laminas ca. 1.7–2.5 times longer than wide; base usually attenuate; adaxial surface at maturity lustrous, dark green, smooth, the hairs restricted to veins and 1 in center of each areole, small, weak, often deciduous; abaxial surface pale gray-green, almost glabrous, the hairs very sparse, weak, strongly appressed, the higher-order and usually secondary veins not keeled. .... *Lantana hodgei.*
1. Hairs of abaxial leaf surface usually abundant and crowded, at least along crevice between major veins and laminar surface, usually occurring on all veins including areolar veinlets and often on noninnervated laminar tissue, filiform (or also gland tipped), straight or gently curved from basal insertion, spreading from vein surface or erect on laminar surface. .... *Lantana urticifolia.*

Lantana hodgei is probably closely related to *L. camara* because both species have tapering, geniculate hairs on the abaxial leaf surfaces (FIGURE 2b, d). *Lantana camara* is commonly encountered in both native and apparently naturalized populations throughout the West Indies and northern South America and is a morphologically variable species. Thus, *L. hodgei* has been considered conspecific with *L. camara* in past studies (Moldenke, 1980 and *in*

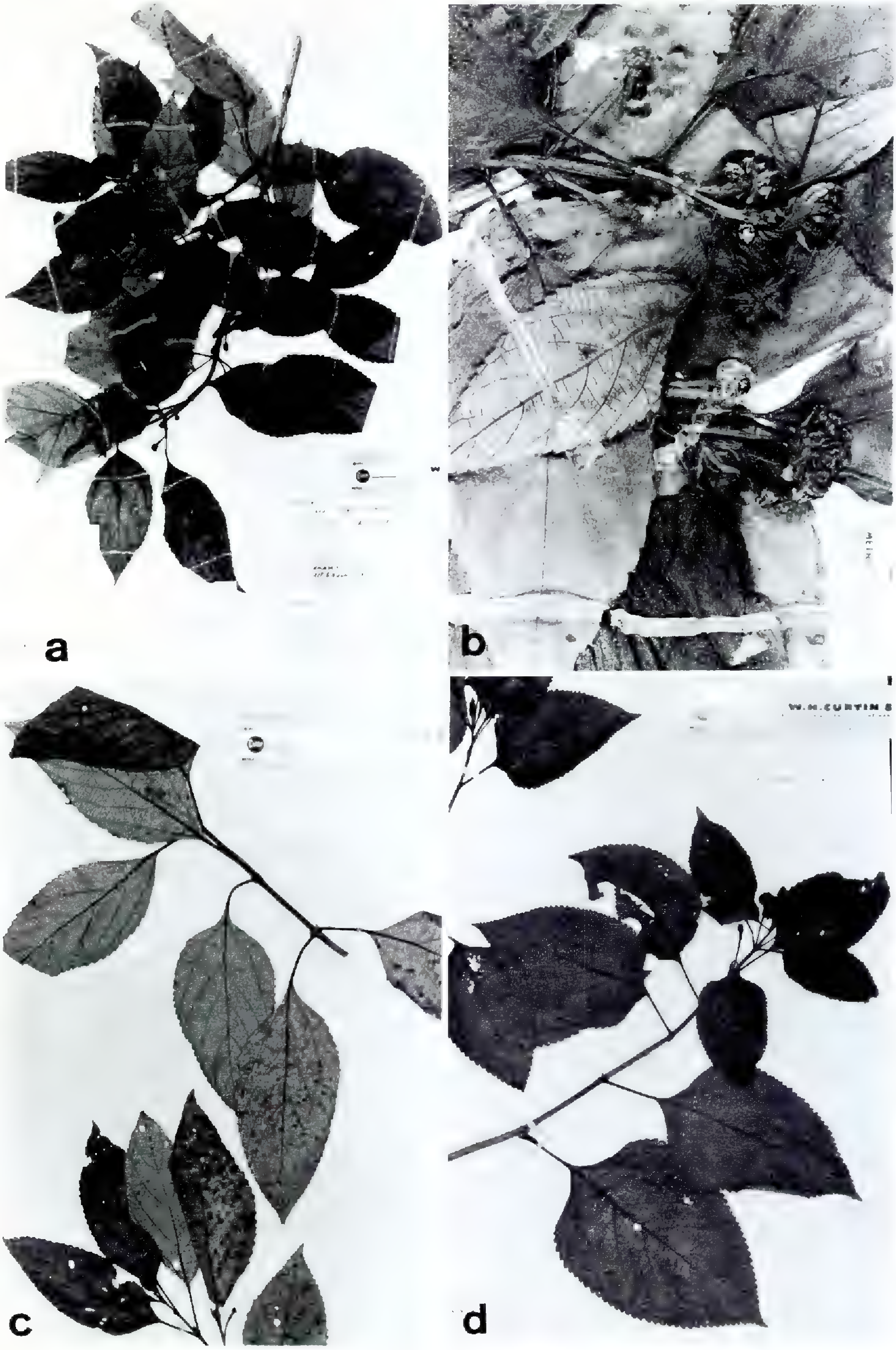

Figure 1. *Lantana hodgei,* habit, inflorescence, and variation in leaf size and shape: a, b, *Fosberg 48269* (holotype, us); c, *Fosberg 48269* (isotype, f); d, *Hodge 1115* (gh). Metric scales numbered in centimeters.

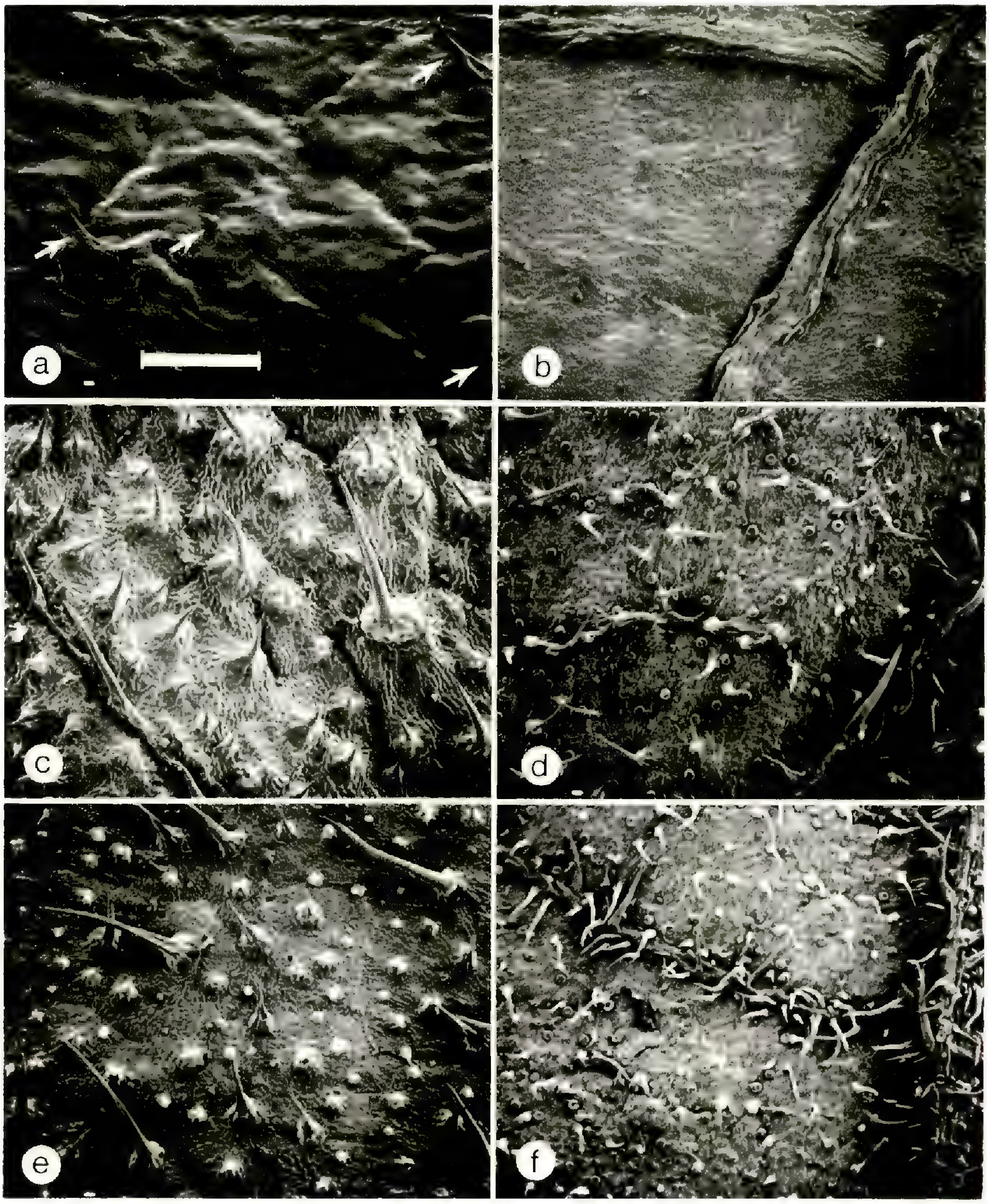

FIGURE 2. Scanning electron micrographs of adaxial (a, c, e) and abaxial (b, d, f) leaf surfaces of *Lantana* species occurring in Dominica: a, b, *L. hodgei* (*Nicolson 2102*, FTG), white arrows pointing to isolated hairs; c, d, *L. camara* (*Wilbur et al. 7665*, FTG); e, f, *L. urticifolia* (*Hodge 859*, GH), apparent basal bending of hairs primarily an artifact of foreshortening. Largest veins shown secondary. Scale bar = 0.5 mm.

schedula). Indeed, some workers would probably submerge all taxa of *Lantana* sect. *Camara* under *L. camara*, as Gibson (1970) did for the *Flora of Guatemala*. Nicolson (unpubl. ms.) calls for new approaches to augment morphology in the delineation of lantanas in the West Indies. Extrapolating from a limited sample of biosystematic and chromosomal studies (Sanders, 1987a, c), I believe there is sufficient reason for separating *L. camara* from *L. hodgei* and other species that have gone under the name *L. camara*. The structure of the abaxial

Pollen stainability of Lantana hodgei, L. urticifolia, and their intermediates.[a,b]

Taxon	Specimen	*N*[c]	% Stainability
L. hodgei	*Cooper 5* (F)	300	85
	Fosberg 48269 (US)	300	65
	Hodge 1115 (GH)	190	81
	Hodge & Hodge 1808 (GH)[d]	200	3
	Nicolson 2102 (FTG)	310	53
	A. C. Smith 10216 (A)[d]	200	4
Intermediate	*Hodge 858* (GH)	203	27
	Hodge 860 (GH)	291	35
	Hodge & Hodge 2592 (GH)	300	33
	Shillingford 120 (MO)	200	29
L. urticifolia	*Dey 69* (A) (Grenada)	303	58
	Hodge 858 (NY)	200	42
	Hodge 859 (GH)	200	35
	Howard 15236 (A) (Redonda)	226	74
	Lloyd 929 (NY)	300	37
	Stoffers 3004 (A) (Saba)	200	81

[a] Pollen from nearly open or open corollas removed from herbarium specimens and stained in lactophenol cotton-blue.

[b] Collections from Dominica unless indicated otherwise.

[c] Total number of pollen grains counted.

[d] Flowers blackened with drying and/or infested with insect larvae.

laminar hairs divides *Lantana* sect. *Camara* into two sets of taxa—a "*camara*-cohort," with conical, geniculate hairs (FIGURE 2b, d), and an "*urticifolia*-cohort," with slender, spreading hairs (FIGURE 2f). Each set includes one or more morphologically distinctive, endemic, and often diploid taxa, in addition to the more morphologically generalized (and hence overall "*camara*-like"), widespread, tetraploid ones (Sanders, 1986, 1987a–c). Characters with generalized states in both groups of tetraploids include growth habit, leaf shape and size, hairs of adaxial leaf surfaces (FIGURE 2c, e), bract shape and size, and flower size. Although the chromosome number of *L. hodgei* is unknown, in other characters this species exceeds the limits of variation of *L. camara* as much as do the other distinctive endemics of the "*camara*-cohort."

Lantana camara, as delimited here (including *L. aculeata* L.), is apparently infrequent on Dominica (Dominica, 1 km NW of Salisbury, *Wilbur et al. 7665* (F, FTG, LL, MO, US—*n.v.*)).

Lantana urticifolia (including *L. arida* Britton and *L. moritziana* Otto & Dietr.) is a widespread and variable species, ranging from Mexico and Cuba to Brazil. It is commonly encountered in Dominica in low-elevation scrub and man-made openings on the lower slopes (Dominica: without further locality, *Imray 229* (GH); Belle View, *Hodge 857* (GH); Fern Villa, *Hodge & Hodge 2177* (GH); Marigot, Mantipo R., *Hodge 858, p.p.* (NY, US); Roseau, *Hodge 859* (GH), *Lloyd 929* (NY); between Salybia and Hatton Garden, *Hodge 3201* (GH)).

Where human disturbance has allowed *Lantana hodgei* and *L. urticifolia* to come in contact, a spectrum of morphological intermediates between the two are found (Dominica: Belfast, *Shillingford 120* (MO); between Belle View and Grand Bay, *Hodge 860* (GH); Marigot, Mantipo R., *Hodge 858, p.p.* (GH); Milton Estate, *Hodge & Hodge 2592* (GH)). Presumably these intermediates are hybrids, like those documented in Florida (Sanders, 1987a). The laminas of these plants are more nearly rounded to cordate at the base, adaxially sublustrous, and abaxially with a moderately dense mixture of filiform straight hairs and tapering geniculately antrorse hairs. The percent stainable pollen is low compared to that of either *L. hodgei* or *L. urticifolia* (TABLE). Indeed, the lower stainability of pollen of *L. urticifolia* from Dominica compared to that from other islands in the Lesser Antilles may suggest that Dominican *L. urticifolia* has undergone widespread introgression from *L. hodgei.* Note especially the apparent co-occurrence of *L. urticifolia* and intermediates (e.g., *Hodge 858,* cited above) on that island.

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I am grateful to the curators of A, F, FTG, GH, LL, MO, NY, UC, and US for loans of specimens. I used the scanning electron microscope at Florida International University, and I am indebted to J. H. Richards, who instructed me in its operation. I thank D. H. Nicolson for making available unmounted specimens of *Lantana* from Dominica and for providing a typescript copy of his treatment of *Lantana* from his unpublished *Flora of Dominica.* He and C. H. Stirton reviewed drafts of the manuscript.

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NOTE ADDED IN PROOF. A specimen documenting the occurrence of *Lantana hodgei* outside of Dominica (Martinique, beyond L'Alena, *Bailey & Bailey 240* (NY)) has recently come to my attention.—R. W. S.

A COMPARATIVE STUDY OF ROOT AND STEM WOODS OF SOME MEMBERS OF THE MIMOSOIDEAE (LEGUMINOSAE)

K. Ranjani and K. V. Krishnamurthy[1]

A comparative study of the root and stem woods of 11 members of the Mimosoideae revealed that the two woods were more alike than had been thought. The only feature of consistent difference was the presence of a greater amount of thinner-walled elements in root wood than in stem wood.

Although structural variation in stem wood has been studied in several arborescent plants, so far less attention has been paid to root wood (Fayle, 1968). This has mainly been due to the assumptions that the structure of root wood is similar to that of stem wood and that root wood has only slight economic importance. It has also been due to the difficulties in procuring authentic root-wood samples (Cutler, 1976). We therefore undertook this comparative study on root and stem woods. We chose subfamily Mimosoideae for investigation not only because of the easy availability of specimens but also because of the lack of study on its root wood.

MATERIALS AND METHODS

Eleven species of Mimosoideae were selected for the study: *Acacia arabica, Acacia auriculiformis, Acacia leucophloea, Adenanthera pavonina, Albizzia amara, Albizzia lebbeck, Dichrostachys cinerea, Enterolobium saman, Leucaena leucocephala, Pithecellobium dulce,* and *Prosopis spicigera.* Wood samples were collected at chest height from the main stem and from the strong, laterally spreading roots at 0.5–1 m below soil level. The collected samples were trimmed to 1 cm^3 in such a way as to include both heartwood and sapwood, and as many growth rings (if present) as possible. Transverse, radial-longitudinal, and tangential-longitudinal sections were taken using a Bright cryostat microtome at a thickness ranging from 15 to 30 μm. The wood was pretreated in boiling water, 10 percent hydrofluoric acid, or a glycerine-alcohol mixture singly or in combination if there was difficulty in sectioning the wood. Sections were stained with safranin alone or with safranin and Delafield's haematoxylin. In addition, macerations of the wood were prepared using Jeffrey's fluid (Johansen, 1940); the macerated elements were also stained with safranin. For all features recorded, 100 random measurements were made. Sample size was accounted for using Student's t test, and levels of significance were calculated

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Comparison of root and stem woods of the taxa of Mimosoideae investigated.

SPECIES	CHARACTER*																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Acacia arabica Willd.	R	A	Dp	15	145	315	20	Ac, Cp	22	Ho	370	35	20	10	L, Sp, St	1430	(-)	680	48
	S	D (IP)	Dp	10	145	300	20	V, Ac, R, Cp	23	Ho	340	35	30	10	L, Sp, St	1200	(-)	690	47
Acacia auriculiformis A. Cunn. ex Bentham	R	A	Dp	20	75	270	4	Ac, Cp	25	Ho	125	15	70	4	L, Sp	825	(-)	-	67
	S	D (CF, IP)	Dp	20	110	280	12	Ac, R, Cp	12	Ho	130	20	65	8	L	730	-	-	68
Acacia leucophloea Willd.	R	A	Dp	10	270	450	28	Ac, Cp	47	Ho	365	35	25	10	L	1655	-	-	15
	S	A	Dp	10	130	290	11	Ac, Cp	33	Ho	330	30	45	9	L	1310	-	-	47
Adenanthera pavonina L.	R	A	Dp	10	180	780	10	V, Ac, Cp	30	Ho	395	30	30	13	L, St	1255	-	(-)	47
	S	D (CF)	Dp	10	130	510	9	V, Ac, Cp	26	Ho	305	30	40	15	L, St	1450	-	645	50
Albizzia amara Boivin	R	D (CF)	Dp	6	165	330	7	Ac, R, Cp	22	Ho	180	15	35	4	L, Sp	1070	1140	(-)	67
	S	D (CF)	Dp	6	140	300	10	Ac, Cp	16	Ho	230	15	60	12	L, Sp, St	1130	1150	670	62
Albizzia lebbeck Bentham	R	A	Dp	5	95	210	2	Ac, Ap, Cp	7	Ho	260	70	25	23	L, Sp, St	705	1075	520	68
	S	A	Dp	5	110	240	7	V, Ac, Cp	15	Ho	250	50	45	19	L, Sp, St	1085	1075	(-)	59
Dichrostachys cinerea Wight & Arn.	R	D (CF)	Dp	20	110	210	5	V, Ac, R, Cp	8	Ho	160	30	80	5	L	955	-	-	82
	S	D (CF)	Dp	20	100	230	8	V, Ac, R, Cp	9	Ho	220	30	50	17	L	960	-	-	76
Enterolobium saman (Jacq.) Prain	R	I (IP)	Dp	10	130	240	16	Ac, Cp	20	Ho	190	30	140	12	L, Sp, St	900	(-)	595	52
	S	I (CF)	Dp	10	125	335	10	Ac, Cp	10	Ho	140	15	65	15	L	805	-	-	65

Leucaena leucocephala (Lam.) De Wit	R	D (CF)	Dp	10	100	330	12	Ac, Cp	21	Ho	260	35	40	7	L, Sp, St	1105	950	(-)	60
	S	D (CF, IP)	Dp	10	160	230	15	Ac, R, Cp	23	Ho	295	20	30	6	L	840	-	-	56
Pithecellobium dulce Bentham	R	I (IP)	Dp	10	90	420	7	V, Ac, Cp	22	Ho	270	40	30	13	L, Sp	1180	1270	-	58
	S	D (CF, IP)	Dp	12	140	435	17	Ac, Cp	11	Ho	210	25	60	8	L, Sp, St	1090	935	(-)	64
Prosopis spicigera L.	R	A	Dp	14	130	295	13	Ac, Cp	20	Ho	295	20	63	12	L, Sp	795	(-)	-	55
	S	A	Dp	13	130	225	15	Ac, Cp	30	Ho	315	30	68	10	L, Sp	905	(-)	-	45

*Key to characters:

1. Portion of plant where wood samples taken: R = root, S = stem.
2. Growth rings: A = absent, D = distinct, I = indistinct, CF = marked by compressed late-wood fibers, IP = marked by initial parenchyma.
3. Porosity: Dp = diffuse porous.
4. Mean number of vessels per mm^2 in transection.
5. Mean vessel diameter (µm).
6. Mean vessel-element length (µm).
7. Percentage of area of transection occupied by vessels.
8. Nature of parenchyma: Ac = aliform confluent, Ap = apotracheal diffuse, Cp = compartmented crystal, R = restricted to side facing periphery of wood, V = vasicentric.
9. Percentage of area of transection occupied by parenchyma.
10. Nature of rays: Ho = homogeneous.
11. Mean height of rays in tangential-longitudinal section (µm).
12. Mean width of rays in tangential-longitudinal section (µm).
13. Mean abundance of rays per mm^2 in tangential-longitudinal section.
14. Percentage of area of transection occupied by rays.
15. Type of fibers: L = libriform, Sp = septate, St = substitute (predominant type underlined).
16. Mean length of libriform fibers (µm).
17. Mean length of septate fibers (µm); - = absent, (-) = data unavailable due to rarity of fibers.
18. Mean length of substitute fibers (µm).
19. Percentage of area of transection occupied by fibers.

for $P = 0.01$ and 0.05. Microphotographs were taken with a Nikon Labophot microscope. Terminology is in accordance with the IAWA Multilingual Glossary (International Association of Wood Anatomists, 1964).

OBSERVATIONS AND DISCUSSION

The TABLE provides the data on all qualitative and quantitative features of the root and stem woods.

GROWTH RINGS

Although variability in growth rings has been studied in detail (Carlquist, 1980), the degree of expression of the ring within the stem and root woods of the same plant has not yet been adequately investigated. Fayle's (1968) statement that growth-ring boundaries are better marked in the stem than in the root is supported by Cutler (1976), Fahn (1982), and Zimmermann and Brown (1971). This is the case in four of the eleven species we studied (*Acacia arabica, Acacia auriculiformis, Adenanthera pavonina,* and *Pithecellobium dulce*) but not for *Albizzia amara, Dichrostachys cinerea, Enterolobium saman,* or *Leucaena leucocephala*; growth rings were absent in the other three species investigated (*Acacia leucophloea, Albizzia lebbeck,* and *Prosopis spicigera*). The presence of growth rings and the degree of their distinction have been reported to be highly variable even in the stem woods of the Mimosoideae (Ramesh Rao & Purkayastha, 1972). In other words, the degree of distinction shown by growth rings may not be directly related to the organ in which the growth ring is present. The reason for this variability is difficult to explain since several intrinsic and extrinsic factors (such as hormone levels, availability of carbohydrates, climatic factors, and soil moisture) appear to control the expression of growth rings.

It is generally believed that the feature or features marking the growth ring are specific for each plant, irrespective of the organ (see Carlquist, 1980). Although this was true of *Albizzia amara* and *Dichrostachys cinerea,* where compressed late-wood fibers marked the growth ring in both stem and root woods, it was not true of other taxa, in which the growth rings of stem and root woods were marked by quite different features (see TABLE).

VESSEL AND VESSEL ELEMENTS

Root wood has been reported to have a greater abundance of vessels and vessel multiples per unit area than stem wood (Carlquist, 1978; Carlquist *et al.,* 1983; Gómez-Vázquez & Engleman, 1983). Fayle's (1968) results, however, did not agree with this (see also Zimmermann & Brown, 1971). Cutler (1976), in discussing the subject, cautioned that further research was necessary before specific conclusions could be drawn. He made this statement because in his study of *Acer* stem and root woods, he found certain samples of root wood to have more abundant vessels than stem wood, while one sample showed no difference in quantity. In nine of the 11 taxa we investigated, pore abundance was the same in both root and stem woods. Only in *Acacia arabica* and *Pithecellobium dulce* was there a difference at the 1 percent level of significance; in the former abundance was greater in the root wood, while in the latter the contrary was true.

Pore Diameter

Presence of wider pores in root wood has been considered to be the most consistent distinction between root and stem woods (Bhat, 1982; Carlquist, 1975, 1977, 1978; Chalk, 1983; Fahn, 1982; Fayle, 1968; Gómez-Vázquez & Engleman, 1983; Plank, 1976; Zimmermann & Brown, 1971; Zimmermann & Potter, 1982). Cutler (1976) was cautious enough to state that further research into this matter was warranted in view of the number of exceptions to the above observation. In the individuals we studied there was no significant difference even at the 5 percent level in mean pore diameter of stem and root woods of *Acacia arabica, Enterolobium saman,* or *Prosopis spicigera.* The difference was significant at both levels in the rest of the species, with greater diameter being exhibited by the stem-wood vessel elements in *Acacia auriculiformis, Albizzia lebbeck, Leucaena leucocephala,* and *Pithecellobium dulce* and by the root-wood vessel elements of the other four species. Thus, mean pore diameter does not appear to be a feature of consistent difference between root and stem woods.

Vessel-Element Length

Whether the length of vessel elements depends upon the organ is a question often debated in the literature. Carlquist (1976) believed that the elements were longer in root wood than in stem wood. This opinion was also held by Fayle (1968), Plank (1976), and Zimmermann and Potter (1982). The data obtained in the present study revealed that longer vessel elements were present in the root wood of *Acacia leucophloea, Leucaena leucocephala,* and *Prosopis spicigera,* but in the stem wood of *Adenanthera pavonina* and *Enterolobium saman.* In all of the above, the difference in length was significant at the 1 percent level. In *Albizzia lebbeck* the stem wood had longer elements, but the difference was significant only at the 5 percent level. In *Acacia arabica, Acacia auriculiformis, Albizzia amara, Dichrostachys cinerea,* and *Pithecellobium dulce* there was no significant difference in length of vessel elements between root and stem woods. We therefore inferred that vessel-element length has no correlation with the organ of the plant in which it occurs, at least in the plants we investigated. Indeed, Carlquist (1976) himself recorded longer vessel elements in the stem woods of *Grubbia rourkei* Carlq.

There was no difference between root and stem woods in qualitative features such as vessel-element pitting, type of perforation, type of axial parenchyma, nature of the ray, or type of fibers. We could not confirm the earlier reports (Lebedenko, 1961, 1962; Patel, 1965; Shimaji, 1962; see also Cutler, 1976) that xylem rays of certain plants tend to be heterogeneous in root wood but homogeneous in stem wood.

AMOUNT OF PARENCHYMATOUS ELEMENTS

The amount of parenchymatous tissue present was considered by some earlier workers to be a consistent difference between root and stem woods, with the root wood tending to be more parenchymatous than the stem wood (Chalk, 1983; Esau, 1965; Fahn, 1982; Fayle, 1968; Lebedenko, 1959, 1961, 1962; Zimmermann & Brown, 1971). However, it is not very clear whether the increase is due to axial parenchyma content, ray content, or both. With respect to rays alone, root wood was reported to have more ray content than stem wood. This may be due to the presence of broader rays, more rays per unit area, or both. In the species we investigated, ray width in tangential-longitudinal section, calculated either in microns or in number of cells across, showed no correlation to the organ. In some taxa the root wood had broader rays, in others the stem wood did (see TABLE). With respect to ray abundance (number of rays per mm^2 in tangential-longitudinal section), there was no consistency either. Of the 11 species studied, only *Dichrostachys cinerea* and *Enterolobium saman* showed greater ray abundance in root wood.

The fibers of the root wood were very much thinner walled and contained starch grains and phenolic inclusions that were generally restricted to parenchyma in the stem wood. Therefore, it can be said that in all the taxa we studied, the root wood had more thin-walled elements than the stem wood.

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ARMORACIA LACUSTRIS (BRASSICACEAE), THE CORRECT NAME FOR THE NORTH AMERICAN LAKE CRESS

IHSAN A. AL-SHEHBAZ[1] AND VERNON BATES[2]

A new combination is proposed for the North American lake cress. A county distribution map is included.

Lake or river cress is one of the most remarkable heterophyllous North American aquatic plants. It grows in quiet waters of lakes, ponds, streams, rivers, and springs, as well as on flood plains, mud flats, and muddy shores. Any part of the root, stem, or leaf is capable of regenerating a new plant. The species is widely distributed in North America east of the 95th meridian from Wisconsin and Michigan eastward to Quebec and northwestern Vermont, southward to Florida, westward to eastern Texas, and northward to eastern Oklahoma, Missouri, eastern Iowa, and southeastern Minnesota (see MAP). Despite its perennial habit, its regenerating ability, and its apparent wide distribution, the species is not very common anywhere. In the northern parts of its range, it has very rarely been collected with good fruits and seeds and appears to regenerate and reproduce primarily asexually (La Rue, 1943).

The nomenclature of lake cress, *Armoracia lacustris* (which now replaces *A. aquatica*), has been confused at both the specific and the generic ranks. Eaton (see below) originally described it as a variety of horseradish (*A. rusticana* Gaertner, Meyer, & Scherb., as *Cochlearia armoracia* L.) but later recognized it as a distinct species of *Cochlearia* L. Other authors treated it as a species of *Nasturtium* R. Br., *Rorippa* Scop., *Neobeckia* Greene, *Radicula* Moench, or *Armoracia* Gaertner, Meyer, & Scherb. Under the last genus it has been known as *A. aquatica* (Eaton) Wieg., but this is a later homonym of *A. aquatica* Kostel. The latter is a synonym of *Rorippa amphibia* (L.) Besser, an entirely different Eurasian species. Therefore, the specific epithet *aquatica* cannot be used for the North American plant under the genus *Armoracia*. A new combination based on *Nasturtium lacustre* A. Gray is proposed.

Armoracia lacustris (A. Gray) Al-Shehbaz & V. Bates, comb. nov.; based on *Nasturtium lacustre* A. Gray, Gen. Pl. U. S. **1:** 132. 1848. TYPE: same as that of *Nasturtium natans* DC. var. *americanum* A. Gray. Gray cited no specimens under *N. lacustre* but listed this varietal name as a synonym.

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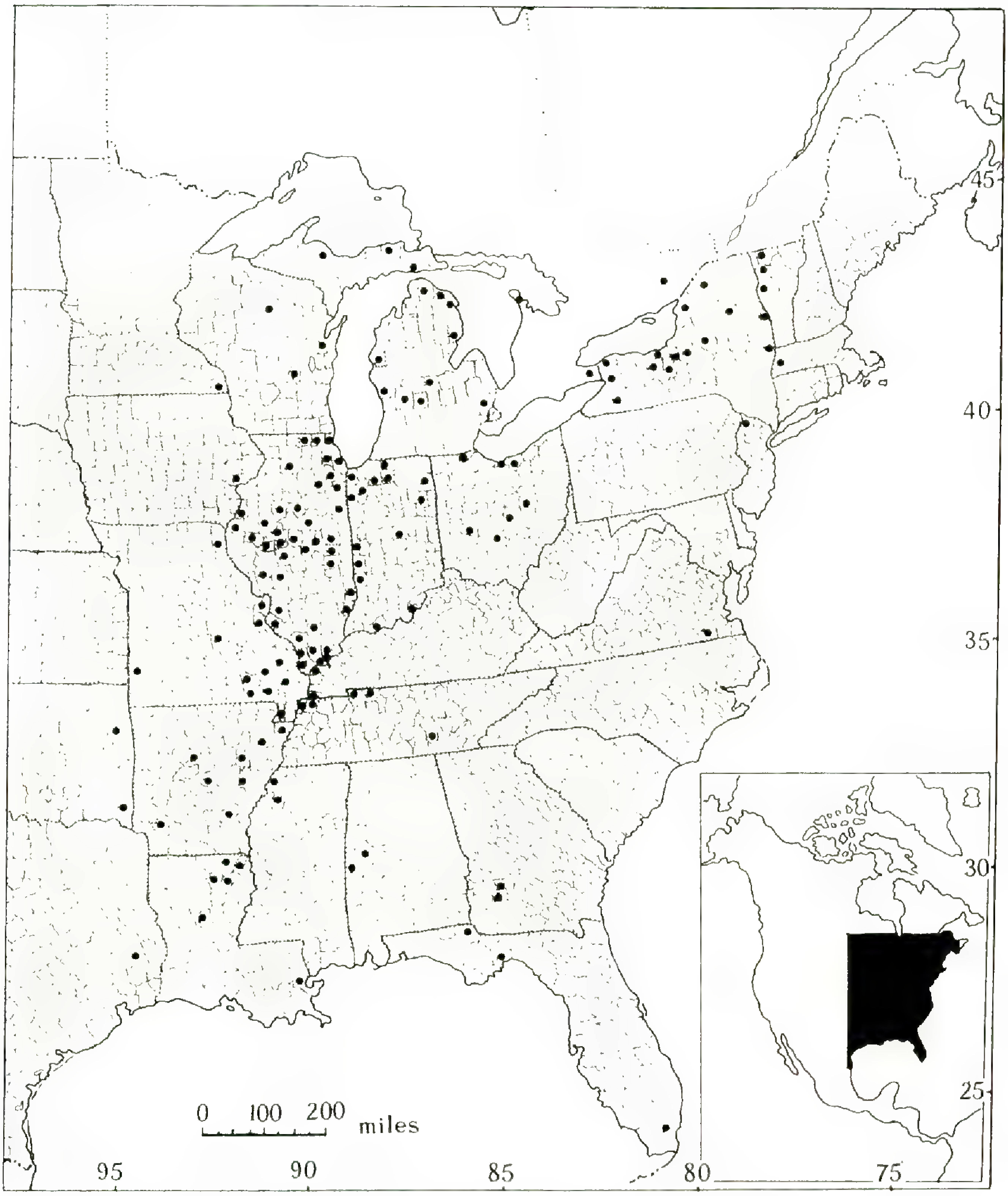

County distribution map of *Armoracia lacustris.*

Cochlearia armoracia L. var. *aquatica* Eaton, Man. Bot. N. Amer. ed. 3. 243. 1822. TYPE: Massachusetts, Berkshire County [*A. Eaton s.n.*, not seen].

Cochlearia aquatica (Eaton) Eaton, Man. Bot. N. Amer. ed. 5. 181. 1829.

Nasturtium natans DC. var. *americanum* A. Gray, Ann. Lyceum Nat. Hist. New York **3:** 223. 1835. LECTOTYPE (here designated): W. New York, Oneida Lake [*A. Gray s.n.*] (GH!).

Armoracia americana (A. Gray) Hooker & Arnott, Brit. Fl. ed. 6. 28. 1850.

Rorippa americana (A. Gray) Britton, Mem. Torrey Bot. Club **5:** 169. 1894.

Neobeckia aquatica (Eaton) Greene, Pittonia **3:** 95. 1896.

Radicula aquatica (Eaton) Robinson, Rhodora **10:** 32. 1908.

Armoracia aquatica (Eaton) Wieg. Rhodora **27:** 186. 1925; non *A. aquatica* Kostel. Allg. Med. Pharm. Fl. **5:** 1571. 1836.

Rorippa aquatica (Eaton) Palmer & Steyerm. Rhodora **40:** 132. 1938.

A few authors have questioned the placement of *Armoracia lacustris* and *A. rusticana* in the same genus, and Rickett (1967, p. 236) stated that they "seem to have nothing in common except that they are both crucifers." Schulz (1936) treated the former species as a *Nasturtium* (sect. *Rorippa* (Scop.) Prantl) in the tribe Arabideae DC. and retained the latter in *Armoracia,* which he placed in the tribe Drabeae O. E. Schulz. In our opinion, both species share a number of characters (e.g., white flowers, biseriately arranged seeds, incomplete septum, oblong to ovate fruits, dissected lower leaves) that support their disposition in *Armoracia,* as was proposed by Wiegand (1925).

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JOURNAL OF THE ARNOLD ARBORETUM

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CONTENTS OF VOLUME 68, NUMBER 3

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VOLUME 68 OCTOBER 1987 NUMBER 4

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

GORDON C. TUCKER[2]

CYPERACEAE A. L. de Jussieu, Gen. Pl. 26. 1789, nom. cons.

(SEDGE FAMILY)

Small to large perennial or annual herbs of aquatic or terrestrial habitats. Roots fibrous; many species rhizomatous or stoloniferous. Plants glabrous or

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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-8415367 (Norton G. Miller, principal investigator), under which this account was prepared, and BSR-8415769 (Carroll E. Wood, Jr., principal investigator). This treatment, 118th 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. Those references I did not verify are marked with asterisks.

Preceding the reference for each genus, a paragraph is given listing by author all familial or tribal references pertinent to that genus.

I have enjoyed working with Norton Miller and Carroll Wood on the Generic Flora Project, and I thank them for their interest and assistance. Thomas J. Rosatti has given helpful advice on many occasions. Stephen A. Spongberg and Elizabeth B. Schmidt improved the final manuscript with their editorial expertise. Melinda F. Denton helped initiate my interest in the Cyperaceae, and Robert L. Wilbur ably supervised my graduate studies on *Cyperus*. Thanks are extended to the staffs of the New York State Library (especially Alta Beach, Senior Librarian), the Missouri Botanical Garden Library, the New York Botanical Garden Library, and the Libraries of the Arnold Arboretum and the Gray Herbarium for providing access to the needed literature. I am grateful to the curators at A, AC, ALU, CCNL, CONN, DUKE, E, F, FSU, GA, GH, KIRI, MASS, MUHW, NASC, NCBS, NCSC, NCU, NEBC, NY, NYS, PENN, PH, SD, SMU, UC, UNA, US, USCH, WRSL, WVA, and YU who have sent specimens or provided access to collections and hospitality during my visits. Charles T. Bryson, Patricia L. Forbes, Paul Goetghebeur, Encarnación R. Guaglianone, Robert Kral, Anton A. Reznicek, Alfred E. Schuyler, Lisa A. Standley, Wm. Wayt Thomas, Marcia J. Waterway, and Karen L. Wilson have shared information and discussed nomenclatural matters. Thomas J. Rosatti, William R. Linke, Jr., Bruce A. Sorrie, Jason R. Tucker, and Joshua D. Tucker have helped with field work. Vicky Martin Tucker, my wife, has been supportive (and tolerant) of my weekend collecting trips, week-long research trips, and numerous evenings given over to sedges; her understanding is deeply appreciated.

The illustrations were prepared by Karen Stoutsenberger under the supervision of Carroll Wood or Kenneth R. Robertson, from plants collected by Carroll Wood or from specimens in the herbaria of Harvard University (A, GH).

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scabrellate. Culms single, approximate, or caespitose, trigonous, triquetrous, or terete, the cortex chlorenchymatous, the central region aerenchymatous or hollow; cortical bundles with sheaths like those in the leaves. Leaves basal or both basal and cauline; sheaths closed; blades linear to lanceolate, flat, conduplicate, plicate, or involute; stomata paracytic, sometimes surrounded by 1–4 porrect or arching cuticular papillae; anatomy non-kranz or kranz, if kranz, the bundle sheaths 2-layered ("*Cyperus* type") or 3-layered ("*Fimbristylis* type"). Inflorescences spicate or umbelliform [corymbose], sessile, simple, or with second- and third- [to fifth-]order branching. Spikelets 1- to many-flowered, basally subtended by a scalelike prophyll, above which may be 1 or more sterile scales; flowers perfect or imperfect and monoecious (rarely dioecious), each borne in the axil of a scale ("glume" of some authors), anemophilous (infrequently entomophilous); perianth absent or comprising 1 or 2 series of smooth or barbed bristles, at maturity shorter to several times longer than mature achene. Stamens (1, 2, or) 3; filaments ribbonlike or capillary; anthers broadly ellipsoid to linear, basifixed; pollen maturing as cryptotetrads (pseudomonads), subspheroidal, trinucleate (binucleate?) when shed. Gynoecium tricarpellate and stigmas 3, or bicarpellate (dorsiventrally or laterally compressed) and stigmas 2; styles and stigmas capillary, glabrous or glandular-pubescent; ovules basal, anatropous, bitegmic, crassinucellar; megagametophyte (embryo sac) of the Polygonum type. Achene trigonous or lenticular, ovoid, obovoid, or ellipsoid, smooth, puncticulate, or papillose; endosperm mealy, with starch grains, protein crystals, and oil droplets, filling most of the achene; embryo small; embryogeny of the Onagrad (*Juncus* variation) or Asterad type; germination epigeal. Base chromosome numbers 5, 6, 7, 8. TYPE GENUS: *Cyperus* Linnaeus.

A large family of about 80 genera and 3500 species, worldwide in distribution. Seventeen genera occur in our area, including *Carex* L., with 165 species, the largest genus of seed plants in the Southeast.

There is general agreement that the Juncaceae are the closest relatives of the Cyperaceae (Thorne; Dahlgren & Rasmussen). Both families have tristichous phyllotaxy, simultaneous microsporogenesis, post-reductional meiosis, nonlocalized (diffuse) centromeres, anatropous ovules, and Onagrad embryogeny. The Cyperaceae are distinguished from the Juncaceae in having conical silica bodies in the epidermal cells, solitary ovules and basal placentation, pollen-grain formation in which three of the meiotic products degenerate, nuclear endosperm, and indehiscent fruits (achenes). North American Cyperaceae lack a perianth or have one of bristles; North American Juncaceae have expanded chartaceous tepals. This is useful regionally for distinguishing the two families, but it cannot be used on a worldwide basis because *Oreobolus* R. Br. and several other genera of Southern Hemisphere Cyperaceae also have chartaceous tepals.

Some authors (e.g., Fernald, Cronquist) have treated the Gramineae as the closest relatives of the Cyperaceae. However, the grasses have apical placentation, orthotropous ovules, distichous phyllotaxy, and open leaf sheaths, and their affinities are with the Restionaceae and the Flagellariaceae (Thorne; Dahlgren & Rasmussen). Also, the grasses are chemically unlike the sedges (Harborne, 1971). For example, anthocyanins are common in grasses but unknown in sedges, while aurones are common in sedges and unknown in grasses (and in the Juncaceae).

The tribal classification was first elaborated on a worldwide basis by Nees von Esenbeck and Kunth and has been rather stable since. Some authors recognized tribes only; some, subfamilies and tribes; and others, subtribes also. Two subfamilies, both distributed worldwide, are accepted in this treatment: the Cyperoideae (Scirpoideae Pax, flowers perfect) and the Caricoideae Pax (flowers imperfect). Included in the Cyperoideae are four tribes, of which the Scirpeae Dumort. (including Fimbristylideae Raynal; spikelets with 1 or 2 sterile basal scales, numerous fertile scales spirally arranged, perianth bristles generally present, embryos well differentiated), the Cypereae (1 or 2 sterile basal scales, several to many fertile scales distichously arranged, perianth absent, embryos well differentiated), and the Schoeneae Dumort. (Rhynchosporeae Fenzl; spikelets with several sterile basal scales, fertile scales 1 or 2 (to several), perianth bristles generally present, embryos slightly differentiated) are represented in our area. No members of tribe Hypolytreae Fenzl (Mapanieae Koyama) of the tropics grow in North America. Subfamily Caricoideae is divided into two tribes: the Scleriae Fenzl (achenes naked, borne on a hardened disk), represented in North America by a single genus, *Scleria* Berg.; and the Cariceae Dumort. (achenes enclosed in a perigynium), represented in the Southeast by *Cymophyllus* Mack. and *Carex* (and also in North America by *Kobresia* Willd., a circumboreal genus occurring in the northern United States and Canada, and *Uncinia* Pers., an austral genus extending north to Jamaica and Mexico).

Microsporogenesis in sedges differs markedly from that in other angiosperms. The nucleus of the microsporocyte divides meiotically, but cytokinesis does not follow immediately. Rather, three nuclei migrate to one end of the pollen mother cell, where they begin to disintegrate. The fourth nucleus remains in the center of the cell, where it divides mitotically. One of the resulting daughter nuclei migrates to the end of the cell, joining the other three disintegrating products of meiosis. The remaining haploid daughter nucleus divides mitotically, forming generative and tube nuclei. The generative nucleus divides again as the exine matures, resulting in the trinucleate pollen grain characteristic of the family. The four degenerated nuclei often remain visible as dark streaks near the exine. The wall of the mature pollen grain is thus homologous to the wall of the pollen mother cell. This pattern of microsporogenesis, presumably characteristic of the entire family, has been reported in *Abildgaardia* Vahl, *Bulbostylis* Kunth, *Carex, Cladium* P. Br., *Eleocharis* R. Br., *Fimbristylis* Vahl, *Fuirena* Rottb., *Scirpus* L., *Scleria,* and *Rhynchospora* Vahl. In the closely related Juncaceae cytokinesis is delayed in the pollen mother cells until each daughter nucleus has divided a second time. Thus, the Juncaceae provide a pattern of microsporogenesis intermediate to that in the Cyperaceae and other monocots, and emphasizing the relationship of the Cyperaceae and the Juncaceae.

Embryology is nearly uniform in the Cyperaceae. Endosperm formation is nuclear in all genera that have been investigated. Endosperm wall formation is complete in most genera, but incomplete in *Rhynchospora* and *Scleria.* The mature embryos of the Cyperaceae vary considerably in shape and in the position of the cotyledon and the radicle. As a rule, each genus has its characteristic type of embryo (Van der Veken). When the achenes mature, the embryos of tribe Schoeneae are considerably less differentiated than those of other tribes (Vanhecke).

The sedges are incompletely investigated chemically, although *Cyperus* is much better known than other genera. Ethereal oils occur in the roots of three species of *Cyperus* (Hegnauer). Cyanogenesis is evidently uncommon but has been reported for three species of *Cyperus* and for one each of *Fimbristylis* and *Kyllinga* Rottb. (Gibbs). This is surprising because it is widespread in the closely related Juncaceae. Tannins occur in many sedges, having been reported in *Cyperus, Dulichium* Pers., *Fuirena,* and *Scirpus* (one species each). Alkaloids are rare; brevicarine, brevicolline, and harman occur in *Carex brevicollis* DC. (Gibbs). Some terpenoids have been reported. Citral, a monoterpenoid, occurs in species of *Kyllinga* (Gibbs), and several sesquiterpinoids are known from species of *Cyperus* (Hegnauer). Quinones are found in both *Cyperus* and *Fimbristylis* (Allan *et al.*). Leucoanthocyanins are reported from species of *Carex, Cyperus, Dulichium, Kyllinga,* and *Scirpus.* Anthocyanins are absent from the family (Harborne; Harborne *et al.*).

Flavonoids occur in many genera (Kukkonen, 1969; Harborne). Recently, Harborne and collaborators have done much to expand what is known about flavonoids in sedges. Among this class of compounds are aurones, which give a yellowish tint to the inflorescences of many sedges. These are absent from the Gramineae and the Juncaceae. Flavonols were present in only 15 percent of 11 genera tested by Harborne. Flavonoid aglycones, especially quercetin and luteolin, are widespread in the family, as are proanthocyanidins (particularly in the leaves). Harborne and colleagues (p. 765) concluded that there are "no dramatic correlations between flavonoid distribution and higher level classification of the Cyperaceae." However, certain genera or subgenera are distinguished chemically from closely related groups (see under *Cyperus* and *Abildgaardia*). Flavonoid profiles have been shown to distinguish between related taxa in *Carex* and *Cyperus* (discussed under those genera).

Metcalfe presented much useful information on the anatomy of the Cyperaceae, including clear illustrations and insightful comments on the taxonomic significance of anatomical features. Many of his descriptions were derived from studies of specimens collected in the Southeast, particularly Florida.

Developmental anatomy and morphology have received some attention (Barnard). The apex of spikelets in all examples studied conforms to the tunica-corpus pattern. Periclinal division of dermatogen and hypodermal cells gives rise to tissues that develop into the scales subtending flowers (*Scirpus, Cyperus*), the carpels (in all species), the perianth bristles (*Scirpus*), and the perigynia (*Carex*).

The first fossil remains of the Cyperaceae date from the Eocene. Fruits of *Carex, Scleria,* and *Scirpus* are known from the Eocene and Oligocene of Eurasia and North America; those of *Dulichium* and *Cladium* from the Oligocene and Pliocene of Europe. Reports of Cyperaceae from pre-Tertiary strata (i.e., *Caricopsis* Samylina) are not considered reliable (Daghlian).

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KEY TO THE GENERA OF CYPERACEAE IN THE SOUTHEASTERN UNITED STATES

General characters: *perennial (occasionally annual), often rhizomatous herbs of diverse, usually wet, often disturbed habitats; rhizomes frequently present; leaves linear, the sheaths usually closed; inflorescences simple or variously branched, lateral or crowded at the apices of the culms; flowers perfect or imperfect (the plants very rarely dioecious), borne in the axils of scales or in perigynia; perianth bristles present or absent; fruit an achene; embryo small; endosperm abundant.*

A. Flowers perfect (staminate or carpellate flowers infrequently formed at base or apex of spikelets).
  B. Scales of the spikelets spirally arranged.
    C. Achenes without obconical or pyramidal apical tubercle, but sometimes with persistent swollen style base much less than half as wide as the achene.
      D. Achenes subtended by 15–20 cinnamon or whitish, silky bristles 5–10 times as long as the achenes. . . . . 2. *Eriophorum.*
      D. Achenes subtended by bristles at most 3 times as long as the achenes, or with bristles lacking.
        E. Inner whorl of perianth bristles with expanded spongy petaloid blades. . . . . 3. *Fuirena.*
        E. Perianth bristles absent or lacking expanded blades.
          F. Bulbous base of style persistent on mature achenes. . . . . .6. *Bulbostylis.*
          F. Base of style not persistent.
            G. Styles fimbriate. . . . . .5. *Fimbristylis.*
            G. Styles smooth.
              H. Spikelets maturing a single achene; bristles absent. . . . . 14. *Cladium.*
              H. Spikelets maturing several to many achenes; bristles usually present.
                I. Spikes and spikelets borne on rays, rarely sessile; achenes and scales appressed to rachilla. . . 1. *Scirpus.*
                I. Spikelets sessile; achenes and scales borne at right angles to rachis. 10. *Lipocarpha.*
    C. Achenes with pyramidal or obconical apical tubercle ½ to nearly as broad as the achene.
      J. Leaf blades absent; inflorescences unbranched, a single spikelet terminating the culm. . . . . 4. *Eleocharis.*
      J. Leaf blades present; inflorescence of several to many spikelets, some usually borne on branches. . . . . 11. *Rhynchospora.*
  B. Scales of the spikelets distichously arranged.
    K. Perianth bristles absent.
      L. Plants bulbous-thickened basally; style base sclerified, persistent; spikelets 1(–3). . . . . .7. *Abildgaardia.*
      L. Plants not bulbous-thickened basally; style base soft, deciduous; spikelets numerous.
        M. Inflorescences branched; spikelets 1- to many-flowered; rachilla elongate; scales broadly rounded. . . . . 8. *Cyperus.*
        M. Inflorescences unbranched (spikes sessile); spikelets 1- (infrequently 2-)flowered; rachilla not or barely elongate; scales conduplicate, conspicuously keeled. . . . . .9. *Kyllinga.*
    K. Perianth bristles present.
      N. Leaves cauline; inflorescences several, axillary. . . . . .12. *Dulichium.*
      N. Leaves basal; inflorescence solitary, terminal. . . . . .13. *Schoenus.*

A. Flowers strictly imperfect.
  O. Achenes naked, often borne on a discoid hypogynium. .... 15. *Scleria.*
  O. Achenes enclosed in perigynia.
    P. Spikes single, white; leaf blades broadly lanceolate, the apices broadly rounded, the midvein not distinguishable from other veins. .. 16. *Cymophyllus.*
    P. Spikes 1 to several, greenish, yellowish green, or light brown; leaf blades linear, the apices acute, the midvein much larger and more conspicuous than other veins. .... 17. *Carex.*

Subfamily CYPEROIDEAE

Tribe SCIRPEAE Kunth ex Dumortier, Fl. Belg. 143. 1827.

1. **Scirpus** Linnaeus, Sp. Pl. **1:** 47. 1753; Gen. Pl. ed. 5. 26. 1754.

Small to medium-sized perennials or annuals of shallow fresh or tidal waters, disturbed moist soils, moist [mesic to dry-mesic] woodlands, marshes, open mountaintops, and grassy balds. Roots fibrous; perennial species with rhizomes short, branched, producing loose to dense tussocks of culms; annual species without rhizomes, forming dense clumps of culms. Culms trigonous (with planar, concave, or slightly convex surfaces) or terete, smooth throughout or scabrellate distally. Leaves all basal or scattered along the culm; sheaths closed, smooth or sometimes with conspicuous cross veins, greenish white, reddish brown, or blackish; blades flat, conduplicate, or subterete, ½ to nearly as long as the culm, stiff or arching (limp when growing underwater); stomata paracytic; chlorenchyma not radiate; longitudinal air chambers often present. Involucral leaves (1 or) 2–10, the blades resembling cauline ones but sheaths generally much shorter, approximate at the summit of the culm or rather widely spaced over the upper ⅓ of it, horizontal to ascendent, or the longest nearly vertical and simulating a continuation of the culm. Inflorescences composed of primary and secondary (sometimes tertiary) rays, in many species reduced to glomerulate clusters or heads, in some to a cluster of several more or less sessile spikelets or a single sessile spikelet; prophylls of the rays tubular, obtuse to acute apically, smooth but usually conspicuously costate; primary rays smooth, or scabrellate distally or throughout, terete, stiff or flexuous, secondary (and sometimes tertiary) rays similar to primary ones, but shorter and usually more slender. Spikelets ovoid to linear-oblong. Scales (3 to) 20 to about 100, spirally arranged and closely imbricate, with 2 lowermost sterile and others fertile, all deciduous at maturity, ovate to oblong, with 1–9 subtle to conspicuous nerves and sometimes a conspicuous midrib, the apex obtuse to acute, entire or mucronulate to strongly cuspidate, the awn straight to strongly excurved. Flowers perfect, protogynous. Perianth bristles 3–6(–8) or lacking, smooth or retrorsely scabrellate, straight, highly curled, or crinkled at maturity, from ⅓ to 4 times as long as the mature achene, deciduous or remaining attached to the mature achene. Stamens (2 or) 3; filaments slender, about equaling the subtending scales; anthers broadly ellipsoid to narrowly linear, the apices of the connectives in some species prolonged as subulate appendages up to ¼ the length of the anther, sometimes tipped with crystalline prickles; pollen uniaperturate, subspheroidal in polar view and triangular to obovoid in equatorial view, psilate,


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bi- or trinucleate. Styles capillary; stigmas 2 or 3, about equaling the style in length. Achenes lenticular to trigonous, equilateral in transverse section, or slightly to strongly dorsiventrally flattened, the base stipitate or cuneate, the apex apiculate, beaked, or entire, the surface essentially smooth, finely pitted, reticulate, or rugulose. Embryos ellipsoid, turbinate, or fungiform, the radicle lateral or basal. Base chromosome numbers 5, 7. LECTOTYPE SPECIES: *Scirpus sylvaticus* L.; see Hitchcock & Green, Prop. Brit. Bot. 118. 1929. (Latin name for a bulrush, probably *Scirpus Tabernaemontani* Gmelin.)—BULRUSH, REED, CLUB-RUSH, WOOL-GRASS, THREE-SQUARE.

Scirpus, the third-largest genus of the Cyperaceae, with about 300 species worldwide, is best represented in temperate regions. North America (including Mexico), with about 80 species, is the center of diversity. Only about 15 species occur in the West Indies and Central America, and about 30 in all of South America, most of these in Argentina and Chile. Twelve species occur in Europe, and perhaps 50 in Africa. It is difficult to estimate the number of species in all of Asia; 24 grow in the Soviet Union, and ten in Malesia. A recent synopsis included 44 in Australia (Wilson).

Studies in *Scirpus* have been hampered by lack of a worldwide treatment (such as those prepared for several other large genera of the family, i.e., *Carex, Cyperus, Eleocharis,* and *Rhynchospora*). Some botanists (e.g., Wilson, Koyama) have recognized each of the sections at the generic level. Most American authors (Fernald, Schuyler), however, have recognized the genus in a broad sense; this traditional circumscription is accepted here. Although several researchers have lamented the "diverse" nature of the genus, most of the kinds of variation that are represented in *Scirpus* are also present in *Cyperus,* which

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FIGURE 1. *Scirpus* sect. JUNCO-SCIRPUS. a–h, *S. Tabernaemontani* (*S. validus*): a, underwater rhizome collected late in season, apex at right (note remains of shoot of current season and developing shoots of next year's growth), × ½; b, apex of culm with inflorescence, × 1; c, single spikelet with lower flowers past anthesis (filaments visible), upper ones with anthers visible and styles exserted, × 12; d, flower and subtending scale removed from spikelet, view of adaxial surface, stigmas exserted, anthers still included (note barbed bristles), × 20; e, flower, showing different maturation of stamens, the stamen to right with elongate filament and anther ready to dehisce, the middle stamen with anther fallen, the stamen to left before elongation of filament, × 12; f, spikelet at stage later than that in "c," immature achenes below and flowers with receptive stigmas above, × 6; g, mature achene with persistent bristles, × 12; h, same, in vertical section, fruit wall hatched, endosperm stippled, embryo unshaded (seed coat too thin to show), × 12. i, j, *S. cespitosus:* i, spikelet, lower flowers with persistent filaments, upper ones with exserted stigmas, involucral bracts greatly reduced, scalelike, spikelet solitary, × 6; j, achene with smooth bristles, × 12. k, l, *S. koilolepis:* k, solitary spikelet, subtended by scalelike involucre, scales keeled, × 6; l, mature, trigonous, bristleless achene, × 12. m–o, *S. Erismaniae:* m, basal flower in axil of leaf, × 6; n, achene from basal flower, × 12; o, achene from cauline spikelet, × 12. p, *S. cyperinus:* achene with elongate bristles, × 12.

has traditionally been maintained as one genus. Moreover, there has yet to appear a thorough study of *Scirpus* that presents compelling arguments for recognizing *Schoenoplectus* (Reichenb.) Palla, *Trichophorum* Pers., *Baeothryon* A. Dietr., and other segregate genera. Many useful papers on the taxonomy of single species or groups of species have been written by several authors, most notably Schuyler.

The achenes of species of *Scirpus* are probably dispersed after being eaten by waterfowl (McAtee) (wild ducks in the case of *S. paludosus* Nelson). Most are digested, but those that survive have 94 percent germination, compared with two or three percent for those treated with acid or alkali, and nine percent after fermentation treatment (Low). Light is required for germination (Isely). Achenes of many species, particularly *S. cyperinus* (L.) Kunth, are probably dispersed by the wind, although their long, contorted perianth bristles likely also cause them to cling to fur or feathers.

Some 30 species of *Scirpus*, representing six sections, occur in our area. Following is a brief account of these.

Species with leafy stems are classified in three sections. In all of these, leaves are borne along the length of the culm, while in plants of other sections they are basal. Schuyler (1961, 1962, 1963, 1964, 1966, 1967a, 1967b, 1967c, 1971b) has studied the species with leafy stems and has provided most of the available information on morphological variation, cytology, hybridization, and distribution.

Section SCIRPUS (sect. *Taphrogeton* (Reichenb.) Ascherson; plants leafy stemmed; spikelets in dense heads; achenes ellipsoid, with perianth bristles straight, about as long as the achenes) includes the type species, the Eurasian *Scirpus sylvaticus* L., $n = 31, 32$. The section is represented by seven species in our area, which fall into three groups. The first includes the North American relatives of *S. sylvaticus*, among which the only representative occurring in the Southeast is *S. expansus* Fern., $n = 32$. This bulrush grows mostly in the Northeast, but it ranges south in the Appalachians to northern Georgia and northern Alabama. A second eastern North American species, *S. microcarpus* Presl (*S. rubrotinctus* Fern.), $n = 33$, occurs southward to the uplands of West Virginia and also in western North America and eastern Asia.

The second group (leaves tristichous, spikelets in glomerules, plants typically viviparous, bristles straight) includes what was treated as *Scirpus atrovirens* Willd. by Fernald (1950). Schuyler (1967a, 1967b, 1967c) demonstrated that there are four species in this group that can be distinguished morphologically and separated geographically and phenologically. *Scirpus georgianus* Harper, $n = 25, 26, 27$, is the most common in our area (specimens examined from every state). It lacks a perianth and leaf cross veins (these are present in the more northern *S. atrovirens* Willd., $n = 28$, which is occasional in our area from the Ridge and Valley Province westward). *Scirpus Hattorianus* Makino, $n = 28$, is a northeastern species known in our area from only six collections from the uplands of North Carolina, Tennessee, and Alabama. *Scirpus flacidifolius* (Fern.) Schuyler, $n = 27$, is endemic to river bottoms in eastern Virginia and northeastern North Carolina.

The third group of sect. SCIRPUS (leaves distichous, spikelets in glomerules, plants not viviparous, bristles contorted) is represented by a single species in North America, *Scirpus polyphyllus* Vahl, $n = 29$, which is known from all the Southeastern States.

Section ANDROCOMA (Nees) Bentham (plants leafy stemmed; perianth bristles smooth, approximately as long as the subtending scales) is represented in our area by three species. *Scirpus pendulinus* Muhl. (*S. lineatus* auct., non Michx.), $n = 20$, has the greatest range of the three, occurring from Maine to Minnesota south to the Gulf Coast. *Scirpus lineatus* Michx. (*S. fontinalis* Harper), $n = 18$, is found along the Coastal Plain from Virginia to Florida; *S. divaricatus* Ell., $n = 14$, has a similar range but is found westward to Louisiana.

Section TRICHOPHORUM (Pers.) Darl., the wool grasses (plants leafy stemmed; perianth bristles contorted, several times longer than the achenes), comprises several species of cold-temperate regions. At maturity the elongate, crinkled bristles give the spikelets and the inflorescences a woolly appearance. Extensive hybridization in this group has resulted in a nomenclatural mire of species, varieties, and forms. Schuyler (1962, 1967a) has carefully documented infraspecific variation, cytology, and hybridization; he concluded that only a single species, *Scirpus cyperinus* (L.) Kunth (including *S. rubricosus* and *S. eriophorum* Michx.), $n = 33$, should be recognized in the Southeast. Three others that hybridize with *S. cyperinus*, *S. pedicellatus* Fern., $n = 34$; *S. Longii* Fern.,[3] $n = 33$; and *S. atrocinctus* Fern., $n = 34$, occur in the Northeast.

Section OXYCARYUM (Nees) Beetle (plants rhizomatous; heads of spikelets ovoid, pedunculate; scales acute, excurved) is represented in the Southeast by a single species, *Scirpus cubensis* Poeppig & Kunth. In our area the species occurs from southern Florida to Louisiana in brackish or freshwater marshes. The affinities of this section are unclear, and no chromosome counts are available.

Section BOLBOSCHOENUS (Ascherson) Beetle (plants tall; spikelets large, few; scales awned, pubescent) is represented in our area by two species of freshwater or tidal wetlands. *Scirpus robustus* Pursh grows in tidal marshes and estuaries from eastern Canada to Texas. A second species, *S. cylindricus* (Torr.) Britton, occurs in marshes from Delaware to Georgia. It was confused with *S. robustus* and *S. etuberculatus* until it was restudied by Schuyler (1975). The third species, *S. etuberculatus* (Steudel) Kuntze, grows in brackish waters and is known near the coast from Delaware to Louisiana. It is morphologically transitional to the next section (Fernald, 1950).

Section JUNCO-SCIRPUS Syme[4] (sect. *Pterolepis* Beurl., sect. *Schoenoplectus* (Reichenb.) Bentham) (plants tall; culms often leafless; involucral leaves 1 or 2, more or less erect; achenes sessile, beaked, with bristles persistent) is represented in the Southeast by seven species. *Scirpus pungens* Vahl (*S. americanus*

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[3] Reported from North Carolina by Cappel and Radford and colleagues. I was unable to locate any specimens to substantiate this. According to Schuyler (1962; pers. comm.), records of *S. Longii* from south of New Jersey were the result of misidentifications of *S. cyperinus*.

[4] *Scirpus* sect. JUNCO-SCIRPUS Syme in Sowerby, Engl. Bot. ed. 3. **10:** 62. 1870. LECTOTYPE SPECIES (here designated): *S. lacustris* L. Syme included three species in this section, *S. lacustris*, *S. triqueter* L., and *S. pungens* Vahl; *S. lacustris* is the only one with terete culms suggesting those of plants of the genus *Juncus* L., a feature emphasized by the sectional name.

auct., non Pursh), $n = 39$, of sunny wetlands, is widespread in temperate North America and occurs in all the southeastern states. It is closely related to *S. americanus* Pursh (*S. Olneyi* Gray), $n = 39$, a taller, thicker-stemmed species of tidal, alkaline, or saline marshes from Massachusetts to Florida and west to southern California. The two species occasionally hybridize in brackish upper edges of tidal marshes, but in general they are isolated ecologically. A recently described species, *S. deltarum* Schuyler, $n = 39$, occurs in the Mississippi Delta region, the Mobile Bay area, and disjunctly in the prairie marshes of eastern Kansas and Missouri. A fourth species, *S. subterminalis* Torrey, $n = 37$, is widespread in eastern North America but is known in the Southeast from only a few collections from the Coastal Plain and Piedmont of North and South Carolina. Two growth forms exist: submersed, in which the leaves are filiform and flaccid, and terrestrial or stranded, in which they are conduplicate and stiff (Schuyler, 1972b). The highly reduced inflorescence consists of a single spikelet subtended by one erect involucral bract. The species has an unusual photosynthetic metabolism: the tissues of the stem, leaf, and rhizome accumulate malic acid at night, providing a reservoir of fixed carbon for photosynthetic reactions during daylight (Beer & Wetzel). Such physiology is similar to that of terrestrial plants having crassulacean-acid metabolism.

The remaining three species of sect. JUNCO-SCIRPUS were once segregated as sect. *Pterolepis* (Fernald, 1950). These reportedly differ in having plumose bristles and pedunculate clusters of spikelets. However, on a worldwide basis several extraregional species are intermediate with respect to these two characters; Koyama (1963) therefore concluded that the two sections should be merged. *Scirpus Tabernaemontani* Gmelin (*S. validus* Vahl), $n = 21$, grows in freshwater marshes nearly throughout the United States and southern Canada and in much of the Old World; it is common throughout the Southeast. *Scirpus acutus* Bigelow, $n = 19$, a species of the Midwest and Great Plains, is represented in our area by a few collections from North Carolina and Tennessee. Dabbs studied these two species in Saskatchewan and found that they were morphologically distinct. Hybrids were occasionally found, but these were sterile and spread only by rhizomes. A western species, *S. californicus* (C. Meyer) Steudel, $n = 34$, is known from a few places in Louisiana, Mississippi, and South Carolina. Other North American species of *Scirpus* lack its plumose perianth bristles. *Scirpus heterochaetus* Chase, $n = 19$, might be found in the northwestern part of our area; it is a species of quiet calcareous waters of the St. Lawrence and upper Mississippi drainages.

Section BAEOTHRYON Dumort.[5] (plants caespitose, often forming tussocks; leaves basal; inflorescences of a single terminal spikelet; involucral bract greatly reduced, resembling a fertile scale of the spikelet) is represented by four species in northeastern North America. Only one of these, the circumboreal *Scirpus cespitosus* L., reaches our area, growing in the grassy balds of the high mountains of North Carolina, Georgia, and Tennessee. The southeastern populations are disjunct from the nearest occurrences of the species in the northeastern United

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[5] *Scirpus* sect. BAEOTHRYON Dumort. Fl. Belg. 143. 1827. Fernald (1947, 1950) and other authors have attributed the sectional name to Endlicher (Gen. Pl. 118. 1836).

States (in the Adirondack Mountains of New York) by some 1200 km. A widespread but easily overlooked species of the northeastern and midwestern United States, *S. verecundus* Fern., has not yet been collected in our area but might occur in the uplands of North Carolina, Tennessee, or Arkansas. It is perhaps the most mesic species of the genus in North America, inhabiting dry woodlands and basic ledges, in contrast to the aquatic habitats of most species of *Scirpus*.

Section ISOLEPIS (R. Br.) Griseb. (plants annual; inflorescences unbranched; spikelets sessile, few) is represented in our area by five species. *Scirpus koilolepis* (Steudel) Gleason probably occurs in all the states in our area, as well as in the Midwest and the Great Plains. The remaining species are much less frequent and are local in range. *Scirpus Erismaniae* Schuyler, $n = 5$, is recorded from Georgia, western Florida, and Alabama. This species produces basal spikelets on very short culms (see FIGURE 1), as do several African species of this section (Haines). *Scirpus molestus* M. C. Johnston, described from Texas, also occurs in southern Louisiana. The remaining species have perianth bristles (in most collections) and have been distinguished by some authors (e.g., Fernald, 1950) as sect. *Actaeogeton* (Reichenb.) Beetle. *Scirpus Hallii* Gray, $n = 11$, known from widespread localities in the eastern United States, has been collected in Georgia; and *S. Purshianus* Fern., $n = 19$, a primarily northeastern species, is known in the Southeast from North and South Carolina, Tennessee, and Georgia.

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2. **Eriophorum** Linnaeus, Sp. Pl. **1:** 52. 1753; Gen. Pl. 27. 1754.

Small to medium-sized, single-stemmed or loosely caespitose [densely caespitose or tussock-forming] perennials of bogs, swamps, and pocosins. Roots fibrous; rhizomes short, horizontal to oblique. Culms terete or nearly so, glabrous. Leaves basal and cauline; sheaths glabrous, ligules lacking; blades flat [conduplicate], the midrib conspicuous, the margins scabrellate, especially distally; chlorenchyma not radiate; air chambers present. Inflorescences of 1 to several sessile or pedunculate spikelets; bracts 1–6, closely spaced at the summit of the culm, oblique or slightly reflexed [ascendent to erect], sheaths very short, blades leaflike; rays short [elongate and drooping or absent]. Spikelets oblong-ovoid; empty basal scales 3–5[–15]. Scales 50–150, oblong-ellipsoid, acute to obtuse, 1- to 5-nerved, deciduous after the achenes mature. Flowers perfect. Perianth bristles [6 to] 12 to ca. 50, about equaling the scales at anthesis but elongating greatly as the achenes mature. Stamens 1 [or 2 or 3]; filaments flattened; anthers linear [ellipsoid], the apices of the connectives not prolonged. Styles capillary, glabrous; stigmas 3, about as long as the style. Achenes trigonous, slightly compressed dorsiventrally, oblong-ellipsoid (widest in distal half), the apex obtuse, apiculate, the base sessile, the surface smooth, glossy. Embryos more or less turbinate [obconical or ellipsoid], the radicle sublateral. Base chromosome number 29. TYPE SPECIES: *E. vaginatum* L.; see Britton & Brown, Illus. Fl. No. U. S. Canada, ed. 2. **1:** 322. 1913. (Name from Greek, *erios,* cotton or wool, and *phoros,* bearing, in reference to the cottony mature inflorescence.)—COTTON-GRASS, BOG-COTTON.

A genus of about 12 species of boreal regions. About eight species are circumpolar, occurring in both northern Eurasia and northern North America. There is relatively little endemism. Only *Eriophorum virginicum* L. occurs in the Southeast; it ranges from Newfoundland to Minnesota southward and is known in our area from a few scattered collections made in the mountain bogs of North Carolina and Tennessee and the Coastal Plain swamps of North Carolina, South Carolina, and Georgia (southern limit in the Okefenokee Swamp). No species of the genus is reported from Missouri or Kentucky, and only *E. virginicum* occurs in Virginia and West Virginia.

A few workers (e.g., Koyama) have treated the cotton grasses as constituting *Scirpus* sect. *Vaginati* (Andersson) Koyama, but most have kept *Eriophorum* separate from *Scirpus.* The two genera are readily distinguished by the number and the length of the perianth bristles. *Eriophorum* is divided into two sections (Goncharov *et al.*), each with about six species: sect. ERIOPHORUM (sect. *Vaginati* Andersson) contains those species in which the inflorescence is a single sessile spike, while sect. PHYLLANTHELA Andersson comprises those (including *E. virginicum*) in which the inflorescence consists of several pedunculate spikes.

The genus is almost uniform cytologically; ten of the 12 species have been counted as $n = 29$. Two are $n = 27$, and in the case of *Eriophorum angustifolium* L., $n = 29$ and $n = 35$ have been reported.

Hybridization is known among both the Eurasian and the North American species. Although it is generally not difficult to distinguish *Eriophorum virginicum* from the other members of the genus, there are species pairs that appear to intergrade—for example, *E. angustifolium* and *E. viridicarinatum* (Engelm.) Fern. It is surprising that the genus has not received more systematic study, considering its broad distribution.

The circumboreal *Eriophorum alpinum* L., $n = 29$, was placed in *Scirpus* (as *S. hudsonianus*) by Fernald. Following a survey of epidermal features of achenes of *Scirpus* and *Eriophorum,* Schuyler concluded that the species belongs in *Eriophorum.* Its chromosome number also supports this placement.

In the Arctic, species of *Eriophorum* are dominant and sometimes form a vegetation type known as "tussock tundra." The plants provide an important forage for deer and caribou in North America and for sheep, ponies, and reindeer in northern Europe and Asia. In the United States the plants are seldom dominant (except in alpine grasslands in limited montane areas). However, they sometimes form a conspicuous element of fen and bog vegetation because of their showy fruiting heads.

Wein summarized ecological information about *Eriophorum vaginatum,* a circumboreal tussock-forming species. Species of *Eriophorum* occurring in the eastern United States are rhizomatous or rather loosely caespitose. There is much information on the autecology and physiological ecology of the genus, although nearly all is derived from studies of *E. vaginatum.*

Despite its abundance in arctic regions, *Eriophorum* has conspicuously few insect herbivores. Larvae of the cottongrass moth, *Celaena haworthi* Curtis, tunnel in the culms of *E. vaginatum* in Europe, but no macrolepidopteran species is reported to feed on *Eriophorum* species in North America (Tietz). The aphid *Rhopalosiphum eriophori* (Walker) is reported on *E. angustifolium* and *E. vaginatum.* The larvae of the beetle *Plateumaris discolor* (Panzer) live in anaerobic conditions among the roots of *E. vaginatum* in Europe, obtaining needed oxygen by tapping into the intercellular air spaces in the cortex of the roots.

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3. **Fuirena** Rottboell, Descr. Icon. 70. 1772.

Rhizomatous perennials or caespitose annuals of sunny, wet, often disturbed soils. Rhizomes horizontal, covered with persistent lanceolate scales, producing cormlike axillary offshoots from which new culms arise. Culms erect or slightly inclined, unbranched, terete, hollow. Leaves with sheaths tubular, costate, pubescent, barely reaching to decidedly separated from the base of the next sheath, the ligules hyaline, hispid (or glabrous) apically; basal leaves bladeless, cauline leaves with blades lanceolate to linear, flat or slightly conduplicate [crescentiform], pubescent (blades absent or reduced to an awned apex of the sheath in 1 species); stomata paracytic; chlorenchyma not radiate. Inflorescences of 1 to several sessile or pedunculate glomerules in the axils of the upper leaves; rays lacking or 1–4, smooth or hispidulous. Spikelets 1–6, ovoid to oblong. Scales 30–60(–100 or more), ovate to oblong, widest at or above the middle, hispid adaxially, less often glabrous or glabrescent, 3- to 9-nerved, the 3 central nerves prolonged into a cuspidate, straight, or excurved apex ⅕ as long as to nearly equaling the length of the body of the scale, the 3 basal scales sterile, longer, narrower, and more conspicuously awned than the fertile ones. Flowers perfect, protogynous. Perianth biseriate [uniseriate or absent], outer whorl (sepals) of 3 smooth or retrorsely scabrellate bristles, ¼ to nearly as long as the achene; inner whorl (petals) of bristles bearing expanded, entire [fimbriate], hyaline to somewhat spongy blades with obtuse, acute, aristate, or emarginate apices. Stamens 3 (infrequently 1, 2, or 6); filaments ribbonlike, about as long as the subtending scale; anthers linear to ellipsoid; pollen grains uniaperturate, obovoid to subspheroidal, psilate, trinucleate. Styles linear, frequently hispid; stigmas 3, linear, about as long as the styles, pubescent. Achenes trigonous with conspicuous ridged angles, ellipsoid, the apex acute but not apiculate, the base stipitate (usually conspicuously so), the faces flat to slightly concave, delicately striate or smooth [cancellate], glossy. Embryo fungiform. Base chromosome number 23. (Including *Vaginaria* Persoon.) LECTOTYPE SPECIES: *F. umbellata* Rottb.; see Britton & Brown, Illus. Fl. No. U. S. Canada, ed. 2. **1:** 337. 1913. (Named for Joergen Fuiren, 1581–1628, Danish physician.)

A warm-temperate and tropical genus of about 30 species. Seven occur in the Southeast; these are well known through Kral's recent revision. An additional three occur in the southwestern United States. *Fuirena repens* Boeck. is endemic to Mexico, while five primarily South American species extend northward into Central America, Mexico, and the West Indies. About 12 species occur in South America, and about as many in Africa. Only *F. umbellata* is recorded in Europe, and it is limited to the southern part of the continent. Five species occur in southern Asia, but none is recorded from the Soviet Union.

Most of our species are distributed from Texas to Florida along the Gulf Coastal Plain and northward on the Atlantic Coastal Plain. *Fuirena scirpoidea* Michx. and *F. longa* Chapman occur only as far north as southern Georgia, *F. breviseta* Cov. as far as eastern Virginia, *F. squarrosa* Torrey north to Long Island, and *F. pumila* to Cape Cod. The last species is disjunct in southern Michigan and northern Indiana. Two others in our area, *F. Bushii* Kral and *F. simplex* Vahl, are southern Great Plains species that occur eastward to Louisiana, Arkansas, and Missouri.

All of the southeastern species have haploid chromosome numbers of 23. The only exception is *Fuirena simplex,* for which $n = 15$ has been reported from Texas populations, in addition to $n = 23$ from southeastern representatives (Kral).

Plants of *Fuirena* have no reported economic significance in North America, although *F. glomerata* Lam. and *F. umbellata* have been reported as important weeds in Borneo, India, Taiwan, and Malaysia (Holm *et al.*).

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HOLM, T. Studies in the Cyperaceae. V. *Fuirena squarrosa* Michx. and *F. scirpoidea* Vahl. Am. Jour. Sci. **154:** 13–26. 1897. [Morphological and anatomical study of two species of the Southeast; illustrations.]

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4. **Eleocharis** R. Brown, Prodr. 224. 1810.

Small to medium-sized, loosely to densely caespitose or single-stemmed, rhizomatous or stoloniferous, submersed, emergent, or littoral perennials (rarely annuals) of marshes, ditches, and pond and river shores. Roots fibrous; rhizomes (lacking in some species) slender, horizontal, covered with appressed ovate to lanceolate scales. Culms terete or ellipsoid (less often trigonous, quadrangular, or flattened), solid or hollow (sometimes with thin transverse parenchymatous septa), smooth, with numerous paracytic stomata (submersed lower portions of culms with few or no stomata); in submersed species secondary branches present, very closely spaced and seemingly verticillate. Leaves 1–4; sheaths closely fitting the base of the culm, the summit firm or scarious (sometimes apiculate); blades lacking. Inflorescences single spikelets terminating the culms. Spikelets slenderly cylindrical to ovoid, slightly less than to about 3 times thicker than the summit of the culm. Scales (2–)20–100, oblong, lanceolate, obovate, or orbiculate, hyaline, firm, or coriaceous, strongly to weakly nerved or nerveless, deciduous or persistent. Flowers perfect. Perianth bristles (3–)6(–12) or absent, extrorsely or retrorsely barbed or smooth, persistent on the base of the mature achene or falling from it. Stamens 3; filaments hyaline, about equaling to shorter than the subtending scale; anthers ellipsoid to linear; pollen grains 1- [to 4-]aperturate, obovoid to subspheroidal, psilate (scabrellate), trinucleate. Styles with swollen, bulbous base; stigmas 2 or 3, capillary. Achenes lenticular or trigonous, ovoid, obovoid, or ellipsoid, the base broadly rounded, the apex capped by a small to large, pyramidal, conical, or swollen tubercle, the surface smooth or variously reticulate, dull, frequently glossy, or iridescent. Embryos turbinate to fungiform. Base chromosome number 5. TYPE SPECIES: *E. palustris* (L.) Roemer & Schultes (*Scirpus palustris* L.); see Britton & Brown, Illus. Fl. No. U. S. Canada, ed. 2. **1:** 310. 1913. (Name from Greek, *helos,* marsh, and *charis,* grace, from the paludal habitat of most species.)—SPIKE-RUSH, DOG'S-HAIR GRASS.

A genus of about 250 species, worldwide in distribution. *Eleocharis* is evidently closely related to *Scirpus* but is distinguished by its leafless culms and its single, erect, terminal spikelets. Although the apical tubercles of the achenes of *Eleocharis* are similar to those of some species of *Fimbristylis* Vahl, suggesting that *Eleocharis* is most closely related to that genus (Svenson, 1929), recent evidence supports a closer relationship between *Scirpus* and *Eleocharis.* Both of these genera have non-kranz anatomy, while *Fimbristylis* has kranz anatomy (Metcalfe). The embryos of *Eleocharis* (turbinate to fungiform, radicle basal, coleoptile lateral) are similar to those of species in *Scirpus* sect.

Bolboschoenus (Van der Veken), rather than to those of *Fimbristylis* (turbinate to fungiform, radicle lateral, coleoptile basal).

Some 40 species occur in the Southeast, and many of these have rather wide ranges. Holarctic, neotropical, and pantropic groups are represented in our area. Svenson's (1929, 1957) division of the genus into seven series has received wide acceptance, and our species are presented here according to his classification. The two largest are ser. Eleocharis (ser. *Palustriformes* Svenson) and ser. Tenuissimae Svenson, having 13 and ten species in our area, respectively.

Plants of ser. Eleocharis are characterized by slender culms and a stoloniferous habit; there are both tristigmatic and distigmatic species. Our representatives are mostly northeastern species that occur southward only as far as Virginia, Tennessee, or Arkansas. However, *Eleocharis fallax* Weatherby, $2n = 42$, and *E. arenicola* Torrey, $2n = 20$, both of the Coastal Plain, are found in most of the Southeastern States. *Eleocharis montevidensis* Kunth, $2n = 10, 20$, is a neotropical species that has been found north to the Carolinas and California; it is sometimes treated as conspecific with *E. arenicola.*

Plants of ser. Tenuissimae are loosely caespitose and have slender, wiry culms. Our species are mostly restricted to the Coastal Plain. In the Southeast the neotropical *Eleocharis nana* Kunth has been found only in southern Florida, while *E. nodulosa* (Roth) Schultes occurs along the Gulf Coast from Florida to Louisiana. The most widely distributed of our species, *E. tuberculosa* (Michx.) Roemer & Schultes, $2n = 30$, is found throughout the Southeast northward to Nova Scotia. It is distinctive in having perhaps the largest tubercle in any species of the genus—as large as the body of the mature achene.

Plants of ser. Mutatae Svenson are the tallest in the genus; three of our species regularly reach 1 m. The plants are characterized by spikelets that are barely wider than the apices of the subtending culm and that have persistent scales. The plants are unusual ecologically because they grow in ponds or pools with a stable water level. Most other species of the genus grow where receding water levels leave the plants exposed in summer. Species of ser. Mutatae have very high chromosome numbers. Briggs has made counts for the Australian *Eleocharis equisetina* Presl, $2n = 172$, and *E. sphacelata* R. Br., $2n = 94$–100, 140, 180, 188. Six species of the series occur in our area: *E. equisetoides* (Ell.) Torrey and *E. quadrangulata* (Michx.) Roemer & Schultes are reported throughout the Southeast and range north to southern New England; *E. cellulosa* Torrey, *E. interstincta* (Vahl) Roemer & Schultes, and *E. elongata* Chapman are restricted to the Coastal Plain; and *E. Robbinsii* Torrey, a species mainly of the Northeast, ranges south to Virginia and northern Florida along the Coastal Plain. Tubers of *E. dulcis* (Burman f.) Trin. ex Henschel, $n =$ ca. 100, provide the familiar water chestnut of Oriental cuisine. The juice of the tubers is strongly antibiotic (Hegnauer). The species is closely related to the eastern North American *E. equisetoides,* and the pair serve as an example of the eastern Asian–eastern North American pattern of disjunction (Wood).

Species of ser. Pauciflorae Svenson are tiny plants with few-flowered spikelets. *Eleocharis parvula* (Roemer & Schultes) Link, $2n = 8, 10$, *E. rostellata* Torrey, and *E. melanocarpa* Torrey occur in the Southeast, and all have broad ranges in our area.

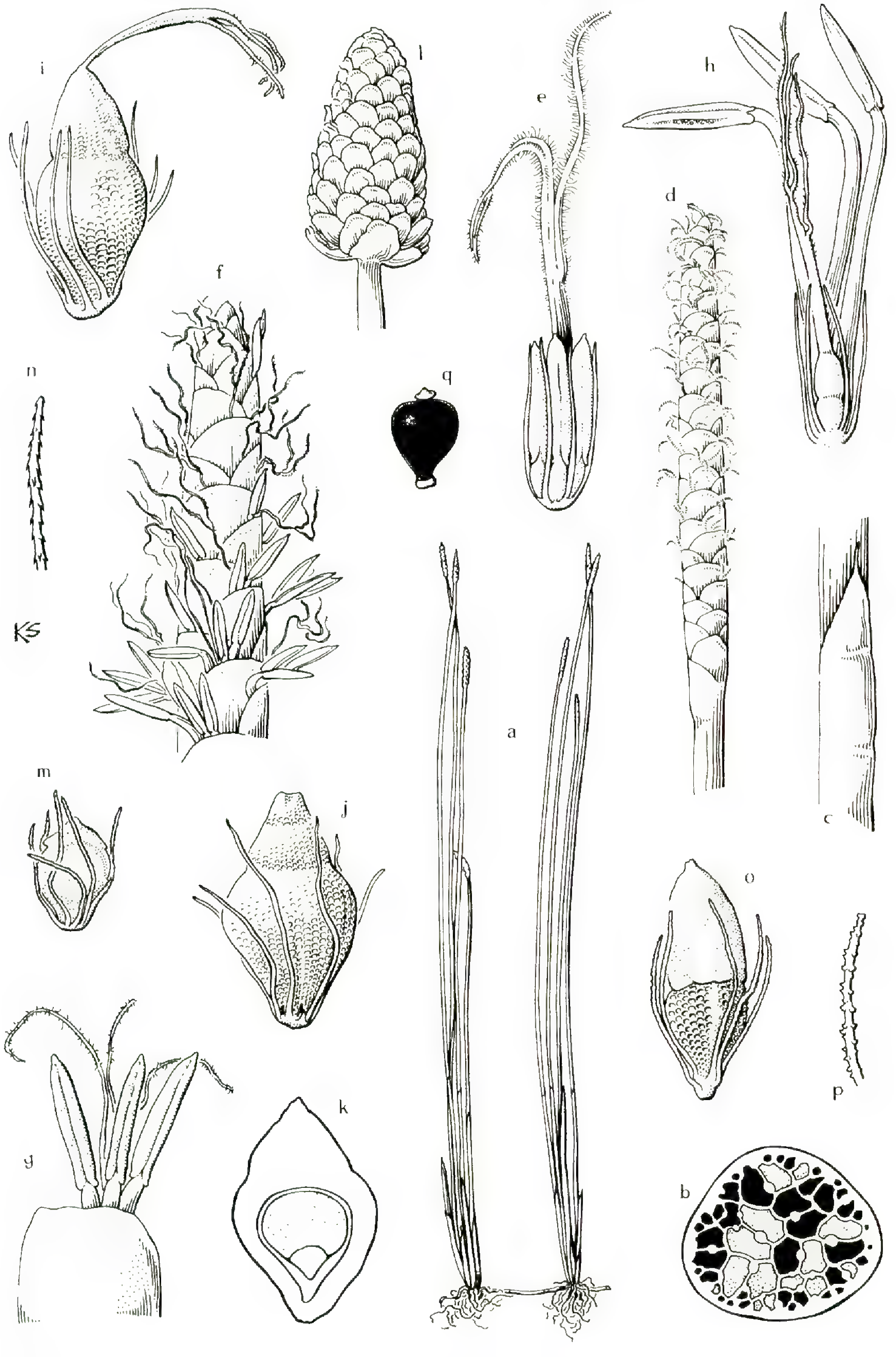

FIGURE 2. *Eleocharis.* a–k, *E. cellulosa:* a, habit of stoloniferous plants, × ¼; b, cross section of culm, showing air spaces (black) with cross partitions (stippled—cellular detail too small to be shown), × 10; c, detail of culm with apex of bladeless sheath, × 2; d, spike of flowers in carpellate phase (flowers protogynous), styles protruding (note flowers with either 2 or 3 stigmas), × 2; e, abaxial side of flower, stigmas receptive, filaments

Plants of ser. ACICULARES Svenson are also small. Three species occur in our area, and their contrasting distribution patterns are notable. The northern *Eleocharis Wolfii* Gray is found southward to Tennessee and Louisiana, while the neotropical *E. radicans* (Poiret) Kunth ranges northward to Virginia and Oklahoma. However, *E. acicularis* (L.) Roemer & Schultes, $2n = 20$, 30–38, 50–58, a widespread north-temperate species, is reported from throughout eastern North America. Both emergent and submersed growth forms of *E. acicularis* have been described. Submersed plants have three large lacunae per culm, while emergent plants have about ten small ones. These forms are genetically identical and fully interconvertible, as is demonstrated by reciprocal transplants (Rothrock & Wagner). The plants are able to grow in acidic runoff from Appalachian coal mines and flourish in streams with pH as low as 2.8. This is odd and suggests some overlooked variability in the species, because in northern Europe it nearly always occurs in basic waters (Iversen).

The plants of ser. OVATAE Svenson have broadly ellipsoid to ovoid spikelets. Three species are in our area: *Eleocharis obtusa* (Willd.) Schultes, $2n = 10$, in every Southeastern State, is one of the commonest spike-rushes in eastern North America; the closely related *E. Engelmannii* Steudel, $2n = 10$, occurs from Georgia and Missouri south to the Gulf Coast; and *E. lanceolata* Fern. is a southwestern species that just extends into our area in Arkansas and Louisiana.

Plants of ser. MACULOSAE Svenson are characterized by dark purple to black, biconvex achenes. Some species grow submersed, while others are found in littoral habitats. There are four species in our area: *Eleocharis caribbaea* (Rottb.) Blake is pantropic (northward to South Carolina and Texas); *E. olivacea* Torrey, $2n = 20$, is endemic to the Coastal Plain from Virginia to Florida; *E. atropurpurea* (Retz.) Kunth is widely but sporadically distributed in the Southeast (but otherwise is found throughout temperate and tropical regions of both the Old and New Worlds); and *E. flavescens* (Poiret) Urban is neotropical, growing north along the Coastal Plain to Delaware.

Plants of ser. WEBSTERIA (S. H. Wright) G. Tucker[6] are submersed, flaccid,

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[6] *Eleocharis* ser. WEBSTERIA, comb. nov., based on *Websteria* S. H. Wright, Bull. Torrey Bot. Club **14:** 135. 1887.

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of stamens not yet elongated, 4 of 6 perianth bristles visible, × 10; f, apex of spikelet, carpellate phase past, lower flowers with protruding stamens, × 5; g, flower in staminate phase with apex of subtending scale, × 10; h, abaxial view of flower in staminate phase (note 4 of 6 perianth bristles, ovary with enlarged stylar base), × 10; i, adaxial view of mature achene with persistent stylar base and smooth perianth bristles, achene lenticular, × 12; j, mature achene, abaxial view, × 12; k, longitudinal cross section of achene (tubercle, pericarp, seed coat, and basal embryo unshaded, endosperm stippled), × 12. l–n, *E. obtusa:* l, spikelet with mature achenes (hidden by subtending scales, few stigmas visible at upper left), × 5; m, abaxial side of mature achene crowned by tubercle (persistent style base) and with perianth bristles, × 12; n, detail of perianth bristle to show retrorse barbs, × 25. o, p, *E. tuberculosa:* o, abaxial side of mature achene (trigonous in cross section) with tubercle, × 12; p, detail of perianth bristle, × 25. q, *E. atropurpurea:* abaxial side of mature achene (lenticular in cross section) with tubercle, perianth bristles absent, × 25.

slender-branched plants of shallow, still waters. There are one or perhaps two pantropic species (Eiten, 1976b). *Eleocharis confervoides*[7] is an uncommon plant of cypress swamps and lakes in Florida, southern Alabama, southern Georgia, and Louisiana. It is also known from widely scattered localities in the neotropics and in tropical Africa and Sri Lanka. The species has been variously placed in *Rhynchospora* Vahl (Bentham; Kükenthal, 1948), *Scirpus,* and the monotypic *Websteria.* The slender, leafless culms are similar to those of other species of *Eleocharis.* Additional submersed one-flowered species of *Eleocharis* occur in Brazil and Africa (Nelmes). At anthesis, the one-flowered spikelets of *E. confervoides* are exserted just above the water surface. The achenes lack the differentiated tubercle of most species of *Eleocharis,* but the embryos are typical of the genus (Van der Veken).

Rikli reported that the inner parenchymatous layer was absent from the bundle sheaths in many species of *Eleocharis,* a feature on which he based the segregate genus *Chlorocharis.* Metcalfe could not confirm this in any species including those investigated by Rikli but suggested that further study might be profitable.

Chromosomes of *Eleocharis* have been extensively studied. Cytologically, the genus is the best known in the Cyperaceae. Most species have the diffuse centric condition typical of the family; some have holocentric chromosomes (Battaglia). Although aneuploidy has been frequent in most other genera of Cyperaceae, polyploidy has been important in the evolution of this genus. Several species have tetraploid (and sometimes hexaploid) races or subspecies. Strandhede (1965, 1966) studied about 1100 European populations of species of ser. ELEOCHARIS (ser. *Palustriformes*) and reported that chromosome breakage and refusion were common. Most species had several cytotypes, and various kinds of multivalents were frequent at meiosis. Heterovalents formed in meiosis, and aberrant but apparently viable gametes were often observed. Similar reports of chromosomal variability have been made for North American species. Karyotypic rearrangements have been noted in *Eleocharis flavescens* (Poiret) Lam., which had 30 chromosomes in various combinations of univalents, bivalents, tetravalents, and ring complexes (Schuyler, 1977).

When the sample size is large, chromosome number can be correlated with morphology within species and between species pairs. For example, the European *Eleocharis uniglumis* (Link) Schultes consists of two subspecies that differ in ecology and in features of the spikelet scales. Subspecies *uniglumis* has $n = 46$, while subsp. *Sterneri* Strandhede has $n = 74$–82. Apparently, the latter taxon was derived from the former by tetraploidy followed by fusion of some of the chromosomes, but fusion of different chromosomes in different populations has also resulted in mixoploidy. In some cases affinities between species can be confirmed cytologically. For example, *E. Engelmannii* Steudel and *E. obtusa* are both $n = 5$ and have very similar karyotypes.

Species with different chromosome numbers are known to hybridize in the wild. Some hybrids (e.g., *Eleocharis mamillata* × *E. palustris* subsp. *palustris*)

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[7] *Eleocharis confervoides* (Poiret) G. Tucker, comb. nov., based on *Scirpus confervoides* Poiret in Lam. Encycl. Méth. Bot. **6**: 755. 1804.

have greatly reduced fertility, while others (e.g., *E. palustris* subsp. *palustris* × subsp. *vulgaris*) have fertility comparable to that of the parent species.

Several species are important weeds, especially of rice fields.

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5. **Fimbristylis** Vahl, Enum. Pl. **2**: 285. 1805.

Small to medium-sized annuals or perennials of disturbed, open, wet habitats. Roots fibrous; rhizomes regularly present in some species. Culms slender, terete or nearly so, glabrous. Leaves all basal; sheaths smooth or pubescent, with ligule present or not, glabrous or ciliate; blades linear to filiform, flat, conduplicate, or involute, glabrous or pubescent, the margins glabrous or scabrellate; chlorenchyma radiate; bundle sheaths 3-layered ("*Fimbristylis* type"). Inflorescences terminal, branched (rarely sessile, capitate); bracts 1–6, erect to oblique, the sheaths greatly reduced to essentially absent, the blades leaflike; primary rays absent or 1–10, glabrous or scabrellate, secondary rays regularly produced in some species. Spikelets single or in clusters of 2–5, ovoid to lanceolate. Scales 5–100, ovate to oblong, obtuse or acute, blunt or mucronate [aristate], glabrous or puberulent abaxially, 1- to 5-nerved medially, nerveless laterally, deciduous at maturity. Flowers perfect. Perianth lacking. Stamens (1, 2, or) 3; filaments about as long as the subtending scales, flattened; anthers oblong, the apices of the connectives sometimes prolonged; pollen grains uniaperturate, obovoid, subspheroidal, or spheroidal, scabrate, trinucleate. Styles slender, terete throughout or trigonous basally, usually fimbriate distally, deciduous from the mature achene; stigmas 2 (or 3), about as long as the style, glabrous. Achenes lenticular or trigonous, ovoid, oblong, or obovoid, the apex broadly rounded to subacute, apiculate or not, the base cuneate or stipitate, the surface smooth, warty, or reticulate with isodiametric or horizontally arranged rectangular cells, these cells concave or with a central papilla. Embryos turbinate, radicle lateral, coleoptile basal. Base chromosome number 5. TYPE SPECIES: *F. dichotoma* (L.) Vahl, *typ. cons.* (Name from Latin *fimbria,* fringe, and *stylus,* style, referring to the fringed style of most species.)

A genus of about 200 species, mainly pantropic but also well represented in warm-temperate regions. Most of the species grow in disturbed wet habitats, especially roadsides and croplands. The center of diversity is southeastern Asia (Goetghebeur & Coudijzer). Thirteen species are recorded from the United States. Twelve of these occur in the Southeast, while *Fimbristylis thermalis* S. Watson is endemic to California, Arizona, and Nevada (Kral). Kral's thorough monograph includes illustrations and chromosome counts for all species in North America.

Fimbristylis is closely related to *Bulbostylis* and *Abildgaardia.* Chromosome numbers in the three genera are based on five (Gordon-Gray, Kral), and their kranz anatomy is similar (three-layered bundle sheaths). Such anatomy is not reported in any other genera of the Cyperaceae (Metcalfe; Raynal, 1972). The three genera have been distinguished from the remainder of the Scirpeae as tribe Abildgaardiae Lye (Fimbristylideae Raynal).

Koyama (1961) treated *Bulbostylis* as a subgenus of *Fimbristylis,* while Kral recognized three genera, *Bulbostylis, Abildgaardia,* and *Fimbristylis.* Additional information supports Kral's belief. Gordon-Gray made a careful study of the southern African representatives of the three genera. *Abildgaardia* can be distinguished from *Bulbostylis* and *Fimbristylis* by its distichous spikelet scales. *Bulbostylis* and *Fimbristylis* are separated by a suite of characters. The embryos are consistently different (in *Fimbristylis* the radicle is lateral, the coleoptile basal; in *Bulbostylis,* the radicle is basal and the coleoptile lateral), although there is no single morphological character that separates the two genera. The styles of *Fimbristylis* are usually fimbriate (occasionally entire) and are deciduous, while those of *Bulbostylis* are always entire and have a persistent base. The spikelet scales of *Fimbristylis* are generally glabrous, while those of *Bulbostylis* are generally puberulent. The ligules of *Fimbristylis* are glabrous, while those of *Bulbostylis* are hispid. Species of *Fimbristylis* always lack intraprophyllar buds at the base of the inflorescence rays, while such buds are frequently present in *Bulbostylis* (Guaglianone). Species of the two genera differ in surface ornamentation of the achenes. Goetghebeur & Coudijzer examined about 100 species from throughout the world and found that the epidermal cells of *Fimbristylis* are horizontally elongate (infrequently isodiametric) and in vertical bands, but those of *Bulbostylis* are vertically elongate in horizontal bands. The two genera also differ in habit and habitat: *Fimbristylis* species are mostly perennials of moist soils, while *Bulbostylis* species are generally annuals of dry sandy soils.

Svenson recognized two sections in *Fimbristylis*; Kral did not comment on the infrageneric classification. Plants of sect. FIMBRISTYLIS (sect. *Dichelostylis* Bentham) have two stigmas, lenticular achenes, and styles commonly fringed apically. This section includes eleven of the fourteen species of the southeastern United States. Most of our species are somewhat weedy plants of disturbed wet habitats: *Fimbristylis tomentosa* Vahl, $n = 5$; *F. dichotoma* (L.) Vahl, $n = 10, 15$; *F. decipiens* Kral, $n = 10$; *F. annua* (All.) Roemer & Schultes, $n = 15$; *F. Vahlii* (Lam.) Link, $n = 10$; *F. puberula* (Michx.) Vahl, $n = 10, 20$; and *F. perpusilla* Harper, $n = 5$. In general these are widely distributed in the Southeast. *Fimbristylis perpusilla,* endemic to southeastern North America, is a notable exception. Kral knew of only two localities in southwestern Georgia for this tiny annual. Recently, the species has been reported in Horry County, South Carolina (Leonard) and in eastern Maryland (Schuyler, pers. comm.). The four remaining southeastern species of sect. FIMBRISTYLIS, *F. caroliniana* (Lam.) Fern. ($n = 10, 20, 30$), *F. schoenoides* (Retz.) Vahl ($n = 5$), *F. spathacea* Roth ($n = 24$), and *F. castanea* (Michx.) Vahl ($n = 10$), are tall plants of tidal marshes.

Plants of sect. TRICHELOSTYLIS Bentham have three stigmas, lenticular achenes, and entire styles. In our area this section is represented by *Fimbristylis autumnalis* (L.) Roemer & Schultes, *F. complanata* (Retz.) Link, and *F. miliacea* (L.) Vahl, all $n = 5$.

Fimbristylis autumnalis and *F. miliacea* are detrimental weeds in rice fields in the Southeast and California (Smith *et al.*), as well as in Asia and Africa (Holm *et al.*). *Fimbristylis tomentosa* is rapidly becoming a common weed in rice fields from South Carolina to Texas (Kral).

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6. **Bulbostylis** Kunth ex C. B. Clarke in Hooker f. Fl. Brit. India **6:** 651. 1983, *nom. cons.*

Small to medium-sized, tufted (solitary-stemmed) perennials or annuals of open or disturbed, dry or wet habitats. Roots fibrous; rhizomes lacking [present]. Culms slender, terete, glabrous. Leaves all basal; sheaths expanded basally or not, with ligule fimbriate or ciliate apically; blades filiform or narrowly linear, shorter than to slightly exceeding the culm, conduplicate or involute, often pubescent on one or both surfaces, the margins and midvein scabrellate or smooth; chlorenchyma radiate; bundle sheaths 3-layered ("*Fimbristylis* type"). Inflorescences terminal, capitate or branched; bracts 1–4, erect to oblique, shorter than to exceeding the length of the rays; primary rays lacking or 1–6, erect or spreading, subterete, glabrous or scabrellate, secondary rays absent. Spikelets solitary or in small clusters, ovoid to oblong or lanceolate. Scales 2–50, ovate to oblong, mucronulate, mucronate, or aristate, glabrous or scabrellate, or puberulent abaxially, 3- to 7-nerved, deciduous at maturity, the 1–4 lowest ones sterile. Flowers perfect. Perianth lacking. Stamens (1, 2, or) 3; filaments slender, hyaline, about as long as the subtending scales; anthers oblong, the apices of the connectives prolonged as tiny subulate tips; pollen grains uniaperturate, subspheroidal or obovoid, psilate or scabrate, trinucleate. Styles papillate, the bulbous basal portion persistent on the mature achene; stigmas 3, slender, glabrous, equaling to exceeding the style in length. Achenes trigonous (rarely biconvex), ovoid to oblong or ellipsoid, the apex obtuse to acute, crowned by the persistent bulbous style base, the base cuneate to stipitate, the surface smooth or reticulate with vertically elongate, rectangular (rarely isodiametric) cells, these cells smooth or sometimes with a single central papilla. Embryos turbinate, radicle basal, coleoptile lateral. Base chromosome number 5. TYPE SPECIES: *B. capillaris* (L.) C. B. Clarke, *typ. cons.* (Name from Latin *bulbus,* bulbous, and *stylus,* style, referring to the characteristic bulbous style base.)

A genus of about 120 species, mostly pantropic but with some in the warm-temperate regions. The genus is related to *Abildgaardia* and *Fimbristylis.* (A discussion of the distinguishing features of these genera appears under *Fimbristylis.*) *Bulbostylis* was first distinguished from *Fimbristylis* as the genus *Stenophyllus* Raf. (Neogenyton, 4. 1828). Although the generic name *Bulbostylis* Kunth was published in synonymy (Kunth) and validated by Clarke (q.v.), it has been conserved over *Stenophyllus.* Kral's illustrated monograph (including chromosome numbers) is the basic reference for the North American species.

Bulbostylis is represented in the United States by eight species, five of which occur in the Southeast. *Bulbostylis barbata* (Rottb.) C. B. Clarke, $n = 5$, *B. capillaris* (L.) C. B. Clarke, $n = 36$, and *B. ciliatifolia* (Ell.) Fern., $n = 30$, have each been reported from all or nearly all the southeastern states. *Bulbostylis stenophylla* (Ell.) C. B. Clarke and *B. Warei* (Torrey) C. B. Clarke, both $n =$

15, are more restricted in range than the three preceding species. Both occur along the Coastal Plain from Florida to North Carolina. Three more species, *B. Funckii* (Steudel) C. B. Clarke, $n = 10$, *B. juncoides* (Vahl) Kükenthal, $n = 60$, and *B. Schaffneri* (Boeck.) C. B. Clarke, occur in the Southwest. About 15 species occur in Mexico, Central America, and the West Indies, with perhaps 20 in all of South America. The center of diversity for the genus is tropical Africa, where 30–40 species are reported.

The southeastern species of *Bulbostylis* are generally found in open, dry, sandy places, such as pine flatwoods, sand hills, palmetto scrub, roadsides, and shores. They are annuals or short-lived perennials. The neotropical *B. paradoxa* (Sprengel) Lindm., a long-lived perennial that flowers in response to fires (Kral), occurs in pinelands and savannas in Cuba and from Mexico to northern South America.

Plants with basal clusters of spikelets are occasionally encountered in several species of *Bulbostylis* (e.g., *B. capillaris* and *B. Funckii*). Formation of such spikelets may be the result of drought, but no studies have been made to document this supposition. In some species achenes produced by the basal spikelets are 1½–2 times larger than those produced by typical elongate culms. Such amphicarpy has also been reported in certain African species (Haines).

Bulbostylis barbata is a weed of old fields and sandy croplands in the southeastern Coastal Plain. Three species (including *B. barbata*) are reported as significant weeds in tropical Africa and Asia (Holm *et al.*).

REFERENCES:

Under family references see BARROS (1945); BEAL; BENTHAM; BROWN; CAROLIN *et al.*; CLARKE (1908, 1909); GODFREY & WOOTEN; GONCHAROV *et al.*; HAINES; HARBORNE; HARBORNE *et al.*; HOLM *et al.*; HOLTTUM; HUANG; J. HUTCHINSON; J. H. KERN; KUKKONEN (1969); KUNTH; LE MAOUT & DECAISNE; LERMAN & RAYNAL; METCALFE; NAPPER (1965); NEES VON ESENBECK; O'NEILL; RAYNAL (1972, 1973, 1978); RIKLI; SCHULZE-MOTEL (1959, 1964); STANDLEY; TEERI *et al.*; TORREY; VAN DER VEKEN; and WINFREY & SAMSEL.

Under *Fimbristylis* see GORDON-GRAY, KRAL, and SVENSON.

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7. **Abildgaardia** Vahl, Enum. Pl. **2:** 296. 1805.

Small, single-stemmed or tufted, bulbous-based, glabrous perennials of tropical and subtropical grasslands. Roots fibrous; rhizomes lacking. Culms subterete, smooth. Leaves about ½ as long as the culms; sheaths expanded, their overlapping bases forming the bulblike base of the plant, ligules lacking; blades linear-filiform, slightly involute, thickened at margins, scabrellate distally; chlorenchyma radiate; bundle sheaths 3-layered ("*Fimbristylis* type"). Inflorescences simple cymes of 1–3[–6] sessile or pedunculate spikelets; bracts solitary, filiform. Spikelets broadly lanceolate, slightly compressed, the scales distichous or essentially so. Scales 3–15, ovate, acute, mucronate, 3- to 5-nerved medially, nerveless laterally, deciduous as the achenes mature. Flowers perfect (although frequently the distal flowers of a spikelet staminate only). Perianth lacking. Stamens (1, 2, or) 3; filaments flattened; anthers linear, the apices of the connectives not prolonged; pollen grains uniaperturate, obovoid to subspheroidal, scabrate, trinucleate. Style trigonous basally, slender and capillary distally, deciduous from the mature achene; stigmas 3, linear, about as long as the style, glabrous. Achenes rounded-trigonous, ovoid, the apex broadly rounded, apiculate, the base abruptly contracted to a stipe, the surface pebbled. Embryo turbinate, radicle basal. Base chromosome number 10. (Named for P. S. Abildgaard, an eighteenth-century Danish botanist.) TYPE SPECIES: *A. ovata* (Burman f.) Kral (*Carex ovata* Burman f.; *A. monostachya* (L.) Vahl); see Britton & Millspaugh, Bahama Fl. 52. 1920.

A pantropic genus of about 15 species, distinguished from *Bulbostylis* and *Fimbristylis,* with which it has been united, by its distichous spikelet scales and its deciduous style bases. Chemical data support the recognition of *Abildgaardia.* The four Australian species produce the flavones luteolin and tricin, whereas the 15 species of *Fimbristylis* and *Bulbostylis* examined had only tricin (Harborne *et al.*).

Abildgaardia is represented in the New World by two species. *Abildgaardia mexicana* (Palla) Kral, $n = 10$, is endemic to grasslands of the Mexican High Plateau. The southeastern representative, *A. ovata,* $n = 10$, occurs in Florida, the West Indies, and the lowlands of Central and South America. *Abildgaardia ovata* is found in grasslands over limestone in southern Florida (Dade and Monroe counties) and in the vicinity of Tampa (Citrus County; Kral).

Species of *Abildgaardia* have no reported economic significance. None has been noted as a weed.

REFERENCES:

Under family references see BARROS (1945); BENTHAM; CLARKE (1908); GODFREY & WOOTEN; HARBORNE; HARBORNE *et al.*; HUANG; KUNTH; LERMAN & RAYNAL; METCALFE; NAPPER (1965); NEES VON ESENBECK; O'NEILL; SCHULZE-MOTEL (1959, 1964); and VAN DER VEKEN.

Under *Fimbristylis* see KRAL and SVENSON.

LYE, K. A. Studies in African Cyperaceae VIII. The taxonomic position of *Abildgaardia* Vahl and *Nemum* Hamilton. Bot. Not. **126:** 325–329. 1973.

Tribe CYPEREAE

8. **Cyperus** Linnaeus, Sp. Pl. **1:** 44. 1753; Gen. Pl. ed. 5. 27. 1754.

Tufted or rhizomatous, perennial or less often annual herbs of disturbed wet to dry soils, marshes, ditches, shallow swamps, and shores in full sun or light shade. Roots fibrous; rhizomes or stolons sometimes present, horizontal to oblique. Culms trigonous (sometimes with winged angles) or terete, smooth or scabrellate. Leaves all basal; sheaths glabrous, sometimes with conspicuous cross veins, especially in emergent plants, ligule present or lacking; blades linear to lanceolate, flat, conduplicate, plicate, filiform, crescentiform, or involute, the margins and midvein usually scabrellate; stomata paracytic, sometimes surrounded by 1–4 papillae; chlorenchyma radiate or not (if radiate the bundle sheaths 2-layered—"*Cyperus* type"). Inflorescences terminal, diffusely branched, spicate, or capitate; bracts (1–)3–6(–22), the sheaths very short, the blades leaflike, closely spaced and appearing verticillate at the apex of the culm, usually ascendent but in some species erect (the inflorescence thus appearing lateral), horizontal, or reflexed, forming a conspicuous involucre; rays glabrous (rarely scabrellate or hispidulous), unequal in length, produced singly from the axils of the inflorescence bracts; spikes digitate, glomerulate, or spicate; rachis smooth, rarely scabrellate. Spikelets (1–)5–30(–150), cylindrical to compressed, ovate, lanceolate, or linear, the scales distichous; rachilla deciduous or persistent, internodes winged or wingless, spongy and thickened in a few species. Scales (1 or) 2–20(–80), oblong, elliptic, or ovate, obtuse, acute, mucronulate, or cuspidate, 3- to 11-nerved, deciduous or persistent, the 2 lowermost (bract and prophyll) sterile. Flowers perfect [imperfect, the plants dioecious]. Perianth lacking. Stamens (1, 2, or) 3; filaments ribbonlike, usually as long as the subtending scales; anthers ovoid, ellipsoid, or linear, the apices of the connectives sometimes prolonged as small, reddish, entire or scabrellate appendages; pollen grains obovoid, subspheroidal, rectangular, or triangular, (1- or) 4-aperturate, psilate, trinucleate. Styles slender, the base sometimes persistent as an apiculus or beak on the mature achene; stigmas capillary, shorter than, equaling, or exceeding the style in length, glabrous [glandular]. Achenes trigonous or lenticular, ovoid, ellipsoid, or narrowly oblong, obtuse or acute, apiculate or not, stipitate, substipitate, or sessile, smooth, puncticulate, or reticulate. Embryos broadly to narrowly ellipsoid. Base chromosome number 8. (Incl. *Pycreus* Beauv., *Mariscus* Vahl, *Juncellus* (Griseb.) C. B. Clarke, *Acorellus* Palla, *Remirea* Aublet, *Torulinium* C. B. Clarke.) LECTOTYPE SPECIES: *C. esculentus* L.; see Britton & Brown, Illus. Fl. No. U.S. Canada, ed. 2. **1:** 297. 1913. (Name from Greek *kupeiros,* ancient name for *C. longus* L.)—FLAT-SEDGE, UMBRELLA-SEDGE, SEDGE-GRASS, GALINGALE (Britain).

A very large genus of about 650 species widely distributed throughout the tropical and warm- and cool-temperate regions of the world. It is the second largest genus of the Cyperaceae; only *Carex* L. is larger. *Cyperus* is morphologically coherent and is readily recognized by the distichous arrangement of scales on the spikelets. Six subgenera have been recognized: subg. CYPERUS, subg. PYCNOSTACHYS C. B. Clarke,[8] subg. PYCREUS (Beauv.) Gray,[9] subg. JUNCELLUS (Griseb.) Kükenthal, subg. TORULINIUM (Desv.) Kükenthal, and subg. FIMBRICYPERUS K. A. Lye. These are circumscribed by features of the achenes, spikelets, and vegetative anatomy. Most recent workers have followed

[8] *Cyperus* subg. PYCNOSTACHYS C. B. Clarke in Hooker f. Fl. Brit. India **6:** 597. 1893. LECTOTYPE SPECIES (here designated): *C. diffusus* Vahl. Synonym: *Cyperus* subg. *Protocyperus* K. A. Lye, Nordic Jour. Bot. **1:** 54. 1981. TYPE SPECIES: *C. difformis* L.

[9] *Cyperus* subg. PYCREUS (Beauv.) Gray, Man. Bot. ed. 1. 517. 1848. This combination is consistently, but erroneously, attributed to C. B. Clarke, Jour. Linn. Soc. Bot. **21:** 33. 1884.

Kükenthal and Fernald, who treated the genus in the broad sense. Others (Koyama, 1962b; Vorster; Raynal, 1972, 1973) have followed Clarke (1908) and recognized the subgenera as genera. Subgenera PYCREUS and JUNCELLUS differ from the others in having the derived conditions of lenticular (vs. trigonous) achenes and bifid (vs. trifid) styles (Blaser, 1941a; Raynal, 1972). In subg. PYCREUS the achenes are laterally compressed, while in subg. JUNCELLUS the compression is dorsiventral, suggesting that the bicarpellate condition evolved twice. Several other genera of the family (e.g., *Carex* and *Bulbostylis*) are divided into subgenera on the basis of carpel number.

Subgenus TORULINIUM differs from all other subgenera in having the rachilla articulate at the base of each scale (i.e., an abscission layer forms) (vs. continuous or articulate only at the base of the spikelet). Thus, the mature spikelet of plants of subg. TORULINIUM breaks up into one-fruited segments, each consisting of an internode of the rachilla, a scale, and an achene.

Subgenera JUNCELLUS, PYCREUS, and TORULINIUM are readily distinguished from each other and from the remaining subgenera. However, the subgeneric classification of the remaining species of the genus has been a matter of long debate. Traditionally, the species here recognized as constituting subgenera PYCNOSTACHYS and CYPERUS (Lye, 1981) have been circumscribed differently as subgenera *Mariscus* and CYPERUS. Clarke (1908) and Kükenthal (1935–1936) defined subg. CYPERUS as differing from subg. *Mariscus* in having the spikelet rachilla firmly attached to the rachis, while the scales are deciduous, falling from the rachilla as the achenes mature. In species of subg. *Mariscus,* the scales remain firmly attached to the rachilla even after the spikelet has fallen from the rachis. O'Neill (1942) listed some twenty species (e.g., *Cyperus strigosus* L., a common species throughout the United States) having characteristics of both subgenera—both the rachillas and the scales are more or less deciduous. Kükenthal placed such intermediate species in his concept of subg. *Mariscus,* but they are clearly transitional between subg. CYPERUS and subg. *Mariscus.* Also, as O'Neill (1942) observed, *C. rotundus* L. and *C. esculentus* L., both of which have always been placed in subg. CYPERUS, have persistent scales, a feature attributed solely to subg. *Mariscus* by Kükenthal. Federowicz surveyed the epidermal features of leaves and achenes of both subgenera and found no consistent differences between the two. There is no single character that consistently separates them. O'Neill (1942, p. 47) stated: "It is ill-advised to maintain *Mariscus* as a genus when it is very ill-defined even as a subgenus." More recently, Koyama (1962b) and Vorster have recognized *Mariscus* at the generic level.

Rikli surveyed the anatomy of the leaves and culms of many genera of the Cyperaceae. He divided *Cyperus* into two genera, *Eucyperus* (= *Cyperus*) and *Chlorocyperus.* The latter was characterized by having radiate chlorenchyma (i.e., kranz anatomy), while the former had nonradiate. Lerman & Raynal examined the distribution of the C_4 photosynthetic pathway in the family and found that *Cyperus* contained both C_3 and C_4 species. These physiological differences were correllated with the division that Rikli had based on anatomical information. Subgenus PYCNOSTACHYS corresponds to "Pars Pycnostachys" (not a valid taxonomic rank) in Kükenthal's monograph of the genus. Lye concurred with O'Neill that *Mariscus* could not be maintained even at the subgeneric rank but ought to be included in subg. CYPERUS. The recognition of subgenera PYCNOSTACHYS and CYPERUS (rather than subgenera *Mariscus* and CYPERUS *sensu* Kükenthal) is a natural classification that reflects current knowledge of the phylogeny of the genus, as outlined by Raynal (1973).

Van der Veken surveyed variation in embryo shape within the subfamily, including 162 species of *Cyperus.* Throughout this genus the embryos were broadly ellipsoid. There were interspecific differences in size, but these did not follow taxonomic lines. Van der Veken's data supported a broad concept of the genus.

Harborne and colleagues surveyed the distribution of flavonoids in South American, African, and Australian species of *Cyperus.* They examined about 150 species and reported that each subgenus had a distinct profile of compounds. Subgenus PYCNOSTACHYS is characterized by flavonols, which are absent in the other subgenera (these have flavones instead). Aurones, which give a yellowish hue to the inflorescences, are present in subgenera CYPERUS (including subg. *Mariscus*) and TORULINIUM but lacking in subgenera PYCREUS and PYCNOSTACHYS. These investigators believed the differences they reported confirmed the recognition of PYCNOSTACHYS as a subgenus distinct from subg. CYPERUS. They also concluded that the flavonoid data indicated that no subgenus was sufficiently unlike the others to merit generic status. Thus, these authors also favored a broad concept of the genus.

Chromosome numbers have been reported for about 40 species of *Cyperus.* However, even this limited number of counts gives some information about evolution in the genus. One significant trend is that subg. PYCNOSTACHYS has haploid numbers from 8 to 28 (mostly 15–20), while subg. CYPERUS has n = 8–86 (mostly 45–60). The generally lower chromosome numbers of subg. PYCNOSTACHYS suggest that it is the most primitive subgenus; this is also indicated by its being the only subgenus with the C_3 pathway. Different chromosome numbers have been reported for several species. In some species (e.g., *C. rotundus,* n = 16, 48, 54, 76) polyploid races are indicated; in others (e.g., *C. Houghtonii* Torrey, n = 84, 85, 86), mixoploid.

Cyperus in the southeastern United States comprises 63 species in four subgenera: five species are adventives from the Old World, seven are endemic, 17 are shared with the northeastern states, 15 are shared with the neotropics, and the remaining ones have either pantropic or cosmopolitan distributions.

Subgenus PYCNOSTACHYS (C_3 photosynthesis, spikelets in glomerules or digitate clusters, achenes trigonous), with 150 species worldwide (Lye), includes 14 in our area. Eight of these belong to the New World sect. LUZEOLOIDEI (Kunth) Clarke (spikelets in glomerulate clusters, scales with proximal abaxial groove, stamen one per flower). The group has been revised by Denton (1978, 1983), who has also investigated the morphology of the achenes and leaf blades. She showed that epidermal features of the achenes could be used to distinguish species. Only one chromosome count is available for this section: *Cyperus Eragrostis* Lam., $2n$ = 42. This species has been collected as a waif in South Carolina; it is native to the Pacific coast of the United States and temperate South America and is naturalized in southern Europe and southeastern Texas.

The remaining six southeastern species of the subgenus are scattered among four sections. Section HASPANI (Kunth) Clarke[10] (wetland plants; spikelets digitate; achenes ovoid, papillose), is represented in our area by three species. *Cyperus Haspan* L. occurs in Coastal Plain wetlands from Virginia southward. It is one of the few truly pantropic species and is believed to be native to southeastern Asia, tropical Africa, and the New World tropics. *Cyperus dentatus* Torrey, $2n = 34$, is a northeastern species of pond shores that extends southward to South Carolina and Tennessee. This is the only species of the subgenus with tuberiferous stolons. It is closely related to the southeastern endemic *C. Lecontei* Torrey ex Steudel,[11] a Coastal Plain species ranging from North Carolina to Louisiana.

Section FUSCI (Kunth) Clarke[12] (plants annual; scales ovate; styles and stigmas very short; achenes ovoid, glossy) is represented in the Southeast by one introduced species. *Cyperus difformis* L., $2n = 34$, a weedy Asian species, was first collected in the eastern United States in Norfolk Co., Virginia, in 1935 by Fernald (Tyndale). Lipscomb (1980b) has provided an interesting account of the spread of this species in North America. The species was first collected in the New World in New Mexico in 1850. It is a significant weed of rice fields in California but has not yet become a problem in the southern rice-producing states (Bryson). In contrast to the other weedy species of the genus (e.g., *C. esculentus*), *C. difformis* is an annual that is capable of completing its life cycle in only one month; a single plant can produce thousands of achenes. The species is adapted to ground that is frequently flooded, such as rice fields. The seeds germinate best under shallow water (McIntire). The type species of the section, *C. fuscus* L., $2n = 72$, is Eurasian; it is sparingly adventive from Massachusetts to Nebraska and Virginia but has not yet been reported from the Southeast.

Subgenus PYCREUS is characterized by having lenticular, laterally compressed achenes and C_4 photosynthesis. There are about 120 species worldwide, of which eight occur in our area. All our species are fibrous-rooted annuals, mostly less than 30 cm tall, of disturbed wet soils. One, *Cyperus louisianensis* Thieret, is endemic to southeastern Louisiana. Five pantropic species occur in our area: *C. flavescens* L., $2n = 50$, *C. pumilus* L., $2n = 94$, *C. flavicomus* Michx. (*C. albomarginatus* "Nees," see Tucker, 1985a), *C. polystachyos* Rottb., and *C. lanceolatus* Poiret. *Cyperus bipartitus* Torrey (*C. rivularis* Kunth, see Tucker, 1983a), $n = 27$, is a widespread North American species that also occurs in the mountains of Mexico, Central America, and southern South America (Tucker, 1983a). *Cyperus filicinus* Vahl is endemic to eastern North America (tidal marshes from Maine to Louisiana).

Subgenus JUNCELLUS has only about six species worldwide. The pantropic *Cyperus laevigatus* L., $2n = 80$–84, was collected as a ballast plant in Wilmington, North Carolina (*G. McCarthy s.n.* in 1888, GH!). It apparently never

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[10] *Cyperus* sect. HASPANI (Kunth) Clarke, Jour. Linn. Soc. Bot. **21**: 119. 1884. TYPE SPECIES: *C. Haspan* L.

[11] The name has been attributed to Torrey, but he published it provisionally under *C. dentatus* var. *multiradiatus* Torrey (Ann. Lyc. Nat. Hist. New York **3**: 273. 1836). The name *C. Lecontei* was first validly published by Steudel (Syn. Pl. Glum. 2: 17. 1854).

[12] *Cyperus* sect. FUSCI (Kunth) Clarke, Jour. Linn. Soc. Bot. **21**: 131. 1884. TYPE SPECIES: *C. fuscus* L.

became established in the eastern United States. This species, which grows in alkaline or brackish soils, is native to the area from western Texas to southern California and southern Mexico, to the Lesser Antilles, and to South America.

Subgenus CYPERUS contains about 400 species worldwide and about 35 in the Southeast. Among these are pantropic, neotropical, and cosmopolitan representatives. About half of the 35 are endemic to the United States, and many of these are endemic to the Southeast; four are introduced from the Old World.

Plants of sect. UMBELLATI C. B. Clarke are characterized by their caespitose habit, deciduous rachillas, and appressed, mostly persistent scales. This pantropic group has twelve species in the southeastern United States: *Cyperus croceus* Vahl (*C. globulosus* auct., non Aublet), *C. echinatus* (L.) Wood (*C. ovularis* (Michx.) Torrey), *C. Plukenetii* Fern., *C. ovatus* Baldwin (*C. Pollardii* Britton), *C. hystricinus* Fern., *C. refractus* Torrey, *C. retrofractus* (L.) Torrey (*C. dipsaciformis* Fern., see Carter & Jarvis), *C. lancastriensis* Porter, *C. retrorsus* Chapman (*C. Nashii* Britton), n = ca. 90 (Marcks, 1972a), *C. thyrsiflorus* Jungh., *C. retroflexus* Buckley (*C. uniflorus* Torrey & Hooker, non Thunb.), and *C. lentiginosus* Millsp. & Chase. Carter (1984) revised the North American representatives, some of which were also studied by Marcks (1972b) and Tucker (1983a, 1985b).

Plants of sect. LAXIGLUMI[13] are characterized by their rhizomatous, single-stemmed habit, deciduous rachillas, and spreading, more or less deciduous scales. Species of this section infrequently hybridize with those of the preceding one (Marcks, 1972a, 1972b). Eight species occur in the eastern United States, of which four are in our area; there are ten in the mountains of the southwestern United States, Mexico, and Central and South America. The plants typically grow in open, dry, sandy or gravelly habitats. The American species were studied biosystematically by Marcks (1972a, 1972b), and the Mexican and Central American ones by Tucker (1983a, 1984, 1985a). The species are cytologically similar: all are $n = 82$ except *Cyperus Schweinitzii* Torrey, $n = 84$, 85 (Marcks, 1972b). *Cyperus filiculmis* Vahl (*C. Martindalei* Britton), *C. lupulinus* (Sprengel) Marcks (*C. filiculmis* auct., non Vahl), *C. Grayi* Torrey, and *C. Grayoides* Mohlenbrock occur in our area.

The remaining southeastern species are scattered among six mainly pantropic sections. Section CYPERUS (sects. *Esculenti* Kükenthal and *Rotundi* C. B. Clarke) is most diverse in Australasia (Blake, J. H. Kern). In members of this section both the scales and the spikelets are persistent (a combination of characters unknown elsewhere in the genus), and the stolons are tuberiferous. *Cyperus rotundus* L., purple nut-sedge, is generally acknowledged to be the world's worst weed. It occurs throughout the Southeast, except in the mountains, but extends only as far north as southern Missouri and southeastern Virginia. It does not grow north of the mean 1°C January isotherm (Stoller). *Cyperus esculentus* L., yellow nut-sedge, is able to tolerate winter air temperatures as low as −18°C and is a serious weed in much of the world, especially in cooler regions where

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[13] *Cyperus* sect. LAXIGLUMI (C. B. Clarke) Kükenthal, Pflanzenr. IV. **20**(Heft 101): 220. 1936; based on *Mariscus* subsect. *Laxiglumi* C. B. Clarke, Kew Bull. Add. Ser. **8:** 103. 1908, "*Laxiglumae.*" LECTOTYPE SPECIES (here designated): *Mariscus Manimae* (HBK.) C. B. Clarke (= *C. Manimae* HBK.).

the more tropical *C. rotundus* does not grow. These two species also differ in their thermal optima for growth. In Mexico *C. esculentus* is found from sea level to about 2600 m, while *C. rotundus* occurs from sea level to about 1500 m (Tucker, 1985b). It is unclear whether these species are native to the New World. *Cyperus esculentus* now occurs in all 50 states and in southern Canada.

The stoloniferous nature of these two species underlies their success as weeds. A single tuber can produce a population covering 2–4 m^2 in two months (Horowitz). The sharp-pointed stolons can cause puncture wounds in the hands of farm workers and curious agronomists and penetrate root crops such as potatoes and yams. In 1821 Elliott noted that *Cyperus rotundus* was a great problem for farmers in Georgia and South Carolina. He outlined a method for removing an infestation by cultivating a fallow field weekly for a year (including winter), thus allowing the tubers to be killed by exposure to drying and cold air. Mulligan & Junkins provided a thorough summary of its biology, emphasizing weed control and management. Horak & Holt analyzed isozymes in ten widely separated populations of *C. esculentus* in California. Genetic variation served to determine the relative importance of sexual and asexual reproduction. Results indicated that reproduction by seeds is unimportant in maintenance of populations in croplands. Stolons and tubers are the primary means of reproduction. Germinability of seeds from northeastern populations ranged from 7 to 95 percent; such variation was believed to be genetic (Mulligan & Junkins). Seeds from a 50-year-old herbarium specimen had 5 percent germination (Mulligan & Junkins). *Cyperus esculentus* is self-incompatible (Horak & Holt).

Members of sect. COMPRESSI Nees[14] are caespitose annuals with cuspidate scales and emarginate achenes. Most of the species are native to the Old World tropics. The pantropic *Cyperus compressus* L., $n = 64$, is the only representative in the United States. It is found throughout the Coastal Plain and Piedmont, as far north as Pennsylvania and Missouri. The only other New World species, *C. Wilburii* G. Tucker, is endemic to the lowlands of southern Mexico. Its larger size suggests that it may be a tetraploid derived from *C. compressus.*

Section IRIOIDEI Nees[15] comprises several tropical and temperate eastern Asian species. The plants are annual and have ascending-appressed spikelets and three-nerved, orbiculate scales. *Cyperus Iria* L. is an adventive in all tropical and temperate regions of the New World and is a common weed throughout the southeastern Coastal Plain and Piedmont. Apparently, the plants are cleistogamous. The staminal filaments elongate only enough to bring the minute anthers into contact with the very short stigmas, which remain inside the scales at anthesis. Often the anthers are later found agglutinated to the stigmas.

Section VISCOSI C. B. Clarke[16] is endemic to the New World and is represented

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[14] *Cyperus* sect. COMPRESSI Nees, Linnaea **9:** 234. 1834. TYPE SPECIES: *C. compressus* L.

[15] *Cyperus* sect. IRIOIDEI Nees, Linnaea **9:** 235. 1834. TYPE SPECIES: *C. Iria* L. Synonym: sect. *Iriae* (Kunth) C. B. Clarke, Kew Bull. Add. Ser. **8:** 99. 1908.

[16] *Cyperus* sect. VISCOSI C. B. Clarke, Jour. Linn. Soc. Bot. **21:** 114. 1884. TYPE SPECIES: *C. viscosus* Aiton (= *C. elegans* L.). Synonym: sect. *Glutinosi* (Böck.) Kükenthal, Pflanzenr. IV. **20**(Heft 101): 163. 1936.

by two species in the Southeast. Plants of this section have spicate inflorescences; the spikes are short and dense and appear glomerulate, which apparently caused Kükenthal to believe them to be closely related to plants of sect. LUZEOLOIDEI (subg. PYCNOSTACHYS). The plants have kranz anatomy, further supporting their placement in subg. CYPERUS (Tucker, 1985b). They secrete a viscid fluid and are sticky when living, hence the appropriate sectional name. Two species occur in the Southeast. *Cyperus elegans* L. grows from southern Florida and Texas south to Ecuador. *Cyperus oxylepis* Nees ex Steudel is a South American species that has recently become an adventive in the United States, where it was first noted in Texas (O'Neill). More recently it has been reported in Louisiana (Thieret, 1964) and in Charleston County, South Carolina (*MacDougal 1501,* 5 Aug. 1981, DUKE, NCU, NYS).

Subgenus TORULINIUM has a single representative in our area, the pantropic and warm-temperate *Cyperus odoratus* L. It is a common species of disturbed, wet soils, especially pond shores and stream banks. Five segregate species (e.g., *C. Engelmannii* Steudel, *C. ferruginescens* Böck.) have been recognized at various subspecific ranks. Evidence for treating these segregates as conspecific with *C. odoratus* has been published (Tucker, 1984). Three other species of this subgenus occur in the New World tropics: *C. Correllii* (Koyama) G. Tucker in the Bahamas, *C. rhizophorae* (C. B. Clarke) Standley along the Pacific Coast of Central America, and *C. filiformis* Sw. in the Greater and Lesser Antilles.

Section REMIREA (Aublet) Kern contains a single pantropic species, *Cyperus pedunculatus* (R. Br.) Kern (*Remirea maritima* Aublet), beach-stars. In our area it occurs only in Peninsular Florida. The rhizomatous plants form mats that bind sand dunes. This species has been treated as constituting a monotypic genus, *Remirea,* which Kükenthal placed in the Rhynchosporoideae. Metcalfe and Oteng-Yeboah showed convincingly that the anatomy of *C. pedunculatus* is similar to that of the kranz species of *Cyperus.* Within *Cyperus,* the thickened upper internode ("corky organ") of the one-flowered spikelets suggests a relationship with subg. TORULINIUM (*C. odoratus* typically has spongy, thickened rachilla internodes). Such internodes may serve to make the achenes buoyant, thus contributing to dispersal by water, but experimental evidence for this supposition is lacking.

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9. **Kyllinga** Rottboell, Descr. Icon. Rar. Nov. Pl. 12. 1773, *nom. cons.*

Small, rhizomatous or tufted perennials (1 species annual). Culms trigonous or roundly trigonous, smooth. Leaves 1–5, basal; sheaths short, closely fitting the culms, ligule lacking; blades flat or V-shaped in cross section [lacking], the margins and keels scabrellate, especially distally; chlorenchyma radiate; bundle sheaths 2-layered ("*Cyperus* type"). Involucral bracts 2–4, leaflike, horizontal to slightly reflexed or erect. Spikes 1–4, sessile, densely ovoid to cylindrical. Spikelets 15–150 per spike, not readily distinguishable without magnification, ovate to lanceolate, decidedly flattened. Scales 4, the 2 basal minute, the 2 distal much longer, making up the bulk of the spikelet, the lower of these (the third scale of the spikelet) subtending a perfect flower, the upper (fourth scale) slightly smaller, sterile or infrequently bearing 1 or 2 (often abortive) stamens. The fertile scale of the spikelet ovate, conduplicate, with a conspicuous smooth or spinulose-scabrellate [fimbriate or erose] keel terminating in a mucronate or mucronulate [aristate] apex, laterally 2- to 4-nerved. Flowers perfect. Perianth lacking. Stamens 1–3; filaments ribbonlike, about as long as the subtending scales; anthers oblong-elliptic to linear, the apices of the connectives not prolonged; pollen grains 4-aperturate [uniaperturate], obovoid, psilate, trinucleate. Styles capillary, smooth; stigmas 2, about as long as the styles. Achenes lenticular, laterally compressed, narrowly ovoid to oblong or ellipsoid, about ½ the length of the subtending scale, the apex obtuse, apiculate, the base cuneate to rounded, barely to decidedly stipitate, the surface puncticulate. Embryos narrowly ellipsoid. Base chromosome number 60. (*Cyperus* subg. *Kyllinga* (Rottb.) Valck.-Suringar.) TYPE SPECIES: *K. monocephala* Rottb., *nom. illeg.* (= *K. nemoralis* (J. R. & G. Forster) Dandy ex Hutchinson & Dalz., *typ. cons.*). (Named for Peter Kylling, Danish botanist, d. 1696.)

A genus of about 40–45 species, nearly all of which are tropical. The greatest diversity is in tropical East Africa and Madagascar, where there are 30–35 species. Eight occur in southern Asia, three or four in eastern Asia, and two in Australasia. Two (neither endemic) grow in the Hawaiian Islands, but none occurs in Europe. There are eight species in the New World; three of these, *Kyllinga pumila* Michx., *K. odorata* Vahl, and *K. brevifolia*, $2n = 120$, which occur in the Southeast, are pantropic. *Kyllinga vaginata* Lam. and *K. tibialis* Ledeb. are species of littoral habitats in the Caribbean, South America, and tropical West Africa. *Kyllinga nudiceps* C. B. Clarke is endemic to Isla del Coco, in the Pacific some 300 km southwest of Costa Rica. *Kyllinga squamulata* Thonn. ex Vahl (*Cyperus Metzii* Mattf. & Kükenthal), from tropical Asia, is introduced in Florida and the West Indies; *K. brevifolioides* (Delahoussaye & Thieret) G. Tucker,[17] from temperate eastern Asia, has become sparingly established in the eastern United States in the area from Connecticut to western North Carolina and Tennessee. The four southeastern species are mostly weedy plants of disturbed, usually moist, sunny places. *Kyllinga pumila* is a common

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[17] *Kyllinga brevifolioides* (Delahoussaye & Thieret) G. Tucker, comb. nov., based on *Cyperus brevifolioides* Delahoussaye & Thieret, Sida **3**: 131. 1967.

weed of lawns and croplands in the eastern United States from Pennsylvania and Missouri south to the Gulf Coast.

Kyllinga differs from *Cyperus,* with which it has been combined by some workers, in its very short rachilla and in the two lowest sterile scales of its spikelets being greatly reduced. Taxonomically useful characters have been reviewed by Tucker. The most important of these are habit (rhizomatous perennials or caespitose annuals), length and orientation of the involucral bracts, and length of the anthers. Such characters as number of stamens and presence of spinulose prickles on the keels of the scales have previously been used (Delahoussaye & Thieret) but frequently vary within individuals of the same species and sometimes within spikes of a single plant.

The plants are probably at least partly wind pollinated. However, because of the close spacing of the spikelets within an inflorescence, some anthers probably shed their pollen directly onto stigmas of adjacent spikelets. Insect pollination may be important in some species with conspicuous, whitish or cream-colored spikes (e.g., *Kyllinga odorata*), as it is in many species of *Rhynchospora* sect. DICHROMENA. Syrphid flies have been observed visiting individuals of *K. tibialis* in Costa Rica (*MacDougal 1190,* DUKE) and *K. odorata* in Mexico (*Tucker 2222,* DUKE).

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10. **Lipocarpha** R. Brown in Tuckey, Narr. Exped. Congo **5:** 459. 1818, *nom. cons.*

Small, caespitose annuals of wet sandy or peaty soils. Roots fibrous, rhizomes absent. Culms 1–20(–100), usually densely clustered, erect, spreading, or curved, filiform, terete, glabrous. Leaves 1 or 2, basal, filiform, about as wide as the culms, the lower reduced to a bladeless sheath or a sheath bearing merely an involute appendage, the upper with blade up to ⅓ as long as the culm, or reduced like the lower one; stomata paracytic; chlorenchyma radiate; the bundle sheaths 2-layered ("*Cyperus* type"). Inflorescences unbranched, a sessile cluster of 1–4 dense spikes; bracts 1–4, filiform, 1–4 times as long as the spikes, leaflike, the longest erect, appearing as a continuation of the culm, the other(s) shorter than or equaling the spikes, borne approximately perpendicular to the culm; rays none. Spikes ("spikelets") 1–4, sessile, ovoid [globose]; denuded rachis persistent, with rhombic scars where the spikelets were attached. Spikelets ("flowers") [20–]50–150, densely spirally arranged, borne approximately perpendicular to the rachis, deciduous. Scales (1, 2, or) 3; outer scale lanceolate to ovate-lanceolate, planar or nearly so, with 2 conspicuous medial veins and a less conspicuous central one, laterally weakly 1- or 2-nerved or essentially nerveless, mucronulate [aristate]; inner scale hyaline, equaling or shorter than the outer, or reduced to a scalelike appendage much shorter than the outer, with 3–5 inconspicuous veins or veinless, or absent; third scale present between the outer scale and the achene in some species, similar to or smaller than the second. Flowers perfect. Perianth lacking. Stamens 1 or 2; filaments capillary, about ¾ as long as the outer scale; anthers ovoid, the apices of the connectives not prolonged; pollen grains 4-aperturate, obovoid to subspheroidal, psilate or scabrate. Styles filiform; stigmas 2, about ½ as long as the styles, minutely swollen apically, glabrous, deciduous before the achenes mature. Achenes trigonous to terete, obovoid to cylindrical, slightly shorter than the outer scale, the base sessile to stipitate, the apex obtuse to subtruncate, apiculate, the surface papillose. Embryos ellipsoid. Base chromosome number 6. (Incl. *Ascolepis* Nees ex Steudel, *Hemicarpha* Nees ex Arnott.[18]) TYPE SPECIES: *L. senegalensis* (Lam.) T. & H. Durand (*L. argenteum* (Vahl) R. Br., *nom. illeg.*; see Haines & Lye). (Name from Greek, *lipo,* to fall, and *carpha,* chaff, referring to the deciduous hyaline inner scale of the spikelet.)

A genus of about eight species occurring in tropical and warm-temperate regions. Five grow in North America: *Lipocarpha maculata* (Michx.) Torrey, on the Coastal Plain from Virginia to Texas, southward into the tropics; *L. occidentalis,* restricted to the Pacific coast; *L. Drummondii,* from Oklahoma and Texas west to New Mexico; *L. aristulata,* across the United States from South Carolina and Florida west to Washington and California; and *L. mi-*

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[18] The inclusion of *Hemicarpha* in *Lipocarpha* necessitates the following new combinations for species occurring in the New World:

Lipocarpha aristulata (Cov.) G. Tucker, based on *Hemicarpha micrantha* var. *aristulata* Cov. Bull. Torrey Club **21:** 36. 1894.

L. Drummondii (Nees) G. Tucker, based on *Hemicarpha Drummondii* Nees in Martius, Fl. Brasil. **2**(1): 62. 1842.

L. micrantha (Vahl) G. Tucker, based on *Scirpus micranthus* Vahl, Enum. **2:** 254. 1806.

L. occidentalis (Gray) G. Tucker, based on *Hemicarpha occidentalis* Gray, Proc. Am. Acad. **7:** 391. 1868.

L. Schomburgkii (Friedl.) G. Tucker, based on *Hemicarpha Schomburgkii* Friedl. Am. Jour. Bot. **28:** 860. 1941.

crantha, throughout the United States and southeastern Canada, southward to tropical South America. *Lipocarpha Schomburgkii* is known only from the Guyana region of northern South America.

All species are small, inconspicuous plants of disturbed wet soils, especially shores of ponds and pools. Because of their small size (less than 30 cm tall, and often less than 1 cm!), they are easily overlooked and are probably more frequent and widely distributed than available collections indicate.

Raynal's view that *Lipocarpha* is a highly reduced derivative of *Cyperus* seems well founded and is accepted here. The fact that both genera have "*Cyperus*-type" kranz anatomy (Metcalfe) further strengthens this conclusion. The achene and subtending scales of *Hemicarpha* are probably homologous to a single spikelet of *Kyllinga* or *Cyperus.* Friedland suggested that the inner hyaline scale represented five perianth members that correspond to the bristles subtending the achenes in some species of *Scirpus.* Raynal's interpretation of the inner scales of *Lipocarpha* (and *Hemicarpha*) as reduced scales of a spikelet appears more plausible than Friedland's view.

Haines & Lye studied the African species previously assigned to *Hemicarpha* and *Lipocarpha* and concluded that the two genera should perhaps be merged. Goetghebeur (pers. comm.) has recently studied all the Old World species of these genera, as well as those of the closely related genus *Ascolepis.* He concluded, as I had from my independent investigations, that the three genera should be combined.

Chromosome numbers have been reported for *Lipocarpha argentea* R. Br. ($2n = 26$) and *L. microcephala* Kunth ($2n = 46$). This suggests a base chromosome number of 6.

No species is gathered as food or for medicinal purposes. *Lipocarpha argentea* and *L. microcephala* (R. Br.) Kunth are recorded as weeds in eastern Asia (Holm *et al.*).

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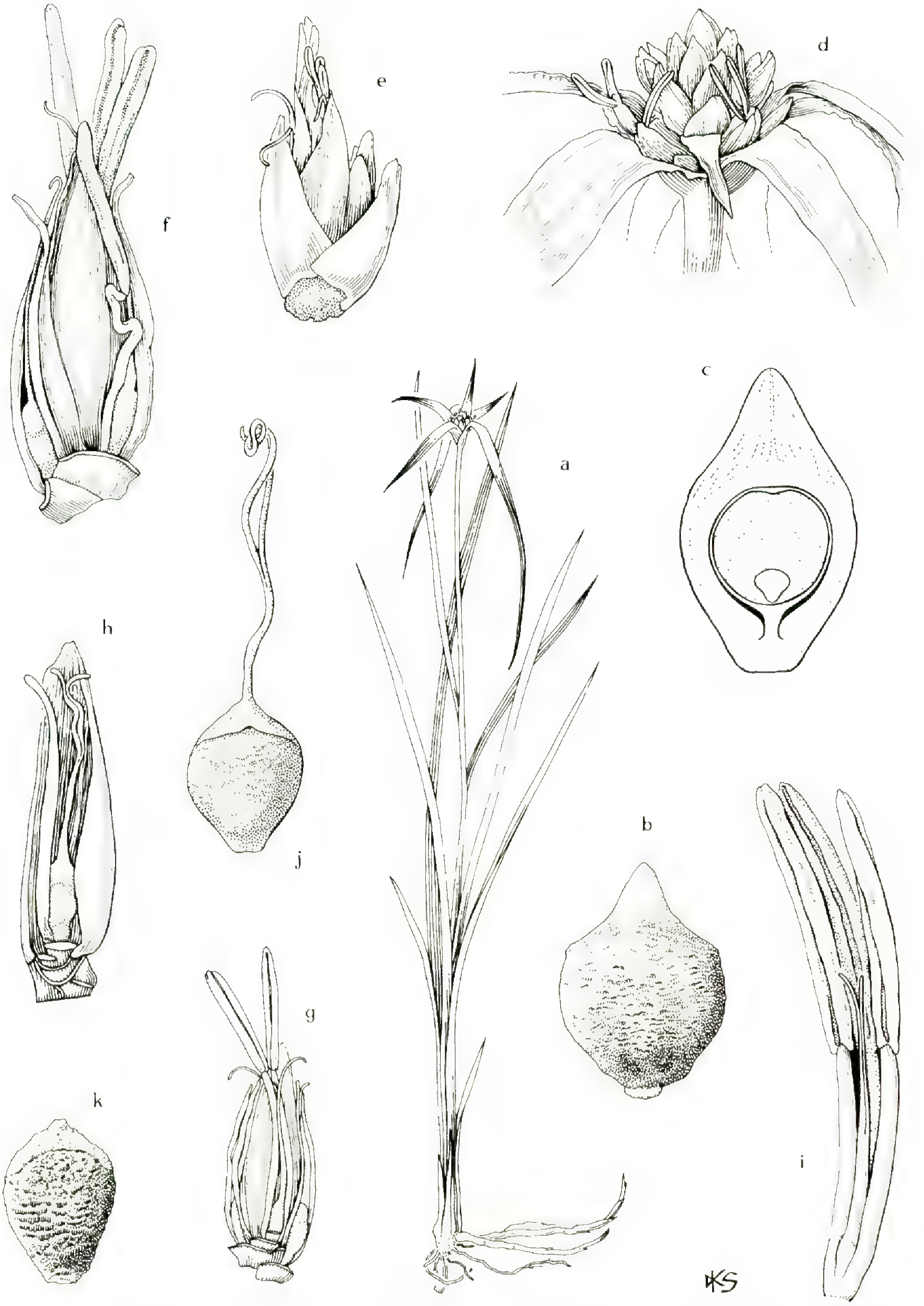

FIGURE 3. *Rhynchospora* sect. DICHROMENA. a–c, *R. colorata:* a, habit (note rhizomes to right), × ½; b, mature achene, tubercle scarcely decurrent on body of achene, × 20; c, same, in longitudinal section, the 2 layers of the achene wall separated by dotted line, seed coat unshaded, endosperm stippled, embryo unshaded, × 20. d–k, *R. floridensis:* d, head of spikelets subtended by involucral bracts, × 3; e, 1 large and 1 small spikelet enclosed by 2 scales, × 6; f, abaxial surface of spikelet, 2 scales removed, flowers protandrous, × 10; g, same spikelet, adaxial surface, 1 stamen and 3 scales removed, × 6;

Tribe SCHOENEAE Dumortier, Fl. Belg. 144. 1827. (Tribe Rhynchosporeae Fenzl in Endlicher, Gen. Pl. 2: 115. 1836.)

11. **Rhynchospora** Vahl, Enum. Pl. 2: 229. 1806, *nom. cons.*

Small to large, caespitose or single-stemmed, perennial [annual] herbs of moist open woods, bogs, pocosins, ditches, and pond shores. Roots fibrous; rhizomes or stolons present in a few species. Culms trigonous, subtrigonous, or terete, smooth throughout or ribbed just below the inflorescence, glabrous, leafy [leafless]. Leaves numerous, basal, cauline, or both; basal leaves with blades flat to conduplicate or involute-filiform, the margins and midveins generally scabrellate with unicellular [multicellular] prickles, the surfaces glabrous or with prickles like those on the margins, or pubescent with long, flexible, unicellular hairs, or papillose (in *R. alba*); cauline leaves shorter than but otherwise similar to the basal ones; stomata paracytic, generally confined to the abaxial surface; chlorenchyma not radiate [radiate in some tropical species]. Inflorescences terminal (sometimes also lateral, the lateral ones smaller and less branched than the terminal), fasciculate or cymose; bracts 1–6, leaflike (sometimes basally whitened); rays slender, terete, smooth or scabrellate; heads loosely to densely ovoid or capitate. Spikelets solitary, globose, ellipsoid, or slenderly lanceolate, the 1–5 basal scales sterile. Scales spirally arranged, closely imbricate, ovate to lanceolate, entire or mucronulate at apex, nerveless to rather prominently nerved, the midvein most conspicuous. Flowers perfect (the terminal 1 or 2 scales sterile or subtending rudimentary ovaries and functional stamens). Perianth bristles lacking or 1–6(–20), smooth, barbed, or plumose, persistent. Stamens (1–)3(–12); filaments capillary or ribbonlike; anthers elliptic to oblong, the apices of the connectives not prolonged; pollen grains uniaperturate, obovoid, psilate or scabrate, binucleate. Styles glabrous; the stigmas longer than, equaling, or much shorter than the style. Achenes lenticular (dorsiventrally flattened), ovoid to slenderly ellipsoid, crowned with a pyramidal to subulate tubercle shorter than to 3 times longer than the body of the achene, the base sessile to conspicuously stipitate, the lateral edges often raised to form a conspicuous ridged margin, the surface alveolate to cancellate (rarely smooth or nearly so), transversely rugulose or not. Base chromosome number 5. (Incl. *Psilocarya* Torrey, *Dichromena* Pers., *Calyptrostylis* Nees.) TYPE SPECIES: *R. alba* (L.) Vahl (*Schoenus albus* L.), *typ. cons.* (Name from Greek, *rhynchos,* snout, and *spora,* seed, in reference to the prominently beaked achenes.)

A genus of about 225 species, worldwide in distribution, with greatest diversity in the New World tropics; about 60 occur in the southeastern United States. Temperate North America, especially the southeastern Coastal Plain, is rich in species, and there are many others in the Old World tropics. Only a

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h, flower with subtending scale, anthers fallen, 5 scales and rachilla of spikelet removed, × 10; i, flower removed from spikelet, anthers dehiscing, styles not yet elongated, stigmas not receptive, × 12; j, nearly mature achene with persistent style and stigmas, × 20; k, mature achene, tubercle decurrent on body of achene, × 20.

few species are indigenous to temperate Eurasia—three species in Europe and four in the Soviet Union east of the Urals.

Kükenthal's worldwide monograph (1949, 1950, 1951) provided a basis for identification and further study of the genus *Rhynchospora*. Gale, in her careful, well-illustrated monograph, did much to clarify the taxonomy of the North American species. Thomas (1984) has recently investigated the tropical section DICHROMENA (Pers.) Pfeiffer and confirmed its inclusion in *Rhynchospora*.

The genus is little known cytologically; chromosome numbers have been published for only ten species (summarized by Thomas, 1984). These suggest a base chromosome number of 5, in keeping with the base number for other genera of the family.

There are three subgenera in *Rhynchospora* (Kükenthal, 1949, 1950, 1951). The largest of these, including about 54 of the 60 species in our area, is subg. RHYNCHOSPORA (*Eurhynchosporae* Gray), species of which have papery spikelet scales and stigmas equaling or longer than the styles. Complete descriptions of the southeastern species were provided by Gale.

Species of sect. DICHROMENA have sessile capitate inflorescences and whitish spikelets often subtended by whitish bracts and lack perianth bristles. The section is primarily neotropical in distribution and contains 23 species, of which four are present in the United States. Three occur in the Southeast. Insect pollination has evolved in plants of this section, as was first noted in 1893 by De Lagerheim and later studied by Uphof and Leppik.

Thomas (1984) reviewed previous investigations of entomophily in species of sect. DICHROMENA and made thorough field and laboratory studies. Fifteen species of bees (Hymenoptera) visit flowers of plants included in this section. The bees exhibit constancy, visiting four to ten inflorescences in a population before leaving. The flowers have no fragrance and no nectar; the white color of the bracts and spikelets attracts the bees, and pollen is the only reward. The pollen grains have a sticky "pollenkit"; thus, they aggregate and stick to the bee's body and legs. There is probably some transfer of pollen by the wind. All species of sect. DICHROMENA are self-compatible. Thomas (1984) postulated that the evolution of entomophily may have permitted the species to radiate into shaded tropical forests, where a lack of air movement necessary for wind pollination is compensated for by insect and self-pollination.

No species of *Rhynchospora* is gathered for food or medicinal uses. Several species are detrimental weeds in rice fields, both in the Old World and in the southeastern United States.

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12. **Dulichium** Persoon, Syn. Pl. **1:** 65. 1805.

Perennial herbs of swamps, fens, and shores. Roots fibrous; rhizomes horizontal. Culms 1–3, terete, hollow, glabrous. Basal leaves bladeless; sheaths appressed; cauline leaves several, the blades lanceolate, about 1–2 times longer than the sheaths, auriculate, planar, with margins and midveins densely scabrellate abaxially; stomata confined to the adaxial surfaces (sometimes a few present near the margins on the abaxial surface); chlorenchyma not radiate; air cavities present. Inflorescences solitary in the axils of the upper leaves; rays and rachises slender, compressed, scabrellate on the edges; spikes loosely ovoid, appearing flattened from the distichous arrangement of the spikelets. Spikelets 3–20, linear-lanceolate, flattened; rachilla persistent, the internodes with hyaline margins, the lowermost scale sterile (except in the terminal spikelet). Scales 3–9, deciduous as the achenes mature, lanceolate, conduplicate, acute, 5- to 9-nerved, the midveins scabrellate. Flowers perfect. Perianth bristles 6–9, 1–2 times as long as the mature achene, retrorsely barbed. Stamens 3; filaments ribbonlike, nearly as long as the scales; anthers linear, the apices of the connectives minute. Style capillary, glabrous; stigmas 2, about as long as the style, glandular-pubescent. Achenes planoconvex, narrowly ellipsoid, the apex acute, the base stipitate, the surface puncticulate. Embryos turbinate. Base chromosome number 16. TYPE SPECIES: *D. arundinaceum* (L.) Britton. (Name from the Greek *duo,* two, and *leichon,* scale, referring to the two-ranked scales of the spikelets.)

A monotypic genus of wetland plants endemic to temperate North America. *Dulichium* is easily distinguished from other Cyperaceae by its characteristic distichous spikelet scales and its three-ranked cauline leaves. An interesting, apparently uninvestigated feature of the plants is that in adjacent culms arising from the same rhizome, the leaves are spiraled clockwise in one and counterclockwise in the next. The single species, *D. arundinaceum,* is distributed from Newfoundland to southeastern Manitoba, south to southern Florida and eastern Texas, and disjunctively in the area from northwestern Montana and southwestern British Columbia south, mostly west of the Cascades and the Sierra Nevada, to central California (Wood, 1972, *map*). The genus had a wider distribution during the Pleistocene when it occurred in Europe (Wood, 1971, *map*). Fossils of this species are known from the Pliocene in the Soviet Union (Daghlian). Infraspecific variation in fossil achenes from Europe has been studied by Truchanowiczowna.

Dulichium has usually been placed in the tribe Cypereae, near *Cyperus.* Linnaeus (Sp. Pl. **1**: 45. 1753) included the species in *Cyperus,* presumably because of its distichous spikelet scales. The two genera differ, however, in several important features: *Dulichium* has widely spaced axillary inflorescences subtended by leaflike bracts with conspicuous sheaths, while *Cyperus* has apically clustered inflorescence branches subtended by sheathless bracts; *Dulichium* has one sterile scale at the base of each spikelet, and *Cyperus* has two; *Dulichium* has perianth bristles, but *Cyperus* does not.

The embryos of *Dulichium* resemble those found in *Rhynchospora,* rather than those of any genus of the Cypereae (Van der Veken). A new monotypic tribe, the Dulichieae, has recently been proposed for this genus by Schulze-Motel (1959).

Plants of this genus have been neither reported to have economic use nor noted as weeds.

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13. **Schoenus** Linnaeus, Sp. Pl. 42. 1753; Gen. Pl. ed. 5. 26. 1754.

Caespitose perennials of open sunny wetlands. Rhizomes short, oblique. Culms terete, hollow, glabrous. Leaves all basal; sheaths tough, glossy, glabrous, ligule lacking; blades linear, subcylindrical, upper surface flat or broadly convex; stomata paracytic, on both surfaces [mostly adaxial]; chlorenchyma not radiate. Inflorescences terminal, sessile, capitate [diffusely branched]; bracts 1 or 2, oblique to erect, sheathless or essentially so, basally expanded and partly clasping the spikelets, distally linear; rays lacking. Spikelets (1–)10–25, oblong-ellipsoid, flattened, the 2 or 3 basal scales sterile; rachilla wingless, more or less deciduous at maturity. Scales distichous, 3–8, oblong, acute but not mucronate, distally scabrellate, laterally nerveless, medially 1-nerved. Flowers perfect. Perianth bristles lacking to 6, smooth or scabrellate. Stamens 3; filaments ribbonlike; anthers linear, the apices of the connectives subulate, conspicuous; pollen grains 4-porate, obovoid, finely scabrate (pore areas frustillate). Styles trigonous to subtrigonous, glandular; stigmas 3, capillary, shorter than the styles, glandular. Achenes roundly trigonous to subterete, ovoid to ellipsoid, the apex broadly rounded, the base gradually tapered to a stipe, the surface smooth or barely reticulate, glossy. Base chromosome number 20(?). TYPE SPECIES: *S. nigricans* L.; see Britton & Millspaugh, Bahama Fl. 56. 1920. (Name from Greek *schoinos,* for a rushlike plant.)—BLACK-HEADED SEDGE.

A genus of about 80 species, mostly restricted to Australasia but with a few occurring in Africa, Eurasia, and the New World. *Schoenus nigricans* L., $2n =$ 54, 55, is present in North America. It is common in southern Florida but rare in the Florida Panhandle, where it grows in wet grasslands over limestone outcrops; it also occurs in the southwestern United States in the mountains and valleys of western Texas, southern California, and southwestern Nevada, where it grows in marshes and thermal springs. It is also reported from the West Indies, Europe, and Asia.

Kükenthal published a worldwide revision of *Schoenus,* and the genus has received little subsequent systematic attention. The European species have been investigated ecologically. *Schoenus nigricans* requires aluminum ions for growth, and its range in the blanket bogs of the British Isles is thus limited to the coastal region of western Ireland.

Plants of the genus have little economic significance. Wet meadows dominated by *Schoenus ferrugineus* L. are mowed for fodder in northern and central Europe. The species is adapted to low nutrient levels and is quickly displaced by grasses when fertilizers are regularly applied.

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14. **Cladium** P. Browne, Civ. Nat. Hist. Jamaica, 114. 1756.

Stoloniferous, single-stemmed or loosely clustered, medium to large perennials of sunny wetlands. Culms terete, roundly trigonous, or thickly crescentiform, hollow, glabrous. Leaves all cauline; sheaths glabrous, much shorter than the blades; blades flat or slightly conduplicate to subinvolute, the margins and midveins sparsely scabrellate to harshly scabrous; chlorenchyma not radiate; alternate bundles inverted. Inflorescences pedunculate, terminal or both lateral and terminal, diffusely branched; bracts leaflike but with shorter blades; primary rays terete, wirelike and slightly drooping, glabrous; secondary rays similar to primary but shorter and more slender; tertiary and quaternary rays regularly produced in some species, these subtended by lanceolate scalelike bracts and sheathing prophylls (involucels). Spikelets in glomerules of 1–5, narrowly ellipsoid to lanceolate; rachilla wingless. Scales 3–5, the basal 1–3 sterile, ovate to oblong-lanceolate. Flowers perfect or imperfect (the distal flower of a spikelet perfect, the subdistal staminate). Perianth lacking. Stamens 2 or 3; filaments about as long as the subtending scale, flattened; anthers linear, the apices of the connectives subulate; pollen grains 4-porate, narrowly obovoid (sometimes with a peculiar apical appendage containing the degenerate nuclei), scabrate. Styles subtrigonous, glabrous; stigmas 3, longer than the styles, glandular. Achenes terete, ovoid, the apex broadly round (the withered style base sometimes persistent), the base truncate and impressed, sometimes stipitate, the surface smooth or nearly so. Embryos small, broadly obovoid, scarcely differentiated (the first leaf not developed). Base chromosome number 20. TYPE SPECIES: *C. Mariscus* (L.) Pohl (*Schoenus Mariscus* L.; see Britton & Brown, Illus. Fl. No. U. S. Canada, ed. 2. **1:** 347. 1913). (Name from Greek *clados,* branch, referring to the highly branched inflorescences.)—TWIG-RUSH, SAW-GRASS.

Cladium is here accepted in the strict sense—i.e., consisting of three species: *C. Mariscus, C. mariscoides* (Muhl.) Torrey, and *C. jamaicense* Crantz. Kükenthal treated the genus more broadly, including *Machaerina* Vahl. Recent studies by Vanhecke and Metcalfe argue against such a broad circumscription. Species of *Cladium* consistently differ from those of *Machaerina* in their smaller, less differentiated embryos and their isobilateral leaves with inverted bundles (illustrated by Metcalfe).

Two species occur in our area. *Cladium jamaicense,* the saw-grass of the Florida Everglades, grows in tidal marshes and coastal wetlands from eastern Virginia to Mexico and the West Indies. Some authors (Kükenthal, Raynal) included *C. jamaicense* in the European *C. Mariscus*; Kern also included the Australasian *C. procerus* S. T. Blake. The second species in our area, *C. mariscoides,* occurs in brackish wetlands and inland fens and marshes from Newfoundland to Saskatchewan to Florida and Missouri; it is rare in the Southeast. Raynal, without discussion, treated *C. mariscoides* and *C. jamaicense* as synonyms of *C. Mariscus,* an extreme view not followed by anyone else.

Cladium jamaicense is important as the dominant species of much of the Florida Everglades. The culms and leaves of *C. Mariscus* are gathered and used in the manufacture of paper products in the Danube Delta, Romania.

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Tribe SCLERIAE Kunth ex Fenzl in Endlicher, Gen. Pl. 2: 114. 1836.

15. **Scleria** Bergius, Sv. Vet.-akad. Handl. 26: 142. 1765.

Small to medium, erect [scandent], perennial or annual herbs of grasslands, open woods, fens, and shores. Roots fibrous; rhizomes regularly present in many species, indurate, sometimes tuberlike, simple or branched. Culms trigonous, glabrous, pubescent, or scabrellate [retrorsely scabrous], sometimes bulbous basally. Basal leaves bladeless or nearly so. Cauline leaves several; sheaths 3-angled, glabrous or more often scabrellate or pubescent; blades lanceolate to linear or filiform, flat to slightly conduplicate [involute or thickened], glabrous, scabrellate, or pubescent; chlorenchyma not radiate. Inflorescences paniculate, 1 to several, terminal or lateral and terminal; bracts leaflike but shorter than or equaling the cauline leaves; rays trigonous, scabrellate on the angles or smooth, secondary rays regularly produced in some species. Spikelets 1–6, lanceolate to linear or oblong. Scales 1–6, ovate-deltoid, acute, mucronulate to cuspidate, conspicuously medially 1-nerved, laterally nerveless, glabrous or pubescent. Flowers imperfect; carpellate flower(s) 1 (or 2), borne at the base of the spikelets or in separate spikelets. Perianth bristles lacking. Stamens 1–3; filaments capillary; anthers narrowly ellipsoid to linear, the apices of the connectives frequently prolonged as slender, subulate, reddish appendages; pollen grains uniaperturate, obovoid to subspheroid, psilate. Hypogynium, if present, pebbled or warty, entire or with 3 acute to obtuse [truncate or acuminate], ciliate or glabrous lobes clasping the base of the achene. Styles slender, glandular; stigmas 3, capillary, shorter than the styles. Achenes roundly trigonous to terete, globose to ellipsoid, the apex broadly rounded (sometimes apiculate), the base sessile to broadly stipitate, the surface smooth, reticulate, trabeculate, rugose, glabrous, or pubescent. Base chromosome number 7(?). TYPE SPECIES: *S. flagellum-nigrorum* Berg.; see Britton & Brown, Illus. Fl. No. U. S. Canada, ed. 2. **1:** 348. 1913. (Name from Greek *skleros,* harsh, the culms of the type species being bound together into whips for beating slaves in Surinam; often incorrectly said to be derived from Greek *skleria,* tough, in reference to the achene walls; see Holm, 1898).—NUT-RUSH.

A predominantly tropical genus of some 200 to 225 species. Centers of diversity are tropical South America, tropical Africa, and southeastern Asia. Twelve species occur in the United States, all east of the Great Plains. All are present in the Southeast. Several range northward into northeastern North America, reaching Massachusetts, southern Ontario, and southern Minnesota. Two of our representatives occur southward into the West Indies. Many of our species are endemic, as are most other taxa of *Scleria.* Many African species, for example, occur only in Africa, and several are restricted to a single country or are known from only one collection. Such endemism contrasts with the distribution of the other large, mostly tropical genera of the family, such as *Cyperus,* in which about one-fifth of the species are pantropic. Only two species of *Scleria, C. lithosperma* (L.) Sw. and *S. hirtella* Sw., are reported from both the Old World and the New.

The morphology of the achenes and the hypogynia has traditionally provided the chief criteria for the circumscription of species. Core noted that some species—for example, the South American *Scleria leptostachya* Kunth—produced both smooth and verrucose achenes, sometimes within a single collection and sometimes within the same inflorescence. Nelmes (1955, 1956) reported similar problems with certain African species, and he relied on features of the rhizomes, ligules, and inflorescence (in addition to achene morphology) in his classification of the African species. The hypogynium is apparently derived from receptacular tissue, as is shown by its vascularization (Blaser, 1940, 1941b).

Robinson (1966) indicated that many of the southern African species of *Scleria* are strong calcicoles. This autecology contrasts with that of the American species, most of which grow in acidic coastal plain habitats. Apparently only one American species, *S. nitida* Willd. (which Fairey treated as a synonym of *S. verticillata*) is a calciphile (Fernald).

Core recognized five sections in the genus, of which two, sects. SCLERIA (sect. *Euscleria* Endl.) and HYPOPORUM (Nees) Endl., are represented in the Southeast. In sect. HYPOPORUM the species have androgynecandrous spikelets (carpellate flowers below the staminate) and lack hypogynia. There are five species in our area: *S. verticillata* Willd., *S. hirtella* Sw., *S. Baldwinii* (Torrey) Steudel, *S. georgiana* Core, and *S. lithosperma* (L.) Sw. Species of sect. SCLERIA have unisexual spikelets and three-lobed, entire hypogynia. In our area this section includes seven species: *S. triglomerata* Michx., *S. minor* Stone, *S. oligantha* Michx., *S. ciliata* Michx., *S. pauciflora* Willd., *S. Curtissii* Britton, and *S. reticularis* Michx.

The genus is scarcely known cytologically. Reports are available only for *Scleria tesselata,* $2n = 28$, of southeastern Asia. This suggests the base number $x = 7$ for the genus.

Species of *Scleria* have unusual embryological features (Nijalingappa). In *S. foliosa* A. Rich. the embryos have both chalazal and micropylar haustoria. Wall formation in the endosperm is complete in the Cyperaceae, except in *Scleria,* where it is incomplete. The surface of the cotyledon is papillose in *Scleria* but smooth in other genera of the family.

Robinson (1966) stated that several southern African species had "citrus-scented" foliage; in fact, he used this as a lead characteristic in his key. Thus, further investigation of the chemistry of these plants might be fruitful.

The fruits of *Scleria triglomerata* are dispersed by ants. The hypogynium functions as an elaiosome (Gaddy). However, Robinson (1962) suggested that the hypogynium provided buoyancy for the achenes of several southern African species and was thus an adaptation for dispersal along water channels that might later provide appropriate conditions for germination and growth of seedlings.

No species of *Scleria* is gathered for food. Rhizomes of *S. hirtella* have been employed medicinally in Colombia (Core). The tough, scabrous foliage of *Scleria* is unsuitable for cattle forage. About ten species are noted as significant weeds in Central and South America, tropical Africa, and southeastern Asia. *Scleria sumatrensis* Retz. is a detrimental weed in Borneo (Holm *et al.*).

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Tribe CARICEAE Kunth ex Dumortier, Fl. Belg. 144. 1827.

16. **Cymophyllus** Mackenzie in Britton & Brown, Illus. Fl. No. U. S. Can. ed. 2. **1:** 441. 1913.

Loosely caespitose perennials of mesic montane forests. Rhizomes oblique. Culms subterete, smooth, aphyllopodic. Leaves several; lowest with papery sheath only, bladeless; uppermost sheathless, the blade broadly lanceolate, broadly rounded at apex, undulate at margins (especially so when dried), conspicuously multinerved but lacking a differentiated midvein and ligule. Inflorescences single densely ellipsoid spikes, 1 per culm, terminal, with the pistillate flowers below the staminate; bracts single broadly deltoid entire scales, 1 per

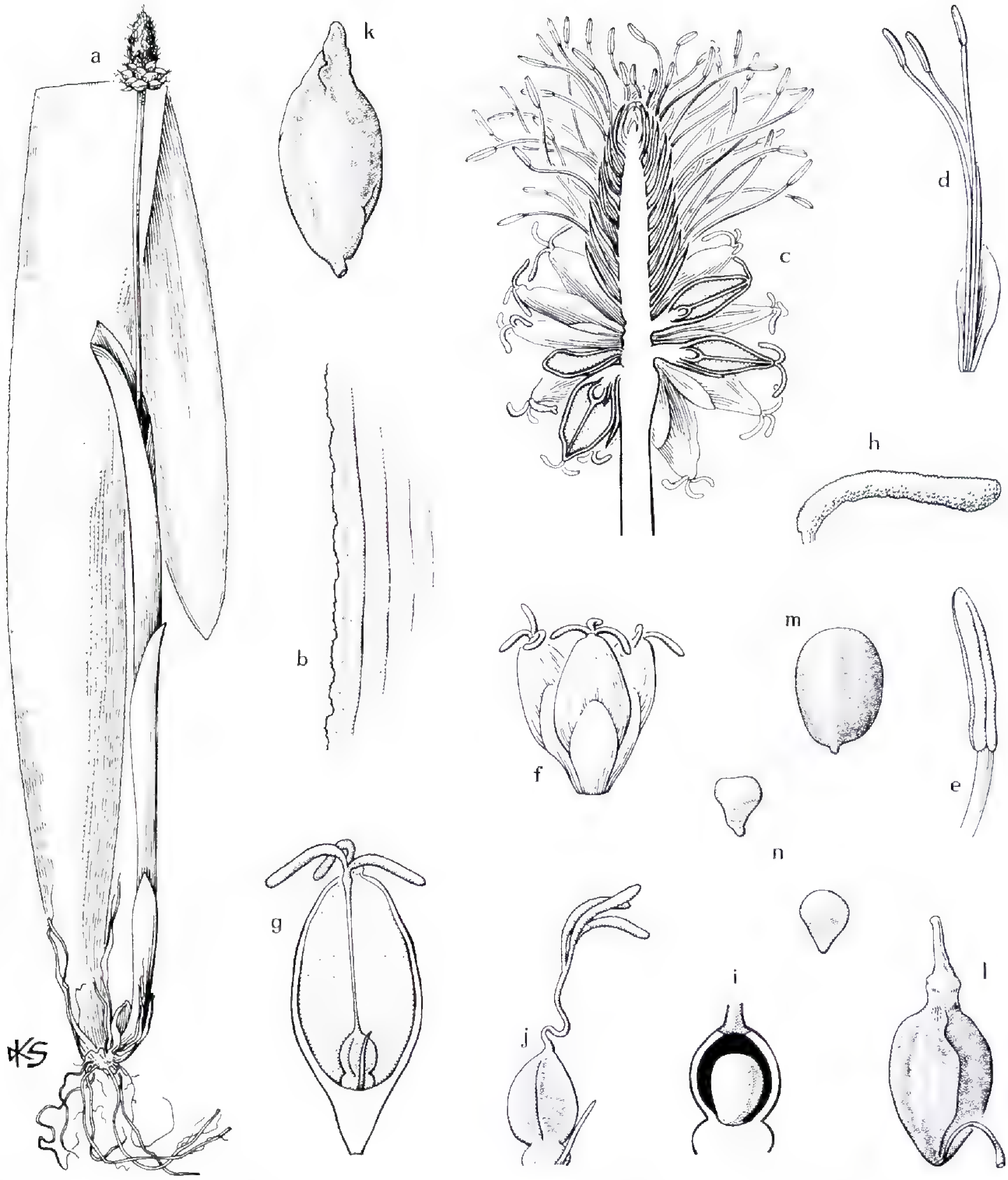

FIGURE 4. *Cymophyllus.* a–n, *C. Fraseri:* a, habit (portion of plant, leaf of preceding season, plus new shoot terminated by inflorescence just past anthesis), × ½; b, detail of undulate leaf margin, × 6; c, longitudinal section of inflorescence, staminate flowers above, carpellate below, × 2; d, staminate flower with subtending scale, × 3; e, anther (basifixed), × 12; f, 3 carpellate flowers enclosed in perigynia, each in axil of a scale, × 3; g, longitudinal section of perigynium to show carpellate flower (note bristlelike rachilla), × 5; h, stigma (note lack of papillae—species is insect pollinated), × 12; i, longitudinal section of gynoecium to show single basal anatropous ovule, × 12; j, early stage of developing fruit, growth of gynoecium producing kink in style, × 5; k, perigynium enclosing mature achene, × 6; l, immature achene (note rachilla at base), × 6; m, achene, × 6; n, embryo, dissected from base of achene, 2 views, × 25.

spike, broader than but otherwise like the pistillate scales immediately above it. Flowers imperfect. Perianth lacking. Scales oblong-ovate, entire, without conspicuous midvein or nerves. Stamens 3; filaments slender, 1–3 times as long as the subtending scales; anthers slenderly ellipsoid, the connectives not prolonged. Perigynia 10–30, broadly ellipsoid, roundly trigonous, abruptly contracted to a short, entire beak, weakly 20- to 30-nerved, glabrous; rachilla filiform, ⅓–½ as long as the perigynium. Styles slender; stigmas 3, slightly longer than the style, exserted from the beak of the perigynium. Achenes trigonous, broadly ellipsoid, the apex broadly rounded, the base abruptly stipitate, the surface smooth, glossy. Chromosome number unknown. TYPE SPECIES: *C. Fraseri* (Andrews) Mackenzie (*Carex Fraseri* Andrews; see Britton & Brown, Illus. Fl. No. U. S. Canada, ed. 2. **1**: 441. 1913.) (Name from Greek *kuma,* wave, and *phyllon,* leaf, in reference to the undulate margins of the leaves.) —FRASER'S SEDGE.

A monotypic genus endemic to the southern Appalachians. The sole species, *Cymophyllus Fraseri,* is well known for its attractive white spikes that are conspicuous when the plants flower in the spring. The plants grow in mesic to somewhat damp soils in mixed hardwood forests, particularly on northern and western slopes at middle elevations. The species is known from eastern Tennessee and northwestern South Carolina, north through the Ridge and Valley and Blue Ridge provinces to extreme south-central Pennsylvania (Somerset County). Clarkson listed known collections arranged by state and county.

The systematic position of the genus has been disputed. Kükenthal treated the species as *Carex Fraseri* (sect. *Leucocephali* Holm of subg. *Primocarex* Kükenthal). Mackenzie, Fernald, Metcalfe, and Reznicek (pers. comm.) recognized *Cymophyllus* as a distinct genus. The conspicuous white inflorescences of *C. Fraseri,* while unique among North American species of the tribe Cariceae, are also known in at least one Old World species of *Carex* (*C. baldensis* L.). White inflorescences are associated with insect pollination (discussed below) and have evolved in *Cyperus* and *Rhynchospora.* In *C. Fraseri* there is a rachilla within the perigynium. While a rachilla is not present in any temperate North American species of *Carex,* it does occur in several other species (e.g., *C. microglochin* Wahlenb. (boreal North America, cold-temperate Eurasia, southern South America, *fide* Fernald)). Anatomical evidence (summarized by Metcalfe) gives the strongest support for the generic status of *Cymophyllus.* In *Cymophyllus Fraseri* the culms are terete (trigonous (rarely hexagonal) in *Carex*); the leaves lack ligules (which are always present in *Carex*); the uppermost leaf lacks a sheath and consists of blade only (sheaths are always present in the cauline leaves of *Carex*); the large leaf blade is broadly rounded apically (acute in *Carex*) and lacks the differentiated midrib and the adaxial layer of bulliform cells typical of *Carex* (Holm; Metcalfe). In *Cymophyllus Fraseri* the median vascular bundle has an incomplete adaxial sclerenchyma cap, and there is an abaxial sclerenchyma girder (Metcalfe). The presence of perigynia in *Carex* and *Cymophyllus* clearly indicates that they are closely related, although it is unclear how. The presence of a rachilla in *Cymophyllus* suggests that this genus might be closer to the Southern Hemisphere *Uncinia* Pers. than to *Carex.*

Cymophyllus Fraseri has long been suspected of being entomophilous (Clarkson), although there has been only a single field study documenting entomophily (Thomas). Four bee and one fly species were observed to visit spikes of this species, which flowers from late April to mid-June. The insects collect pollen for food and transfer it from plant to plant. They land on the lower, relatively broad carpellate portion of the spikes, where they deposit pollen on the stigmas. They then crawl up to the anthers, collect pollen, and fly to another inflorescence. The pattern of stigmas first, then anthers, probably enhances outcrossing (Thomas).

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17. **Carex** Linnaeus, Sp. Pl. **2:** 972. 1753; Gen. Pl. 280. 1754.

Caespitose or single-stemmed, small to medium-sized perennials of wet to dry woods, grasslands, rock outcrops, pocosins, fens, bogs, marshes, and swamps. Roots fibrous, smooth or pubescent; rhizomes (infrequently lacking) short and oblique or long and horizontal, with closely appressed, lanceolate scales. Culms loosely to densely clustered or solitary, fertile or both vegetative and fertile, trigonous [hexagonal], the angles smooth or scabrellate. Basal leaves several to many; sheaths smooth; ligule hyaline, glabrous; blades flat, conduplicate, plicate, or involute, scabrellate (or smooth) on margins and midveins, sometimes microscopically papillate on 1 or both surfaces, infrequently glaucous; stomata paracytic, present on one or both surfaces; chlorenchyma not radiate; air chambers frequently present; cauline leaves similar to basal ones but shorter and fewer, sometimes lacking. Inflorescences simple or compound, monoecious (rarely dioecious); bracts lacking or 1–6; spikes 1 to several, loosely to densely ovoid to slenderly cylindrical, sessile or borne on simple [branched] erect to pendent peduncles; each spike subtended by a leaflike or filiform basal bract; spikes wholly carpellate or wholly staminate or gynecandrous or androgynous.

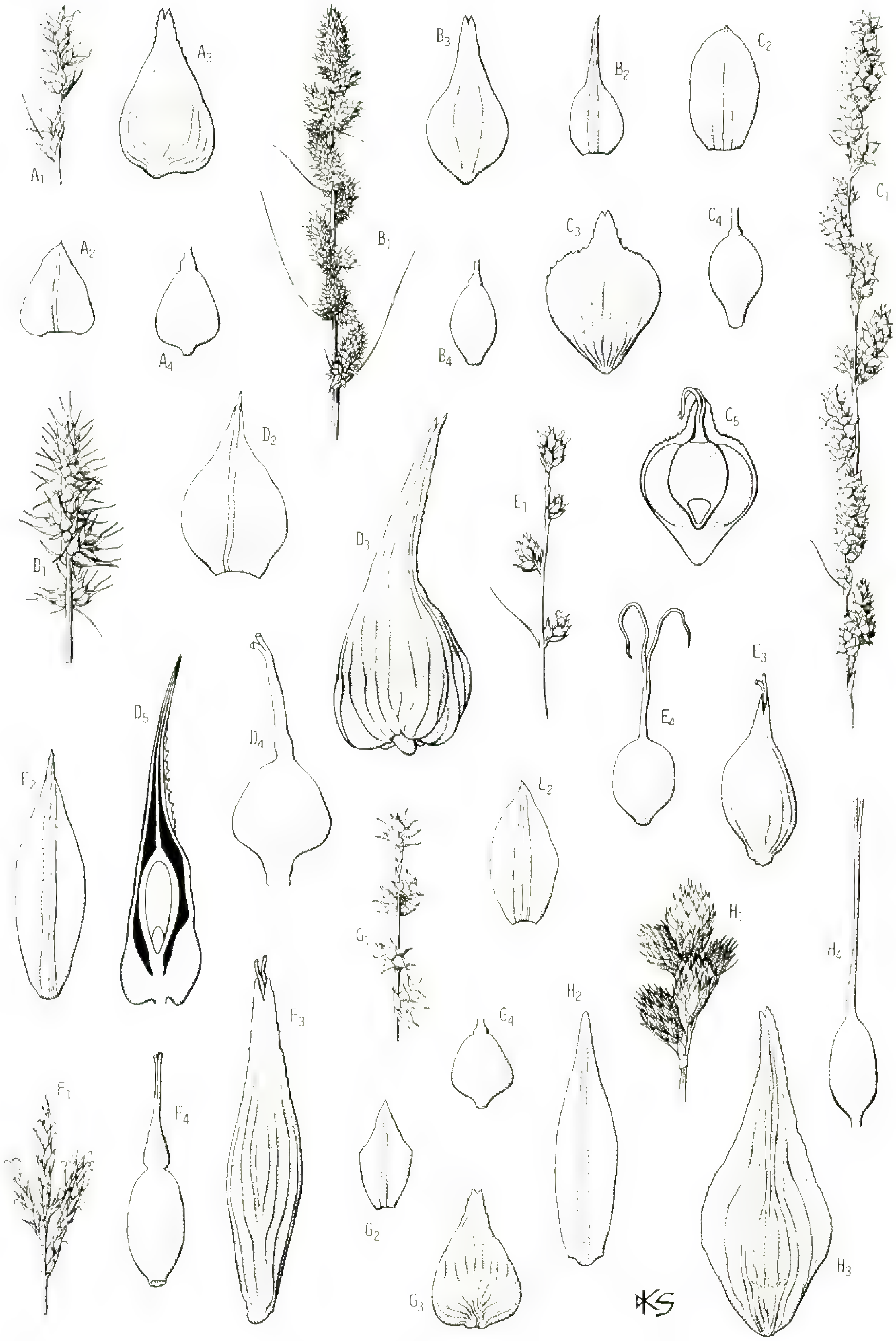

FIGURE 5. *Carex* subg. VIGNEA: 8 species shown, each representing a different section (A, *Carex retroflexa* (sect. PHAESTOGLOCHIN); B, *C. vulpinoidea* (sect. MULTIFLORAE); C, *C. decomposita* (sect. HELEOGLOCHIN); D, *C. laevivaginata* (sect. VULPINAE); E, *C. brunnescens* subsp. *sphaerostachya* (sect. GLAREOSAE); F, *C. bromoides* (sect. DEWEYANAE);

Staminate scales lanceolate (the margins rarely fused basally), hyaline to chartaceous, 1- (to 3-)nerved; carpellate scales lanceolate to broadly ovate, chartaceous, 1- (to 3-)nerved. Flowers imperfect, protogynous or protandrous. Perianth lacking. Stamens 3; filaments capillary or ribbonlike, longer than the subtending scales; anthers broadly to slenderly ellipsoid; pollen grains 1- or 4-aperturate, obovoid or subspheroidal, psilate, trinucleate. Perigynia solitary in the axils of carpellate scales, lenticular, subterete, trigonous, or slightly to strongly compressed (beak, when present, less than to equaling or sometimes longer than the body), coriaceous to chartaceous, the faces nerveless or with 1–15 nerves, minutely papillose or not, scabrellate or essentially smooth, dull or glossy. Styles capillary, straight or curved; stigmas 2 or 3 [or 4], equaling or exceeding the styles in length, smooth, papillose, or glandular, at anthesis exserted through the orifice of the perigynia. Achenes lenticular or trigonous [4-sided], ovoid to ellipsoid, ¼ as long as to nearly as long as the body of the perigynium, sessile or stipitate, apiculate or entire, the faces flat, convex, or concave, the edges obtuse or acute (invaginate in a few species), the epidermal cells translucent, opaque, or glossy. Embryos obconical, the radicle basal. Base chromosome number 5. TYPE SPECIES: *C. hirta* L., not *C. pulicaris* L.; see Hitchcock & Green, Prop. Brit. Bot. 187. 1929, and comments by Voss, Mich. Bot. **11:** 31, 32. 1972. (The classical Latin name, perhaps derived from the Greek *keirein,* to cut, due to the sharp margins and keels of the leaf blades.) —SEDGE.

A very large, cosmopolitan genus, reported to contain from 1000 to 2000 or even 2500 species (Standley, 1985a), including 165 that occur in the Southeast. Four subgenera have been recognized, of which two are represented in the United States. Subgenus INDOCAREX Baillon (inflorescences richly branched, branches subtended by tubular prophylls) comprises about 50 species of the Old World tropics. Subgenus VIGNEA (Lestib.) Kükenthal (spikes all either gynecandrous or androgynous, sessile, stigmas two, perigynia and achenes lenticular) includes about 500 species; it is worldwide in distribution but is most diverse in the northern temperate and boreal regions. Subgenus CAREX (subg. *Eucarex*; spikes sessile or pedunculate, some exclusively staminate or pistillate, stigmas 3 (rarely 2), perigynia and achenes trigonous) is the largest subgenus, with about 800 species. Subgenus PRIMOCAREX Kükenthal (spikes solitary, terminal, stigmas 2 or 3, achenes lenticular or trigonous) is not represented in our area.

The evolution of the tribe Cariceae is largely unclear. Due to shared features of the inflorescences, Smith & Faulkner suggested that it arose from ancestors akin to the Scleriae or the Hypolytreae. Kukkonen (1963), because of similar

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G, *C. Howei* (sect. STELLULATAE); H, *C. scoparia* (sect. OVALES)). Four or 5 items illustrated for each, these drawn at same magnification throughout: 1, inflorescence, × 1; 2, scale subtending perigynium, abaxial surface, × 10; 3, mature perigynium, abaxial surface, × 10; 4, mature achene, abaxial surface, × 10; 5, longitudinal section of mature perigynium and achene (C and D only), × 10.

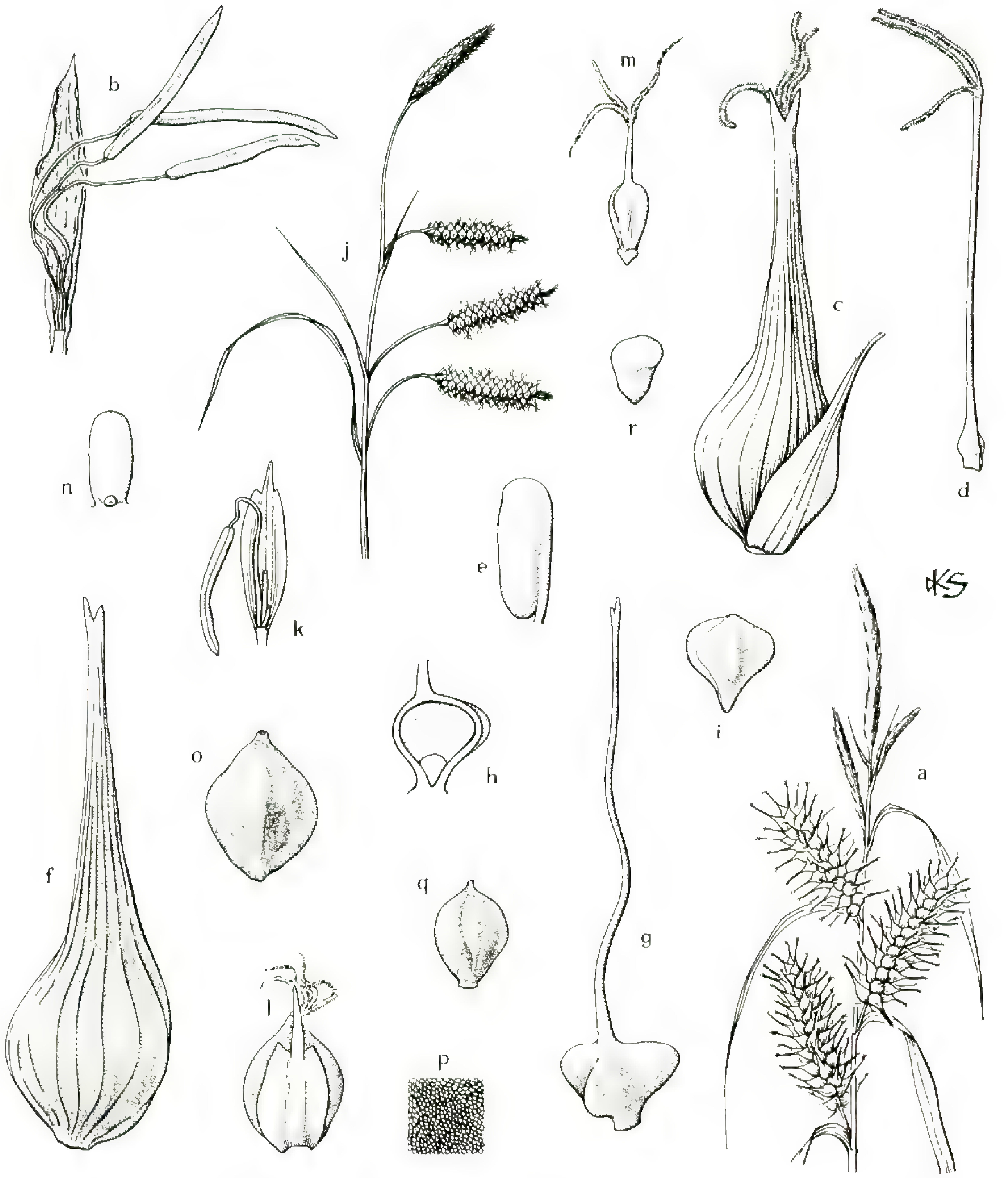

FIGURE 6. *Carex* subg. CAREX (subg. *Eucarex*). a–i, *C. gigantea:* a, inflorescence, uppermost 3 spikes staminate, × ½; b, staminate flower and subtending scale, adaxial view, × 5; c, perigynium in axil of subtending scale, stigmas of carpellate flower protruding, × 5; d, carpellate flower (gynoecium), perigynium removed, × 5; e, ovule, lateral view, micropyle not visible, × 25; f, mature perigynium enclosing achene, × 5; g, achene with persistent style, × 5; h, longitudinal section of achene, seed coat not shown, embryo basal, endosperm above, × 5; i, seed removed from achene, × 5. j–r, *C. glaucescens:* j, inflorescence, staminate spike uppermost, × ½; k, staminate flower and subtending scale, most of 2 stamens removed, × 5; l, perigynium and subtending scale, stigmas of carpellate flower protruding, × 5; m, carpellate flower, × 5; n, ovule, micropyle visible, raphe behind, × 25; o, mature perigynium enclosing achene, × 5; p, perigynium, detail of surface, showing globular to ellipsoid cells that produce glaucous effect, × 25; q, achene, × 5; r, embryo, × 25.

infestations of smut fungi, indicated a probable close relationship with subfam. Rhynchosporoideae; Koyama concurred with this opinion. A clearer understanding of generic relationships of the genus must await a better picture of evolution within the genus. Its very large size and worldwide distribution continue to hamper such studies.

Kükenthal believed that subg. PRIMOCAREX Kükenthal was the most primitive within the genus. A succession of more recent cyperologists (Kreczetowicz; Nelmes; Koyama, 1962a; Le Cohu, 1968; Haines & Lye; Smith & Faulkner; Reznicek, 1986b) have taken the opposite view. In their opinion the unispicate condition of subg. PRIMOCAREX was derived (perhaps polyphyletically) from ancestors with richly branched inflorescences like those of subg. INDOCAREX. However, the presence of a rachilla within the perigynium of some species of subg. PRIMOCAREX suggests that it is the most primitive subgenus. Smith & Faulkner believed that subgenera CAREX and VIGNEA might have evolved from subg. INDOCAREX by reduction in inflorescence structure (a pattern also suggested for several other genera of the family, e.g., *Cyperus* and *Scirpus*). This would have involved loss of cladoprophylls (tubular prophylls subtending branches) and reduction of branching. There are contrasting interpretations of the inter- and infrageneric relationships in *Carex.*

The morphology of the inflorescences, particularly of the spikes and perigynia, has traditionally been most heavily relied upon in distinguishing species and circumscribing sections. Anatomical and cytological features are also taxonomically useful. Anatomical evidence has long been applied to the systematics of *Carex.* Crawford described the stems and leaf blades of the British species. Akiyama presented a systematic study of the eastern Asian species, emphasizing anatomical differences. Several recent revisions have included anatomical descriptions of culms and leaves. Standley (1985a), in her monograph of the northwestern species of sect. PHACOCYSTIS Dum. (sect. *Acutae*), showed that related species differ in the distribution of sclerenchyma and stomata in culms and leaf blades. In certain species stomata are present on one or both surfaces (Standley, 1986). The importance of anatomical features has also been discussed by Le Cohu (1972) and by Metcalfe.

Recent studies with the scanning electron microscope have revealed an interesting variety of surface features in leaves, perigynia, and achenes of *Carex.* The presence of tubercles (Hoshino, 1986) and papillae (Maloney & Evans) and the distribution of stomata (Standley, 1986) are useful in distinguishing species and circumscribing sections.

Cytological studies have been helpful in *Carex,* but chiefly at the specific level. Chromosome numbers in the genus range from $n = 6$ to $n = 56$. The base chromosome number is 5, and the commonest haploid numbers in North American species are 10, 20, 30, and 40 (Wahl). In many instances related pairs of species differ in chromosome number. Aneuploidy is prevalent within the genus. Aneuploid series characterize many sections (Wahl; Davies; Dietrich; Faulkner, 1972). Polyploidy is infrequent.

The pollination biology of *Carex* has received little attention. Most species are anemophilous. Honey bees and beetles visit inflorescences to gather pollen and thus may also be vectors (Leppik). Self-compatible and self-incompatible species have been noted in the genus (Faulkner, 1973; Handel, 1976, 1978a; Schmid, 1984b). It is not known whether the incompatibility is sporophytic or gametophytic. Handel (1976) determined that pollen-flow distances in *C. platyphylla* Carey and *C. plantaginea* Lam. were rarely more than 10 m.

Little is documented about the dispersal of fruits of *Carex*. It has been assumed that species with inflated perigynia are dispersed by floating on water, but experimental verification is lacking. Several North American species (e.g., *C. communis* Bailey, *C. umbellata* Willd., and *C. pedunculata* Willd.) have elaiosomes at the base of the perigynia and are dispersed by ants (Handel, 1978; Gaddy, 1986). *Carex pauciflora* Michx., widespread in northeastern North America, has subulate perigynia that at maturity spring away from the rachis (up to 60 cm) when touched (Hutton).

Flavonoid profiles can be used to distinguish between closely related species. Toivonen (1974) showed this in the Fennoscandian representatives of sect. CANESCENTES (sect. *Heleonastes*). Manhart (1985) demonstrated that classifications based on occurrences of flavonoids were similar to relationships determined by morphology.

The species of *Carex* fall into three broad ecological groups with regard to habitat: wetland, forest, and ruderal. In general the species of a section are ecologically similar. Several sections (e.g., sects. PALUDOSAE G. Don and LUPULINAE Carey) include mostly wetland species. Section ACROCYSTIS Dumort., however, contains species of dry to dry-mesic open or wooded habitats. Several sections (e.g., sect. ALBAE Ascherson & Graebner) are composed mostly of calcicoles.

Most species of *Carex* are rhizomatous perennials. *Carex* is the only large genus of the family containing no annuals. Certain species reproduce mostly vegetatively (e.g., *C. Bigelowii* Torrey, plants of which set abundant seed, with little germination or recruitment of seedlings unless disturbance occurs). In the boreal *C. flava* L. seedlings persist for several years until competition is removed (by disturbance or herbivory) and then grow rapidly to fill in the available space (Schmid, 1986).

The economic importance of the genus lies chiefly in providing fodder for domestic and wild mammals, especially in colder regions. Many Russian species are important in this way (Goncharov *et al.*); *Carex stans* Drejer and *C. discolor* Nylander provide good grazing for cattle and reindeer. In Iceland, meadows of *C. Lyngbyei* Hornem. are managed and yield up to five tons per hectare. The nutritional content is very similar to that of common pasture grasses such as Kentucky bluegrass, *Poa pratensis* L.

The following is a synopsis of the southeastern species, with chromosomal, systematic, and ecological references. The order and circumscription of sections generally follows Mackenzie (1931–1935).

Subgenus VIGNEA (Lestib.) Kükenthal, represented in the Southeast by species belonging to ten sections, is characterized by lenticular achenes, dorsiventrally flattened perigynia, two stigmas, and both carpellate and staminate flowers in each spike of the inflorescence.

Species of sect. AMMOGLOCHIN Dumort. (*Arenariae* Kunth, including sect.

Divisae) are small rhizomatous plants of grasslands and strands. Two Eurasian species, *Carex arenaria* L., $n = 29, 58, 60, 64$ (Noble) and *C. divisa* Hudson, are naturalized in our area. Both grow on coastal sands from eastern Maryland to eastern North Carolina. Several others occur in Canada and the western United States, where *C. Eleocharis* Bailey is an important forage in the Rocky Mountain region (Hermann, 1970).

Section MACROCEPHALAE Kükenthal comprises two eastern Asian species, one of which, *Carex Kobomugi* Ohwi, $2n = 84, 88$, is sparingly naturalized from eastern Virginia (Norfolk Co.) north to Cape Cod; it should be looked for in eastern North Carolina. Standley (1985b) studied its population biology. Although previous authors had described the species as dioecious, she showed that individual rhizomes of a clone were consistently either staminate or carpellate (monoecious).

Section PHAESTOGLOCHIN Dumort. (sect. *Bracteosae* (Kunth) Pax) is one of the most diverse sections of *Carex* in North America; it includes 16 species in our area, all with ranges that extend into the northeastern United States or to Canada. Plants of these species are mostly caespitose, with one to five sessile androgynous spikes. Webber & Ball revised the *C. rosea* complex and corrected the application of the names *C. rosea* and *C. convoluta.* Chromosome numbers are known for six southeastern representatives of this section: *C. sparganioides* Muhl., $n = 23$; *C. cephalophora* Muhl. ex Willd., $n = 24$; *C. retroflexa* Willd., $n = 20$; *C. rosea* Schkuhr (*C. convoluta* Mack.), $n = 26$; *C. appalachica* Webber & Ball (*C. radiata* auct., non (Wahlenb.) Sm.); and *C. radiata* (Wahlenb.) Small (*C. rosea* auct., non Schkuhr), $n = 29$. David & Kelcey summarized the biology of the European species, *C. muricata* L., *C. spicata* Hudson, and *C. divulsa* Stokes, all $2n = 58$. *Carex spicata* and *C. divulsa* are naturalized in the Northeast south to Virginia. They might be found in North Carolina.

Section MULTIFLORAE (Kunth) Mack. contains three species in our area. The commonest of these, *Carex vulpinoidea* Michx., $n = 26, 27$, is known from all of the southeastern states and ranges north into southern Canada. It is also sparingly naturalized in England (Clapham *et al.*). The other southeastern species are *C. triangularis* Boeck. and *C. annectens* Bickn. Both occur in most of the southeastern states, but neither is as common as *C. vulpinoidea.*

Section HELEOGLOCHIN Dumort. (sect. *Paniculatae* G. Don (Hort. Brit. 367. 1830; non Carey) is represented in the Southeast by *Carex decomposita* Muhl., $n = 30, 32, 33$, which occurs in every state in our area. Plants of this section are the only North American representatives of *Carex* with paniculate inflorescences. Certain extraregional species of the section appear to be cytologically conservative (cf. Clapham *et al.*). *Carex diandra* Schrank, $2n = 60$, is circumboreal, while *C. paniculata* L., $2n = 60, 62, 64$, and *C. appropinquata* Schum., $2n = 64$, are European.

In the Southeast, sect. VULPINAE (Carey) Christ is represented by five species of swamps, marshes, and wet meadows. The plants resemble those of the preceding two sections but are distinguished by their long, slender perigynia (1 cm long in *Carex crus-corvi* Shuttlew.). In several species the bases of the perigynia are conspicuously enlarged with aerenchyma, which probably makes the fruits buoyant and allows dispersal by water. *Carex crus-corvi,* $n = 26$, *C.*

laevivaginata (Kükenthal) Mack., $n = 23$, and *C. stipata* Willd., $n = 26$, occur throughout our area.

Section GLAREOSAE G. Don (sect. *Heleonastes* (Kunth) Kükenthal) is a group of circumboreal species of wet woods and bogs. The plants are small and have few-flowered inflorescences. Three species, *Carex brunnescens* subsp. *sphaerostachya* (Tuckerman) Kalela, $n = 27, 28$, *C. canescens* L., $n = 27, 28$, and *C. trisperma* Dewey, $n = 30$, barely reach our area from the north and are found in the mountains of North Carolina and Tennessee.

Section STELLULATAE (Kunth) Christ consists of perhaps 30 species worldwide. The plants are caespitose and have gynecandrous spikes of spreading to reflexed perigynia with serrulate beaks. Reznicek & Ball (1980) revised the North American species and provided excellent keys and descriptions. There are seven representatives in our area. *Carex Ruthii* Mack. is endemic to high elevations in the southern Appalachian Mountains from West Virginia to Georgia. *Carex exilis* Dewey is primarily northeastern, occurring from Newfoundland to Ontario south to Maryland; it is also known from widely disjunct stations in central North Carolina, southern Mississippi, and southern Alabama. The other southeastern species are *C. atlantica* Bailey (including *C. Mohriana* Mack.), *C. Howei* Mack., $n = 27$, *C. incomperta* Bickn., $n = 22$, and *C. angustior* Mack., $n = 26$. The two European species for which counts are available have similar numbers: *C. elongata* L., $2n = 56$, and *C. echinata* Murray, $2n = 56, 58$.

Species of sect. DEWEYANAE (Tuckerman) Mack. are probably closely related to those of sect. STELLULATAE but have fewer, narrower, and appressed rather than spreading perigynia (Reznicek & Ball, 1980). *Carex bromoides* Schkuhr, $n = 31+(4)$, is the sole southeastern representative; it occurs in every state in our area. *Carex Deweyana* Schwein., the only other species of the section, occurs in northeastern North America.

Section OVALES (Kunth) Christ contains about 50 species in North America. It is the largest section in our area, and the 16 representatives occurring in the Southeast have flattened, papery, appressed perigynia in dense, ovoid spikes. The section is taxonomically difficult and needs revisionary work. Several taxa recognized by Mackenzie (1931–1935) have been synonymized by later workers. Most of our species are widespread in eastern North America. For example, *Carex tribuloides* Wahlenb., $n = 35$, and *C. reniformis* (Bailey) Small occur in all the southeastern States, while *C. argyrantha* Tuckerman and *C. aenea* Fern. are northeastern and just enter our area in the mountains of North Carolina. *Carex vexans* Herm. is endemic to central and southern Florida. Among our representatives, chromosome numbers are known only for *C. tenera* Dewey ($n = 26, 27, 28$), *C. straminea* Willd. ($n = 34+(3)$), and *C. cristatella* Mack. ($n = 35$). The type species, the European *C. ovalis* Good., $2n = 64, 66, 68$, is cytologically similar to eastern North American species of the section.

Subgenus CAREX (subg. *Eucarex* Cosson & Germ.) includes the remaining sections of the genus, 26 of which are represented in the Southeast. The plants are characterized by differentiated spikes in which the terminal spike is wholly staminate and the others are wholly or partly carpellate. Except in the distigmatic sect. Phacocystis Dumort. (sect. *Acutae*), the ovaries and achenes are trigonous and there are three stigmas.

Section Polytrichoideae (Tuckerman) Mack. contains only *Carex leptalea* Wahlenb., $n = 26$, an eastern North American endemic growing in damp, mossy woods, often in calcareous soils, from Florida and eastern Texas north into Canada. These are small, thin plants bearing few slender, beakless perigynia and narrowly oblong, truncate achenes.

Section Phyllostachyae (Tuckerman) Bailey has four North American species, characterized by androgynous spikes and staminate scales with basally fused margins. Two, *C. Jamesii* Schwein., $n = 35$, and *C. Willdenovii* Schkuhr, $n = 31$, occur in the Southeast. In addition to features of the perigynia, these species are distinguished by the distribution of micropapillae on the leaves and culms (Maloney & Evans).

Section Acrocystis Dumort. (*Montanae* (Kunth) Carey) comprises ten species in the Southeast and nearly 30 worldwide. The plants grow in the most xeric habitats of any species of *Carex* in our area, typically dry woodlands and rock outcrops. They are small and tufted, with the leaves stiff, the carpellate spikes few flowered, and the perigynia globose to ovoid, closely covering the roundly trigonous achenes. Chromosome numbers are reported for half of our representatives and indicate an aneuploid series: *C. communis* Bailey, $n = 14$, *C. nigromarginata* Schwein., $n = 17$, *C. artitecta* Mack., $n = 18$, *C. pensylvanica* Lam., $n = 18$, and *C. lucorum* Willd. ex Link, $n = 20$. The European species are more diverse cytologically ($n = 9, 15, 19, 33$) but are similar ecologically. The fruits of *C. artitecta* (Handel, 1978) and *C. nigromarginata* (Gaddy, 1986) are dispersed by ants.

Section Pictae Kükenthal has two representatives in eastern North America, *Carex picta* Steudel and *C. Baltzellii* Chapman ex Dewey. Both are local, dry-woodland species of the unglaciated eastern United States. *Carex Baltzellii* is endemic to Georgia and northern Florida. *Carex picta,* occurring from southern Indiana to Georgia and Louisiana, is a curious species. It is the only native dioecious representative of *Carex* in our area. The plants form "fairy rings" as the rhizomes branch and proliferate dichotomously (see Martens for illustration). Clones from individual rhizomes are consistently staminate or carpellate, and carpellate plants do not always flower every year.

Section Clandestinae G. Don (*Digitatae* (Fries) Carey) consists of four species of the North Temperate Zone. The plants have purple leaf sheaths and perigynia with minute beaks and tapered bases. *Carex pedunculata* Muhl., which grows on wooded, mesic, calcareous slopes, is the only representative of the section in the Southeast. Elaiosomes are borne at the base of the perigynia, which are dispersed by ants (Handel, 1976; Gaddy, 1986). Mackenzie (1931–1935) included the only tetrastigmatic species of *Carex, C. concinnoides* Mack. of the Pacific Northwest, in this section. St. John & Parker established subg. *Altericarex* for this unusual species, but aside from its tetramerous carpellate flowers, *C. concinnoides* fits in sect. Clandestinae rather well, both morphologically and ecologically.

Section Triquetrae (Carey) Kükenthal comprises five species of temperate

North America. The plants are caespitose, and they have greenish sheaths and short-beaked, pubescent perigynia. There are two representatives in the Southeast, *Carex dasycarpa* Muhl. and *C. tenax* Chapman ex Dewey. Both grow in pine forests, mostly from South Carolina to southern Mississippi. Another species of the section, *C. hirtifolia* Mack., $n = 22+(3)+(3)$, of the northeastern United States, reaches its southern limit in the mountains of Virginia.

Section ALBAE Ascherson & Graebner consists of two species, both boreal calcicoles of dry soils. One of these, *Carex eburnea* Boott, the only North American representative, is a stoloniferous plant with glabrous perigynia that is recorded in our area only from Tennessee. The second is *C. alba* Scop., $2n = 54$, of Eurasia.

Section PANICEAE G. Don (non Christ) is a Eurasian and North American section of 12 species, five of which occur in the Southeast. The stoloniferous plants have purple to reddish scales subtending the flowers, and ascending to spreading, more or less ovoid perigynia. A member of this section, the rare southern Appalachian endemic *Carex Biltmoreana* Mack., occurs on wet, shaded cliffs in the Blue Ridge Mountains of North and South Carolina (Gaddy, 1983). Three of our representatives, *C. Woodii* Dewey, $n = 22, 26$, *C. tetanica* Schkuhr, $n = 26$, and *C. Meadii* Dewey, are mostly northern in distribution and just reach our area in the mountains of Tennessee and North Carolina. The fifth species, *C. Chapmanii* Steudel, is endemic to the Coastal Plain between Florida and North Carolina. The European *C. panicea* L. and *C. vaginata* Tausch have lower chromosome numbers: both are $2n = 32$.

Section LAXIFLORAE (Kunth) Kükenthal, containing about 25 species in eastern North America (17 in our area), one in the western United States, and a few in eastern Asia, is the most diverse section of *Carex* in our area. The plants grow in woodlands; they are caespitose and bear conspicuously two-nerved perigynia. Our species have recently been studied by Bryson, and Manhart (1986) has investigated their cytology. Handel (1978a), who investigated the pollination biology of *Carex plantaginea* Lam. and *C. platyphylla* Carey, reported that both are self-compatible and that apomixis is absent. He studied the dispersal of pollen by wind and found that pollen was transported twice as far from *C. plantaginea* as from *C. platyphylla.* This difference was attributed to the greater average height above ground of the staminate flowers in *C. plantaginea.* An aneuploid series is evident in those southeastern representatives of the section for which chromosome numbers have been reported: *C. Manhartii* Bryson, $n = 14$, *C. purpurifera* Mack., $n = 17, 18, 19$, *C. leptonervia* (Fern.) Fern., $n = 18, 19$, *C. blanda* Dewey, $n = 18, 19, 20, 21, 22$, *C. gracilescens* Steudel, $n = 20$, *C. laxiflora* Lam., $n = 20$, *C. laxiculmis* Schwein., $n = 22, 23$, *C. digitalis* Willd., $n = 24$, *C. plantaginea,* $n = 25$, and *C. platyphylla,* $n = 33, 34, 35$. *Carex striatula* Michx. and *C. laxiflora* are myrmecochorous (Gaddy, 1986).

Section GRANULARES (O. F. Lang) Kükenthal includes five eastern North American species, of which four are found in the Southeast. They are calcicoles and have few-flowered pedunculate spikes and perigynia with many fine nerves. *Carex granularis* Muhl. ex Willd., $n = 16+(4)$, occurs in all the southeastern states and is the widest-ranging species of the section. The other southeastern representatives are *C. rectior* Mack., *C. Crawei* Dewey, and *C. microdonta* Torrey & Hooker.

To sect. OLIGOCARPAE (Carey) Kükenthal (including sect. *Griseae* Bailey) belong nine species of eastern North America, of which six are present in our area. Members of this section are ecologically and morphologically similar to plants of sect. GRANULARES but have lower chomosome numbers. *Carex flaccosperma* Dewey (*C. glaucodea* Tuckerman), *C. oligocarpa* Schkuhr, $n = 27$, and *C. grisea* Wahlenb. (*C. corrugata* Fern.), $n = 28$, occur nearly throughout our area and are also found in the northeastern United States.

Species of sect. HYMENOCHLAENAE (Drejer) Bailey (including sects. *Sylvaticae* Boott and *Gracillimae* (Carey) Kükenthal) are widely distributed in the temperate regions of the Northern Hemisphere and in the East African Highlands (Kükenthal; Mackenzie, 1931–1935). The plants have slender, drooping spikes and often strongly beaked perigynia. A European representative of this section, *Carex sylvatica* Hudson, $2n = 58$, is naturalized in southern New England and Long Island. There are six species in the Southeast. The eastern North American representatives are currently being revised (with particular attention to cytology) by Waterway (in prep.). Reznicek (1986a) has provided a detailed illustrated study of the Mesoamerican species. Chromosome numbers have been reported for *C. gracillima* Schwein. ($n = 5, 27$), *C. flexuosa* Muhl. ex Willd. ($n = 27, 28$), *C. aestivalis* Curtis ($n = 28$), and *C. prasina* Wahlenb. ($n = 30$), all of which occur in the Southeast. *Carex cherokeensis* Schwein., wolf-tail, reported from every state in the Southeast, and *C. Sprengelii* Dewey, $n = 21$, of the northeastern United States, are sometimes segregated into sect. *Longirostres* Kükenthal because of their longer perigynial beaks.

Section VIRESCENTES (Kunth) Carey is represented in temperate North America, Eurasia, and the mountains of northern South America. The plants have densely cylindrical, stiffly erect spikes. There are six species in eastern North America, and all occur in the Southeast. Our representatives for which chromosome numbers are known (*Carex Bushii* Mack., $n = 24$, *C. hirsutella* Mack., $n = 26$, *C. Swanii* (Fern.) Mack., $n = 27$, and *C. virescens* Muhl. ex Willd., $n = 30$) provide yet another example of the aneuploidy so frequent in the genus.

Species of sect. CAREX (sect. *Hirtae* (Tuckerman) Christ) are widespread in the Northern Hemisphere, and a few are disjuncts in temperate South America. The plants are stoloniferous and have three to ten spikes of ascending, ovoid perigynia. The section has only two representatives in the Southeast: the Northeastern and midwestern *Carex lanuginosa* Michx., $n = 39$, is known in our area only from Arkansas, while *C. striata* Michx. (non *C. striata* Gilib., *nom. illeg.*; *C. Walteriana* Bailey), of the Coastal Plain, ranges from Georgia north to southeastern Massachusetts. The type species of this section and of the genus, *C. hirta* L., $n = 56$, is sparingly adventive in the northeastern United States (south to the District of Columbia).

Section ANOMALAE Carey includes many species in eastern Asia and Australasia, one in the western United States, and another in the eastern United States, *Carex scabrata* Schwein., $n = 27$, recorded in our area from North Carolina, Tennessee, and northern Alabama. Plants of this species have dense, cylindrical carpellate spikes and perigynia with bidentate beaks; they are stoloniferous and typically grow near woodland springs.

The monotypic sect. SHORTIANAE (Bailey) Kükenthal contains *Carex Shortiana* Dewey, an uncommon but attractive species of the Ohio River valley south to central Tennessee. The plants have culms each bearing four or five gynecandrous spikes of nerveless, corrugated perigynia with stipitate bases and entire beaks.

The species of sect. PENDULINAE (Fries) Christ have a circumpolar distribution and are characterized by pedunculate spikes and closely spaced perigynia. The type species is the European *Carex pendula* Hudson, $2n = 58$ or 60. The three representatives in our area, *C. Joorii* Bailey, *C. verrucosa* Muhl., and *C. glaucescens* Ell., are all widely distributed.

Species of sect. LIMOSAE (Tuckerman) Christ have drooping, few-flowered spikes and broadly elliptic, beakless perigynia. Many are circumboreal in distribution and grow in fens, bogs, or wet woods. A single, primarily northeastern representative, *Carex Barrattii* Schwein. & Torrey, from the mountains of Tennessee and North Carolina, is known in our area. The type species is the circumboreal *C. limosa* L., $2n = 56$.

The diverse and heterogeneous sect. ATRATAE (Kunth) Christ[19] contains many species of the arctic and alpine tundra. The plants are characterized by sessile, erect or drooping spikes, dark pistillate scales, and beaked or beakless perigynia. There are many representatives in the southern Rocky Mountains (Hermann, 1970; Murray), but none of these is shared with our area. The single species of our area, *Carex Buxbaumii* Wahlenb., $n = 37$, ca. 50, reaches its southern limit in North Carolina and Arkansas.

Section PHACOCYSTIS Dumort. (sect. *Acutae* Fries) is also a diverse circumboreal group. The plants are moderately large and have drooping spikes and distigmatic, lenticular achenes. Three northeastern species, *Carex strictior* Dewey, $n = 34$, *C. stricta* Lam., and *C. torta* Boott ex Carey, $n = 33$, reach their southern limits in the northern half of our area. Standley (1985a) revised the 15 representatives of this section in the Pacific Northwest. While none of the species she treated occurs in our area, her thorough investigation of interspecific differences in leaf and culm anatomy, cytology, morphology, and some aspects of ecology is informative and provides a model for future studies.

Species of sect. CRYPTOCARPAE (Tuckerman) Kükenthal are mostly wetland plants. They have drooping, densely flowered spikes and trigonous achenes. *Carex gynandra* Schwein., *C. Mitchelliana* M. A. Curtis, and *C. crinita* Lam., $n = 33$, occur in the Southeast. These have been treated as a single taxon under the last name, but there is good evidence for their specific status (Bruederle & Fairbrothers, 1986). *Carex gynandra* and *C. crinita* hybridize rarely. The hybrids produce aborted achenes (Standley, 1983).

Section COLLINSIAE Mack. contains a single species, *Carex Collinsii* Nutt., that grows in swamps on the Atlantic Coastal Plain from Georgia to Rhode

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[19] *Carex* sect. ATRATAE (Kunth) Christ, Bull. Soc. Bot. Belg. **24:** 15. 1885.

Island (Tucker, 1978). It is characterized by few-flowered inflorescences and subulate perigynia.

Species of sect. FOLLICULATAE Mack. also have subulate perigynia, but the spikes are densely many flowered and the plants are taller. There are two representatives in the Southeast, *Carex lonchocarpa* Willd. ex Sprengel, found throughout our area, and *C. folliculata* L., $n = 28$, a northeastern species growing only in the mountains of North Carolina and Tennessee.

Species of sect. PSEUDO-CYPEREAE (Tuckerman) Christ are tall, paludal plants of circumpolar distribution. They have drooping, slenderly cylindrical spikes and densely arranged, conspicuously bidentate perigynia. There are two representatives in our area, *Carex Schweinitzii* Dewey, $n = 30$, and *C. comosa* Boott, $n = 32$. *Carex pseudocyperus* L., $2n = 66$, is widespread in the Northern Hemisphere and is believed to be native to New Zealand (Clapham *et al.*).

Section PALUDOSAE G. Don[20] has eight species in North America and several in Eurasia. The plants are stoloniferous and bear firm, many-nerved, slightly inflated perigynia. There are two representatives in our area, *Carex hyalinolepis* Steudel, found in wetlands throughout the Southeast, and *C. trichocarpa* Muhl. ex Schkuhr, $n = 55$, a boreal bog species known in the Southeast only from the mountains of North Carolina (Core).

Dense spikes of conspicuously inflated perigynia characterize members of sect. SQUARROSAE Carey, which are endemic to eastern North America. There are three species in our area, *Carex Frankii* Steudel, *C. typhina* Michx., and *C. squarrosa* L., $n = 28$, each occurring in all or most of the southeastern states.

Section VESICARIAE (Tuckerman) Carey is a group of perhaps 20 species, mostly of eastern North America and Eurasia. The plants generally grow in shallow water and are characterized by inflated perigynia. Five representatives occur in our area, but only one, *Carex lurida* Wahlenb., $n = 32, 33$, is common (reported from every state). The others are *C. Baileyi* Britton, $n = 34$, *C. bullata* Schkuhr, *C. Elliottii* Schwein. & Torrey, and *C. rostrata* Stokes, $n = 34$. The type species, *C. vesicaria* L., $n = 41$, and *C. riparia* Curtis, $n = 36$, are cytologically similar Eurasian representatives.

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Under *Rhynchospora* see LEPPIK.

Under *Cymophyllus* see KÜKENTHAL; MACKENZIE (1931–1935).

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[20] *Carex* sect. PALUDOSAE G. Don in Loudon, Hort. Brit. 367. 1830, non (Fries) Christ (1884). TYPE SPECIES: *C. paludosa* Good. (= *C. acutiformis* Ehrh.).

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A NEW SPECIES OF PINUS FROM MEXICO AND CENTRAL AMERICA

J. P. PERRY, JR.[1]

A new species of *Pinus* is described from Mexico and Central America. Specimens were collected in Mexico, Guatemala, El Salvador, and Honduras, and resin samples were taken from trees in Mexico (Chiapas), Guatemala, and Honduras. This species differs from *P. pseudostrobus, P. oaxacana,* and *P. estevezii* both in turpentine chemistry and in leaf and cone morphology. Throughout most of its range, associated species were often *P. pseudostrobus, P. oaxacana,* and *P. montezumae*; field observations indicate that natural hybridization probably occurs between the new species and these taxa.

While carrying out field studies on species of *Pinus* growing in Mexico and Central America, I discovered a number of populations of the genus in Mexico, Guatemala, El Salvador, and Honduras that appear to belong to an undescribed species.

Pinus nubicola J. P. Perry, sp. nov. FIGURES 1–4.

Differt a P. oaxacana et P. estevezii foliis 25–40 cm longis, in fasciculo 5 vel 6 (interdum 7), cernuis vel pendulis; et squamis 20–25 mm latis, ad apicem prominentiis disparibus et umbone parva cum margine depressa instructis.

Tree 25–30 m tall, d.b.h. 0.5–1 m, when mature with open, rounded crown. Spring shoots uninodal; branchlets puberulent, soon becoming glabrous; young trees with smooth bark. Leaves in fascicles of 5 or 6 (occasionally 7, rarely 8), 25–43 cm by 0.6–1 mm, flexible, very drooping, margin serrulate; stomata on all surfaces; hypodermis 2- to 4-layered, with many slight penetrations into chlorenchyma; resin canals 3 or 4, medial (occasionally 1 internal); endodermis with outer cell walls thickened; vascular bundles 2, distinct; fascicle sheaths persistent, 20–30 mm long, pale brown, not resinous. Cones subterminal, 1 to 4 together, subsessile, reflexed, asymmetrically ovoid to long-ovoid, 10–15 by 8–10 cm when open at maturity, peduncle and few basal scales remaining on branch when cone falls. Scales 20–25 mm wide, thick, stiff, with apex obtusely angled, generally with distinct, unequal marginal projections; apophysis 5–8 by 20–22 mm, transversely keeled, abaxial surface raised more than adaxial, the umbo ashy gray, central, 2–3 mm long, margins often slightly depressed, generally curved upward, terminating in small, persistent prickle. Seeds brown or spotted to mottled black, 5–7 by 4–5 mm, with detachable, pale brown wing 20–25 by 8–11 mm; cotyledons (7 or) 8 to 10 (to 13).

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[1] 306 North Front Street, Hertford, North Carolina 27944.

Journal of the Arnold Arboretum **68:** 447–459. October, 1987.

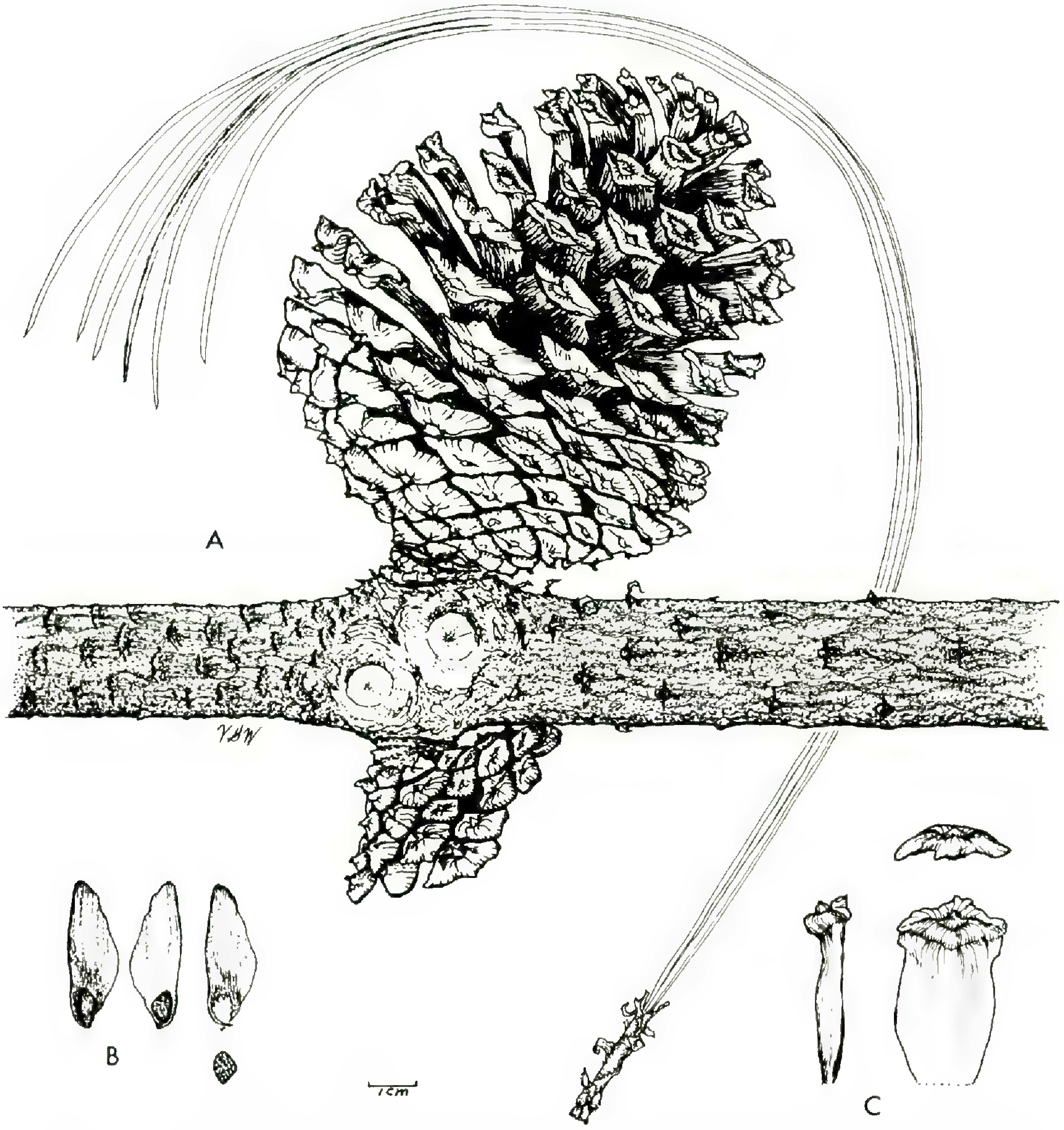

FIGURE 1. *Pinus nubicola:* A, mature cone, foliage, and branchlet, showing nondecurrent bases of foliage bracts; B, seed and seed wing; C, cone scale, showing apophysis, umbo with depressed margins, and apex with unequal projections.

TYPE. Guatemala, Depto. Guatemala, about 40 km E of San José Pinula on dirt road toward Las Nubes, 90°20′W, 14°33′30″N, alt. 2000 m, 25 Feb. 1979, *Perry GUA.32-79* (holotype, GH; isotypes, CHAP, E, GH, K, MEXU, NCSC).

TURPENTINE ANALYSES. Most trees had relatively large amounts of heptane, nonane, and α-pinene; many also had sizeable quantities of limonene, while a few had a great deal of terpinene-4-ol and methyl chavicol. Results of individual analyses performed on 31 specimens from Mexico, Guatemala, and Honduras, as well as approximate mean percent composition, are shown in TABLE 1.

PHENOLOGY. Flowering starting late January, but mainly February and March.

HABITAT AND DISTRIBUTION. Mexico to Honduras (see MAP 1), on cool, moist mountain slopes, 1800–2400 m alt. (see FIGURE 2).

In Veracruz state, Mexico, *Pinus nubicola* was growing at 1800 m on the

FIGURE 2. *Pinus nubicola* growing on slope of Mt. El Pitál, Depto. Chalatenango, El Salvador, showing characteristically drooping foliage.

humid eastern escarpment of the Sierra Madre Oriental. Associated species were *Pinus chiapensis* (Martínez) Andresen, *P. pseudostrobus* Lindley, *P. oaxacana* Mirov, and *Liquidambar styraciflua* L. In Mexico (Chiapas), at a somewhat drier site, associated species were *P. oaxacana, P. pseudostrobus, P. montezumae* Lambert, *P. rudis* Endl., *P. patula* var. *longepedunculata* Loock,[2] *Pinus oocarpa* var. *ochoterenae* Martínez, *Pinus ayacahuite* Ehrenb., and *Quercus* spp. In Guatemala associated species were *P. oocarpa* var. *ochoterenae, P. montezumae, P. rudis, P. maximinoi* Moore, *P. pseudostrobus* (rarely), and *P.*

[2] Styles (1976) pointed out that there has been considerable confusion in the literature and in the field regarding the identification of *Pinus oocarpa* var. *ochoterenae* and *P. patula* var. *longepedunculata*. He attempted to resolve this by combining the two taxa and referring them to *P. patula* Schldl. & Cham. Although there is indeed a great deal of confusion regarding identification of the two taxa, I do not believe the matter has been clarified by referring both varieties to *P. patula*. I prefer, pending the results of further studies, to use the original varietal classification of these taxa.

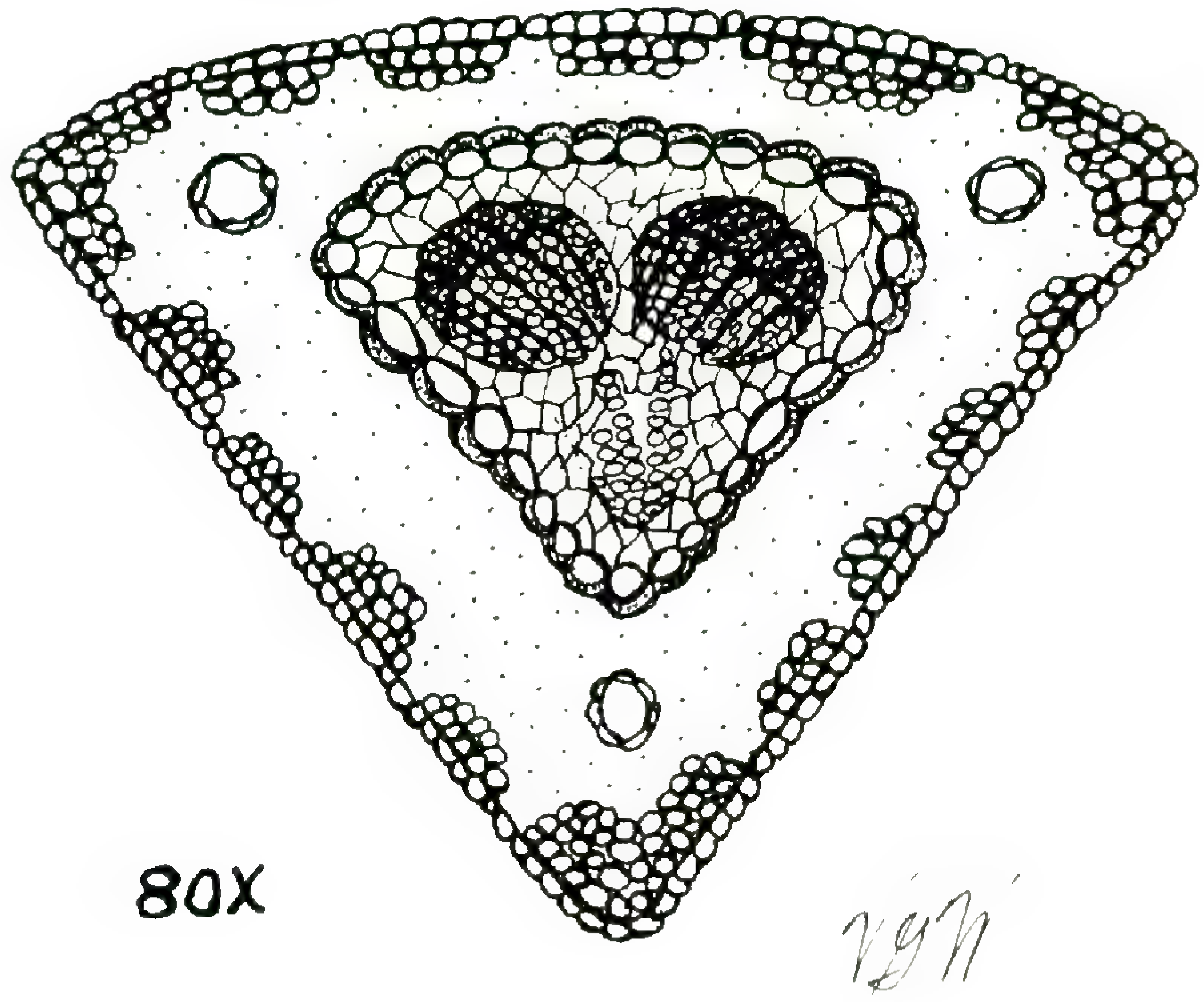

FIGURE 3. Cross section of leaf of *Pinus nubicola.*

tecunumanii Eguiluz & Perry. In El Salvador the species was found growing with *P. maximinoi, P. oaxacana, P. ayacahuite, P. oocarpa* var. *ochoterenae, P. tecunumanii, Abies guatemalensis* var. *tacanensis* Martínez, *Cupressus lusitanica* Miller, *Liquidambar styraciflua,* and *Quercus* spp. In Honduras associated species were *P. maximinoi, P. oaxacana,* and *P. tecunumanii.* At most locations epiphytes were growing in large numbers on the branches and trunks of the trees. In Guatemala and El Salvador some of the larger oaks with massive, horizontal branches were almost covered with orchids and bromeliads. Unfortunately, in most locations—particularly in Guatemala and El Salvador—the forests were rapidly disappearing as the trees were cut for lumber and firewood and the land was converted to pasture and crops.

SPECIMENS EXAMINED.[3] **Mexico.** VERACRUZ: ca. 15 km W of Jalapa, 1800 m alt., *Perry M96-81, M96-81A.* CHIAPAS: ca. 18 km S of San Cristóbal de Las Casas, 2200 m alt., *Perry MEX.24-79*; 15 km N of Comitán, 2200 m alt., *Perry MEX.25-79*; 20 km S of San Cristóbal de Las Casas, 2200 m alt., *Perry MEX.26-79*; E of San Cristóbal de Las Casas, vic. of Las Piedrecitas, 2400 m alt., *Perry MEX.151-83*; ca. 10 km W of San Cristóbal de Las Casas, near Hwy. 190, 2300 m alt., *Perry MEX.74-83*; S of San Cristóbal de Las Casas, vic. of Teopisca, 2300 m alt., *Perry MEX.84-84.* **Guatemala.** QUEZALTENANGO: vic. of Quezaltenango, 2300 m alt., *Perry GUA.3-78.* SOLOLÁ: ca. km 140 W of Guatemala City, 2400 m alt., *Perry GUA.17-78, GUA.19-78*; W of Quezaltenango on hwy. toward San Marcos, ca. km 232, 2300 m alt., *Perry GUA.24-78.* JALAPA: on dirt road from San José Pinula to Mataquescuintla, 2300 m alt., *Perry GUA.112-78* (NCSC), *GUA.112-78A*; E of San José Pinula on dirt road, vic. of Las Nubes, 2200 m alt., *Perry GUA.113-78*; on dirt road from San José Pinula to Las Nubes, ca. km 38, 2250 m alt., *Perry GUA.28-79*; E of San José Pinula on dirt road near Soledad Grande, ca. 2200 m alt., *Mittak 8299* (BANSEFOR[4]); E of San José Pinula on dirt road, vic. of La

[3] Specimens listed are in addition to those collected as vouchers for the trees tapped for oleoresin. Unless indicated otherwise, they are located in the author's personal herbarium.

[4] Banco Nacional de Semillas Forestales, Guatemala.

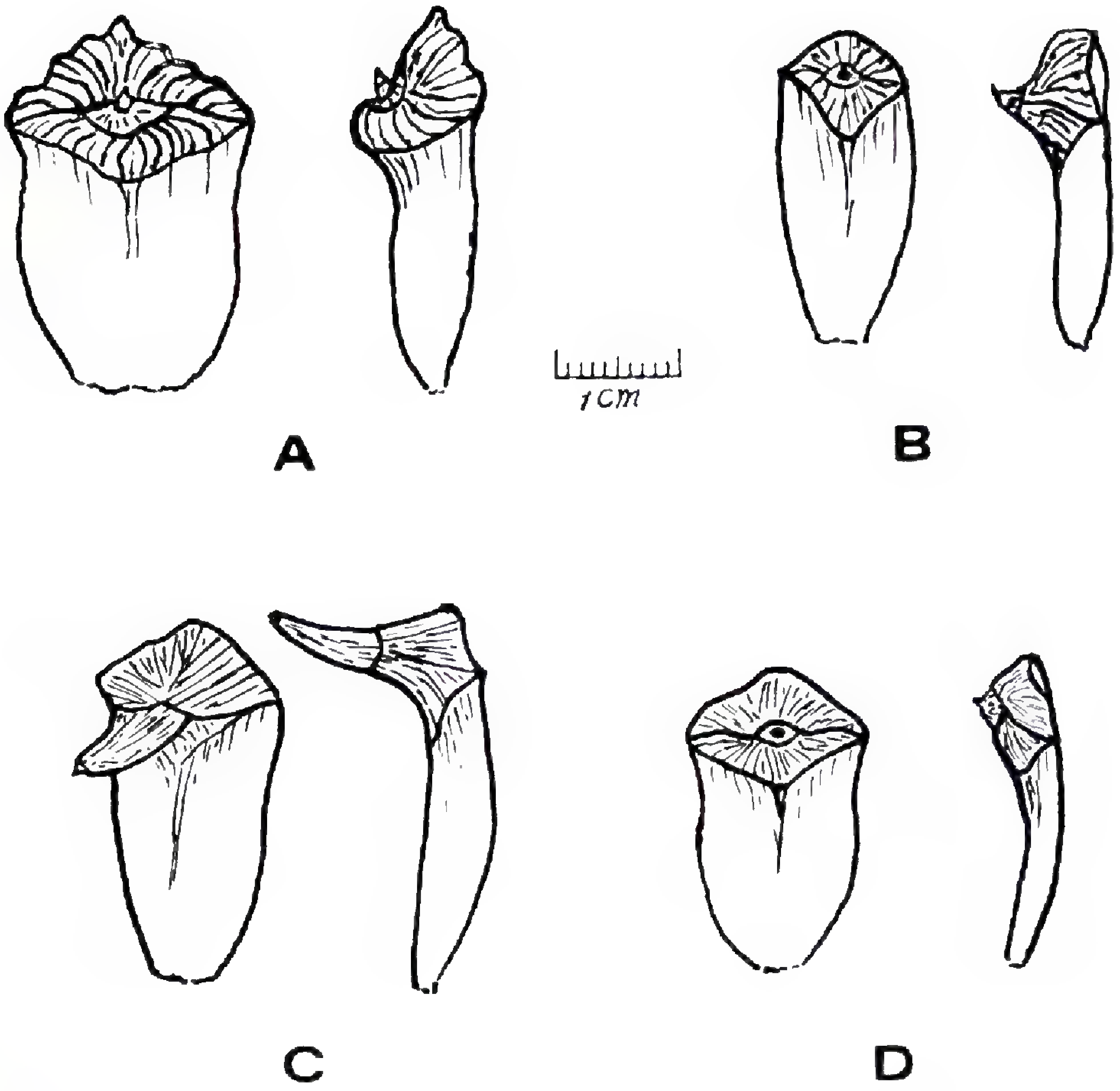

FIGURE 4. Cone scales: A, *Pinus nubicola*; B, *P. estevezii*; C, *P. oaxacana*; D, *P. pseudostrobus.*

Lagunilla, ca. 2100 m alt., *Mittak 9017* (BANSEFOR). **El Salvador.** CHALATENANGO: near Miramundo, 2200 m alt., *Perry SAL.7-77*; near El Aguacatál, 2000 m alt., *Perry SAL.8-77*. **Honduras.** LA PAZ: vic. of Las Trancas, *Perry H-8, H-10* (ESNACIFOR).[5]

RELATIONSHIPS OF PINUS NUBICOLA

Pinus nubicola, with its slender, pruinose branchlets and its smooth-barked young trees, readily falls into the Pseudostrobus group of Mexican pines, which has been variously called a section (Martínez, 1948), a "group" (Loock, 1950; Stead, 1983a; Stead & Styles, 1984), and a "complex" (Mirov, 1967; Stead, 1983b). The other species in the group are *P. douglasiana* Martínez, *P. maximinoi* H. Moore, *P. pseudostrobus, P. oaxacana,* and *P. estevezii* (Martínez) Perry.[6] As determined through chemotaxonomic studies of many of these taxa by Mirov (1958, 1961, 1967), Coyne and Critchfield (1974), Brümmer (1978), Mittak and Perry (1979), and Perry (1982), *P. oaxacana* and *P. estevezii* are most closely related to *P. nubicola.*

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[5] Escuela Nacional de Ciencias Forestales, Siguatepeque, Honduras.

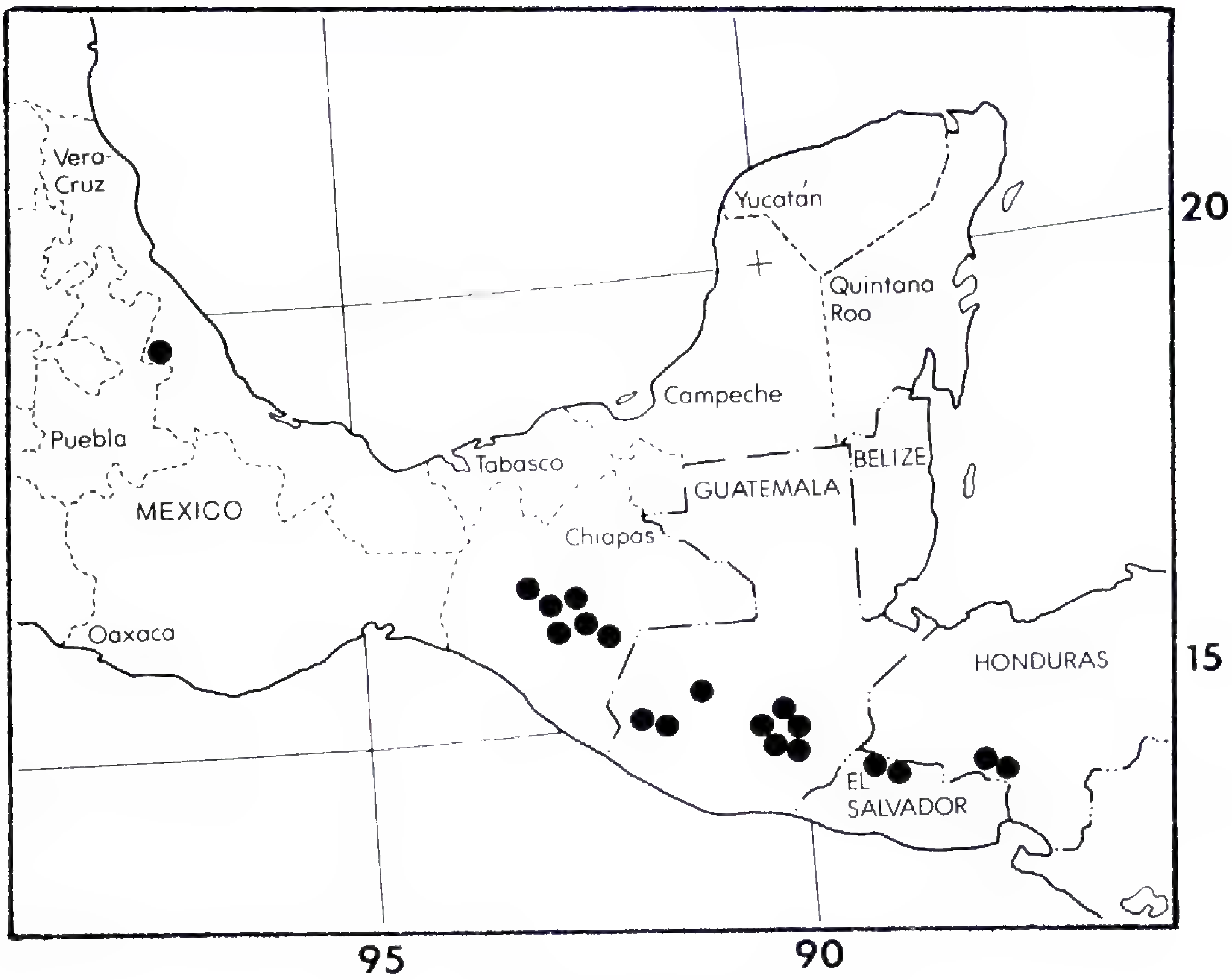
[6] Stead and Styles (1984) criticized the use of resin chemistry by Mirov (1958) and Perry (1982) in elevating var. *oaxacana* and var. *estevezii* to specific status.

TABLE 1. **Turpentine composition* of xylem oleoresin from Pinus nubicola.**

POPULATION	Sample number	Heptane	Octane	Nonane	α-pinene	Camphene	β-pinene	Δ^3-carene	Myrcene	α-terpinene	Limonene	β-phellandrene	P-cymene	Terpinolene	Terpinene-4-ol	Methyl chavicol	α-terpineol
MEXICO																	
Chiapas	1B	25		12	28		10	1		3					18	2	1
State	2B	10		12	31		9	3		30					2	1	
West of San	3B	34		14	6		3	2			39					1	
Cristóbal de	4B	34		15	31		6	7		1					5	1	
Las Casas	5B	5		2	4		2	2			84				Tr	1	
	6B	6		13	8						64					8	
	7B	13		7	44	5	7	7			6	Tr		3	7	1	Tr
	8B	2		12	43		9	3		4					21	6	Tr
	9B	7	8		33		7	8		16				2	4	6	9
	10B	27		11	36		6	2		1					12	4	
	11B	39		12	34	Tr	3	3		3					5	1	Tr
	12B	3		12	54						16	4			3	5	3
	13B			2	81		6								Tr	10	Tr
Station San	M6083	51	Tr	17	12		1	1			6		Tr		7	5	
José	M7283	15		8	36		5	3			21		1		8	1	
	M7383	8		5	39		1	4			31			1	7	4	Tr
Station Las	M12483	9		6	30		8	15			26		1		3	1	
Piedrecitas	M14283	6		12	13			1			40			3	18	4	1
	M15283	12	11	Tr	5			3			53				6	11	
	M14883	7		3	3	1	8	7		64			1	Tr	4	Tr	
GUATEMALA																	
East of	2A	26		8	44		8	Tr		1	2	2			1	4	4
San José	3A	19		12	18		8			3	31				5	2	1
Pinula	4A	42		8	39		6					2				1	
	6A	31	Tr	11	16		10	1		4	17	6			1	2	
	7A	40		8	30		1	1			20					Tr	
	8A	39		15	9		6	1		4	23					2	
	10A	21		10	38		4	3	8	3	13					Tr	
	11A	27		13	24		9	1	6	4	5				10	1	
	12A	32		18	28	4	5			8		4				1	
HONDURAS																	
Las Trancas	H8	42	3	30	5	3	3		Tr	4				2			Tr
	H10	7	3	65	3	5	2		1	3				8			1
Mean		21	1	12	27	Tr	5	3	Tr	3	19	Tr	Tr	1	5	3	1

*Percent of total turpentine.
Tr - trace.

At a number of locations in Mexico (Chiapas), Guatemala, and El Salvador, I have observed trees with cones and foliage that appeared to be intermediate among *Pinus nubicola, P. oaxacana, P. pseudostrobus* var. *apulcensis,* and *P. montezumae.* In all instances the cones were much larger than those of typical *P. pseudostrobus,* the trees were five needled, and the bases of the fascicle bracts were not decurrent. In many instances *P. nubicola, P. pseudostrobus, P. montezumae, P. oaxacana,* and occasionally *P. rudis* formed a part of these mixed stands. It appeared that hybridization and back-crossing had been occurring for many years among these pines. Mirov (1961) stated that *P. oaxacana* apparently crosses naturally with *P. pseudostrobus* and probably also with some varieties of *P. montezumae.* Martínez (1948) pointed out that *P. pseudostrobus* and *P. montezumae* are very closely related. Extensive sampling and analyses



MAP 1. Distribution of *Pinus nubicola.*

of oleoresins from carefully selected trees could, with morphological studies of the cones and foliage, reveal the extent and nature of the hybridization that is occurring in many of these mixed stands.

Because the chemical composition of turpentine is inherited (Squillace, 1976), I believed that information about this character would provide valuable knowledge regarding identification and possible relationships of the new species. Accordingly, I took samples of xylem oleoresin from *Pinus nubicola* trees in Mexico, Guatemala, and Honduras. Results of the analyses are shown in TABLE 1. Information regarding collection and analysis of the oleoresin is given in the APPENDIX.

Although *Pinus nubicola* fits Martínez's and Loock's original concepts of a Pseudostrobus group of the Mexican pines, it (like *P. oaxacana* and *P. estevezii*) differs markedly from *P. pseudostrobus* in the chemical composition of its turpentine. Heptane and nonane are consistently present in the turpentine of *P. nubicola, P. estevezii,* and *P. oaxacana* but usually absent in *P. pseudostrobus* (see TABLE 2). Mirov (1958) stated that the gum turpentine of *P. oaxacana* contained 21 percent heptane, 51 percent d- and dl-α-pinene, 15–16 percent dl-limonene, 1.3 percent n-undecane, and 7.5 percent d-longifolene.[7] There

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[7] Mirov's data were obtained from one sample, in which oleoresin from 25 trees (from near Rancho Nuevo, 25 km SW of San Cristóbal de Las Casas, Chiapas, Mexico) was combined. In other samples the percentages may be different. The presence of large quantities of heptane is significant.

TABLE 2. **Turpentine composition of xylem oleoresin from Pinus nubicola, P. estevezii, P. oaxacana, and P. pseudostrobus.**

	TAXON							
	P. nubicola (n = 31)		P. estevezii (n = 13)		P. oaxacana* (n = 26)		P. pseudostrobus (n = 10)	
TERPENE	Mean†	% High‡	Mean	% High	Mean	% High	Mean	% High
Heptane	21	61	38	100	16	54		
Octane	1		2	4	15			
Nonane	12	61	11	55	10	35		
α -pinene	27	65	19	61	37	77	80	100
Camphene	Tr		3		3	12	1	
β -pinene	5	29	4		4	15	2	
Δ^3-carene	3	16	Tr		4	4	1	
Myrcene	Tr		9	30			11	40
α -terpinene	3	6			Tr			
Limonene	19	48	3	8	10	27	1	
β -phellandrene	Tr		4	15	Tr			
P-cymene	Tr						Tr	
Terpinolene	1		Tr		1	4	Tr	
α -fenchol					Tr		Tr	
Terpinene-4-ol	5	16			2	8		
β -caryophyllene					Tr			
Methyl chavicol	3	16	6	15	4	12		
α -terpineol	1	3			1	4	1	

*Samples collected by the author in Mexico (Puebla, Oaxaca, and Chiapas states) and Guatemala.
†Mean percent of total turpentine
‡Percent of trees having relatively high amounts. (For mathematical procedure see Squillace *et al.*, 1980).

thus appears to be a cluster of species within the Pseudostrobus group of Mexican pines that differ from typical *P. pseudostrobus* in the morphology of their cones and in the presence of heptane and nonane, usually in high amounts, in their turpentine. Further studies of oleoresins from the remaining taxa included in Martínez's sect. *Pseudostrobus* are required in order to clarify these relationships.

DISTINCTION AMONG PINUS NUBICOLA, P. ESTEVEZII, P. OAXACANA, AND P. PSEUDOSTROBUS

Although the principal identifying characteristics of the Pseudostrobus group (i.e., the smooth stems of young trees and the nondecurrent bases of the needle

TABLE 3. **Summary of differences among Pinus nubicola, P. estevezii, P. oaxacana, and P. pseudostrobus.**

	TAXON			
CHARACTER	*P. nubicola*	*P. estevezii*	*P. oaxacana*	*P. pseudostrobus*
FORM OF MATURE TREE	25-30 m tall: stem clear; crown open, rounded	12-20 m tall: stem often limby; crown dense, low, broadly rounded	25-30 m tall; stem clear; crown moderately dense, rounded	30-40 m tall; stem clear; crown narrow, rounded
LEAVES				
Number per fascicle	5 or 6 (occasionally 7, rarely 8)	5 (rarely 4)	5 (rarely 6)	5
Habit	Flexible, very drooping to pendent	Stiff, erect, not flexible	Flexible, slightly drooping	Flexible, slightly drooping to drooping
Dimensions	25-40(-43) cm x 0.6-1 mm	20-30(-35) cm x 1 mm	20-30(-33) cm x ca. 0.8 mm	20-25(-30) cm x ca. 0.7 mm
Anatomy	Hypoderm irregular, with many shallow penetrations into chlorenchyma; resin canals 3 (or 4), medial	Hypoderm irregular, with many shallow penetrations into chlorenchyma; resin canals 3 (to 5), medial (rarely with 1 internal)	Hypoderm uniform, with few slight penetrations into chlorenchyma; resin canals 2 (to 4), medial	Hypoderm uniform, with few slight penetrations into chlorenchyma; resin canals 2 (to 4), medial (rarely with 1 internal or external)
CONES	10-15 x 8-10 cm, asymmetric, reflexed	10-13 x 7-8 cm, asymmetric, usually reflexed	10-14 x 9-11 cm, asymmetric, usually reflexed	8-10 x 5-7 cm, slightly curved, not reflexed

TABLE 3. *(continued)*.

	TAXON			
CHARACTER	*P. nubicola*	*P. estevezii*	*P. oaxacana*	*P. pseudostrobus*
CONE SCALES	20–25 mm wide, hard, strong, thick; apophyses unequally raised, transversely keeled; umbo small, margins slightly depressed, usually up-curved with small, persistent prickle; margin of apex with unequal projections	12–15 mm wide, hard, strong, thick; apophyses raised to subpyramidal, prominently transversely keeled; umbo raised, with persistent up-curved prickle; margin of apex smooth	12–20 mm wide, hard, strong, thick; apophyses with pronounced, unequal projections (to 22 mm long); umbo hard, with small, deciduous prickle; margin of apex smooth	15–18 mm wide; apophyses slightly raised to flat, slightly transversely keeled; umbo small, occasionally depressed, with small, deciduous prickle; margin of apex smooth
TURPENTINE	Usually large amount of heptane and smaller amount of nonane; usually large amounts of α-pinene and limonene; sometimes large amount of terpinene-4-ol; very small amount of myrcene and small but consistent amount of methyl chavicol	Usually large amount of heptane and smaller amount of nonane; often large amount of α-pinene; sometimes large amounts of myrcene, methyl chavicol, and β-phellandrene	Usually large amount of heptane and smaller amount of nonane; usually large amount of α-pinene and smaller amounts of limonene and methyl chavicol	Heptane, octane, and nonane usually absent; usually very large amount of α pinene, occasionally with large amount of myrcene; usually small amounts of Δ^3-carene, limonene, and α-terpineol
ALTITUDINAL RANGE (m)	1800–2400	800–1800	1500–3200	1600–3200

bracts) are shared by *Pinus nubicola, P. estevezii, P. oaxacana,* and *P. pseudostrobus,* the four species can be readily separated by combinations of characters (see TABLE 3).

Pinus nubicola is easily distinguished in the field from the other three species by its long, very drooping needles (see FIGURE 2) five or six (occasionally seven) in a fascicle, and its large, ovoid to long-ovoid cones with unusually wide, thick cone scales having unequal apical projections and a small depressed umbo (FIGURE 4). Cones of *P. oaxacana* are readily identified by their thick, stiff cone scales with unusual prolongation of the apophysis and umbo. *Pinus estevezii* can be distinguished from the other three taxa by its stiff, erect needles and its cones with thick, hard scales armed with a persistent up-curved prickle on the umbo. *Pinus pseudostrobus* is easily separated from the other three species by its much smaller cones having thin, flexible scales with a flat to slightly raised apophysis and a small umbo tipped by a small deciduous prickle (FIGURE 4).

A comparison of the oleoresin components also reveals significant differences among the four species (see TABLE 2). Outstanding among these was the presence of high amounts of limonene in 48 percent of *Pinus nubicola* trees. In addition there were trees of *P. nubicola* with high amounts of terpinene-4-ol (16%) and methyl chavicol (16%).

There appeared to be some population differences, but samples were too few for this to be determined with certainty. For example, all of the *Pinus nubicola* trees in the Guatemalan population had high heptane levels while only about half of the trees in the Mexican population did (see TABLE 1). It is interesting to note that the two trees in Honduras had the highest nonane levels of all the trees sampled.

As in most species, individual trees varied greatly in monoterpene composition. It would have been helpful to have oleoresin samples from *Pinus nubicola* trees growing in El Salvador. Unfortunately, the very unsettled political situation in that country, particularly in Depto. Chalatenango, made it unwise to attempt any resin collections there.

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I would like to express my appreciation for the help received from a number of friends and colleagues during this study. Suggestions and comments on the manuscript from P. C. Mangelsdorf, B. Zobel, J. W. Duffield, W. B. Critchfield, and P. F. Stevens were invaluable, as were P. F. Stevens's assistance with the Latin diagnosis and E. B. Schmidt's editing of the manuscript. Suggestions from A. E. Squillace and E. C. Franklin regarding the turpentine analyses and the presentation of the data were very useful. I am also grateful for J. Drew's advice and comments on analyses of the oleoresins. My thanks are expressed here for V. G. Wright's drawings, and for W. L. Mittak's help with the collection of oleoresins and herbarium specimens in Guatemala. Similar collections in Mexico and Honduras were made possible by the assistance of W. S. Dvorak, Director of CAMCORE, and staff members J. K. Donahue and E. G. Ponce; my deep appreciation for their help is expressed here.

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APPENDIX. **Collection and analysis of oleoresins.**

COLLECTION

In Guatemala samples of xylem oleoresin were collected from nine trees of *Pinus nubicola* (d.b.h. 30–60 cm) growing near San José Pinula at the location described for the type.

At about 75 cm above the ground, a hole ca. 1 cm in diameter was drilled into the stem of each tree (22 February 1979) and a threaded glass vial was immediately screwed tightly into the hole. Three days later the vials were collected and each one covered with a threaded, gasketed cap. *Perry GUA.28-79* was collected as a composite voucher for these trees and has been deposited in the herbaria at GH and NCSC.

In Chiapas, Mexico, samples of xylem oleoresin were taken from 13 trees of *Pinus nubicola* (d.b.h. 35–90 cm) about 10 km west of San Cristóbal de Las Casas, near highway 190. Vials were placed on the trees 2 March 1979 and collected two days later. *Perry*

MEX.7B-12B and *Perry MEX.1B-14B* were collected as composite vouchers for these trees.

East of San Cristóbal de Las Casas, near Las Piedrecitas, oleoresin was collected from four trees of *Pinus nubicola* (d.b.h. 32–50 cm). Vials were placed on the trees 31 January and 1 February 1983 and collected the following day. *Perry M-12483, M-14283,* and *M-15183* were collected as vouchers for these trees.

West of San Cristóbal de Las Casas, near San José, oleoresin was collected from three trees of *Pinus nubicola* (d.b.h. 35–80 cm). Vials were placed on the trees 27–28 January and collected 30 January 1983. *Perry M-6083* and *M-7283* were collected as vouchers for these trees.

In Honduras oleoresin was collected from two trees of *Pinus nubicola* in the Departamento de La Paz, near the village of Las Trancas. Collections were made in October 1982 by W. S. Dvorak, Director of CAMCORE (Central America and Mexico Coniferous Resources Cooperative), and E. G. Ponce, staff member of ESNACIFOR (Escuela Nacional de Ciencias Forestales), Honduras. *Ponce H-8* and *H-10* were collected and deposited in the herbarium at ESNACIFOR, Siguatepeque, Honduras.

The sampling procedure described for collections in Guatemala was followed for all collections in Mexico and Honduras.

ANALYSIS

Analyses of the pine-resin samples were performed by a chemical consulting laboratory, with the following gas-chromatographic conditions and equipment.

Turpentine from each sample was separated from the resin and extraneous matter by steam distillation (alkalinity was maintained to prevent acid isomerization).

The chromatograph used was a Varian Series 1700 with a thermal conductivity detector. A 10′ × ⅛″ diameter stainless-steel column packed with 15% carbowax 20M on "chromosorb W" was injected with 1.5 μl of sample. The injector temperature was 210°C, the detector temperature 225°C, and the column oven programmed from 75° to 220°C with a 4°C per minute temperature rise. The carrier gas was helium.

Components were identified by comparison of elution times against standard chromatographs made from combinations of pure compounds. When a question arose as to the identity of a compound, the sample was reshot with known components added until the presence of overlapping peaks or increase in peak size eliminated any uncertainty.

ARCHIATRIPLEX, A NEW CHENOPODIACEOUS GENUS FROM CHINA

GE-LIN CHU[1]

A new genus of Chenopodiaceae (*Archiatriplex*) and its sole species (*A. nanpinensis,* from northern Sichuan Province, China) are described. The genus is characterized by unisexual flowers, foliaceous bracts subtending the carpellate flowers, and annular embryos; it therefore belongs in tribe Atripliceae. Its relationships and morphology are discussed, and a key to the genera of this tribe is given.

In 1974, as I was finishing the manuscript of the Chenopodiaceae for the *Flora Reipublicae Popularis Sinicae* (Kung & Tsien, 1979), my attention was drawn to an unidentified fragmentary specimen (*K. T. Fu 2166*) in the herbarium of the Institute of Botany, Academia Sinica, Beijing. Its surprising floral morphology—unisexual flowers with the staminate ones fasciculate in terminal, interrupted spikes and the carpellate ones below—suggested that the plant could be placed in the tribe Atripliceae C. Meyer, but in floral and inflorescence morphology it matched no genus in the tribe. Although I located another specimen of the same taxon in the herbarium (*T. P. Wang 7967*), it was also fragmentary.

In 1980 I had the opportunity to visit Nanping, on the northern flank of the Tsinling mountain range in Sichuan Province (MAP 1), where both of the specimens had been collected. While there, I was fortunate to re-locate the population and was able to re-collect more complete specimens and make field observations. Study of the ample material gathered at that time has shown that the plant is a new species that also comprises a new genus. I propose the new genus and species below, followed by a discussion of its relationships and morphology.

Archiatriplex G. L. Chu, gen. nov.

Proximum Microgynoecio J. D. Hooker sed in floribus femineis basi et in stipitibus bractearum insertis, perianthio evoluto, et staminibus differtibus, dissimilis.

Monoecious herbs. Leaves opposite or alternate, petiolate, complanate, slightly succulent, serrate, with unicellular inflated trichomes. Flowers unisexual. Staminate flowers in interrupted spikes at apexes of branchlets, lacking bracts; perianth 5-parted, segments membranaceous, slightly succulent on back near apex, lacking nerves; stamens 5, inserted on disc. Carpellate flowers under

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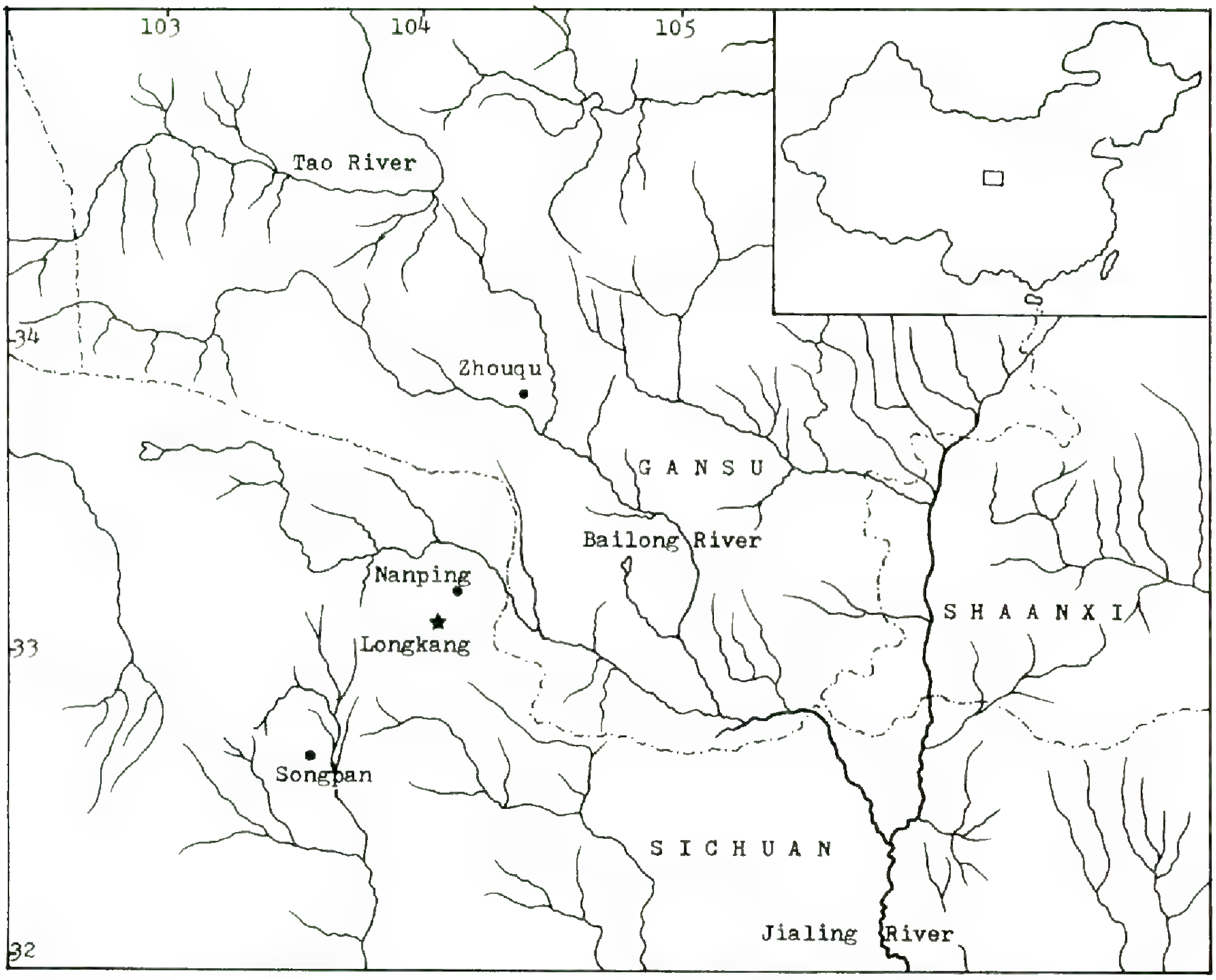


MAP 1. *Archiatriplex* area, showing major river-system involving tributaries of Huanghe and Changjiang rivers, and 4 towns on border of Sichuan and Gansu provinces, with ★ indicating type locality of *A. nanpinensis.*

staminate inflorescences, attached to base and petiole of bracts; bracts foliaceous, short-petiolate or nearly sessile, smaller than leaves; perianth 3- or 4-parted, the segments with longitudinal midrib, slightly enlarged in fruit; ovary obovoid, smooth, with 2 stigmas, style inconspicuous. Utricle slightly compressed, papillate; pericarp membranaceous, adnate to seed. Seeds laterally compressed, lenticular, testa crustaceous; embryo annular, perisperm copious.

TYPE SPECIES: *Archiatriplex nanpinensis* G. L. Chu.

Archiatriplex nanpinensis G. L. Chu, sp. nov. FIGURE 1.

Herbae annuales, usque ad 1.2 m altae; caulis erectus vel ascendens, ramosus, leviter tetragonus, striatus; rami ascendens ramosi, ramulis 1–5 cm longis, saepe gracilibus. Folia late ovata vel triangulari-hastata, 2–10 cm longa, latitudine longitudinem fere aequante, supra viridia, subtus pallide viridia, apice breviter acuminata, basi cordata, margine irregulariter laxe dentata; petiolus tenuis, 0.5–8 cm longus. Inflorescentiae masculinae graciles, interdum ramis brevibus praeditae; flores masculini multi in glomerulis dispositi; segmenta perianthii obovata vel oblanceolata, circa 1 mm longa, basi tantum connata, prope apicem leviter succulenta, apice paulo cucullata; stamina 5, filamentis filiformibus,

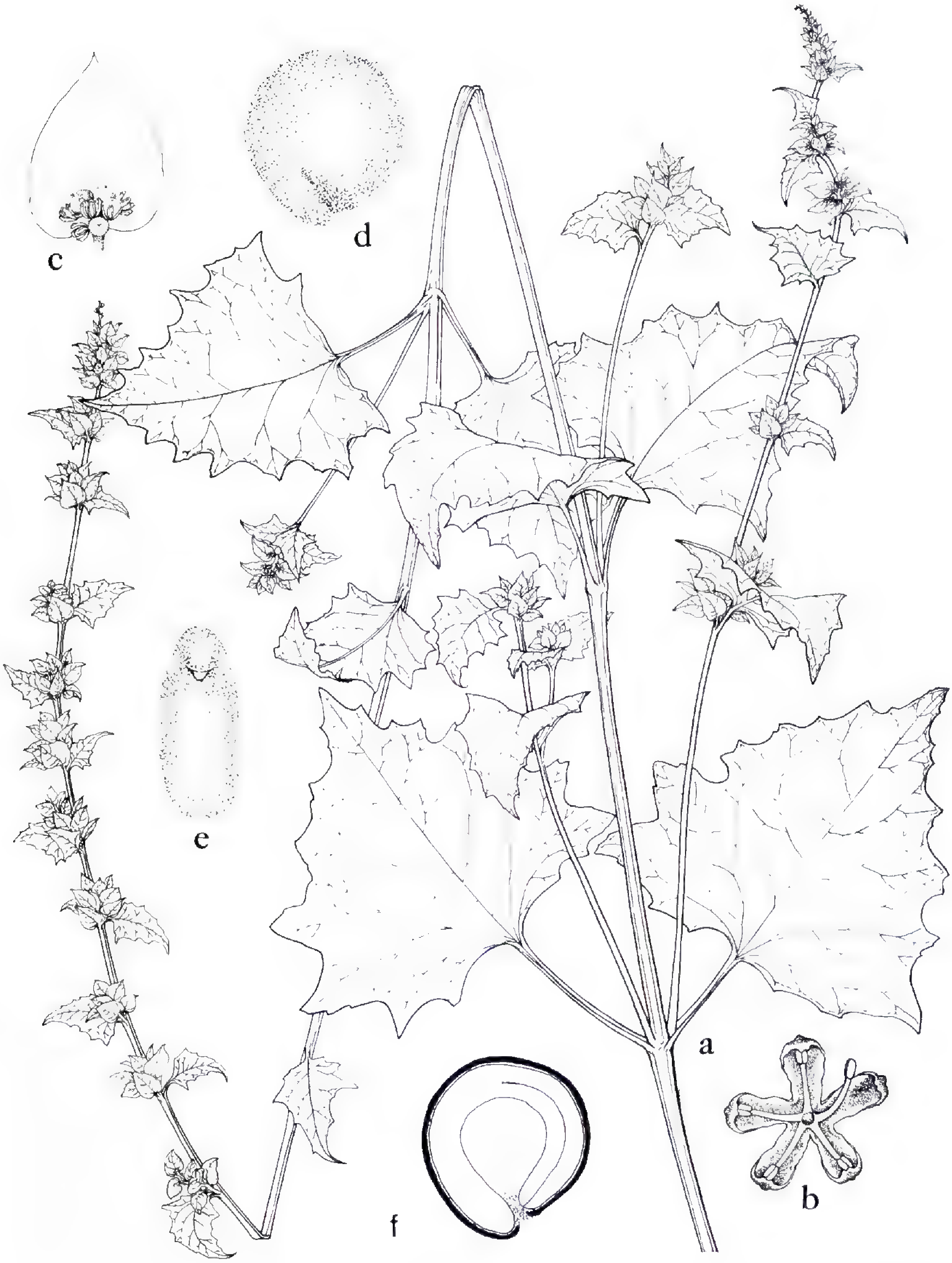


FIGURE 1. *Archiatriplex nanpinensis:* a, flowering shoot, × 0.5, showing opposite leaves on lower nodes and alternate leaves on upper ones, terminal staminate inflorescences, and carpellate inflorescences with foliaceous bracts; b, carpellate flower, × 10, showing 5 perianth lobes and 5 stamens; c, foliaceous bract subtending fascicle of carpellate flowers, × 2; d, utricle, × 7.5, showing tuberculate surface of pericarp; e, seed, lateral view, × 7.5, showing position of radicle and hilum; f, seed, longitudinal section, × 7.5, showing testa, curved embryo with radicle, 2 cotyledons, and central endosperm. (a–c drawn by Xia Quan.)

planis, segmentis perianthii fere aequilongis, antheris late oblongis vel late ovatis, circa 0.3 mm longis. Flores feminei 4–7 simul in glomerulo, basim bracteae inserti; bracteae ovatae vel cordatae, 4–20 mm longae, margine integrae vel serratae; segmenta perianthii basi fructificationis lineari-elliptica vel obovata, 0.7–1 mm longa, basi tantum connata, patentia, margine integra vel leviter lacerata; stigmata circa 0.2 mm longa. Utriculus oblique ovatus, tuberculatus. Semen rubiginosum vel nigrum, nitidum, circa 1–1.5 mm diam.

Annual herbs to 1.2 m tall; stems erect or ascending, ramified, slightly tetragonal, striate, the branches ascending, ramified, with the branchlets 1–5 cm long, usually gracile. Leaves with petiole 0.5–8 cm long; blade broad-ovate or triangular-hastate, 2–10 cm long and nearly as wide, short-acuminate at apex, cordate at base, irregularly coarsely dentate at margin, dark green above, light green below. Staminate inflorescences slender, sometimes short-branched; flowers several in glomerules; perianth segments obovate or oblanceolate, ca. 1 mm long, connate at base, slightly succulent and somewhat cucullate near apex; stamens 5, the filament filiform, complanate, nearly as long as perianth segments, the anther broad-oblong or broad-ovate, ca. 0.3 mm long. Carpellate flowers 4 to 7 per glomerule, inserted at base and petiole of bracts; bracts ovate or cordate, 4–20 mm long, entire or serrate; perianth segments in fruit linear-elliptic or obovate, 0.7–1 mm long, connate at base, patent, entire or slightly lacerate; stigmas ca. 0.2 mm long. Utricles oblique-ovate, the pericarp membranaceous, papillate. Seeds red-brown or black, ca. 1–1.5 mm in diameter.

TYPE. People's Republic of China, Sichuan Province, Nanping, Longkang, 2100 m alt., at edge of bush-wood, 30 September 1980, *G. L. Chu 80040* (holotype, herbarium of the Institute of Botany, NW Teachers' College, Gansu; isotype, A).

ADDITIONAL SPECIMENS EXAMINED. **People's Republic of China.** SICHUAN PROVINCE: Nanping, Longkang, 2100 m alt., *K. T. Fu 2166* (PE), *T. P. Wang 7967* (PE); on banks of terraced farm, *G. L. Chu 80041, 80073, 80086* (all at Herb. NW Teachers' College, Gansu).

MORPHOLOGICAL OBSERVATIONS

SEEDLINGS. Approximately 25 seeds were taken from unfumigated isotypes and were sown on 28 May 1982. Germination was first observed on 2 June and proved to be epigeal. On the eighth day after germination, the first pair of photosynthetic leaves appeared; the cotyledons were then ovate-elliptic, 4–6 × 1–1.5 mm, and light green above and purplish beneath. At the first eight nodes the photosynthetic leaves were opposite, but at the ninth node only one emerged, and thenceforth the leaves were alternate.

POLLEN. Pollen of *Archiatriplex nanpinensis* was taken from fresh material and prepared for examination with a scanning electron microscope. The tuberculate, punctate ektexine of the spherical, polyporate grains corresponds to the general pattern of chenopodiaceous pollen. The grains are ca. 26 μm in diameter and have approximately 60 circular apertures scattered on the tuberculate and finely punctate surface (FIGURE 2a). Each aperture is ca. 2 μm in diameter, with six

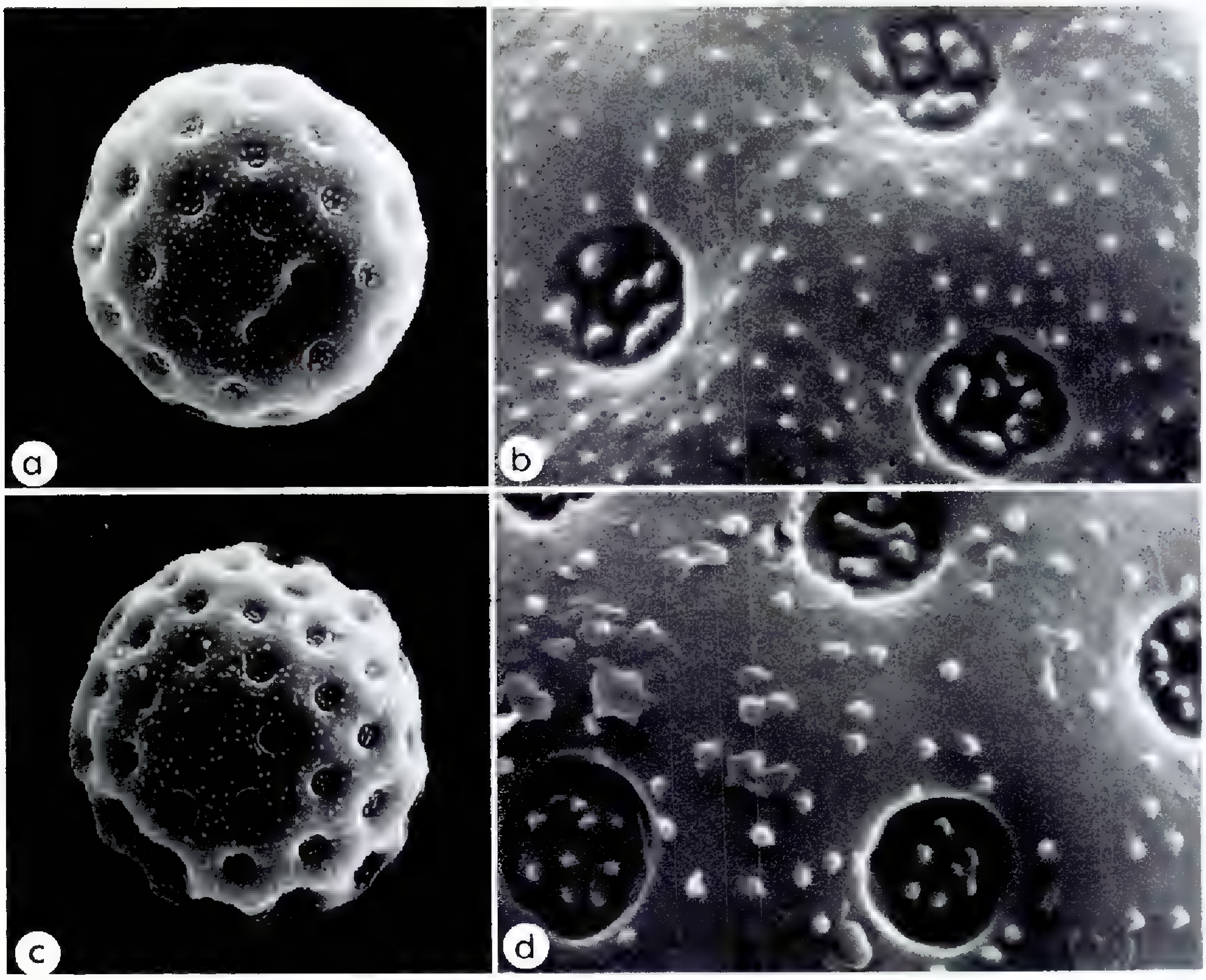


FIGURE 2. Scanning electron micrographs of pollen grains: a, b, *Archiatriplex nanpinensis,* showing numerous circular apertures, and tuberculate and punctate ektexine; c, d, *Microgynoecium tibeticum,* showing more numerous and larger apertures and smooth ektexine (a, c, × 1240; b, d, × 6200).

to nine free or coalescent tubercles (FIGURE 2b). Compared with the pollen of *Microgynoecium tibeticum* Hooker f. (FIGURE 2c, d), the grains of *A. nanpinensis* have fewer apertures but more tubercles.

CYTOLOGICAL OBSERVATIONS

Very young buds of staminate flowers from greenhouse-grown plants of *Archiatriplex nanpinensis* were fixed in Carnoy's solution, and pollen mother cells were stained and prepared in the normal manner for microscopic observation. It was determined that the species is a diploid with $2n = 18$. At meiosis bivalent pairing is regular (see FIGURE 3).

GENERIC RELATIONSHIPS OF ARCHIATRIPLEX

Including *Archiatriplex,* the tribe Atripliceae consists of 13 genera, of which *Atriplex* L. is the largest, with more than 100 species widely distributed in Asia, North America, Europe, Australia, and Africa. *Axyris* L. and *Ceratoides* (Tourn.) Gagnebin are represented in the floras of Eurasia and North America, while

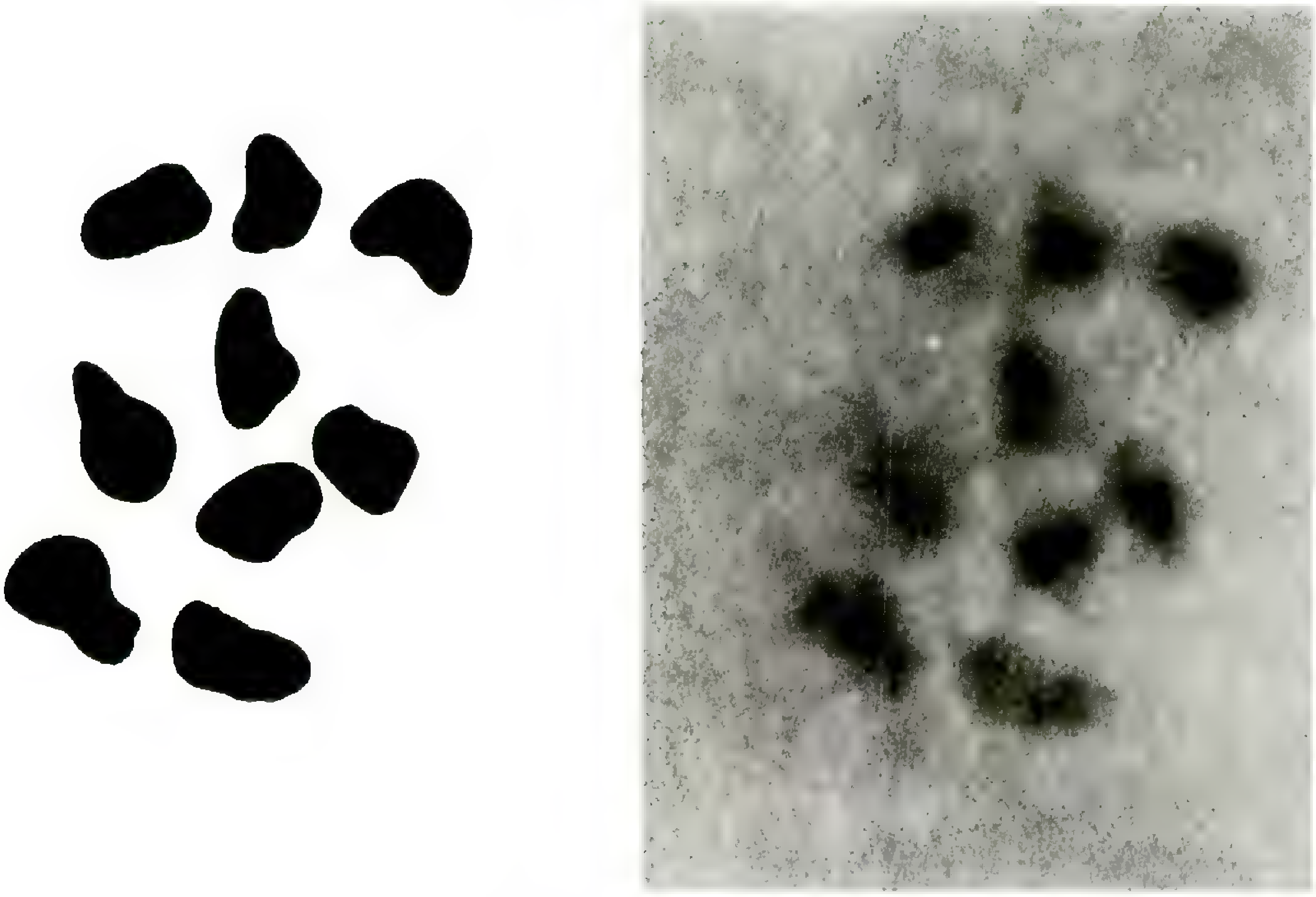
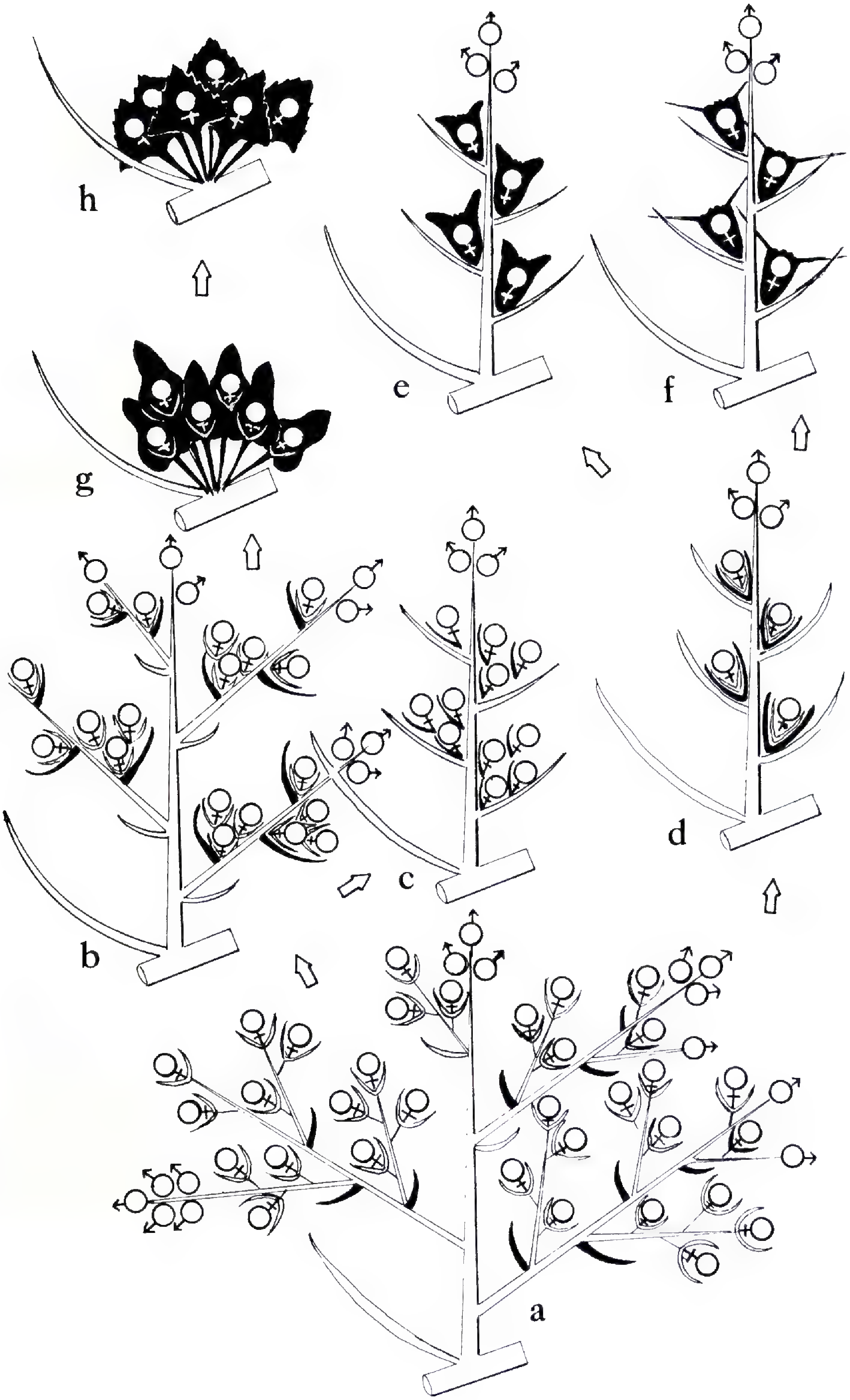


FIGURE 3. Chromosomes of dividing microsporocyte of *Archiatriplex nanpinensis*, $n = 9$, metaphase 1 (voucher specimen, *G. L. Chu 80084*).

Spinacia L. and *Ceratocarpus* L. are confined to Eurasia. The remaining genera are endemics, with distributions restricted to Asia (*Microgynoecium* and *Archiatriplex*), North America (*Endolepis* Torrey, *Suckleya* A. Gray, *Zuckia* Standley, and *Grayia* Hooker & Arn.), Africa (*Exomis* Fenzl ex Moq.), or Australia (*Theleophyton* (Hooker) Moq.).

Archiatriplex has close affinities to *Microgynoecium*. The two species are characterized by similar foliaceous bracts subtending the carpellate flowers, with each bract containing several flowers; the carpellate flowers of *Microgynoecium*, however, lack perianths. The other genera in the tribe differ from *Archiatriplex* in having a single carpellate flower included between two opposite and specialized bracts and (except for *Exomis* and *Endolepis*) in lacking a perianth, or in the stellate hairs covering the plant.

FIGURE 4. Inflorescences in tribe Atripliceae, showing possible evolutionary changes that led to present forms. a, hypothetical prototype with numerous branches, each with staminate flowers at distal end, carpellate at proximal (dark bracts subtending lateral branches indicate key area of evolutionary change). b, *Archiatriplex*, fascicles of 1 to 7 carpellate flowers subtended by bract (black). c, *Microgynoecium*, reduction of rachis and perianth segments. d, *Axyris*, branch of much-reduced panicle, solitary carpellate flowers with perianth subtended by 2 bracts (black). e, *Eurotia*, f, *Ceratocarpus*: bracts (black) fused, carpellate flowers lacking perianth. g, h, fascicles of solitary flowers subtended by enlarged bracts: g, *Endolepis*, carpellate flowers with perianth; h, *Atriplex*, carpellate flowers lacking perianth.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KEY TO THE GENERA OF THE ATRIPLICEAE

1. Plant glabrous, or covered with simple or ramified inflated hairs.
   2. Carpellate flowers with perianth.
      3. Carpellate flowers subtended by single foliaceous bract, axil of each bract usually with several flowers. . . . . *Archiatriplex.*
      3. Carpellate flowers each subtended by 2 opposite, separate bracts, these not foliaceous.
         4. Radicle oriented downward; perianth with 5 segments; bracts succulent. . . . . *Exomis.*
         4. Radicle oriented upward; perianth with 3 or 4 segments; bracts not succulent. . . . . *Endolepis.*
   2. Carpellate flowers lacking perianth.
      5. Stigmas 2; plants monoecious, rarely dioecious.
         6. Carpellate flowers subtended by single foliaceous bract, axil of each bract usually with several flowers. . . . . *Microgynoecium.*
         6. Carpellate flowers each subtended by 2 opposite bracts, these partially or totally fused.
            7. Seeds oriented vertically in fruit.
               8. Bracts of carpellate flowers inflated, saclike; inflated hairs indurated into cubic crystals. . . . . *Theleophyton.*
               8. Bracts of carpellate flowers compressed; inflated hairs scurfy when dry.
                  9. Inflated hairs not ramified; radicle oriented upward, rarely downward.
                     10. Bracts of carpellate flowers bilobed at apex. . . . . *Suckleya.*
                     10. Bracts of carpellate flowers entire or serrate, not bilobed. . . . . *Atriplex.*
                  9. Inflated hairs ramified; radicle oriented downward. . . . *Grayia.*
            7. Seeds oriented horizontally in fruit. . . . . *Zuckia.*
      5. Stigmas 4 or 5; plants dioecious. . . . . *Spinacia.*
1. Plant covered with stellate hairs.
   11. Carpellate flowers with evident perianth, each subtended by 2 separate, foliaceous bracts. . . . . *Axyris.*
   11. Carpellate flowers lacking perianth, each subtended by 2 opposite bracts, these partially or totally fused.
       12. Shrubs or subshrubs; bracts of carpellate flowers fused below middle, forming tube furnished with 4 fascicles of villose hairs. . . . . *Ceratoides.*
       12. Annual herbs; bracts of carpellate flowers fused their entire length, furnished with acicular appendage on both sides near apex. . . . . *Ceratocarpus.*

Compared with the other genera in tribe Atripliceae, the most distinctive primitive character of *Archiatriplex* is its large, loose panicles (FIGURE 4b). Such an inflorescence probably developed from a prototype with flowers protected by a perianth, the staminate flowers located at the distal end of the branches and the carpellate ones below (FIGURE 4a). Evolutionary change from the *Archiatriplex* type of inflorescence led to fasciculate carpellate flowers lacking a perianth and to a reduction in the length of the rachis and in the number of flowers, leaving small bracts as in *Microgynoecium* (FIGURE 4c). It seems that also through reduction of the rachis, the fasciculate *Endolepis*- and *Atriplex*-type inflorescences (FIGURE 4g, h) evolved from the *Archiatriplex* type. In the *Endolepis* type of inflorescence, the flowers have a perianth, while in the *Atriplex* type they do not. Another trend in the inflorescence can be traced from the prototype: through reduction in flower number and rachis length and by fusion of the bracts, the *Axyris* type of inflorescence (FIGURE 4d) resulted. Here, two bracts subtend a single carpellate flower with a segmented perianth. Further evolutionary changes led to the *Eurotia* and the *Ceratocarpus* types (FIGURE 4e, f). In these the carpellate flowers lack a perianth, and the subtending bracts have become highly specialized and fused.

From the above interpretation, it is clear that the discovery of *Archiatriplex* provides a better understanding of the evolutionary changes in tribe Atripliceae.

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SOME BOTANICAL REMINISCENCES OF GEORGE R. COOLEY, 1896–1986

Richard A. Howard[1]

Several years ago I suggested to George Cooley that he divide his life into chapters and begin dictating his memoirs. He had led such a diverse and interesting life and had contributed so much to so many people and organizations that only he could supply a complete accounting. I then knew little of his early years, his short career at Colgate University, his service in World War I, or his employment in investment banking firms, which led to the start of his own financially successful company. Why he began collecting botanical specimens was never clear to me, although it was somewhat illuminated by his statement years later: "Plants and the people who study them are both intriguing organisms."

I met George in 1951, when he came to the Gray Herbarium seeking aid in identifying specimens of *Solidago* from New York State and a miscellany of plants from Florida. I remained associated with him and knew of his botanical pursuits for 35 years; I saw him last at his favorite spot, his home at Hickory Hill, Rensselaerville, New York, a month before his death. I would divide the botanical life of this devoted amateur into several chapters: the flora of Albany County, New York; the reprinting of Small's Manual; the flora of Sanibel Island, Florida; the initiation of the Generic Flora of the Southeastern United States and his Research Fellow appointment at Harvard; Chinsegut Hill and the University of South Florida; the AETFAT meeting and our trip around the world; the flora of St. Vincent, West Indies, and the two-hundredth anniversary of the establishment of the Botanic Garden; his continuing generosity to botany and botanists of the United States; and the Cooley prizes of the American Society of Plant Taxonomists. I offer vignettes of some of these.

SOUTHEASTERN UNITED STATES

George Cooley's greatest impact came from his interest in the flora of the southeastern United States. To the best of my knowledge, he visited Florida first in 1951 and was attracted to Sanibel Island. For many years after that, he spent several winter months on the island. One of his early collections on Sanibel was *Eragrostis traceyi* A. Hitchc., which had not been collected since the original gathering in 1901. He even grew seeds of this plant to have additional herbarium specimens for distribution. The available "wild flower"

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books did not meet his needs, and when Small's Manual was recommended to him he learned it was out of print, out of date, and controversial in its treatment of genera. He was unable to find any botanist or department willing to undertake an immediate revision, so he financed the reprinting of the manual (1954) to make it available. After prolonged discussions he was finally convinced that additional collections of both native and cultivated plants of Florida were needed. To this end he supported the collecting of others and did a considerable amount himself. The idea of an annotated checklist of the Sanibel vegetation appealed to him. In 1954 he published a more elaborate study, "The Vegetation of Sanibel Island, Lee County, Florida" (Rhodora **57**: 269–289), profusely illustrated and definitive as to the location and abundance of each species. Perhaps this work was the start of his concern for conservation and the preservation of endangered species and habitats. The paper clearly shows Cooley's broad interests and keen observation. He noted 672 plants of poison ivy in a quadrat 20 × 20 feet. On one branch four feet long he counted 6130 "blossoms," not learning until later that it was a staminate inflorescence. To do this work on the Sanibel vegetation, he perused the library and herbarium of the Gray Herbarium/Arnold Arboretum, with an appointment as a research fellow (1954) to use the facilities. George and his wife, Myra, moved to Cambridge for six months and took full advantage of his Harvard appointment, both intellectually and socially.

The lack of a proper manual for the southeastern United States still bothered him, but for ten years he gave financial support to the work his Harvard colleagues felt was basic: a consideration of the generic limits of the flora, the assembly of a bibliography, and the preparation of new, accurate illustrations of each genus. This work, under the direction of Dr. Carroll E. Wood, was to become the Generic Flora of the Southeastern States. The first paper, "The Genera of the Woody Ranales in the Southeastern United States," was published in 1958 (J. Arnold Arbor. **39**: 296–346) and has been followed by 115 papers by 38 authors. After Cooley's initial grants, generous support for this work has been received from the National Science Foundation.

CHINSEGUT HILL AND THE UNIVERSITY OF SOUTH FLORIDA

When an old friend, Dr. James Allen, was appointed president of the new University of South Florida, George Cooley "adopted" the school and directed his support and energy to the establishment of a botany department with a herbarium, a library, and a botanic garden. The university acquired, presumably with his help, a property known as Chinsegut Hill, near Brooksville, which Cooley decided could be a center for botanical studies. His first chore was to supply a new roof for the building, and then he started local collecting. Cooley invited old friends and acquaintances to Florida and put them to work collecting, mounting, and inserting specimens in the young herbarium. Henry Gleason, Stanley Pease, Lily Perry, Leonard Brass, Richard Eaton, William Weston, and Mackenzie Lamb were among the hard-working "volunteers." Cooley sought advice on books he bought for the library, and he cajoled curators of major herbaria to work over collections long in storage to find duplicates to send to South Florida. Among the rare plants he collected at Chinsegut was the new species *Justicia cooleyi* Monach. & Leonard. He also gathered the abundant and pestiferous *Dioscorea bulbifera.* Cooley and his volunteers filled a dump truck with the unwanted "bulbs" of this species, which he proclaimed was a suitable entry for the *Guinness Book of Records.* He admitted defeat, however, in his efforts to prepare an edible dish from the bulbs—perhaps the only time when his persistence did not succeed. Before the first undergraduate class had graduated, the University of South Florida had a biological study area, a botanical garden, a creditable botanical library, a herbarium, and an enthusiastic supporter. Cooley was honored at the university's first convocation with an honorary Doctor of Science degree.

SOUTH AFRICA AND AROUND THE WORLD

In 1963 the National Botanical Gardens of South Africa invited about 50 botanists to a celebration of their fiftieth anniversary, followed by a month-long bus tour of the country. For a taxonomist teaching a course in plant families, it was an opportunity not to be missed, and I planned to go. George Cooley applied and received an invitation, and we traveled together. Our first stop was the AETFAT meeting in Florence, Italy. Then we visited Cairo, Addis Ababa, Nairobi, and Capetown before taking the country-wide tour of South Africa. Our wives joined us in Johannesburg for the flight to Mauritius, then to Perth, Melbourne, Canberra, Brisbane, Port Moresby, and Sydney. There we parted company, the Cooleys visiting New Zealand and my wife and I continuing to Fiji, Hawaii, and home to Boston. In two months of travel with a companion, you learn all of his social tricks, foibles, and moods. George was always cheerful, energetic, and ready to go. At each new social encounter with a botanist, he offered a dollar bill to anyone who could spell Rensselaerville and paid only once to an Afrikaans-speaking person in South Africa. His pants pocket always had a "hole" that surreptitiously dropped shining coins on the grass, to the delight of children. He treated an assembly of Masai gathered at a store to soda pop and gave bubble gum to the young police officers in sarongs at Port Moresby. He joined local botanical societies and natural history clubs, usually with a life membership, asking that the publications go to the University of South Florida. In each country visited he gathered herbarium specimens, depending on the local botanists to identify, press, dry, and ship them to South Florida. He left money behind, knowing that there was more than enough to cover costs. Artifacts he purchased in local markets decorated the guest room in his home, and each had a story, often embellished with the passage of time.

ST. VINCENT

In my work on the vegetation of the Lesser Antilles, George Cooley often asked how he could help, stating that he and Myra needed a winter escape. Finally, I suggested that they might like St. Vincent and that I needed plant specimens from the island and someone to search the archives and botanical-garden records for data on plant introductions. George and Myra traveled to St. Vincent in November, 1961, armed with plant presses and a list of taxa previously collected by H. H. and G. W. Smith. George was determined to regather all the species and add to the known flora. As exact localities for the Smiths' collections were not in the list published in *Kew Bulletin* in 1898, the Cooleys interrupted their stay and took a boat to England to search out the original specimens in the Kew herbarium for locality data. The information was not on the sheets, so the search was futile. Undaunted, Cooley returned to St. Vincent and succeeded beyond my wildest dreams in preparing over 3000 excellent specimens, well documented and with duplicates. He insisted on working up the material himself on his return to Cambridge, and his collections remain some of the best ever assembled from St. Vincent.

While George was collecting plants, Myra searched the archives for the historical material I wanted and carefully copied in notebooks records of plant introductions, trials, and successes. Only a small part of this important detail has yet been published.

In September, 1963, I wrote to the governor of St. Vincent, calling to his attention the bicentennial of the founding of the St. Vincent Botanic Garden two years later. I suggested that the garden might be spruced up, the plants newly labeled, and the attention of tourists directed to the anniversary. When the Cooleys returned to the island in 1964, I asked George to determine what plans were being made for the anniversary. He learned that the idea had local appeal, but little was being done about it. He approached the colonial governor (whom he knew personally), the Department of Agriculture, area naturalists, the press, and local businessmen. Soon committees were actively planning, assured of some financial support from George Cooley.

The celebration was held in March, 1965, and the Cooleys were present. The theme was the arrival of Captain Bligh on the *Providence* with the breadfruit and other plants. "Captain Bligh" came ashore in a small boat with some breadfruit plants in pots. These were "headed" by local volunteers in the same manner as they had been 200 years previously. Some were planted with ceremony. There were special greetings sent from the director of the Royal Botanic Gardens, Kew, and from the president of the International Association of Botanic Gardens and Arboreta. A set of postage stamps commemorated the founding of the garden, the arrival of the breadfruit, and Captain Bligh and the *Providence*. A parade featured floats, bands, and marchers in the prize-winning costumes of the recent carnival. Picnics and flower shows were held in the botanic garden, which was also lighted for nighttime visitation. Historical booklets had been reprinted and were distributed. Two cruise boats were in the harbor for the occasion. In all this George enjoyed his supportive role.

In 1950 I had climbed the Soufrière of St. Vincent, collected specimens, taken many photographs, and made observations on the growth of the vegetation since the last eruption in 1902 had decimated the plants on the eastern slope. On the talus of the Soma, a fragment of an earlier volcanic mass north of the present crater, I had collected an herb thought to be a member of the Gesneriaceae. Conrad Morton examined the material and was not certain of the family assignment, and E. C. Leonard could not accept it as a member of the Acanthaceae; both held decision or description pending the collection of more material. I had asked local naturalists to return to the site for more specimens, but none could find the population. There was also a problem with another species from the area. *Solanum urens* Dunal was described in 1852 from material collected 50 years earlier by Alexander Anderson, the second director of the St. Vincent Botanic Garden, as "Bonhomme de Saint Vincent." In 1909 O. Schulz, unaware of Dunal's species, described *Solanum lobulatum* on sterile material collected by H. H. & G. W. Smith at Morne Garu, a name inaccurately associated with the eruptive massif including the Soufrière.

A trip was planned to St. Vincent in early 1971 to record the summit vegetation 70 years after the volcano had erupted and to look for the two problematic species. George Cooley, then 75 years of age, wanted to go along; he would set his own pace, I was told. The two episodes that occurred on nearly successive days revealed his extraordinary courage and poise.

To search for the *Solanum,* we decided to ascend Richmond Peak, starting from the Richmond River valley. Our local companion, Con de Freitas, determined that the only approach was a stiff climb, essentially up a rock face, to a shoulder where we could climb a ridge to Richmond Peak. There was no trail, and the face of the cliff required climbing in a crevasse, which was exhausting. From the shoulder the going was easier in some spots and required machete clearing in others, but the collecting was good and the stops frequent. The final few hundred yards were a dense tangle of *Clusia* and intertwined shrubs, which meant we left packs, field presses, lunches, and water behind. George trailed the party for a while, but after we found the plant we sought in flower and fruit and stopped to prepare specimens and take photographs, he announced he was turning back and would wait for us lower down. Over an hour later we started down, arms loaded with specimens to be put in the field presses that were with our packs, water, and lunches. We passed another hour arranging our presses before we continued down the mountain, wondering where we would overtake George. At the base of the ridge and near the cliff face, we made a shift of several hundred yards to the crevasse we had ascended, still without encountering him. We yelled, to no avail, and assumed he had found his way down the cliff in spite of our suggestion that he wait for us to descend together. We returned to our car at dusk and found no sign that George had been there. Again we called and waited. We knew of a small store several miles down the road and drove there to ask if George had stopped for a cold drink. No one had seen him, so we returned to our starting point. In the path of our headlights we saw a very tired, dirty George Cooley walking toward us along the road. He said little beyond the fact that he had not found the crevasse and so came down the cliff face anyway. How, we will never know.

Two days later we planned to climb the Soufrière from the east, search for the unidentifiable plant, circle the crater to take photographs of the vegetation on close radii, and descend the west slope. We left Kingstown before sunrise to drive to Orange Hill and as far as possible up the mountain. The climb was fairly easy up to the area of cinders. We reached the rim and walked clockwise to the point of eventual descent, where we left our packs. We reversed direction, photographing as we walked to the northern point of the crater rim, and then traveled north across the dry crater to the talus slopes of the Soma wall. On the third or fourth talus slope we explored, we rediscovered the unknown plant that was to be described later as *Lindernia brucei* Howard (Scrophulariaceae). It was then after lunchtime, and we knew several additional hours would be required to complete the circuit of the rim. George Cooley decided not to accompany us on the circuit but to return to our packs and wait for us there. Again we admonished him to be careful, and we started off in different directions. Clouds had already formed and periodically obscured the visibility, so we often had to wait to take our photographs. About 5 P.M., later than we expected, we returned to our packs. There was no sign of George's having been there. We had settled down to eat something and wait when we heard a faint yell of what we thought was "hello" across the crater. We replied and realized the answering shout was "help!" By then some of us had stiffened up from the walk and the wait. Con de Freitas started off at a run, while the rest of us followed as fast as we could. Con outdistanced us but from the clouds soon called "bring the rope," for we had carried a stout climbing rope with us. One local aide went back for the rope, and the rest of us continued until we found Con de Freitas flat on his stomach at the fragile edge of the crater.

George Cooley, returning alone, had become lost in the clouds, put down the package he was carrying, and approached the rim to determine where he was in relation to the crater. The edge gave way, and he fell down the crater wall. Somehow he managed to turn on his stomach in the fall and grasp for something to stop his slide. Several bromeliads growing in the cinders served the purpose. It was truly a miracle, for the steep slope became vertical a few yards below, with a straight drop of several hundred feet to the crater lake. While holding onto the *Guzmania* plants, Cooley was able to scrape a toehold in the cinders of the slope and eventually made it wide and deep enough to support his weight. As he could not climb upward, he widened the shelf he had created and eventually released his hold on the bromeliads and perched on his small ledge. So he was found, about 30 feet below the crater rim. Only the bag he had left above indicated where he was. He reported afterward that he was so tired from his exertions he had trouble staying awake, but he didn't dare fall asleep, so he recited all the poetry he recalled, prayed, and sang the hymns of his childhood. His periodic calls were eventually heard. We estimated that he must have been there three hours before we located him.

The retrieval process was not an easy one. Although one end of the rope was tossed over repeatedly, the strong winds up the crater wall invariably placed it outside of George's reach. Finally it was decided to tie the rope in a bowline and lower the lightest member of our party over the crater rim. An unnamed St. Vincentian accepted the role. I, being the tallest and heaviest of the party, anchored the rope around my waist and spread-eagled on the cinder slope outside of the crater. The others lowered the young man, who reached Cooley and joined him on the shelf he had created. The rope was tied around Cooley under his arms, and he was hauled back to safety. Fortunately, the next toss of the rope reached the volunteer, who was also pulled up. Our transport was to meet us at the coast on the leeward side of St. Vincent, so we had no choice but to walk back to our packs and descend the Soufrière. Our one flashlight gave out at this point, and we were forced to proceed in total darkness. We had Cooley on the trail, his left arm over my shoulders and his right over Dick

Weaver's, as we worked our way around the crater rim and then down the several miles to the coast. Once there, we still had two miles of beach ahead of us and a pair of rivers to ford. Cooley was completely exhausted by the time we reached the contact point, but fortunately our driver had waited. We returned to our hotel at midnight, grateful for our beds.

A knock on my door early the next morning awakened me. There was George Cooley in sparkling white shirt and shorts, white socks, and clean sneakers. He looked ready for a tennis match and was his usual joking self for a few minutes but then admitted he was having severe chest pains. Hastily we located a doctor and rushed George to her office, fearing the worst. The pains proved to be from a chest bruise derived from the bowline knot and the drag on his chest as we pulled him from the crater wall of the Soufrière. Characteristically, George had packed his bags before awakening me and wanted to return to New York immediately. We put him on a plane for Barbados in less than two hours. When we returned to Boston a week later and called him, he said he was fine but added, "Don't tell Myra." To my knowledge, she has never known this story of true courage, the result of foolish behavior on his part and negligence on mine for letting him start back alone. Anyone who knew George Cooley will understand that he wasn't to be dissuaded when he had made up his mind. The story of "the man who fell into the crater and survived" persists on St. Vincent in several versions. One of these was written in *Boy's Life* magazine (August, 1974) as a legend of St. Vincent.

In the winter of 1971–1972, extruded cinders from the bottom of the crater lake formed a cone in the crater, and the rising hot water destroyed vegetation at the lake edge but not that of the crater rim. A massive eruption of the crater in 1979, however, did destroy all plants on the upper levels of the volcano, and our photographic record is useful now only to document the regrowth of vegetation in the 1902–1971 period.

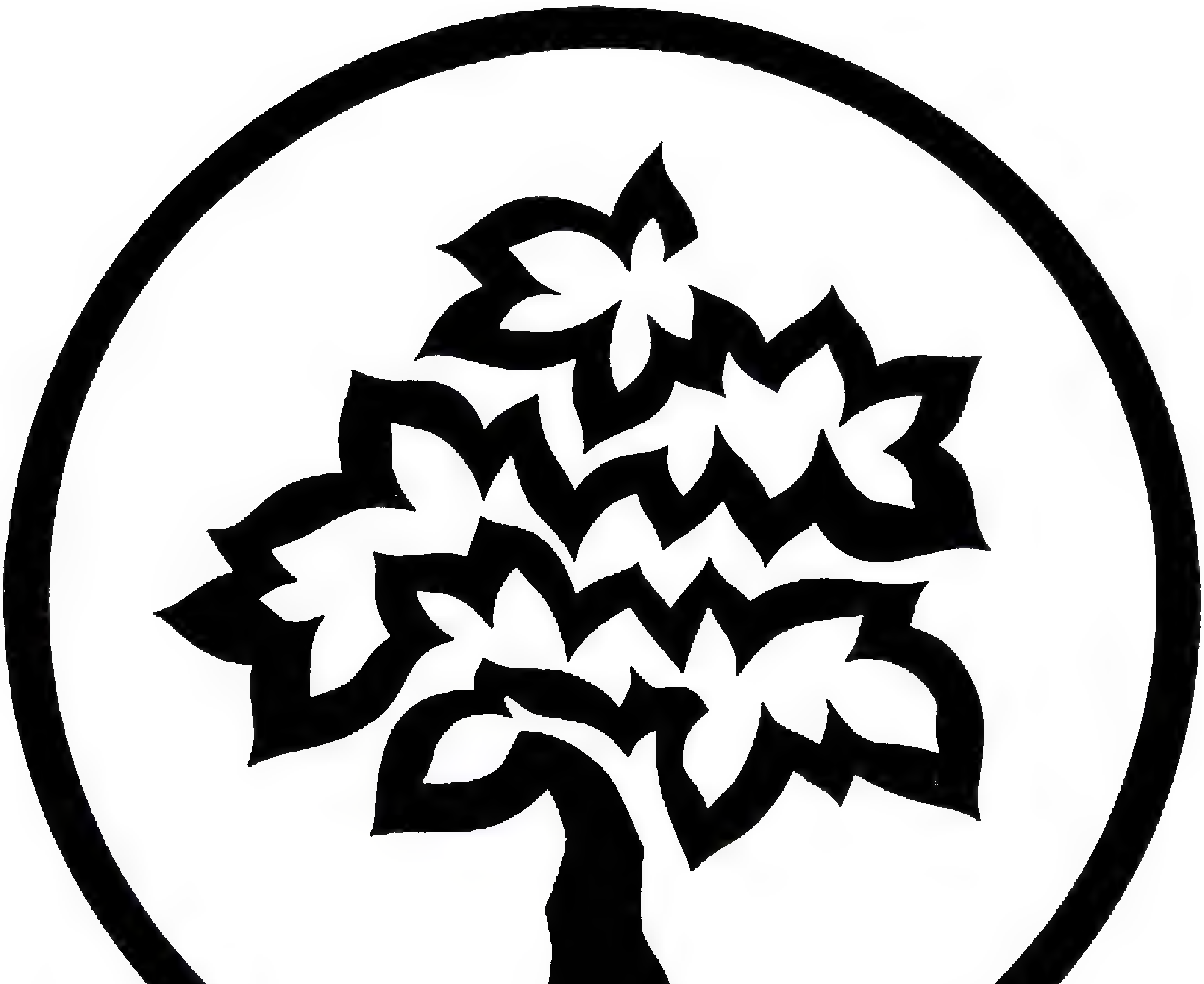
CONTINUING GENEROSITY

The adventures of 1971 may have been George Cooley's last field trip. He returned to Sanibel Island many times. There he helped to create the Sanibel-Captiva Conservation Foundation and to establish a nature preserve, cutting brush and establishing trails in his energetic way. He was the "local" guide for many of the visitors. His interest and support turned to the Nature Conservancy, where he served on the national board of governors and was awarded the Conservancy's Oak Leaf Award in 1984. He spearheaded the protection of Florida's Tiger Creek near the Bok Tower and helped establish reserves in several areas, including the Big and Little Bear swamps in New York State. He was generous to Colgate University (which he attended for only six months), where a library and herbarium, as well as a chair in Peace studies, are named for him. To encourage botanical studies in the southeastern states, he supported local floras, herbarium development, and lecture series, many named for him. Nationally, he funded the Cooley prizes of the American Association of Plant Taxonomists. One was for the outstanding paper published during the previous year, but this was not continued beyond the initial five-year period for lack of suitable papers. The other was for the best paper presented at an annual meeting of the American Society of Plant Taxonomists. Since its inception in 1956, this prize has been awarded to over forty individuals, who are eligible to win but once. After Cooley's death, when it seemed the prize would lapse, his wife and daughters added to the available funds to permit the award to be endowed and the prize continued. Former award winners have added to this fund with gifts in his memory. In addition, *Justicia cooleyi* Monach. & Leonard, *Thalictrum cooleyi* Ahles, and *Thelypteris cooleyi* Proctor honor his role in plant taxonomy.

George Ralph Cooley was born May 29, 1896, in Troy, New York, and died September 27, 1986, at his home in Rensselaerville, New York. He was a valued, sincere, and thoughtful friend to many of us and a devoted, loving husband, father, and grandfather.

INDEX

JOURNAL OF THE ARNOLD ARBORETUM



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Contents of Volume 68 *1987*

Journal of the Arnold Arboretum *October, 1987*

CONTENTS OF VOLUME 68, NUMBER 4

Volume 68, Number 3, including pages 269–359, was issued July 8, 1987.