JOURNAL OF THE ARNOLD ARBORETUM

HARVARD UNIVERSITY VOLUME 66 NUMBER 1

ISSN 0004–2625

Journal of the Arnold Arboretum

The *Journal of the Arnold Arboretum* (ISSN 0004-2625) is published quarterly in January, April, July, and October for $50.00 per year, plus $5.00 postage for addresses outside of the United States, by the Arnold Arboretum of Harvard University. It is printed and distributed by the Allen Press, Inc., 1041 New Hampshire Street, Lawrence, Kansas 66044. Second-class postage paid at Lawrence, Kansas. POSTMASTER: send address changes to *Journal of the Arnold Arboretum,* ℅ Allen Press, Inc., P. O. Box 368, Lawrence, Kansas 66044.

Subscriptions and remittances should be sent to *Journal of the Arnold Arboretum*, 1041 New Hampshire Street, Lawrence, Kansas 66044, U. S. A. Claims will not be accepted after six months from the date of issue.

Volumes 1–51, reprinted, and some back numbers of volumes 52–56 are available from the Kraus Reprint Corporation, Route 100, Millwood, New York 10546, U. S. A.

Printed at Allen Press, Inc., Lawrence, Kansas

COVER: The stylized design appearing on the Journal and the offprints was drawn by Karen Stoutsenberger.

JOURNAL
OF THE
ARNOLD ARBORETUM

VOLUME 66 JANUARY 1985 NUMBER 1

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

GEORGE K. ROGERS

PHYTOLACCACEAE R. Brown in Tuckey, Narr. Exped. Congo, 454. 1818, "Phytolaceae," nom. cons.

(POKEWEED FAMILY)

Herbs, shrubs, vines [or sometimes trees], with lateral expansion normal or by successive cambia. Plants with betalain pigments, rich in saponins (Phytolaccoideae). Sieve-tube plastids usually containing globular crystalloids [these polygonal in *Stegnosperma* and cubic in *Limeum*]. Calcium oxalate mostly

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[1] Prepared for the Generic Flora of the Southeastern United States, a long-term project made possible by grants from the National Science Foundation and currently supported by BSR-8111520 (Carroll E. Wood, Jr., principal investigator), under which this account was prepared, and BSR-8303100 (Norton G. Miller, principal investigator). This treatment, the 105th 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.

Special thanks are extended to my brother, James Rogers, for enthusiasm beyond mere tolerance while I collected and observed "*Phytolacca rigida*" during a trip made to North Carolina for multiple purposes. Ihsan Al-Shehbaz, Michel Lelong, James E. Rodman, and Won S. Woo generously helped fill gaps in my information. I am indebted to George Staples for photographing *Trichostigma* in Florida. That Elizabeth Kellogg made available her treatise on Phytolaccaceae prior to its publication in the *Flora of the Lesser Antilles* is acknowledged with gratitude. The late Dorothy H. Marsh, Diane C. Johnson, and Karen Stoutsenberger, supervised by Carroll Wood and/or Kenneth R. Robertson, drew the three illustrations using materials collected in Mississippi, Virginia, and Florida by R. B. Channell, Carroll Wood, and Frank C. Craighead, Jr. Supplementary materials of *Petiveria* came from specimens from Florida in the Harvard University Herbaria (g, h, *Long & Broome 2543*, GH) and Puerto Rico (l–s, *Wagner 1629*, A). Reviews of the manuscript by Carroll Wood and Stephen Spongberg yielded important improvements, and the paper would be poorer if not for Elizabeth Schmidt's editorial talents. Barbara Nimblett moved the project along quickly by helping with the typing.

Journal of the Arnold Arboretum **66**: 1–37. January, 1985.

present as styloids (Rivinoideae) or raphides (Phytolaccoideae, Agdestidoideae) [or spherical aggregates of crystals in Barbeuioideae, Microteoideae, Stegnospermatoideae], and in additional forms. Leaves alternate, simple, entire, usually petiolate, often with crystals bulging on blades (when dry) or appearing as translucent dots; stomata anomocytic or paracytic. Inflorescences mostly racemose, paniculate, or spicate, the rachises sometimes terminated by flowers, frequently bearing simple or compound lateral dichasia; bracts and bracteoles usually small. Flowers perfect [or imperfect], usually actinomorphic (regular), or slightly irregular or zygomorphic, usually with a hypogynous disc. Perianth uniseriate [or biseriate by virtue of petaloid staminodes in *Stegnosperma* and in *Anisomeria coriacea* var. *petalifera* fide Walter], the tepals usually 4 or 5, inconspicuous or infrequently showy, usually greenish or white, separate or slightly [or rarely strongly] coalescent basally, usually persistent. Stamens [3 or] 4 to numerous, in 1 or 2 whorl(s) or inserted irregularly; filaments separate or connate basally; anthers usually elongate. Pollen grains 2- (*fide* Davis) or 3-celled when shed, 3-colpate [3-colporoidate], pantocolpate [or pantoporate], the exine not reticulate, the tectum spinulose and usually punctate-perforate. Gynoecium of 1 to many [apparently separate or] connate, superior (partly inferior in *Agdestis*) carpels, each with 1 style (styles connate in *Agdestis*), 1 locule, and 1 adaxial-basal ovule, this (ana-)campylotropous to (among our genera, *Petiveria*) erect and straight with the micropyle adjacent to the funiculus, in pluricarpellate species the micropyle abaxial to the floral axis [adaxial in *Stegnosperma*]. [Gynoecium compound and unilocular in Microteoideae.] Fruits berries or drupes, or dry and indehiscent [or capsular, or with separate fleshy or dry carpels], sometimes winged by the persistent tepals [or with wing derived from pericarp], barbed or hooked in some genera. Seeds erect, usually compressed and circular to reniform in outline, sometimes elongate (*Petiveria*), lacking arils (or minutely arillate in *Rivina*) [or strongly arillate in *Stegnosperma* and *Barbeuia*]; seed coat usually smooth and dark, sometimes adherent to pericarp. Embryo annular or sharply bent, sometimes plicate. Megagametophyte (embryo sac) of the Polygonum type (deviating slightly in *Rivina*). Endosperm formation initially nuclear. Principal nutritive tissue in mature seed perisperm. (Including Agdestidaceae Nakai, Barbeuiaceae Nakai, Petiveriaceae Agardh, Rivinaceae Agardh, Stegnospermataceae Nakai.) TYPE GENUS: *Phytolacca* L.

A poorly delimited family of about 17 mostly small and often monotypic genera collectively including about 120 species. *Phytolacca,* with about 25 species, is the largest genus; *Seguieria* Loefl. is slightly smaller. Concentrated in the American tropics and subtropics, the family is represented as far north as southern Canada (*Phytolacca americana*); at the southern extreme distributions of about half the genera include or lie within Argentina or Chile. The Old World indigens are *Barbeuia* Thouars in Madagascar, *Monococcus* F. Mueller in and near Australia, *Lophiocarpus* Turcz. in Africa, and species of *Phytolacca* in Africa and Asia. *Petiveria alliacea, Rivina humilis, Trichostigma octandrum, Phytolacca americana, Agdestis clematidea,* and the debatably phytolaccaceous *Gisekia pharnacioides* L. (see footnote in key) occur in the area of the Generic Flora. *Phaulothamnus spinescens* Gray, which may or may not belong in the Phytolaccaceae, ranges as close as Texas.

The Phytolaccaceae, clearly a family of the order Centrospermae (Caryophyllales), is composed of a diverse assortment of usually unarmed herbs, vines, and trees. Members usually have fairly nonsucculent, *alternate leaves* (vs. leaves mostly opposite in Caryophyllaceae, Aizoaceae, and Nyctaginaceae), betalain pigments (rather than anthocyanins as in Caryophyllaceae and Molluginaceae), and usually globular crystalloids in sieve-tube plastids (vs. crystalloids absent in Chenopodiaceae and Amaranthaceae and polygonal in Caryophyllaceae). The *inflorescences are predominantly racemes or racemelike* but are often partly cymose (vs. more distinctly cymose in most relatives or potential members) and bear *unspecialized bracts* (in comparison with those of Nyctaginaceae and Amaranthaceae, and the "sepals" of Portulacaceae). Phytolaccaceous flowers are generally perfect with *nonshowy perianths* (unlike Portulacaceae, somewhat showy in *Agdestis*) composed of *one whorl of basally connate or separate tepals* (tepals or "sepals" connate in Nyctaginaceae and Aizoaceae). Stamens in Phytolaccaceae vary widely in number and arrangement—in some genera they are numerous and inserted irregularly. With exceptions, the stamens are not elaborated into attractive organs (as they are in some Aizoaceae and Molluginaceae and possibly Caryophyllaceae) and tend only slightly toward connation (thus differing from staminal tubes of some Amaranthaceae). The pollen is variable. Most genera have either a *solitary carpel or several carpels with varying degrees of fusion, each carpel typically with a free style, one locule, and one ovule.* (Compound unilocular or partly unilocular ovaries characterize Amaranthaceae, Chenopodiaceae, Portulacaceae, and Caryophyllaceae. With exceptions, Aizoaceae, Caryophyllaceae, Molluginaceae, and Portulacaceae tend to have multiplication of ovules on variously specialized placentas.)

The six subfamilies recognized in Nowicke's "palynotaxonomic study" (1968) of Phytolaccaceae are congruent with Heimerl's (1934) five tribes and one set of anomalous genera. In the principal revision prior to those of Nowicke and Heimerl, Walter (1909) divided a more broadly circumscribed Phytolaccaceae into two subfamilies, three tribes, and two subtribes. All three monographers perceived *Anisomeria* D. Don, *Ercilla* A. Juss., and *Phytolacca* to constitute a coherent assemblage. This trio, which is characterized by raphides and multiple carpels with as many locules and styles, makes up the entire Phytolaccaceae *sensu* Hutchinson and the entire subfam. Phytolaccoideae in Nowicke's treatment. Walter, Heimerl, and Nowicke agreed further on the boundaries of the group now known as subfam. Rivinoideae Nowicke,[2] characterized by styloid crystals and flowers with single carpels.

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[2] With their authorships brought into accordance with the 1983 International Code of Botanical Nomenclature, the tribes Nowicke recognized under subfam. Rivinoideae are Seguierieae Moq. (two extralimital genera with paniculiform inflorescences and samaroid fruits) and Rivineae Endl. (seven genera, including our *Petiveria, Rivina,* and *Trichostigma,* with spikes or racemes and nonsamaroid fruits). Although some botanists attributed C. A. Agardh with the authorship of tribe Rivineae in his *Aphorismi Botanici,* he evidently published Rivineae as an "order" nomenclaturally equivalent to a modern family (see Agardh, p. 61, and ICBN, 1983, Art. 18.2).

The affinities of the remaining members or potential members of the family have spawned disagreement and remain unsettled. Subfamily Microteoideae Eckardt ex Nowicke is made up of *Lophiocarpus* and *Microtea* Sw. in Nowicke's classification. Walter did not include *Lophiocarpus* in the Phytolaccaceae and listed *Microtea* under *genera anomala.* Heimerl listed both as anomalous. Both Heimerl and Walter placed the three genera corresponding to Nowicke's subfamilies Barbeuioideae Nowicke, Agdestidoideae Nowicke, and Stegnospermatoideae H. Walter in the Phytolaccaceae at various infrafamilial ranks or among *genera anomala.* Other botanists have excluded them from the Phytolaccaceae as *incertae sedis* or as distinct families.

Heimerl, Nowicke, and most recent authors departed from Walter and from Dahlgren and colleagues by treating *Achatocarpus* Triana and *Phaulothamnus* Gray together as the family Achatocarpaceae. They further disagreed with Walter by excluding Gyrostemonaceae from Phytolaccaceae. Evidence that the former is out of place even in the Centrospermae comes from palynology, floral morphology, cytology, chemistry, and the nature of sieve-tube plastids and vacuoles in companion cells (Behnke, 1977; Goldblatt *et al.*; Keighery).

The foregoing historical sketch underscores the need for new research aimed toward a better circumscription of the Phytolaccaceae. The confusion comes largely from the fact that to some degree the family comprises the *taxonomic* residue left after the other Centrospermae are sorted into separate families based on apparent specializations. (From here it is a small jump to the common perception of the family as a *phylogenetic* residue left after the evolutionary radiation of other Centrospermae.) An ostensible shared absence of derived distinctions, leaving suspected ancestral traits as similarities, is at best flimsy evidence for phylogenetic relationship.

Yet, even if the family Phytolaccaceae is a repository for residual unspecialized traits, past authors have probably overemphasized its primitiveness. Thus, a few apparently derived characters should be mentioned. Rohweder's conclusion that ovaries in *Phytolacca* separate by bulging from an ontogenetically originally syncarpous region raises the possibility that near-apocarpy in subfam. Phytolaccoideae is phylogenetically secondary. This challenges the hypotheses that the occurrence of near-apocarpy in the Phytolaccaceae is a tie to apocarpous Ranales (see Buxbaum, 1961), and that this condition reflects the starting point for gynoecial evolution in the rest of the Centrospermae. As a second example, the racemes and racemelike inflorescences that predominate in the Phytolaccaceae are interpretable as having evolved by reduction from cymose inflorescences. Cymose arrangements characterize most other Centrospermae and a minority of Phytolaccaceae (mostly peripheral groups), and racemose inflorescences in the Phytolaccaceae (e.g., species of *Phytolacca*) sometimes have dichasial branches. (For an argument that the general evolutionary trend proceeds in this direction, see Stebbins.) To add a third example, Cronquist doubted that the phytolaccaceous trait of one ovule per carpel is primitive in the Centrospermae. Lastly, recent authors have noted that it is simpler to postulate that the betalain pigments of Phytolaccaceae and most other centrosperms are derived than to interpret their presence as ancestral in the order. The latter interpretation requires acceptance of the anthocyanins in Molluginaceae and Caryophyllaceae as arising anew via reversal.

Specializations are to be expected, and these do not rule out a more or less central position for Phytolaccaceae in the Centrospermae. Support for this position appears in apparent spokelike links to disparate satellite groups and centrospermous families through morphological similarities and transitional genera. As examples of the latter, *Stegnosperma* Bentham forms a much-discussed bridge to Molluginaceae or Caryophyllaceae, and *Lophiocarpus* and *Microtea* have repeatedly been mentioned as ties to Chenopodiaceae and Amaranthaceae. *Gisekia* resembles species of Phytolaccaceae in having raphides, betalains, and gynoecia that agree developmentally, but it leans toward Molluginaceae in habit, cymose inflorescences, androecial morphology, nectaries, and embryology. (For comparative details see Bogle; Hofmann, 1973; Mabry *et al.* Note that Ehrendorfer, 1976b, placed *Gisekia* in Aizoaceae.)

The structures termed stipules in literature on Phytolaccaceae are probably prophylls in some, if not all, genera in which they occur (Eckardt, 1964; see also Buxbaum, 1949). In *Petiveria alliacea* stipulelike axillary emergences can be seen to be attached like reduced leaves to developed axillary shoots, and multiple pairs of emergences appear to correspond to multiple axillary shoots.

According to the sketchy data on hand, chromosome numbers in Phytolaccaceae range as polyploids, but not aneuploids, from $2n = 18$ to $2n = 108$. (Keighery provided a survey.)

Most economic uses for members of the Phytolaccaceae appear in the generic treatments. Among extralimital genera *Ercilla spicata* (Bert.) Moq. is a minor ornamental, while species of *Anisomeria, Gallesia* Casar., *Hilleria* Vell., *Microtea,* and *Seguieria* find uses in folk remedies. Roots of *Stegnosperma scandens* (Lunan) Standley serve as a soap in Mexico (Standley & Steyermark).

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KEY TO THE GENERA OF PHYTOLACCACEAE IN THE SOUTHEASTERN UNITED STATES

A. Carpel 1; stigma 1; style 1 or absent; crystals predominantly styloids.

  B. Inflorescences spicate or nearly so; flowers distinctly zygomorphic; ovaries densely pubescent; fruit dry, cuneiform, armed with 4 or more hooks at apex; seed much longer than wide. .... 4. *Petiveria.*

  B. Inflorescences racemose; flowers actinomorphic or nearly so; ovaries glabrous or glabrate; fruit fleshy, rounded in outline, unarmed; seed more or less lenticular.

    C. Plants usually herbs or subshrubs (sometimes scandent); leaf blades often deltoid; stamens 4; style well developed, stigma capitate or lobed; fruit bright red or orange; seed covered with "hairy" remnant of pericarp (this sometimes wearing off, leaving bare seed coat). .... 3. *Rivina.*

    C. Plants usually robust woody vines, sometimes somewhat arborescent; leaf blades ovate or lanceolate to elliptic; stamens 8 or more; style absent or inconspicuous, stigma penicillate; fruit black or dark reddish; seed bare or covered with "nonhairy" remnant of pericarp. .... 2. *Trichostigma.*

A. Carpels usually 4 or more, apparently apocarpous or syncarpous; stigmas and styles usually 4 or more (except *Agdestis,* with solitary style crowned with usually 4 conspicuous stigmas); crystals predominantly raphides.
  D. Plants climbing vines; leaf blades mostly cordate, often about as long as wide; ovary partly inferior, syncarpous and usually 4-locular (becoming unilocular in fruit by abortion); style solitary; fruit dry, only 1 per flower (not an aggregate). .... 5. *Agdestis.*
  D. Plants nonclimbing herbs; leaf blades linear-oblong to elliptic or ovate, longer than wide; ovary superior, apparently apocarpous with 5 carpels or syncarpous with usually 10 carpels and locules; styles as many as carpels; fruit baccate or an aggregate of nutlets.
    E. Leaves alternate, usually separated by well-developed internodes, usually wider than 1 cm; inflorescence racemose, uncrowded; stamens usually 10; gynoecium syncarpous, carpels usually 10; fruit baccate. .... 1. *Phytolacca.*
    E. Leaves often opposite or subopposite, sometimes clustered at nodes, narrower than 1 cm; inflorescence fundamentally cymose, more or less umbelliform and fasciculate, crowded; stamens 5; gynoecium apparently apocarpous, carpels 5; fruit an aggregate of warty nutlets. ...... [*Gisekia pharnacioides* L.[3]]

Subfamily PHYTOLACCOIDEAE

1. **Phytolacca** Linnaeus, Sp. Pl. **1:** 441. 1753; Gen. Pl. ed. 5. 200. 1754.

Large, perennial [or sometimes annual?], erect [or scandent or procumbent], often shrublike herbs [*Phytolacca dioica* and *P. Weberbaueri* becoming large trees], expanding laterally by successive cambia [or *P. Meziana* with a continuous ring of secondary xylem *fide* Wheat]. Stems and axes of inflorescences often purplish or reddish, the pith diaphragmed [or absent] in mature stems. Patterns of growth monopodial or sympodial, the branching frequently pseudodichotomous, sometimes with multiple shoots emerging from one leaf axil. Taproots often large (reaching several dm in diameter in *P. americana*). Plants mostly glabrous, frequently scurfy-puberulent on axes of inflorescences [and infrequently elsewhere]. Raphide bundles usually bulging on dried specimens. Leaves petiolate [or nearly sessile], the blades thin to slightly succulent, often crisped-undulate, usually elliptic (often narrowly so) to ovate or lanceolate, mostly variously pointed apically, often asymmetric and usually tapered and decurrent onto the petiole basally; stomata anomocytic. Inflorescences terminal, often overtopped by axillary growth, then usually borne opposite a leaf or nearly so [infrequently axillary or arising from old growth], pedunculate [or nearly sessile], nodding to erect, the straight central rachis bearing numerous radiating much shorter [to virtually absent] pedicels, each of these subtended by a scarious elongate bract and bearing 2 small bracteoles, these sometimes subtending second- [or third-]order axes, especially toward the inflorescence base. Flowers small, perfect [or imperfect, the plants dioecious, probably infrequently polygamous], actinomorphic or nearly so. Perianth uniseriate, with 5 [rarely 3 or 4], white to pink or reddish [or yellowish, greenish, or purple],

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[3] Adventive in our area. Bogle treated *Gisekia* for the Generic Flora under Molluginaceae.

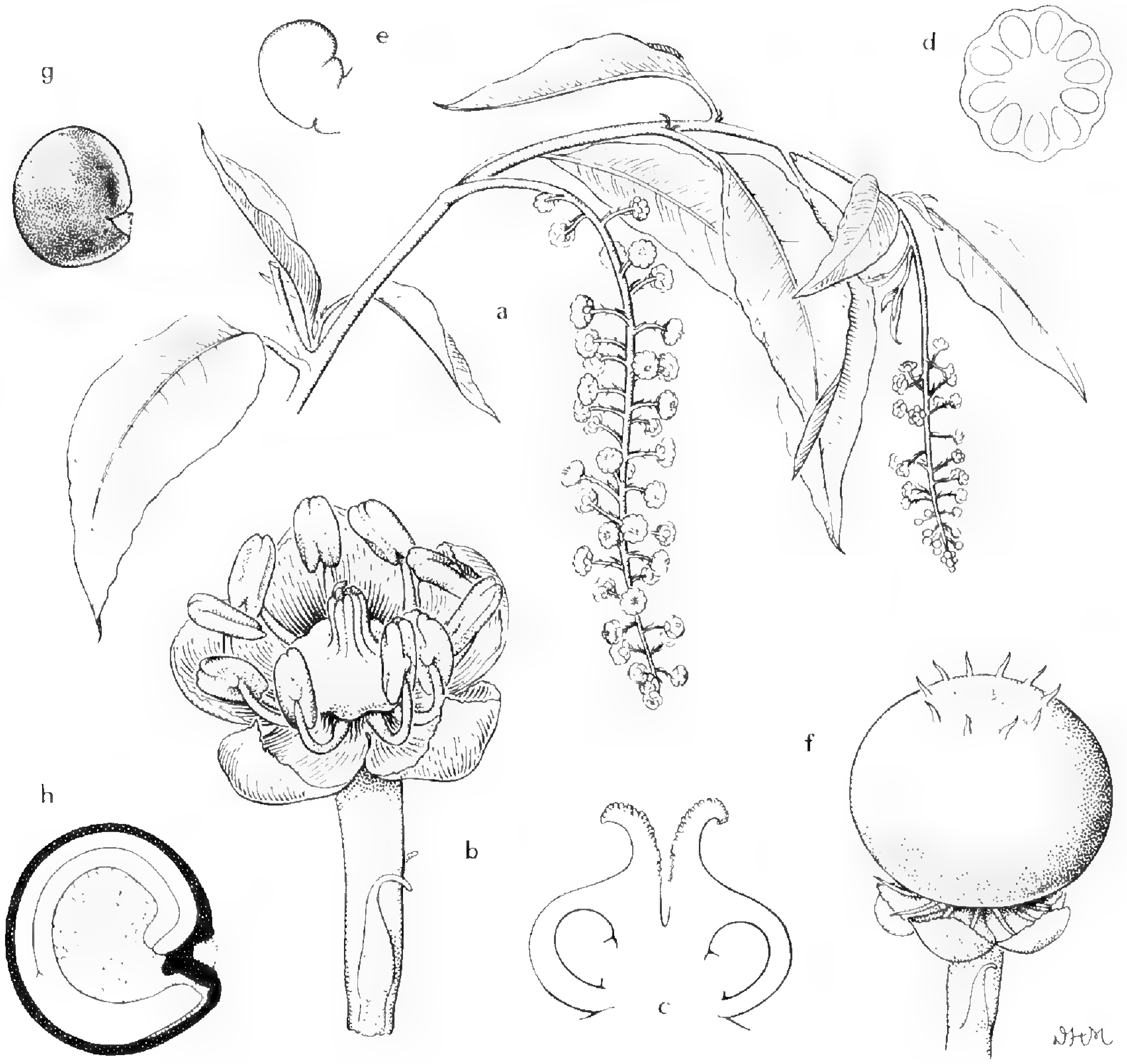

FIGURE 1. **Phytolacca.** a–h, *P. americana*: a, branchlet with flowers and immature fruits, × ½; b, flower, stigmas not yet receptive, × 8; c, gynoecium with receptive stigmas, semidiagrammatic, vertical section, 2 ovules visible, × 15; d, gynoecium, diagrammatic cross section, with ovule filling each locule, × 10; e, ovule, lateral view, micropyle below, × 22; f, mature fruit, × 3; g, seed, lateral view, funicular remnant to right, × 5; h, seed in section, semidiagrammatic, seed coat black with white stipples, embryo unshaded, perisperm in center, × 8.

broad, entire or erose, persistent [or caducous], separate or nearly separate tepals. Stamens [ca. 5 to] usually 10 in *P. americana* [to ca. 33], usually in 1 [or 2] series; filaments distinct [or connate basally], broadened at the bases [to filiform]; anthers dorsifixed. Pollen grains prolate to spheroidal, 3-colpate, the tectum spinulose and punctate-perforate. Gynoecium usually of 10 [or ca. 5 to ca. 17] connate [to nearly distinct] carpels arranged in a ring, each bearing a recurved to erect style with the stigmatic surface decurrent adaxially. Fruit a smooth globose to depressed berry (sulcate when dry), usually 10-locular (*P. americana*) [or carpels remaining separate], usually bearing the stylar remnants, purple-black [or reddish]. Seeds usually 10 (*P. americana*), nearly circular to lopsided reniform [to obovate], flattened, the testas hard and shining, black or nearly so except for light-colored funicular remnants. Embryo annular. Endosperm persisting as a vestige in the mature seed. $2n = 18, 36, 72$. (Including

Sarcoca Raf., *Pircunia* Moq.). LECTOTYPE SPECIES: *P. americana* L. (*P. decandra* L.); see Britton & Brown, Fl. No. U.S. Canada, ed. 2. **2:** 26. 1913. (Name from Greek *phyton,* plant, and *lacca,* a Latinized reference to the pigment variably known as lake, lac, or laque.) — POKE,[4] POKEBERRY, POKEWEED.

Approximately 25 species in three subgenera[5] of two sections each, distributed mostly from southeastern Canada, southward throughout most of North, Central, and South America, and in the West Indies. In the Old World a small number of species range from Africa and Madagascar into Asia Minor and eastward across southern Asia to Korea, Japan, and Taiwan. The unusually wide range of *Phytolacca acinosa* Roxb. (*P. esculenta* Van Houtte), from Pakistan to Japan and elsewhere, is no doubt partly attributable to its culinary history. *Phytolacca dodecandra* L'Hér. is widespread in Africa. *Phytolacca americana, P. icosandra* L., *P. octandra* L., and *P. purpurascens* A. Br. & Bouché are adventive in scattered, usually warm regions worldwide. Outside of our area, but in the United States, *P. brachystachys* Moq. is Hawaiian; *P. heterotepala* H. Walter, an otherwise Mexican species, appeared in San Francisco, California (Howell); and *P. dioica* L. is grown in California.

Sect. PHYTOLACCA (flowers perfect) of subg. PHYTOLACCA (carpels completely connate, styles more or less connivent) is represented in the southeastern United States by *P. americana,* $2n = 36$, which occurs in southern Quebec and Ontario, in every state of the United States east of or intersected by a longitudinal line crossing eastern Nebraska, and in northeastern Mexico. Populations in Arizona, Oregon, and California probably started from introductions by humans. *Phytolacca americana* is widely scattered adventively in the Old World.

A possible second species in our area, *Phytolacca rigida* Small inhabits seaside habitats from North Carolina to Texas and extends inland across much of Florida and into Alabama (Harper). Authors are divided as to whether *P. rigida* ought to be recognized as distinct from *P. americana.* The most salient distinguishing feature of the former, infructescences remaining erect (vs. usually nodding), proved to have a genetic basis in the transplant experiment reported by H. J. Rogers. A second conspicuous difference is that *P. rigida* has somewhat succulent leaves, a distinction undermined by Lloyd's (1914) demonstration of plasticity in leaf thickness in *P. "decandra"* (*P. americana*). My own observations complicate evaluation of this character.[6]

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[4] "Poke" is thought to come from "pocan" or "puccoon," probably an Algonquin term for a plant that contains dye.

[5] *Phytolacca* subg. *Pircunia* (Moq.) H. Walter is a later homonym of *Phytolacca* subg. *Pircunia* Poeppig & Endl. (Nov. Gen. **1:** 26. 1836, two species now placed in *Anisomeria*). Sections "*Pircunia*" and "*Pircuniopsis*" should be called by their older names, sects. *Pircuniastrum* and *Pseudolacca,* due to changes in the International Code of Botanical Nomenclature since Nowicke's revision. These appeared as sections of the genus *Pircunia* in Moquin-Tandon (1849) and as sections of *Phytolacca* in Baillon (1872). (Section "*Pircunia*" also contradicts Art. 64.3.)

[6] In August, 1983, I observed *Phytolacca rigida* and *P. americana* at Emerald Isle, Carteret County, North Carolina, represented at A by *G. Rogers 107* and *108.* Plants of *P. rigida* at that locality had thick leaves, while those of *P. americana* nearby were thin, suggesting genetic difference. But indicating plasticity, two young plants of *P. rigida* (seeds from my no. *107*) have leaves only barely perceptibly thicker than two plants of *P. americana* (seeds obtained inland in Massachusetts) of the same age in

Selected additional differences are that *Phytolacca rigida* tends to have narrower leaves with more gradually tapered bases (which held up on the potted plants), shorter inflorescences bearing fewer flowers, broader bracteoles, shorter pedicels (often shorter than the fruits), and peduncles with vascular cylinders of smaller diameter but with thicker xylem (broader sampling needed). Hardin compared *P. americana* and *P. rigida* in detail, and my comparison leads me to agree that differences between the two taxa are blurred by overlap. Perhaps *P. rigida* would be best recognized at the varietal level. The combination remains to be made.

Phytolaccas are usually large herbs (or even trees) often having reddish axes, pseudodichotomous branching, diaphragmed pith, and conspicuous raphide bundles. The inflorescences are usually pedunculate, cylindrical, racemose (although often with lateral dichasia toward the base), fundamentally terminal, and displaced laterally by axillary growth. (Inflorescences in *Ercilla* usually are nearly sessile, more or less spicate, and axillary, with those of *Anisomeria* condensed and more obviously terminal.) Species of *Phytolacca* usually have five small, nonshowy, thin, and nearly equal tepals (vs. tepals fleshy and unequal in *Anisomeria*). Five to more than 15 carpels range from near apocarpy to pronounced syncarpy. In most species these mature into a reddish to black berry containing numerous flat, blackish seeds. (The 5(–8) or fewer carpels of *Anisomeria* and *Ercilla* usually remain separate.)

Nowicke (1968) noted that interspecific hybridization, infraspecific variation, and apparent weak genetic control of many qualitative characters have obscured boundaries between species.

A familiar weed, *Phytolacca americana* is a tolerant pioneer in disturbed sites but a poor competitor when young. Evidently limited to the north mainly by summer temperatures and to the west by dry conditions, the perimeter of the range of this species has possibly changed little in response to human activity. Nevertheless, it has certainly escaped from scattered habitats, probably mostly along streams, where the taproot has been observed to withstand flooding, to places disturbed by humans. Fassett & Sauer concluded that ecological disruption in Colombia broke down barriers between *P. rugosa* A. Br. & Bouché and *P. rivinoides* Kunth & Bouché. (This paragraph based largely on Sauer, 1952.)

The ability of pokeweeds to become established quickly far from parental plants upon disturbance of soil and vegetation draws attention to their seeds. These remain viable in fecal deposits from birds, which undoubtedly are the primary agents of dispersal (Edmisten, Armesto *et al.*). Shown to withstand burial for almost 40 years (Toole & Brown), the seeds germinate in response to a complex set of factors or to artificial scarification. Farmer & Hall found

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the same pot indoors in Cambridge, Massachusetts. (It must be stressed that my observations on potted specimens are preliminary, based on a small number of specimens only a few inches tall.) Detracting further from the significance of succulent leaves, I have seen seaside plants of *P. americana* with thickened leaves in Hudson County, New Jersey, and Plymouth County, Massachusetts (*G. Rogers 109* and *110*). Plants with thickened leaves tapering at the base and with horizontal to erect inflorescences occur on Nantucket Island, Massachusetts (C. E. Wood, obs. July, 1984).

the inability of fairly fresh seeds to sprout in the dark to be largely overcome by stratification, although a functional dimorphism appeared since some seeds required light even after stratification. Seeds from one or from different individuals responded variably to a given combination of conditions (Farmer & Hall, Armesto *et al.*). Thus, longevity, efficient translocation, and nonuniform requirements for germination allow pokeweed seeds to be delivered to and/or to await disturbances, ensuring continued production of seedlings despite environmental vagaries.

Armesto and colleagues interpreted the ample fruit set of *Phytolacca americana* as a sign of autogamy; the same observation plus release of pollen followed by partial breakdown of stigmas before anthesis led Meehan to the same conclusion.

Young shoots or leaves from *Phytolacca* "*esculenta*" (*P. acinosa*), *P. americana,* and other phytolaccas can serve as food after being boiled once or twice to deactivate toxins. American Indians ate *P. americana,* and it remains a favorite wild delicacy commonly served as poke salad or "sallet." It has even been marketed canned. However, pokeweed believed to have been properly prepared sickened a group of campers, according to a report cited by Edwards & Rodgers, and contemplation of the potency of pokeweed mitogens (discussed below) may dishearten would-be enthusiasts. Despite their toxicity, pokeberries have filled pies and have colored confections and wines (Braun; Shultz; Sauer, 1950). Renewed interest in derivation of food coloring from *Phytolacca* hinges on removal of offensive substances (e.g., see Driver & Francis, Forni *et al.*). The berries have also been employed as sources of ink, as rather poor dyes for fabrics, and (at least in certain extralimital species) as a substitute for soap. *Phytolacca americana* and other species have served in the Old World as ornamentals. The principal shade tree of the Argentinian pampas, *P. dioica* (*ombú* or *bella sombra*), is planted in warm, dry regions.

A formidable brew of bioactive compounds in all parts of the plants clearly lies behind most remaining roles of *Phytolacca* in human affairs, including its use as a narcotic and as a medicine in both hemispheres. (For amplification of the rich medicinal history of *P. americana,* see Byrd; Shultz; Sauer, 1950; and Steinmetz.) Even though remedies incorporating phytolaccas are obsolete, their bioactivity remains of interest as outlined in the paragraphs that follow.

Phytolacca americana is a common and conspicuous toxic hazard. From the use of the root as a medicine and from its being mistaken at times for horseradish or parsnip, the drastic and sometimes fatal consequences of eating it are well known (Ahmed *et al.*; Anonymous; Guthrie; Jenkins; Macht; Sauer, 1950; Shultz). The threat extends to farm animals, especially pigs, which occasionally dig out lethal quantities (Barnett, Hansen, Patterson). The colorful berries are dangerous, too, although they affect various people differently. In gathering data on ca. 100 ingestions of pokeberries, O'Leary uncovered only two mentions of human fatalities. One was a two-year-old child in Rhode Island (whose case Kingsbury discussed in 1980). The other is Chesnut's old report that fruits or seeds are held to blame for deaths of a "few" children. As related in a second-hand report in Wood & Bache, a double handful killed a woman following purgation, prostration, and coma. Hansen recorded with no elaboration another fatality from the berries; and Hardin & Arena documented the death of a five-year-old girl who drank a beverage made from the berries. On the other hand, Hardin & Arena asserted that a small number of berries is generally harmless to adults and older children. Shultz likewise noted that some people eat pokeberries with no harm, but cautioned that this is not usually the case and mentioned gastrointestinal distress suffered by others after dining on birds fed pokeberries. Individuals from a group of Boy Scouts in Kentucky variously had diarrhea, cramps (possibly due to a different cause), or no symptoms after a meal of pokeberry pancakes and some raw berries (Edwards & Rodgers).

In addition to gastric irritation, symptoms of poisoning by phytolacca berries in humans include hematological alterations and probably depression of the central nervous system with inhibition of the heart and respiration, mental aberrations, and convulsions. The three last symptoms have been induced in various experimental animals by the berries and are brought about in humans by poke root. Handling plants of *Phytolacca americana* and other species may cause dermatitis (Sauer, 1950). Relating the toxicity of phytolaccas to their chemistry demands continued research on the classes of bioactive compounds discussed individually below; the high concentrations of oxalic acid and contradictory reports concerning alkaloids (*cf.* Ahmed *et al.*, Goldstein *et al.*, Jack & Rogers, Jenkins, Lascombes & Bastide, Steinmetz, Wall *et al.*, L. Webb) should not be overlooked.

A rich array of triterpenoid saponins and their free nonsugar (aglycone) components occurs in roots, fruits, and other parts of species of *Phytolacca.* In several papers, Woo, Kang, and collaborators reported ten "phytolaccosides," along with the structures of some, in *P. americana* and other species. Similarly, Suga and colleagues detected and in some cases determined structures for over eight saponins in roots of *P. americana* and concluded that the "phytolaccatoxin" of earlier literature was a mixture of more than three saponins. The principal aglycone in *P. americana* is evidently the triterpenoid phytolaccagenin; others include phytolaccagenic, jaligonic, and esculentic acids. Saponins from berries of *P. dodecandra* have aroused interest as biodegradable, ostensibly fairly safe, locally producible molluscicides for controlling schistosomiasis (Lemma, Parkhurst).

A set of single-chain and polymeric proteins associated with carbohydrates, designated mitogens[7] due to their ability to stimulate mitotic proliferation following morphological alteration of lymphocytes, has also received much attention in literature concerning the chemistry of *Phytolacca.* Certain mitogens

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[7] Mitogens from phytolaccas belong to the class of proteins and glycoproteins known as lectins, compounds that bind sugars specifically and agglutinate cells or precipitate sugar-containing compounds. A mitogenic lectin mimics the immunological effect of an antigen by stimulating T- and/or B-lymphocytes. That is, an antigen induces lymphocytes to enlarge into blast cells and proliferate. T-lymphocytes do so directly in response to the antigen, whereas effective contact between B-lymphocytes and antigen is usually mediated by T-lymphocytes. Stimulated B-lymphocytes differentiate into plasma cells and secrete antibodies. Stimulation by mitogenic lectins differs from that of antigens in that mitogens indiscriminately activate large numbers of lymphocytes.

from *Phytolacca* stand out among plant mitogens due to their high potency and/or ability to act upon B-lymphocytes as well as T-lymphocytes. Waxdal (1974) characterized a set of mitogens from *P. americana* as Pa-1 to Pa-5, among which Pa-2 probably corresponds to, or is the chief component of, the original commercially available "pokeweed mitogen" or "PWM." The dangers of pokeweed mitogens to humans are unclear. Accidental exposure to juices from *P. americana* via ingestion, breaks in the skin, and the conjunctiva has brought about hematological changes in numerous people, including researchers studying this species (Barker *et al.*, 1965, 1966, 1967a, 1967b). (A brief review of research on pokeweed mitogens appears in Waxdal, 1978.)

Like many other plants, species of *Phytolacca* contain antiviral proteins. Having been detected early in the course of research on viral inhibitors in plants, and being unusually potent, pokeweed antiviral peptide (PAP) has received special attention. PAP blocks the reproductive cycle of exceedingly diverse viruses in equally diverse hosts, at least in part by interfering with protein synthesis on the hosts' ribosomes. Coupled with an antibody, PAP may serve as a selective antitumor agent (Masuho *et al.*). (For a sampling of the extensive literature concerned with PAP, see Grasso & Shepherd, Irvin, Owens *et al.*, Tomlinson *et al.*, and Ussery *et al.*). A second antiviral protein from *P. americana* recently characterized by Irvin *et al.* is called PAP II.

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Subfamily RIVINOIDEAE Nowicke

Tribe RIVINEAE Endl.

2. **Trichostigma** A. Richard in Sagra, Hist. Fis. Cuba **10:** 306. 1845.[8]

Climbing, shrubby, or somewhat arborescent woody plants, without successive cambia (*Trichostigma octandrum,* stems to 15 cm thick in this species). Plants glabrous or puberulent to hirsute-pilose on young stems, leaves, petioles,

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[8] This work was issued in French (*Trichostigma,* p. 627, 1851?) and evidently a second time in Spanish (*Trichostigma,* **2:** 306. 1853!).

and inflorescence axes. Calcium oxalate present primarily as styloid crystals. Leaves petiolate, the blades sometimes crisped-crenulate, ovate or lanceolate to elliptic, usually pointed and sometimes apiculate apically, mostly cuneate to rounded [or cordate] basally. Racemes borne at ends of minor (or sometimes major) leafy branches or axillary [sometimes displaced by sympodial growth to a pseudolateral position in *T. peruvianum*], sometimes clustered, axes becoming reddish, the slender central rachises bearing many shorter pedicels, each subtended by and usually adnate to one subulate, deciduous or persistent bract and bearing a pair of minute bracteoles. Flowers perfect, fragrant, with 4 subequal, concave, whitish to yellowish or greenish (becoming reddish with age) [sometimes reported as brownish or externally brownish in *T. peruvianum*], separate, oblong-elliptic or tapered tepals, these reflexed or spreading in fruit. Stamens 8–13 (rarely more) [–many]; filaments ± filiform; anthers linear, cleft at the bases. Pollen grains subprolate to spheroidal, mostly 3-colpate [or 11- to 15-colpate], the tectum spinulose. Gynoecium unicarpellate and unilocular; ovary subglobose to elliptic or flask shaped, compressed; style absent or very short, stigma penicillate. Fruit fleshy, nearly globose, black or reddish. Seed lenticular, often plump, dark, glossy and bare or with adherent pericarp tissue. (*Villamillia* Ruiz & Pavon,[9] *Villamilla* Auct.) TYPE SPECIES: *T. rivinoides* A. Richard, nom. illegit. (= *T. octandrum* (L.) H. Walter, *Rivina octandra* L.). (Name from Greek *trichos*, hair, and *stigma*, in reference to the brushlike stigma.)

A small genus of three species distributed throughout most of tropical America. *Trichostigma polyandrum* (Loes.) H. Walter (*Rivina polyandra* Loes.) is found in rain forests from southern Nicaragua to western Panama (for a recent treatment see Burger). Limited to Peru and Ecuador, *T. peruvianum* (Moq.) H. Walter likewise inhabits shady forests, possibly favoring rocky sites. *Trichostigma octandrum* ranges from Argentina northward across South and Central America and the West Indies to a spare representation in Florida only as far north as Collier County (Big Cypress National Preserve, Chokoloskee Island) and Dade County.

Trichostigma octandrum is variously described as a vine, a shrub, or rarely a tree. Numbers of stamens, shapes of tepals, and lengths of racemes fluctuate. Individuals of this species are frequently markedly pubescent, a condition that prompted Kitanov to propose "*T. octandrum* forma *hirsutum*" from Cuba, where this tendency is pronounced. *Trichostigma octandrum* and *T. peruvianum* differ from *T. polyandrum* in having 12 or fewer stamens (vs. over 20) with filaments usually longer than 1.2 mm and (in *T. octandrum*) persistent in

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[9] *Villamillia tinctoria* Ruiz & Pavon, Fl. Peru. Chil. **4:** *pl. 402!* (= *Trichostigma peruvianum*) entered the botanical literature among a set of plates distributed sometime before 1830 and thus prior to Richard's publication in 1845 of *Trichostigma* and its generally acknowledged type species. According to the 1983 International Code of Botanical Nomenclature, Art. 42, the names of a genus and a species "*may be*" simultaneously validated, and a plate published before 1908 with analysis "*is acceptable*" for that purpose (the plate in question contains analysis as explicitly defined therein). I have not accepted *Villamillia tinctoria* as validly published, which appears to be an option implied in the wording of the article.

fruit (vs. under 1 mm and not persistent). Racemes in *T. octandrum* only rarely attain 15(−20) cm in length—those of *T. peruvianum* usually exceed 20 cm, and lengths in *T. polyandrum* are intermediate. Large leaves cordate at base distinguish *T. peruvianum* from its congeners.

Trichostigma is most similar to *Rivina,* in which earlier botanists included all three species, a placement that Burger thought perhaps to be best, although he did not formally merge the genera. A number of characters distinguish the two. Trichostigmas tend to be shrubs or robust climbers to several meters tall with ovate or lanceolate to elliptic leaf blades, as opposed to the herbaceous or suffrutescent, sometimes vinelike *Rivina,* which only rarely grows as tall as two meters and often has deltoid leaf blades. Flowers of *Trichostigma* have 8 to many stamens (vs. 4 in *Rivina*) and sessile or nearly sessile penicillate stigmas (vs. capitate on well-defined styles in *Rivina*). In contrast with Buxbaum's (1955, pp. 209, 210) mention of indument on seeds of *Trichostigma* ("*Villamilla*"), a well-known peculiarity of *Rivina,* I found no "hairy" seeds in any of the three species of *Trichostigma* (herbarium specimens at A and GH). Some seeds of *Trichostigma* do resemble those of *Rivina* in remaining covered by pericarp tissue after most of the flesh of the fruit falls away. With corroborative survey needed, secondary growth in *Trichostigma* is normal and sometimes accumulates massively, unlike the weaker anomalous secondary growth of *Rivina,* which reportedly occurs in thick stems (Metcalfe & Chalk; Walter, 1909; specimen of *T. octandrum, Abbott 1083,* GH). The sole chromosome count for *Trichostigma,* $2n = 72$ for *T. peruvianum,* is two-thirds of the $2n = 108$ reported repeatedly in *Rivina.*

The extensive distribution of *Trichostigma octandrum* is matched by its ecological breadth. In Florida this species grows in or on the margins of hammocks, on swampy ground, on disturbed sites, and in moist woods. Among the habitats throughout its range are gallery forests along tropical rivers, wet evergreen forests, tropical swamps, coastal grassy areas, coastal *Laguncularia* formations, tidal flats, limestone outcrops, and dunes. Rocky and scrubby places predominate, and ruderal sites are not infrequent.

Trichostigma is palynologically heterogeneous. Nowicke (1968) described grains of *T. octandrum* as 3-colpate and those of the other two species as having five colpi at each pole and five more at the equator. Acetolyzed grains from one collection of *T. octandrum*[10] are mostly 3-colpate, but infrequently have four equatorial colpi; they sometimes have extra, perpendicular, polar apertures, thereby approaching grains as described from the other species. Instead of a total of 15 colpi, Bortenschlager counted 12 arranged like the edges of a cube on pollen from *T. peruvianum.*

My observations fail to confirm the presence of minute, deciduous stipules in *Trichostigma* sporadically mentioned in the literature.

Uses of *Trichostigma* are few. In Colombia leaves of *T. octandrum* have been applied to wounds, and in Haiti a decoction of the leaves has been used to counter suffocation or choking. The thin, flexible stems find applications in

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[10] Harvard Palynological Collection, *slide 6300,* Panama, 1940.

basketry and as barrel hoops in the West Indies (Marie-Victorin & León, Morton, Standley). Fruits of *T. peruvianum* have been used for coloring linen, and the dense wood is suitable for handles (Ruiz & Pavon).

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3. **Rivina** Linnaeus, Sp. Pl. **1:** 121. 1753; Gen. Pl. ed. 5. 57 ("*Rivinia*"). 1754.

Often highly branched, perennial (or probably occasionally annual), sometimes scandent herbs, subshrubs, or shrubs, thickening by successive cambia especially at the base, the thin stems with single xylem cylinders. Pattern of branching frequently pseudodichotomous, often with 3 or more shoots arising from 1 node (such branching often taking the form of an inflorescence or vegetative branch, frequently abortive, centered between 2 ± equal divaricate branches). Plants glabrous or scurfy to densely pilose or hispid(ulous) on most organs. Calcium oxalate present primarily as styloid crystals. Leaves alternate or infrequently subopposite, petiolate, the blades usually elliptic or lanceolate to deltoid, generally acuminate apically, the bases usually acute to truncate; stomata rubiaceous or anomocytic. Inflorescences at ends of branches or axillary-lateral, narrow racemes with short pedicels radiating from elongate, straight, central rachises; bracts lanceolate or subulate, bracteoles 2 per pedicel, minute. Flowers perfect. Tepals nearly equal, 4, lingulate to elliptic or oblanceolate, upright to reflexed in fruit. Stamens 4, alternating with and shorter than or about as long as tepals; filaments filiform; anthers oblong-elliptic,

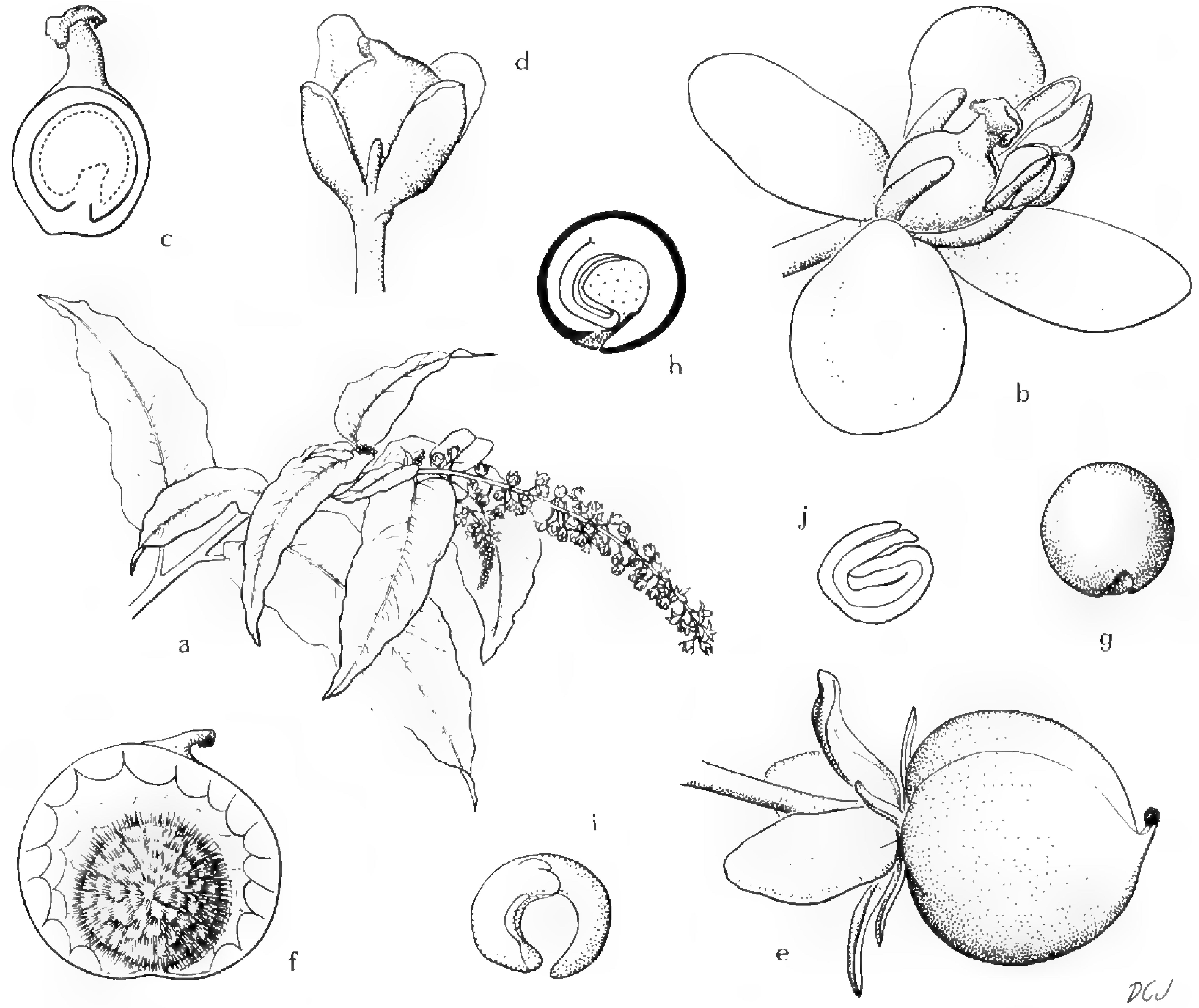

FIGURE 2. **Rivina.** a–j, *R. humilis*: a, tip of flowering shoot, × ½; b, flower, 2 anthers removed, ×12; c, gynoecium in vertical section—note basal ovule, × 6; d, very young fruit, × 6; e, mature fruit, × 6; f, mature fruit, longitudinal section, note hairy endocarp, fleshy mesocarp, and liquid-filled space between mesocarp and endocarp—note that "bumps" in mesocarp fit into "areoles" on very thin endocarp, × 6; g, seed, × 6; h, seed in vertical section, radicle of embryo at micropyle, perisperm stippled, × 6; i, embryo, oriented as in "h," × 6; j, section through center of cotyledons of embryo, oriented as in "i," × 12.

dorsifixed. Pollen grains spheroidal to prolate, the tectum spinulose. Gynoecium unicarpellate; ovary superior, unilocular, compressed, nearly circular to elliptic in outline, grooved adaxially; style filiform, inserted obliquely, (sub)terminal to distinctly eccentric, curved, shorter than to about as long as the ovary; stigma capitate, sometimes irregularly lobed. Drupe bright red or orange, nearly globose, compressed, crowned with the remnant of the style. Seed more or less lenticular, black beneath "hairy" covering derived from pericarp, minutely arillate. Embryo annular, the cotyledons convolute. Endosperm persisting as a cap around the radicle. Megagametophyte (embryo sac) fundamentally of the Polygonum type, although the antipodal cells sometimes proliferating. TYPE SPECIES: *R. humilis* L. (Name commemorating Augustus Quirinus Rivinus (Bachmann), 1652–1723, professor of botany, medicine, and chemistry at Leipzig, early user of binomial nomenclature.) — BLOODBERRY, ROUGE PLANT, BABY PEPPER.

A single polymorphic species ranging from mid-Argentina northward across South and Central America and the West Indies to Mexico and the southern United States; introduced into warm regions elsewhere, including Africa, Asia, Australia, Madagascar, the Malay Archipelago, and scattered islands in the Atlantic and Pacific. In the continental United States, *Rivina humilis* is found across most of Florida and in Louisiana, Arkansas (*fide* Smith), Oklahoma, Texas, New Mexico, and Arizona. I have seen no documentation of the occurrence of *Rivina* in Mississippi or Alabama. It is naturalized in Hawaii.

Rivinas are herbaceous or shrubby, often conspicuously woody only at the base, and sometimes sprawling. Branching tends to be divaricate; often multiple axes arise from a single node. Pubescence is absent or variable. Diverse in shape and size, the leaf blades are frequently deltoid. The small flowers bear four stamens alternating with four tepals. The single compressed carpel is topped with a well-defined, curved style inserted obliquely and generally off center, and the stigma is capitate or lobate. The most outstanding characteristic is the bright reddish, juicy fruit containing one lenticular and "hairy" endocarp.

Rivina has been collected from dunes, rocks, cliffs, waste grounds, stream beds and banks, prairies, roadsides, thickets, seashores, canyons, swampy meadows, hammocks, and "dense," "wet," and "rain" forests. It invades cultivated areas. Sites are frequently shaded but also may be open—some are rich and moist, others dry. Flowering proceeds year-round in Florida.

By excluding *Trichostigma* and by broadening species concepts, modern monographers reduced the number of species in *Rivina* as compared with nineteenth century treatments. Walter (1909) recognized *R. humilis, R. portulaccoides* Nutt.,[11] and *R. purpurascens* Schrader, separated in his key by the relative lengths and degrees of erectness of the inflorescences and by the colors and lengths of the tepals. Nowicke (1968), H. Harms (note in Heimerl, 1934), Standley, and others perceived only one species, for which Raeder listed 37 synonyms. Agreement is general that Walter's (1909) division of his already narrowly defined *R. humilis* into three plus the typical varieties based chiefly on pubescence is excessive splitting (discussion in Raeder).

Repeated counts have yielded $2n = 108$ as the chromosome number for *Rivina humilis*. Joshi's illustration reveals the chromosomes to be short and of fairly uniform length at diakinesis.

Pollen grains from one collection[12] of *Rivina humilis* show that discrepancies in the literature relating to numbers of colpi result from insufficient sampling. Most grains in this collection have five equatorial colpi plus five perpendicular colpi encircling each pole. Also common are grains with 12 colpi arranged similarly, but in fours. Scanning electron micrographs in Bortenschlager show microspines on the tectum and perforations in the endexine.

Nuclei in cells from *Rivina humilis* contain rod-shaped or short-prismatic

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[11] Although in Nuttall's protologue "*R. portulaccoides*" does not sound in some respects like a species of *Rivina*, a specimen so named and labeled "Verdigris" from Nuttall's herbarium at BM is clearly *R. humilis*.

[12] Harvard Palynological Collection, *slides 344*, Texas, 1936.

protein bodies in clusters of up to 10 near nucleoli. As described by Carniel, these may be solid, hollow, or septate and are composed of granular subunits.

Kajale (1954a) determined that cells of the inside ovarian hypodermis elongate radially and differentiate into hairs between the outer tissues of the ovary and the inside epidermis, with the latter adhering to the seed coat. Hence the seed remains covered with a thin shaggy coat after the bulk of the pericarp falls away. (Netolitzky interpreted the "hairy" covering as belonging to the outer integument.)

Because of its attractive divaricate pattern of branching and bright red fruits, *Rivina humilis* is sometimes cultivated as an ornamental, a use dating as far back in Europe as the late seventeenth century. From the very little information that is available, the fruits and other parts are considered toxic (Burlage, Perkins & Payne, Lampe & Fagerström). *Rivina* taints milk of cows that eat it (White). Medicinal uses are listed in Ayensu and in Morton. Red juice from the fruits is said to have been used for dyeing, as rouge and ink, and for coloring cut flowers.

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4. **Petiveria** Linnaeus, Sp. Pl. **1:** 342. 1753; Gen. Pl. ed. 5. 160. 1754.

Herbs, subshrubs, or shrubs, sometimes sprawling, thickening by successive cambia (in root only?). Multiple shoots rising from 1 sometimes rhizomelike root. Branching sparse, multiple axes occasionally branching from 1 node. Plants with garliclike odor. Axes of inflorescences, young stems, petioles, and major foliar veins usually puberulent or tomentose to pilose or villous, additional organs also sometimes pubescent (abaxial surfaces of leaf blades often densely so). Calcium oxalate present primarily as styloid crystals. Leaves petiolate, the blades mostly elliptic to oblanceolate, infrequently rounded to usually acuminate at both ends, often apiculate at the apices; stomata usually with irregular subsidiary cells parallel to the guard cells. Axillary buds flanked by 2 stipulelike (probably foliar) bristles. Inflorescences axillary or terminal, composed of 1 or more long, thin, wandlike, uncrowded spicate axes tending to nod with the apogee of the bend near the youngest open flower, more erect in fruit; when branched, with a small number of lateral axes inserted toward the base of the similar main axis; bracts small, ovate-lanceolate to deltoid, the 2 bracteoles minute. Flowers nearly sessile, zygomorphic, ascending. Tepals 4, glabrous or pubescent abaxially at the bases, elliptic-oblong to narrowly lanceolate or narrowly deltoid, slightly connate basally and slightly adnate to bases of filaments, white or tinged with yellow, green, or pink, becoming green and erect in fruit. Stamens 4–6(–8), unequal, shorter than to about as long as tepals; anthers cleft at both ends. Pollen grains spheroidal or nearly so, 12- (or 15-)colpate [or 12-porate], or reportedly sometimes acolpate, the tectum spinulose and without punctate perforations (*fide* Bortenschlager). Gynoecium unicarpellate; ovary densely pubescent, bearing a set of hooks at the apex (these

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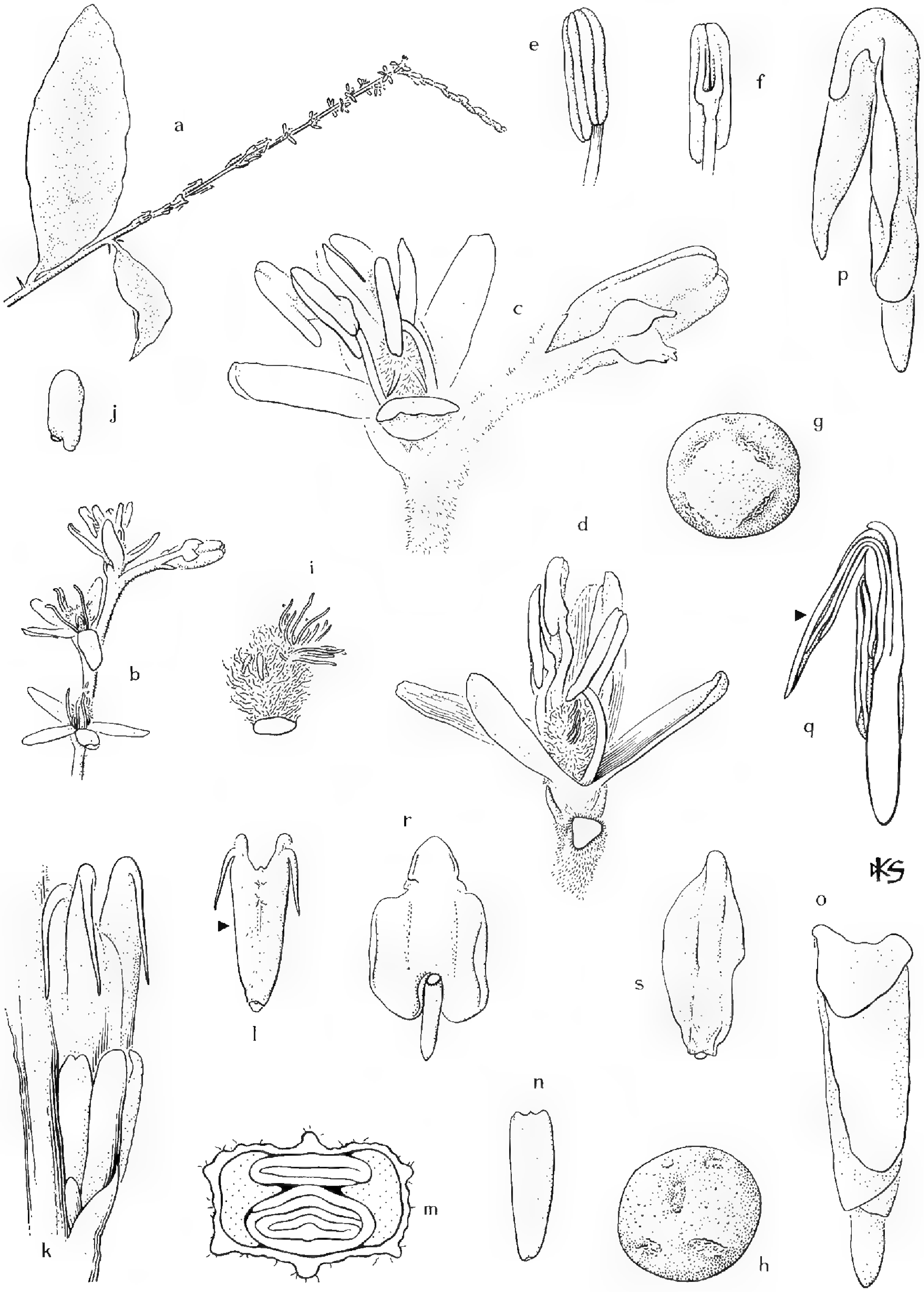
FIGURE 3. **Petiveria.** a–s, *P. alliacea*: a, tip of stem with inflorescence—note bend in rachis at point where flower at anthesis, × ½; b, tip of inflorescence, showing anther-bearing flower at bend, 2 flowers after anthers have fallen (below), and flower buds (above), × 3; c, detail of tip of inflorescence in "b"—note 2 hooks on ovary, × 10; d, adaxial view of flower—note stigma on ovary (unshaded triangular area indicates scar where younger portion of inflorescence removed), × 10; e, f, adaxial and abaxial views of anthers, × 12; g, h, polar and equatorial views (respectively) of pollen grains, pollen 12-colpate with 4 colpi around each pole and 4 perpendicular to the polar colpi around the equator, × 1000; i, side view of gynoecium, style absent, stigma penicillate—



note 2 hooks to left, × 12; j, ovule, attachment point indicated by open circle at bottom left, × 12; k, nearly mature fruit (an achene), with hooks above and persistent tepals below, × 5; l, adaxial side of mature fruit, × 3; m, cross section of fruit at level marked by arrows in "l" and "q," perisperm even-stippled, × 12; n, seed, removed from achene, × 3; o, abaxial surface of embryo, × 6; p, side view of embryo, × 6; q, vertical section of embryo, × 6; r, embryo with longer (inner) cotyledon removed and shorter (outer) one unfolded, × 3; s, unfolded longer cotyledon of embryo in "r."

enlarging considerably in fruit); style absent; stigma penicillate, facing the rachis; ovule straight, the micropyle alongside the funiculus. Fruit dry, indehiscent, cuneiform, longitudinally ribbed, pubescent, armed apically with 4 (or 5) [-13] sharp, stout barbs inserted on 2 lobes and bent back along the surface of the fruit for ca. 1/4–1/2 its length, sometimes with an extra, straight barb rising vertically between the lobes. Seed shaped like the fruit, the testa thin. Embryo with the cotyledons unequal, one wrapped around the other: the outer markedly auriculate basally, wider and shorter than the inner, this rolled into a tube; embryo bent double at about the middle of the inner cotyledon and near the apex of the outer one. TYPE SPECIES: *P. alliacea* L. (Named for James Petiver, ca. 1660–1718, British naturalist and apothecary, Fellow of the Royal Society, noted collector and prolific author.) — GUINEA-HEN WEED, GARLIC WEED.

One variable species distributed across most of Florida and occurring from southern Texas southward through Mexico, Central America, the West Indies, and South America to approximately Buenos Aires, Argentina. *Petiveria alliacea* has escaped from cultivation to a limited extent in warm parts of the Old World.

Long, slender, uncrowded, unbranched or sparsely branched, spicate inflorescences allow recognition of *Petiveria* from a distance. Fresh plants have a skunky or garlicky odor when injured. The small, four-tepaled flowers have a variable number of unequal stamens and a distinctive, densely pubescent ovary bearing hooks at the apex but no style. The brushlike stigma is more or less lateral. The unmistakable long, narrow, tapered, dry fruit is topped by four or more stout hooks. The odd bent embryo has two unequal cotyledons, one wrapped longitudinally around the other.

Investigating different sets of characters, Baillon and Walter (1906) each uncovered evidence suggestive of affinity between *Petiveria* and *Monococcus*. Baillon encountered similarities in vegetative organs, inflorescences, floral organization, and general construction of the embryos. Walter observed that the completely straight (*gerade*) ovules of the two distinguish them together from other Rivineae, in which the funiculus is inserted at the middle of the transversely overlaid nucellus (see Mauritzon for embryological details of *Petiveria*). Walter also mentioned that both genera have tepals overlapping so that one is outside at both edges, one is inside at both edges, and two have one edge inside and the other outside (a trait that reappears in Seguierieae). Further, in 1909, he mentioned similarity in their "*Stipularorgane*," their seed coats, and the general forms of their embryos.

Petiveria differs from *Monococcus* in having perfect (vs. imperfect or polygamous) flowers rotated 45 degrees relative to those of *Monococcus*, spines terminal on (vs. covering) the fruits, fewer stamens, longer fruits, more dissimilar cotyledons, less nutritive tissue in the seed (see especially Baillon), and possibly anomalous secondary growth. (*Monococcus* probably lacks anomalous secondary growth; this is restricted to the root in *Petiveria* according to Holm, 1915; see also Metcalfe & Chalk, and Walter, 1909.)

Among the diverse habitats occupied by *Petiveria* are wet, tropical, evergreen forests, thickets, fields, and even savannas. Soils may be rich or not. Disturbed sites, such as banks of streams, are common. Habitats reported in Florida, where *P. alliacea* flowers year-round, include cultivated land, waste places, hammocks, moist woods, and the top of a limestone cliff. This species at times becomes a weedy pest.

Distribution by animals is clearly effected by the hooks on the fruits. Ormond & Pinheiro (1974) induced autogamy in Brazilian specimens.

In 1909 Walter recognized *Petiveria tetrandra* Gomes as a distinct species, in his key distinguished from *P. alliacea* by six (vs. four) hooks on the fruits, glabrous inflorescence axes (a very unreliable character), and shorter tepals. *Petiveria tetrandra* is centered in or restricted to southern Brazil, northern Argentina, and Paraguay. Hauman-Merck and Nowicke (1968) reduced it to a variety of *P. alliacea*; after studying it at the heart of its range, Santos & Flaster and Hatschbach & Guimarães denied it any taxonomic status. As the result of a multifaceted investigation focused on the problem of the status of *P. tetrandra* and utilizing populations in Brazil, Ormond & Pinheiro (1974, 1975) tentatively advocated maintaining *P. alliacea* var. *tetrandra* (Gomes) Hauman-Merck. The subgroup they cautiously thought to correspond to var. *alliacea* differed from the one they believed probably to represent var. *tetrandra* in having a somatic chromosome number of 72 (vs. 36), four hooks per fruit (vs. 5 or more[13]), and several organs larger, as well as in other ways. The two entities remained phenotypically distinct under uniform cultivation. Crosses in both directions yielded some fruits, a result requiring careful interpretation in view of the alleged difference in chromosome number. Nowicke (1968) raised the possibility of apomixis by suspecting partial sterility in var. *tetrandra* as indicated by apparently acolpate pollen "notwithstanding the setting of fruit" (p. 344). Complicating the palynological picture, Bortenschlager observed porate grains in "*P. tetrandra*" and grains with elongate apertures in "*P. alliacea.*"

The alliaceous odor that gave *Petiveria alliacea* its name, and the enthusiasm for this species in folk medicine, underscore the desirability of chemical studies. Pietschmann obtained evidence of mustard oils in roots and stems, and various other authors have ascribed them to the genus. However, Ettlinger & Kjaer dismissed Pietschmann's evidence as "meaningless"; their own tests on the garlicky seeds were negative for myrosinase and glucosinolates. The odor most likely comes from sulfur-containing compounds other than mustard oils: Von Szczepanski and colleagues established an antimicrobial oil from roots and stems of *P. alliacea* as benzyl-2-hydroxyethyl-trisulfide; Adesogan characterized another sulfur-containing compound from the roots as *cis*-3,5-diphenyl-1,2,4-trithiolan ("trithiolaniacin"). Segelman & Segelman isolated isoarborinol, related compounds, and potassium nitrate from leaves. (For the chemistry of *Petiveria* see also Dias da Silva, Hegnauer, Loustalot & Pagán, Rocha, and Rocha & Da Silva.)

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[13] Specimens displaying the sharpest distinguishing trait of *P. alliacea* var. *tetrandra,* more than four hooks per fruit, occur beyond the boundaries given above. For example, fruits on *Bartlett 10787* (GH) from Mexico have 4, 5, or 6 hooks.

In view of the odor, antimicrobial properties, reputed narcotic effects (Dias da Silva), noxiousness, and toxicity (see symptoms of poisoning in Peckolt & Peckolt) of *Petiveria alliacea,* it is unsurprising that plants of this species are valued and sometimes marketed as a folk remedy. Its attributed benefits are available in numerous references, among them Ayensu, Dias da Silva, Morton, Peckolt & Peckolt, Sorarú & Bandoni, Standley, and Wong. This species is reputed to degrade the milk and meat of cattle, in which it also induces abortion. (The last-mentioned effect applied to humans is one of the most frequently mentioned medicinal uses.) Griffith recounted that a nauseating infusion of roots of *P.* "*foetida*" in rum was employed in the West Indies to instill disgust for liquor. Somewhat insecticidal, *Petiveria* has been used to free woolen goods and chickens of vermin. Harms (note in Heimerl, 1934) and the label of the Brazilian collection *Krukoff's 6th Expedition . . . 7638* (A) mentioned *Petiveria* as an ingredient in curare poison. As related by Peckolt & Peckolt, *P. alliacea* has been used to poison fish. The hooks on the fruits can puncture human skin.

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Subfamily AGDESTIDOIDEAE Nowicke

5. **Agdestis** Moçiño & Sessé ex A. P. de Candolle, Syst. Nat. **1:** 511, 543. 1817 ("1818").

Slightly woody, twining, pungent-smelling vines, sometimes with large napiform taproots. Sieve-tube plastids with globular crystalloids. Plants puberulent on axes of inflorescences, abaxially on leaf blades, and sometimes lightly on young stems. Calcium oxalate present primarily as raphide bundles. Leaves petiolate, the blades suborbicular to usually cordate, rounded to acute and often mucronate apically, often about as wide as long; slender petioles about as long as leaf blades; stomata anomocytic. Inflorescences mostly axillary, sometimes terminal, lax, composed of main axes bearing simple or compound lateral dichasia, or bearing single flowers in axils of bracts (some axes exclusively with such single flowers), or bearing branches resembling the main axes; bracts and bracteoles inconspicuous, subulate to lanceolate. Flowers perfect, pedicellate, strongly scented. Tepals 4 (5 or rarely more), white, elliptic or oblong to oblanceolate, separate or slightly coalescent basally. Stamens 15–30; filaments slender, unequal, shorter than to slightly longer than tepals, threadlike, inserted irregularly; anthers cleft at both ends. Pollen grains subspheroidal to subprolate, tricolpate, the tectum spinulose and punctate-perforate. Gynoecium syncarpous; ovary semi-inferior, (3- or) 4-locular; stigmatic lobes (3 or) 4, thick, papillose adaxially, recurved, shorter than to slightly longer than the single conical, stocky style. Fruit small, dry, indehiscent, obconical, ribbed, surrounded by the enlarged, greenish, spreading, winglike, prominently veined tepals, unilocular and 1-seeded by abortion. Seed with thin testa adherent to pericarp. Embryo annular, the cotyledons linear, slightly wider than radicle. TYPE SPECIES: *A. clematidea* Moçiño & Sessé ex A. P. de Candolle. (Named for a disagreeable hermaphroditic monster because of the anomalous original position of the plant in the dioecious Menispermaceae.[14])

A single species distributed from Texas southward through Mexico to Guatemala, reported from Honduras and Nicaragua, and escaped from cultivation in warm places elsewhere. *Agdestis clematidea* is cultivated at least as far north as Jacksonville, Florida, and occurs outside of cultivation in disturbed sites and hammocks in the southern half of Florida.

Several distinctive attributes allow ready recognition of *Agdestis* and isolate it from other Phytolaccaceae. It is a slender vine capable of forming dense tangles and climbing over shrubs and high into trees. (Taylor estimated growth to be as fast as 40 or 50 feet per year.) The turnip-shaped taproot protrudes above the surface of the ground and, according to Taylor, may weigh as much as 150 pounds (Heimerl, 1934, says six pounds). The cordate leaf blades are highly distinctive. Observers describe odors from the foliage and root as garlicky, skunklike, reminiscent of cabbage, or fetid. Descriptions of the floral scent include "very sweet-scented" (Taylor) and "more fetid than those of the carrion-flower or skunk-cabbage" (Britton). Mexia (*8947*, GH) recorded the stench to have caused headaches. The white flowers in simple or compound dichasia (vs. mostly racemose inflorescences in other Phytolaccaceae) each have four tepals, generally four stigmatic lobes on one compound style (most Phytolaccaceae have one style per carpel), and usually four locules in the ovary, with three aborting. The partly inferior ovary is unique in the family. The single seed adheres to the pericarp of the small indehiscent fruit encircled by spreading tepals.

Bortenschlager found *Agdestis* to agree palynologically with other Phytolaccaceae. While not favoring affinity with Phytolaccaceae in particular, the presence of betalains and P-type sieve-tube plastids confirms *Agdestis* as a member of the Centrospermae (Behnke *et al.*, 1974).

The morphological peculiarity of *Agdestis* is reflected in the taxonomic positions assigned it by different authorities. Most regard *Agdestis* as an isolated member of the Phytolaccaceae. Walter (1909) listed it among *genera anomala*; Heimerl (1934) treated it as the sole genus of tribe Agdestideae Heimerl; and Nowicke (1968) established for it the monogeneric subfamily Agdestidoideae

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[14] According to one version of the Phrygian myth, Cybele—embodied as the Agdus Rock—gave birth unwillingly to Agdestis despite her having thwarted rape by Jupiter. Blood that spilled when the gods tricked the arrogant Agdestis into drunkenness and bound him/her to a tree spawned a second tree, this yielding fruits responsible for the conception of Attis in the princess Nana.

Nowicke. Hutchinson recognized it as the single member of the Agdestidaceae Nakai.

Agdestis resembles other Phytolaccaceae in its weediness, preferring naturally and artificially disturbed sites. It grows in such diverse habitats as tropical forests, dry thickets, rocky places, and clearings.

Ridley (p. 111) observed that a number of taxonomically disparate woody climbers of "rather open jungles in the tropics" produce usually small, one-seeded fruits surrounded by spreading winglike sepals that cause the fruit to rotate rapidly while falling. Among his examples is *Agdestis.* That the falling fruits indeed whirl like the blades of a helicopter is readily demonstrated with fruits from herbarium specimens.

Observations on the nature of secondary growth are contradictory, with the balance tipped toward the presence of successive cambia (*cf.* Cobau; Heimerl, 1934; Metcalfe & Chalk; Walter, 1909).

Agdestis has limited application as an ornamental in circumstances where its odor is not objectionable. It forms a thick cover sometimes used to decorate buildings and hide eyesores.

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JOURNAL OF THE ARNOLD ARBORETUM INDEX TO AUTHORS AND TITLES, VOLUMES 51–65 (1970–1984)

ELIZABETH B. SCHMIDT

IN 1973 the *Journal of the Arnold Arboretum* published an "Index to Authors and Titles, Volumes 1 through 50, 1919–1969," which included a brief history of the *Journal*. Since then 15 years have passed, during which 15 volumes, 326 papers, and 8638 pages have been published. This index is a supplement to the first one; it covers the material published in volumes 61–65 and brings the history up to date.

During this period there have been many changes, some readily visible to readers and some less so. Bernice Schubert, whose capable, tactful, and meticulous direction of the *Journal* began in 1963, stepped down as Editor in 1979, to be succeeded by Stephen Spongberg. An Editorial Committee, originally comprising Bernice Schubert (Chairman), Stephen Spongberg, Peter Stevens, and Carroll Wood, was established in 1975 to redistribute some of the editorial burden. Although committee members have provided reviews and advice and have helped to determine policy, a single botanist must supervise to maintain consistency of policy and quality. Today's committee consists of Stephen Spongberg, Elizabeth Schmidt, Peter Ashton, Kamaljit Bawa (outside member), Peter Stevens, and Carroll Wood.

The amount of assistance available to the editor has increased greatly during this period. In 1970 the only help was a circulation manager; this position was upgraded to editorial assistant, assistant editor, and finally managing editor. These posts have been held by Dulcie Powell (1967–1971), Ellen Bernstein (1971–1973), Kathleen Claggett (1973–1976), and Elizabeth Schmidt (1976–present).

After many years with the Harvard University Printing Office, we changed to Edwards Brothers (Ann Arbor, Michigan) for Volume 61. With this move we hoped to achieve better results at a considerably lower price, we changed from hot to cold type, and we gained sharper reproduction of photographs. Not completely satisfied, however, we changed to Allen Press (Lawrence, Kansas) for Volume 63 and have been extremely pleased with the results. Circulation management has recently been given to Allen Press, as well.

The appearance of the *Journal* has changed considerably over the past 15 years. Basically the same for the first 50 volumes, the cover was redesigned in 1970. From 1972 through 1982, the cover was changed annually, a process that became increasingly expensive and time consuming. In 1981 we had what was to become the *Journal* logo embossed on off-white stock, and we have

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retained this cover ever since. Color plates were included for the first time in 1984—an event perhaps even more exciting for us than for the author!

Other, less visible changes have also taken place. Although still primarily a staff organ, the *Journal* has been accepting an increasing number of papers from outside authors. Consequently, instructions for authors were drawn up—informally (photocopied and sent to authors on request) in 1977, and formally (printed in the back of the *Journal*) in 1983. The review process has also been formalized and tightened, with outside reviewers playing a more and more active role.

The length of papers submitted has been increasing over time. Consequently, fewer papers are published, but several of them have been extremely long. The publication of Peter Stevens's 573-page "A Revision of the Old World Species of *Calophyllum* (Guttiferae)" in 1980 marked the culmination of this trend: three galley readers were never heard from again, and the next six issues appeared off schedule!

To offset skyrocketing costs, we have instituted various measures over the past 15 years. Regretfully, we have had to raise the subscription rate several times: from $10.00 to $16.00 in 1972; to $25.00 in 1978; to $30.00 in 1983; and finally to $50.00 in 1984. Additionally, we added a foreign postage charge of $5.00 and halved agents' discounts. We initiated page charges for manuscripts received after 1 March 1980; however, we have been careful to ensure that inability to pay such charges in no way influences our handling of a manuscript. We are unfortunately no longer able to provide outside authors with free offprints.

In years to come, we hope to continue to offer solid scientific work contained in a carefully produced journal. Despite time, money, and staffing constraints, we strive to provide personalized service to both authors and subscribers. Any comments and suggestions will be gratefully received.

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PERSPECTIVES ON THE ORIGIN OF THE FLORISTIC SIMILARITY BETWEEN EASTERN ASIA AND EASTERN NORTH AMERICA[1]

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The floristic similarity between eastern Asia and eastern North America has been recognized since the time of Linnaeus (see Graham, 1972a; Boufford & Spongberg, 1983) and was emphasized through the work of Asa Gray (1840, 1859). Scientific study of this pattern has continued, and its importance in current botanical thought is shown by the several symposia recently convened on the topic, most notably those at the XI International Botanical Congress in Seattle and the Japanese-American meeting in Corvallis in 1969 (Graham, 1972b), at the Missouri Botanical Garden in 1982, and at the Japanese-American conference held at the Cary Arboretum of the New York Botanical Garden in 1983.

In general, presentations at these conferences have followed one of three approaches: enumeration of taxa exhibiting this pattern; discussion of some aspect of the biology (e.g., anatomy, ecology, cytology, chemistry) of a taxon or taxa exhibiting this pattern; or examination of the paleontological aspects of this question, involving postulated routes of movement or changes over time in one geographic area. However, two major questions have never been directly addressed and have only rarely been alluded to in these symposia: first, is the pattern of similarity between eastern Asia and eastern North America real, and second, if it is, what are all the possible ways by which the pattern might have arisen?

A proper solution to the first question requires a rigorous examination of the patterns of similarity between eastern Asia and eastern North America in light of the larger biogeography of the Northern Hemisphere. In particular, "three-area" tests of the variety suggested by cladistic biogeographers need to be made and analyzed to determine whether the eastern Asian–eastern North American similarity is a unique pattern or simply a distinctive subset of a larger pattern. From a paleontological perspective, I suspect that the latter is both the more correct assumption and the better working hypothesis. I believe that this conclusion is also inherent in reviews of modern angiosperm biogeography (e.g., Thorne, 1972). However, it is the second of the two questions that I wish to explore in depth here, as it places the following paper (Tiffney,

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[1] This is the first of two related papers. The second, entitled "The Eocene North Atlantic Land Bridge: Its Importance in Tertiary and Modern Phytogeography of the Northern Hemisphere," will be published in the April, 1985, issue of the *Journal of the Arnold Arboretum.*

Journal of the Arnold Arboretum **66:** 73–94. January, 1985.

1985) on the importance of early Tertiary North Atlantic land bridges in the historical context of all possible origins of the eastern Asian–eastern North American floristic similarity. For this purpose I will assume that the pattern is "real"; I do not think that this assumption biases the inquiry into its origins.

The purpose of this paper is to call attention to the diverse historical components of this biogeographic pattern and to emphasize that it did not arise as a result of a single historical event. Scientists working with this problem recognize that it is complex but have not presented a logical explanation of its components. A clear exposition of the range of biogeographic factors involved in the origin of the eastern North American—eastern Asian floristic similarity would make it possible to evaluate the individual histories of plant taxa that contribute to the pattern. This information should in turn enhance our knowledge of other aspects of the biology of the plants under investigation. As a general survey, this paper may prove wrong in its particulars but will provide a starting point for an examination of the variables involved.

PATTERNS AND PROCESSES

The origin of the floristic similarity of eastern Asia and eastern North America involves an interplay of three factors: changing geography, changing climate, and evolving (both phylogenetically and ecologically) biota. The last factor is not completely independent of the former two, as physical events are important in both allopatric speciation and natural selection.

Before the interaction of these three factors and the range of possible ways by which the eastern Asian–eastern North American similarity arose can be discussed, three other biogeographic questions must be considered: the concept of a "center of origin" of the flora that now displays this distribution pattern, the nature of past plant movements in general (specifically, the distinction between the dispersal of "floras" and "individuals"), and the biogeographic history of herbaceous angiosperms. These topics have had a strong influence, whether perceived or not, on thought concerning the origin of the eastern Asian–eastern North American floristic pattern.

ELEMENTS OF PALEOPHYTOGEOGRAPHY

Centers of Origin and Associated Problems

The similarity of the extant floras of eastern Asia and eastern North America arose through movements of taxa in the geologic past. Gray (1878), considering the geographic arrangement of the Northern Hemisphere, proposed that the pattern developed due to a glacially induced southward movement of an earlier thermophilic flora with a polar distribution. This perspective was developed by Chaney (1947) and refined by Axelrod (e.g., 1966) as the "geofloral hypothesis." Subsequent workers have found no evidence of a Late Cretaceous/early Tertiary circum-Arctic flora similar to that of the temperate regions of eastern North America and eastern Asia today (see Hickey *et al.*, 1983; Hickey, pers. comm.).

Wolfe (1975, 1977) argued from paleobotanical evidence that the origin of the similarity of the floras of eastern Asia and eastern North America involved the evolution of a large number of modern taxa in the latest Cretaceous and early Tertiary. These first appeared in the mid-latitudes of the Northern Hemisphere and spread by existing land bridges, ultimately forming a relatively homogeneous early Tertiary flora. Both paleoclimatological data (Kennett, 1977; Buchardt, 1978; Collinson *et al.*, 1981) and the taxonomic composition of this early Tertiary flora demonstrate that early Tertiary climates were at least paratropical in the mid-latitudes of the Northern Hemisphere. For this reason, and to distinguish this assemblage from coeval floras in the Southern Hemisphere (Wolfe, pers. comm.), Wolfe (1975) referred to these newly evolved plants as forming a "boreotropical flora."

Wolfe (1975, 1977) did not cite a specific "center of origin" for the boreotropical flora, but certain aspects of its composition and distribution have been taken to suggest such a center. The greatest diversity of modern taxa derived from this early Tertiary flora is now found in eastern Asia. Similarly, the affinities of many fossil representatives of the boreotropical flora found in Europe and North America lie with extant taxa found in Japan, China, northern India, Indomalaysia, and some western Pacific islands. These include plants of temperate, subtropical, and tropical environments. Further, the modern eastern Asian flora includes a host of taxa that are presumed to be phylogenetically primitive, with many occurring as monotypic families or genera (Wang, 1961).

These factors all lead to the common perception that southeastern Asia was the evolutionary source area both of the angiosperms as a whole and of the modern flora of the Northern Hemisphere (e.g., Takhtajan, 1969; Smith, 1970). The interpretation of southeastern Asia as the place of origin of the angiosperms has been rejected in recent years (e.g., Raven & Axelrod, 1974), and its role as the sole source for the boreotropical flora similarly disintegrates under scrutiny. In both cases the alternative interpretation that southeastern Asia was a great refugium or "museum" appears to be correct. Perhaps more importantly, the dismissal of this "center of origin" should not imply the necessity of locating a new one. I agree with Wolfe (1975) that the boreotropical flora probably had a diffuse origin involving several areas of the Northern Hemisphere. Evaluation of the status of southeastern Asia, and of the latter suggestion, requires an examination of what distinguishes southeastern Asia from other areas of the Northern Hemisphere in the past and the present, as well as of what evidence exists for other places of origin of the boreotropical flora. The latter further requires the distinction between a localized center of origin and a diffuse origin of this flora.

Little paleobotanical evidence is available for southeastern Asia in the early Tertiary. Guo (1980) and Hsü (1983) have reviewed evidence of the Late Cretaceous and Tertiary flora and vegetation of China. Although Hsü includes some palynological data, generally at the family level, both reviews are largely dependent on evidence from fossil leaves. Hickey (1973) and Wolfe (see Hickey & Wolfe, 1975) have indicated that many existing identifications of fossil leaves are erroneous and in need of revision. Thus, the composition of these Chinese floras is unclear. Muller's (1968) report on early Tertiary palynology of Borneo indicates that several typical elements of the modern flora did not arrive at the sample site until after the Eocene. This suggests that the extant flora of this area developed through the Tertiary and is not the product of a single, local, early Tertiary origin. Vertebrate evidence (Li & Ting, in press; see also McKenna, 1983b) indicates that the Chinese Paleocene fauna was distinct from that of the rest of the Northern Hemisphere; the same may have been true of its early Tertiary flora. Circumstantial evidence further suggests that southeastern Asia is well suited to preserve taxa of tropical to warm-temperate affinity. During the early to middle Tertiary, it was linked with central Asia and Europe by the Tethys Seaway (see Tiffney, 1985, *map 6*), and to western North America via the Bering land bridge. Southeastern Asia is topographically diverse and was presumably equally so in the later Tertiary, encompassing a wide range of habitats and climates. Further, it was and is protected from invasion of Arctic air masses by east-west oriented mountains that had sufficient gaps to permit the southward movement of plants from the north. In short, southeastern Asia could be expected to serve as a refugium for thermophilic plants in an ice age.

With respect to the second question, the other possible areas of origin of the boreotropical flora involve the Late Cretaceous-early Tertiary low latitudes, high latitudes, and mid-latitudes of the Northern Hemisphere. No real data are available on plant evolution in the tropics at this time; this is one of the challenges to angiosperm paleobotany. Recent evidence (Hickey, 1981a; Hickey *et al.*, 1983; Hickey, pers. comm.) from high latitudes indicates the presence of a species-poor, deciduous flora. Although several components of this flora (e.g., *Betula* L., *Cercidiphyllum* Sieb. & Zucc., *Metasequoia* Miki, Juglandaceae) are members of the boreotropical flora, the latter unit did not evolve here.

For the mid-latitudes the evidence is less direct, but suggestive. In the Late Cretaceous, palynological data indicate that the Northern Hemisphere was broadly divided into two primary floristic provinces: the *Aquillapollenites* Rouse province of western North America and eastern Asia, and the Normapolles province of eastern North America and Europe (Muller, 1970; Srivastava, 1981), which reflect the geography of the time—eastern Asia and western North America were linked by the Bering land bridge, and eastern North America and Europe were linked by a North Atlantic land bridge. Separated by the Turgai Straits and other seaways through central Asia and eastern Europe (Vinogradov, 1967–1968; see Tiffney, 1985), and by the Midcontinental Seaway through central North America, these provinces disintegrated at the end of the Cretaceous (Muller, 1970), shortly before the rise of the boreotropical flora. With their different floristic compositions, they each probably contributed distinctive elements to the succeeding boreotropical flora.

The paleogeography of the early Tertiary also suggests other possible mid-latitude sources of the boreotropical flora. In particular, the island chains of the European and Middle Eastern portions of the Tethys Seaway seem likely to have been excellent sources for the evolution of new taxa through allopatric speciation. The great longitudinal span of the Tethys, from eastern Asia to Europe and west at least as far as Caribbean North America, may have provided a natural route for taxa that evolved in a limited area of the seaway. Certainly both classic boreotropical floras (e.g., the London Clay Flora of England (Reid & Chandler, 1933; Chandler, 1964), the Geiseltal Flora of Germany (Mai, 1976), the Haselbach Flora of Germany (Mai & Walther, 1978), the Burgas Flora of Bulgaria (Palamarev, 1973), the Clarno Flora of Oregon (Scott, 1954; Chandler, 1964; Manchester, 1981a, 1983)) and modern refugia rich in boreotropical elements (Central America, southeastern North America, the Caucasus, the Himalayas, southeastern Asia) lie along the ancestral path of the Tethys. Other mid-latitude areas of the early Tertiary may also have provided the geographic diversity necessary for allopatric speciation. In North America the early Tertiary rise of the Rocky Mountains resulted in an increasingly diverse landscape and was associated with many floristic changes (Leopold & MacGinitie, 1972), which probably involved the evolution of new taxa *in situ* rather than their movement in from other areas.

In summary, no paleontological evidence exists to support the concept of eastern Asia as the sole center of origin of the modern flora of the Northern Hemisphere. A limited number of boreotropical taxa have been recognized in the early Tertiary of the Arctic; geographic considerations suggest that other areas in the mid-latitudes of the early Tertiary could well have served as diffuse centers of origin and speciation. Resolution of the sources of the boreotropical flora will require careful analysis of the geographic history of its specific component lineages (e.g., Manchester's (1981b) survey of the Juglandaceae).

THE BALANCE OF FLORAS AND INDIVIDUALS IN "MIGRATION"

Discussion of the origin of the modern flora of the Northern Hemisphere invariably entails consideration of the "migration" of ancestral communities or floras. This idea can be traced to Darwin (1859) and Gray (1878). However, the first modern concepts of the community can be ascribed to the ecological work of Clements (1916, 1928), who considered the community to be the basic structural unit of the earth's vegetation. He regarded individual communities as tightly interdependent groupings of plants united through adaptation to a particular climate and environment and having almost organismlike emergent properties. Clements argued his case cogently, and his ideas had a strong influence on American botany for many years. One of those influenced was R. W. Chaney, who saw in this approach an ecological explanation to patterns observed in the fossil record. From this arose the geofloral concept—the hypothesis that past phytogeographic changes involved the movement of monolithic "climax" communities of set taxonomic composition across the face of the earth in response to climatic stimuli (Chaney, 1947). In particular, he believed that the present similarity of the floras of eastern Asia and eastern North America resulted from the early Tertiary southward movement from a polar source of a temperate "Arcto-Tertiary Geoflora" of modern floristic and vegetational composition. Viewed in the context of contemporary science, this was an up-to-date, biological explanation of the observed facts.

However, the Clementsian concept of the community as a monolithic unit was not without its detractors. In particular, H. A. Gleason (1926) countered the community concept of plant ecology with what he termed the "individualistic concept." Gleason contended that plant species acted independently, that range expansions and contractions occurred on the level of individual organisms, and that the "communities" of Clements were nothing more than chance aggregations of species sharing some common physiological requirements and tolerances. In some senses the individualistic approach is the dominant perspective in modern community ecology, as reflected both in Whittaker's concept of gradients (1967) and in the general sense that Clementsian "climax" communities do not exist.

The paradox of the Clementsian-Gleasonian debate is that both sides are right. Communities do not move in lockstep, but neither are plant groupings totally completely random associations of species. Davis (1976, 1981) has demonstrated that several taxa that are found together in portions of the modern temperate deciduous forest of eastern North America moved into these communities after the Pleistocene from different refugial sources and following different routes of dispersal. However, although plants disperse as individuals, different taxa may be constrained by similar environmental factors such as moisture, temperature, soils, or dispersal agents in such a way that "communities" of mutual tolerance are maintained as loose but recognizable units. With the loss of resolution dictated by the nature of the fossil record, it is not surprising that paleontologists perceive a pattern involving "floras" rather than individuals. The danger lies in accepting this perception at face value without seeking the dynamic biological factors that underlie it.

The critical response to the geofloral hypothesis has not necessarily followed the community-individual debate, but elements of that discussion are present. Wolfe (1969, 1975, 1977) surveyed the fossil record and found no evidence of a polar Arcto-Tertiary Geoflora, or of phytogeographic evolution of the Northern Hemisphere involving the mass movement of unit floras. However, he has demonstrated the early Tertiary appearance of a floristic unit that he termed the "boreotropical flora." Although Wolfe never envisioned this flora as uniform in its composition, its name conveys the impression that it was fairly homogeneous. This raises conceptual problems, as it might appear that the sole difference between the Arcto-Tertiary Geoflora and the boreotropical flora is that the latter did not "migrate" but simply appeared. In a sense this is true, but the real distinction between the two lies in their internal dynamics. The geofloral hypothesis assumed a stable community with a static composition; the boreotropical flora concept, a constant internal flux of taxonomic composition, both in its origin and during its existence. Thus, the boreotropical flora is envisioned not as sweeping out from a single source but as rapidly accumulating through the dispersal of separately derived taxa into common areas. Although the reason for the initial appearance of so many boreotropical taxa during the early Tertiary is unclear (but see Tiffney, in press, for a possible explanation), the unique proximity of Northern Hemisphere continents in the early Tertiary, together with the warm climates of that time, explains their rapid spread. Similarly, after its establishment the boreotropical flora probably displayed considerable internal variation. I suspect that during the times of maximum land connection in the Northern Hemisphere, although the flora was characterized by a few distinctive taxa that were known from all or most of the range of the flora (e.g., *Nypa* Steck, Icacinaceae, Mastixiaceae), individual species generally occupied only a portion of the range at any one time. As time progressed and climate and geography altered, this level of variation gave way to allopatric speciation and increased local differentiation.

Finally, some word is appropriate regarding one antithesis of floral "migration"—the hypothesis that the floristic similarity of eastern North America arose largely through chance long-distance dispersal (e.g., Iltis, 1982, 1983). This hypothesis is at odds with paleobotanical evidence for the existence of a boreotropical flora. Further, biotas resulting from long-distance dispersal are often dysharmonic; that is, they contain an imbalance of ecological constituents (Carlquist, 1974). The floras (and faunas) of eastern Asia and eastern North America contain a diverse array of constituents and could not have resulted entirely or in large part from the effects of long-distance dispersal. Finally, while long-distance dispersal is significant in explaining the past and present distribution of individual taxa, it is a counterproductive and anarchic hypothesis when used to explain patterns involving entire biotas. A dispersal hypothesis eliminates the ability to make predictive hypotheses and reduces the science of biogeography to chance.

THE DIFFERENTIAL APPEARANCE OF TAXA

Analogous to simplistic models of "single centers of origin" and "migration of unit floras" is the all-too-human tendency to seek a single time for the origin of the similarity of the floras of eastern Asia and eastern North America. Although Wolfe's boreotropical-flora model of the early Tertiary provides much to explain the extant phytogeography of the Northern Hemisphere, I believe that it has given the unintended impression that the eastern Asian–eastern North American similarity is a function of a single time-limited historical event. However, analyses of phytogeographic patterns reveal that the individual taxa involved appeared in the fossil record at different times (which may reflect their evolution at different times), have different ecological adaptations, particularly as reflected in physiognomy, and are presently adapted to different climatic regimes. In short, the observed similarity of the two modern floras involves a range of taxa with rather different histories, habitats, and habits. This suggests that the similarity did not arise as the result of a single past event. Closer examination of the fossil record supports this contention. I will look at three particular aspects: the time of origin of specific families; the time of origin of herbaceous angiosperms, many of which are included in this pattern; and the nature of the different climatic tolerances of taxa constituting the modern eastern Asian–eastern North American pattern.

ORIGINS AND AFFINITIES. Some of the plants now having an eastern Asian–eastern North American distribution pattern belong to families that appeared in the fossil record at different times in the Tertiary. As a sample of the plants now showing this geographic pattern, I take those described in the classic work of H. L. Li (1952, 1972) and those mentioned by participants in the symposium that prompted the present paper, together with a few assembled from other sources (see TABLE 1). For the first occurrences of modern families in the fossil

TABLE 1. **Age of origin of some families held in common between the floras of eastern Asia and eastern North America.**

FAMILY[a]	REPRESENTATIVE GENERA[b]	REFERENCE[c]	POLLEN DATE[d]	FRUIT AND SEED DATE[e]
Aquifoliaceae	*Ilex* L.	5	Turonian	Paleocene
Buxaceae	*Pachysandra* Michaux	4	Campanian	Mid-Miocene
Juglandaceae	*Carya* Nutt.	4	Campanian	Paleocene
Leguminosae	*Gymnocladus* Lam., *Cladrastis* Raf., *Wisteria* Nutt., *Apios* Medikus	4	Maastrichtian	Paleocene
Symplocaceae	*Symplocos* Jacq.	5	Maastrichtian	Early Eocene
Theaceae	*Gordonia* Ellis, *Stewartia* L.	4	Early Eocene	Late Cretaceous
Aceraceae	*Acer* L.	5	Oligocene	Paleocene
Anacardiaceae	*Rhus* L.	5	Paleocene	Early Eocene
Araliaceae	*Panax* L.	4	Paleocene	Mid-Eocene
Caprifoliaceae	*Triosteum* L., *Diervilla* Miller, *Weigela* Thunb.	4	Mid-Eocene	Paleocene
Cyperaceae	*Carex* L., *Schoenoplectus* (Reichb.) Palla	3	Mid-Eocene	Paleocene
Hamamelidaceae	*Hamamelis* L.	4	Paleocene	Early Eocene
Nyssaceae	*Nyssa* Gronov. ex L.	4	Paleocene	Early Eocene
Polygonaceae	*Antenoron* Raf., *Polygonum* L.	4, 5	Paleocene	Late Eocene
Rosaceae	*Rhodotypos* Sieb. & Zucc., *Kerria* DC., *Neviusia* A. Gray	4	Oligocene	Paleocene
Lauraceae	*Sassafras* Trew, *Lindera* Thunb.	4	Paleocene	Late Paleocene
Ericaceae	*Pieris* D. Don, *Lyonia* Nutt., *Epigaea* L.	4	Pliocene	Late Paleocene
Rutaceae	*Zanthoxylum* L.	5	Pliocene[f]	Late Paleocene
Vitaceae	*Vitis* L., *Parthenocissus* Planchon	5, 11	Oligocene	Late Paleocene
Araceae	*Symplocarpus* Salisb.	4	Late Miocene	Early Eocene
Celastraceae	*Celastrus* L.	5	Oligocene	Early Eocene
Cornaceae	*Cornus* L.	6	No data	Early Eocene
Ebenaceae	*Diospyros* L.	5	Early Eocene	Early Eocene
Magnoliaceae	*Liriodendron* L., *Magnolia* L.	4	Mid-Eocene	Early Eocene

TABLE 1 (*continued*).

FAMILY[a]	REPRESENTATIVE GENERA[b]	REFERENCE[c]	POLLEN DATE[d]	FRUIT AND SEED DATE[e]
Menispermaceae	*Menispermum* L.	4	No data	Early Eocene
Santalaceae	*Buckleya* Torrey, *Pyrularia* Michaux	4	Early Eocene	Mid-Eocene
Staphyleaceae	*Staphylea* L.	11	Pliocene	Early Eocene
Styracaceae	*Halesia* J. Ellis ex L., *Styrax* L.	4, 5	No data	Early Eocene
Umbelliferae	*Sanicula* L.	5	Early Eocene	Mid-Miocene
Bignoniaceae	*Campsis* Lour., *Catalpa* Scop.	4	Mid-Eocene	Mid-Eocene
Oleaceae	*Chionanthus* L.	4	Oligocene	Mid-Eocene
Rubiaceae	*Mitchella* L., *Galium* L.	4, 7	Late Eocene	Mid-Eocene
Acanthaceae	*Justicia* L., *Dicliptera* Juss.	11	Early Miocene	Late Eocene
Guttiferae	*Ascyrum* L.	4	No data	Late Eocene
Liliaceae	Tribe Helonieae	9	Late Eocene	No data
Ranunculaceae	*Trautvetteria* Fischer & Meyer, and the closely related genera *Hydrastis* Ellis ex L. (N. Am.) and *Glaucidium* Sieb. & Zucc. (E. Asia)	4	Early Miocene	Oligocene
Labiatae	*Stachys* L., *Agastache* Clayton, *Meehania* Britton	11	Pliocene	Mid-Oligocene
Primulaceae	*Trientalis* L., *Samolus* L., *Lysimachia* L.	11	Pliocene	Mid-Oligocene
Saururaceae	*Saururus* L.	4	No data	Mid-Oligocene
Compositae	19 genera in common	2	Oligocene	Mid-Miocene
Verbenaceae	*Callicarpa* L., *Clerodendrum* L., *Vitex* L.	11	Early Miocene	No data
Loganiaceae	*Gelsemium* Juss.	4	No data	Mid-Miocene
Scrophulariaceae	*Veronicastrum* Moench	4	Mid-Miocene[g]	Mid-Miocene
Saxifragaceae	*Decumaria* L., *Astilbe* Buch.-Ham., *Hydrangea* L.	4	No data	Mid-Miocene

TABLE 1 (*continued*).

	REPRESENTATIVE			
FAMILY[a]	GENERA[b]	REFERENCE[c]	POLLEN DATE[d]	FRUIT AND SEED DATE[e]
Berberidaceae	*Jeffersonia* Bartram, *Podophyllum* L., *Diphylleia* Michaux, *Caulophyllum* Michaux	4	No data	Late Miocene
Cruciferae	*Arabis* L., *Draba* L., *Cardamine* L.	11	Pliocene	Late Miocene
Crassulaceae	*Penthorum* Gronov. ex L.	4	No data	Quaternary
Phytolaccaceae	*Phytolacca* L.	10	No data	Quaternary

[a] Listed in order of age of appearance, then alphabetically when of similar age. Age of first appearance is determined from fossil records of pollen and of fruits and seeds; where the two differ, the older age is used to order the families.

[b] Representative modern genera with an eastern Asian–eastern North American distribution pattern.

[c] Reference(s) to modern distribution pattern by number: 1) Constance, 1972; 2) H. Koyama, 1983; 3) T. Koyama, 1983); 4) H. L. Li, 1952; 5) H. L. Li, 1972; 6) Sharp, 1972; 7) Shimizu, 1983; 8) Tamura, 1983; 9) Utech, 1983; 10) Wada & Ihara, 1983; 11) personal data.

[d] Earliest date recorded for family, based on pollen records (Muller, 1981). Stratigraphy according to individual author's citations, arranged after Van Eysinga (1975).

[e] Earliest date recorded for family, based on fruit and seed records (B. H. Tiffney, unpubl. data). Stratigraphy according to individual author's citations, arranged after Van Eysinga (1975).

[f] Traverse (1955) reported pollen of the Rutaceae from the Brandon Lignite of Vermont (Oligocene?).

[g] Muller indicates (1981) that some Paleocene pollen may ultimately prove to have affinities with the Scrophulariaceae.

record, I refer to Muller's (1981) compilation of the palynological record and to similar unpublished data of my own on fossil fruits and seeds. Such "first occurrence" data are suspect and open to revision with the discovery of new material. Further, Muller queries several of the identifications that he reports; there is no guarantee that all of the individual reports will stand the test of time. However, the parallelism between the two records suggests that these data are useful, and that the general patterns will hold even if specific cases are found to be in error.

Many of the taxa belong to families known in the fossil record by the Early Eocene (see TABLE 1) and could thus have been members of the boreotropical flora. However, many other taxa sharing the modern eastern Asian–eastern North American distribution belong to families that arose long after the boreotropical flora is assumed to have been broken up by drifting continents and cooling climates. These must have had a geographic history separate from that of the more classic early Tertiary taxa, although they share this modern distribution pattern.

HERBS AND TREES. This pattern of different times of origin of different taxonomic groups has a parallel in the histories of herbaceous and woody plants. Many herbaceous taxa (e.g., members of the Araceae, Araliaceae, Compositae, Cyperaceae, Liliaceae, Polygonaceae, Primulaceae, Ranunculaceae, Rubiaceae, Santalaceae, Umbelliferae) have an eastern Asian–eastern North American distribution.

In general, the paleobotanical literature (e.g., Muller's (1981) data on first appearances, which basically agree with my data on fruits and seeds) tends to emphasize the appearance of herbaceous families in the mid-Tertiary. These herbs are generally assumed to have evolved through neoteny from woody ancestors (Takhtajan, 1976) in response to increasing seasonality in rainfall and/or temperature. Often these herbs were important in the expanding grass-dominated biomes of the time, the prairies and savannas. However, this picture is misleading, because herbs were present before the Miocene and may be presumed to have occupied unstable sites or to have formed forest-floor associations in angiosperm and gymnosperm communities. Evidence for this is the occurrence of individual taxa (e.g., *Ranunculus* L., *Polanisia* Raf.) and even entire groups (e.g., the Monocotyledoneae, which are inherently herbaceous) in early Tertiary floras. Thus, all herbaceous angiosperms sharing an eastern Asian–eastern North American distribution may not have had a similar history. Some may have spread with the boreotropical flora as forest-floor herbs or as early successional colonists of disturbed sites. Others may have evolved in the later Tertiary and spread either by continuous range expansion within the deciduous communities of the Bering or North Atlantic land bridges or by chance long-distance dispersal.

This separation of historical types among herbs is both a complication for paleophytogeographic inquiry and an opportunity to break such a study into component parts. Individual groups will have individual histories, but I suggest that at least four broadly overlapping historical patterns (reflecting, in part, the ecologies of the plants involved) can be predicted for herbs. First would be the plants of the forest-floor association. While some members of this group (particularly those adapted to flowering before leaves of the forest canopy appear in the spring) would be expected to evolve with the diversifying mixed-mesophytic forest of the mid-Tertiary, others were likely present in the early Tertiary. These would belong to lineages with at least a Paleogene fossil record, and they would probably be rhizomatous perennials adapted to stable, low-light environments (see Li, 1952). The long fossil history of monocots (Doyle, 1973) suggests that they would play an important role in this group. Second would be plants of disturbed forest sites. Again, these might belong to lineages with a Paleogene fossil record, but they might be biennials or shorter-lived perennials with good dispersal and other adaptations to the patchy and transient nature of disturbed forest sites. Plants in these groups could also have attained an eastern North American–eastern Asian distribution quite early. The third group, which would include plants adapted to continually disturbed or stressed environments, would comprehend herbs of many different life-histories and would be dominated by groups that evolved in the mid-Tertiary (e.g., Compositae). A fourth and unique group would be composed of aquatic angiosperms. Their adaptation to the common, stable but patchy and short-lived habitats of lakes and other bodies of fresh water suits them to a broad distribution. This mode of existence has been present almost since the origin of the angiosperms (Doyle & Hickey, 1976; Hickey & Doyle, 1977), and the inclusion of aquatics in the eastern Asian–eastern North American pattern may predate the boreotropical flora.

These categories are general; variants and intergradations will occur, particularly since members of each category have undoubtedly evolved throughout the Tertiary, although at greater rates during some periods than during others. Further, the fossil record and the biology of individual plants will constrain the success with which these categories can be recognized. For example, *Jeffersonia* Barton, *Podophyllum* L., and *Diphylleia* Michaux (Berberidaceae), and *Dicentra* Borkh. (Papaveraceae) all exemplify the first category of rhizomatous forest-floor herbs that might be expected to trace their eastern Asian–eastern North American distribution to the early Tertiary. However, pollen of Berberidaceae is not known in the fossil record and fruits and seeds appear only in the Late Miocene (TABLE 1), while no record is available for the Papaveraceae. Either the fossil record is incomplete or these taxa moved after the early Tertiary. For the Berberidaceae the fossil record of pollen, fruits, and seeds may be shown to be incomplete since leaves of *Mahonia* Nutt. are known from Late Eocene–earliest Oligocene sediments in the American West (Leopold & MacGinitie, 1972). However, this extension fails to push the family back to the warmest climates of the Early Eocene, possibly indicating that it expanded after the spread of the boreotropical flora.

Although this suggestion of groupings is speculative, it establishes a perspective. More importantly, it emphasizes that herbaceous plants sharing a common distribution pattern in the modern day need not have attained this distribution in the same way or at the same time. The ecology, phylogeny, and fossil record of individual taxa must be studied before an informed hypothesis about the biogeographic history of a group can be made.

BIOGEOGRAPHIC HISTORY AND CLIMATIC REQUIREMENTS. The climate of the past 65 million years has ranged from the widespread, equable conditions of the early Tertiary that brought tropical taxa to far northern latitudes (Reid & Chandler, 1933; Chandler, 1964; Wolfe, 1975) to the glacial maxima of the Pleistocene. The pattern of change from one extreme to the other was not directional and gradual in any but the broadest sense; continued paleoclimatic research (Kennett, 1977; Buchardt, 1978; Wolfe, 1978; Keller, 1983) demonstrates that the overall cooling trend of the Tertiary was marked by fluctuations. The interplay between climatic fluctuations and changing intercontinental geographic connections through the Tertiary has determined the availability of "migration" routes to plants.

The climatic history of the Northern Hemisphere Tertiary commences with temperate (Hickey, 1981b) or cool-paratropical conditions (Wolfe, pers. comm.) in the mid-latitudes from the Cretaceous-Tertiary boundary through the Paleocene. Temperatures warmed, with fluctuations, into the Early and Middle Eocene, supporting tropical vegetation in equable climates at high latitudes, although perhaps with a simultaneous reduction of average annual equatorial temperatures (Shackleton, 1981). In the Middle to Late Eocene, climates gradually cooled, leading to a sharp decline in the latest Eocene or at the Eocene-Oligocene boundary (Kennett, 1977; Buchardt, 1978; Wolfe, 1978; Collinson *et al.,* 1981). Although we have less knowledge of Oligocene climates, evidence suggests a generally cooler period, with a warming trend beginning in Late Oligocene time and extending into the Miocene. Miocene climates were generally equable and fairly warm, but not as warm as those of the Eocene. More importantly, they were characterized by a series of fluctuations (Kennett, 1977; Wolfe, 1978; Mai, 1980) between warmer and cooler temperatures, leading to increasingly cooler climates in the later Miocene. From the Late Miocene through the Pliocene to the Pleistocene, climates cooled off, with fluctuations, to a situation approximating that of the present day.

Changing climates have had a direct effect upon the evolution and distribution of Tertiary plant communities. In particular, Mai (1964) and Wolfe (1969) both discuss the development of the mixed mesophytic forest as a function of Miocene climatic fluctuations. Szafer (1961), Leopold (1967), and Friis (1975) detail the effect of increasing seasonality in the Late Miocene, Pliocene, and Pleistocene on European plant communities. It is clear from such studies that the climatic tolerances of many angiosperm taxa could not be altered; these taxa either moved via dispersal or became extinct. Others were able to adapt to the cooler, more seasonal climates of the later Tertiary, adding to the growth of deciduous communities (Mai, 1964; Wolfe, 1969). In general, the fossil record suggests that the direction of evolution of tolerance was from paratropical to temperate climates; there is no suggestion that paratropical taxa consistently crossed temperate barriers by evolving temperate forms and then reevolving paratropical ones. We may safely assume that the eastern Asian–eastern North American pattern among evergreen or thermophilic taxa arose at a time when these plants could move directly between the two areas and is not a result of parallel evolution from widespread, deciduous, temperate common ancestors.

The floristic similarity between eastern Asia and eastern North America involves "tropical" evergreen and thermophilic taxa, temperate deciduous taxa, and boreal and alpine taxa. Tropical taxa require no frost, adequate moisture, and sufficient year-round light to support an evergreen physiology. These environmental constraints were met in the Early Eocene when the congruence of warm climates and the availability of the North Atlantic bridges and perhaps the southern margin of the Bering bridge (Wolfe, 1978, in press; Tiffney, 1985) provided a connection between the Old and New worlds. We may assume that evergreen or obligate thermophilic taxa with an eastern Asian–eastern North American pattern in the present day generally attained this distribution as part of the boreotropical flora.

The situation is less clear for temperate taxa with this geographic pattern. I see three possible ways in which such taxa could have achieved this distribution. First, as Hickey has implied (Hickey *et al.,* 1983), temperate elements could have evolved near the early Tertiary North Pole, developing a deciduous habit in response to annual fluctuations in day length. These taxa could have moved southward with cooling temperatures in the later Eocene, attaining a "boreotropical" distribution in the process. Some taxa certainly followed this route, but the known early Tertiary Arctic floras are species poor and do not account for all of the temperate taxa presently shared between the Old and New World portions of the Northern Hemisphere. Second, as Wolfe (1969, 1977) suggests, these temperate-adapted taxa could have evolved in parallel in the Old and New worlds from thermophilic ancestors that attained their distribution with the Eocene spread of the boreotropical flora. It seems unlikely to me that this could account for the entire temperate floristic similarity of eastern Asia and eastern North America. However, in many cases (e.g., oaks) where there are good tropical relatives of the temperate taxa in the modern day and/or where a transition from a tropical ancestor to a temperate descendant can be demonstrated in the fossil record (see Wolfe, 1969), this is a reasonable supposition. The third possible explanation is that these temperate taxa evolved in post-Eocene time in one portion of the Northern Hemisphere and moved to other regions during the mid-Tertiary, when temperate vegetation was still present at high latitudes (Wolfe, 1972). Such an exchange could have occurred via the Bering land bridge, which was present through the Tertiary and was closed to temperate plants by climatic barriers only in the latest Tertiary or Quaternary. It is also possible that some exchange could have occurred across the post-Eocene North Atlantic by "island hopping" (see, for example, Heie & Friedrich, 1971; McKenna, 1983b), but supporting evidence for this is less clear.

I believe that the similarity in temperate taxa between eastern Asia and eastern North America has arisen through some combination of (at least) these three patterns. Researchers interested in temperate taxa shared between these areas should examine the history and affinities of individual taxa to see if they fit one of these patterns.

Finally, although the fossil record of boreal and alpine taxa is virtually nonexistent, we may assume that many of these plants evolved in the later Tertiary and Quaternary in response to cooling world climate. Particularly since the Bering bridge lay at a high latitude and was functional in the later Tertiary and Quaternary, there is little difficulty in ascribing the similarities of Asian and western North American montane floras to direct exchange. However, workers should be sensitive to the possibility of parallel evolution of montane taxa in the two areas from related temperate ancestors, as well as to long-distance dispersal.

MAJOR HISTORICAL DISTRIBUTION PATTERNS AND EASTERN ASIAN–EASTERN NORTH AMERICAN FLORISTIC SIMILARITY

In the preceding section perspectives and physical variables involved in the origin of the similarity of the floras of eastern Asia and eastern North America were explored. The apparent independent nature of these factors (e.g., climate, geography, evolution) could be expected to predispose me to the view that the history of this floristic pattern involves so many permutations that it would change continuously through time and not be divisible into stages. However, while the variables are "continuous" in one sense, they are often grouped and form coherent patterns. In particular, climatic variation may be seen as occurring in several "stages" during the Tertiary, and the variables of geography and evolution are not fully independent of climate. Geography may influence climatic change (e.g., moving continents and oceanic currents—Kennett (1977), Berggren (1982)), and climatic change and geography certainly influence evolution. Therefore, one can discern a series of stages in the evolution of the floristic similarity between eastern Asia and eastern North America. These are offered as hypotheses for testing, not as final conclusions destined to replace existing hypotheses or conclusions.

At the outset, it is appropriate to list the variables.

GEOGRAPHY. Two major routes connect the Old and New worlds: the Bering and the North Atlantic land bridges. The former was available throughout the Tertiary, although with occasional breaks enforced by climatic change. The latter involved at least four geographic links, two between North America and Greenland, one between Greenland and Fennoscandia, and one between Greenland and southwestern Europe (McKenna, 1983a, 1983b).

CLIMATES. As detailed above, world climate was cool or, at most, moderately warm at the beginning of the Tertiary. It warmed into the Early Eocene to an Early to mid-Eocene maximum, commenced cooling in the mid-Eocene with a sharp drop in the Late Eocene, remained cool through most of the Oligocene, and then warmed into the Miocene, although not to the degree achieved in the Eocene. A cooling trend began in the Late Miocene and has continued to the present. These general climatic trends were overlain by a secondary pattern of fluctuation that affected the floras of specific times, but not the broad pattern under discussion.

MAJOR PERIODS OF EVOLUTION. Two distinct periods in which modern angiosperm families appeared at an accelerated rate occurred during the Tertiary (see Muller, 1981; Tiffney, 1981, and unpubl. data). From the Cretaceous-Tertiary boundary to the Early Eocene, many modern families appeared. These were largely families dominated by trees. The Late Oligocene and Miocene saw a second diversification, this time largely involving families dominated by herbs. It must be emphasized that, from the Cretaceous to the present, new families were always appearing. The two specific times cited are only times of "increased" rate of family appearance.

POSSIBLE GENERAL PATTERNS

Taking geography, climate, and evolution as the three variables, I suggest that at least five historical patterns contribute to the floristic similarity between eastern Asia and eastern North America.

PRE-TERTIARY. Our knowledge of pre-Tertiary angiosperm evolution and biogeography is limited, but the existence of the Normapolles and *Aquillapollenites* floristic provinces in the later Cretaceous suggests that some Tertiary biogeographic patterns could stem from Cretaceous antecedents. This might be particularly true of aquatic angiosperms and monocots. I suspect that many conifers (perhaps excluding some Pinaceae, a family that shows modernization concomitant with that of the angiosperms—Miller (1976)) and some bryophytes and pteridophytes may also have attained an eastern Asian–eastern North American distribution at this time.

EARLY EOCENE. The basic components of the boreotropical flora evolved in the Paleogene. The combination of warm climates at high latitudes and the existence of the Bering and North Atlantic land bridges made available the boreal land routes necessary for its spread. I expect that the majority of evergreen taxa presently fitting into the eastern Asian–eastern North American pattern (e.g., Magnoliaceae, Lauraceae, Theaceae) attained their distribution at this time via the North Atlantic bridges. These arborescent taxa were probably accompanied by many herbs of the forest floor or disturbed forest sites. Some deciduous trees may have spread about the hemisphere at this time, perhaps occupying marginal sites in the primarily evergreen boreotropical forest.

LATE EOCENE–OLIGOCENE. As the climates cooled during this period, the deciduous taxa of the polar realms (Hickey *et al.*, 1983) spread southward; some may already have spread to marginal sites earlier in the Eocene. The North Atlantic bridges broke up in the Early Eocene (McKenna, 1983a), cutting off direct movement between Europe and North America. Taxa adapted to cooler, more seasonal sites may have moved via the Bering bridge.

MIOCENE. The Bering bridge remained a viable route, but the temperatures at high latitudes dictated that only temperate deciduous plants could be exchanged between Asia and North America. The North Atlantic land bridges may have existed as a series of island "stepping stones" into the mid-Tertiary and might have permitted the passage of some deciduous taxa. Many deciduous tree lineages evolved during this time (Wolfe, 1969). With regard to the origin of the similarity of the deciduous elements of eastern Asia and eastern North America, it is unclear how many of these evolved in one area and moved via the Bering bridge to the other, and how many evolved in parallel in the two separate areas from common ancestors in the boreotropical flora. This period also saw the evolution of many herbaceous angiosperm groups. Many of these exhibit an eastern Asian–eastern North American distribution, which might have arisen in one of two ways: movement via the Bering bridge by colonization of disturbed sites in the existing forests or development of open communities, or spread by long-distance dispersal, a character common in such plants. I think the latter explanation is less important in view of prevailing wind directions.

LATE TERTIARY–QUATERNARY. With the advent of cold climates in the polar region and on high mountains in the latest Tertiary, it is likely that modern Arctic-alpine forms evolved. The widespread high mountains of Asia and western North America and their point of "meeting" in the northern Pacific provide ample explanation for the movement of these taxa from one area to the other. Some of these taxa may also prove to be derived from common herbaceous ancestors that spread to occupy an eastern Asian–North American range earlier in time.

OTHER. In any such generalized series of categories, there must be a repository for organisms that do not fit the other classes. Taxa that fit into this category may be unique in their history or may represent another pattern that I have failed to suggest.

EXHORTATION

Investigators working on specific plants with an eastern Asian–eastern North American distribution should attempt to determine which of these patterns (if any) their taxon exhibits. They should seek out the assumed geologic time of origin of that taxon and ascertain its climatic and ecological affinities. From such data it is possible to hypothesize the earliest time at which the taxon attained its present distribution. Such information will enhance the value of research on individual taxa. For example, knowledge of which pattern most closely agrees with the history of a taxon will provide an approximate time of separation of its eastern Asian and its eastern North American members. This in turn permits the estimation of rate—perhaps of karyotypic or chemical differentiation, perhaps of morphological or ecological evolution. Such data also aid the paleontologist to understand past floristic movements and ultimately to assess the validity of the five models suggested above. It should be clear that the study of this pattern on a geographic basis is *not* the province of the paleontologist and phytogeographer alone, but requires knowledge from all associated fields.

SUMMARY

Discussion of Southeast Asia as the cradle or the grave of the modern flora of the Northern Hemisphere, and of angiosperms, is misleading; this area is a giant refugium. However, this implies that another "center of origin" is to be sought. I do not think that such a center exists. I suggest that the antecedent of the modern flora of the Northern Hemisphere (the boreotropical flora of Wolfe) had its origins from several separate sources.

The debate whether plants move in communities or only as individuals is fallacious. Plants disperse as individuals. Plants having similar ecological tolerances generally respond to similar environmental stimuli in a similar manner. The myopic perspective induced by the fossil record makes it likely that, as environmental factors change through geologic time, the paleontological observer will witness apparent movements of groups of plants. The recognition of a "floral migration" is thus reasonable but must always be tempered by the knowledge of the underlying biological pattern of the dispersal of individuals.

The early Tertiary boreotropical flora developed in a unique geographic situation involving two sets of land bridges (Bering and North Atlantic) existing at different latitudes in a time of warm and equable climates. This permitted a free movement of newly evolved taxa and the development of a hemispheric flora. No evidence exists for monolithic "geofloras" in the classic sense. The boreotropical flora was not homogeneous; local differentiation existed. Individual plant migrations resulted in most taxa occurring in some portion of the range of the boreotropical flora at some time, but few taxa occurring in all of the range of the flora all of the time.

Taxa exhibiting the eastern Asian–eastern North American distribution include forms that evolved in both the early and later portions of the Tertiary. The modern similarity of the two areas is the product of more than one biogeographic event.

The perception of herbaceous angiosperms as primarily a phenomenon of the mid-Tertiary is wrong. Aquatic herbs and monocotyledons have existed almost since the origin of the angiosperms. Forest-floor herbs existed in the Early Eocene boreotropical flora. While the mid-Tertiary did witness a major diversification of herbaceous taxa adapted to disturbed sites, these were not the first, nor the only important, angiosperm herbs.

The modern eastern Asian–eastern North American pattern of distribution did not arise through a single historical event but is the result of a layering of many events. Some aspects of the similarity may trace their roots to pre-Tertiary times. A large number of taxa, many evergreen, achieved this distribution in the warm climates of the Early and Middle Eocene. Deciduous taxa may have accompanied these floras, moved later in the Tertiary during times of cooler climate, or evolved in parallel from evergreen ancestors inhabiting both areas. Herbaceous forms may have achieved the distribution at various times, depending on their particular ecological affinities.

All of these observations complicate our understanding of the origin of this biogeographic pattern and the mechanisms underlying it. However, if the question is broken down into component parts, it may be easier to address the overall pattern.

ACKNOWLEDGMENTS

I wish to thank Leo J. Hickey (Peabody Museum of Natural History, Yale University), Karl J. Niklas (Cornell University), Stephen A. Spongberg (Arnold Arboretum, Harvard University), Scott L. Wing (U. S. Geological Survey, Washington, D. C.), Malcolm C. McKenna (American Museum of Natural History), Alan Graham (Kent State University), and Jack A. Wolfe (U. S. Geological Survey, Denver, Colorado) for comments and criticisms on the content of this paper, and Willard W. Payne, Thomas S. Elias, and Tetsuo M. Koyama (all then at the New York Botanical Garden) for organizing the conference that spurred me to consider this line of thought. Research was supported in part by NSF grants DEB 79-05082 and BSR 83-06002.

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

IHSAN A. AL-SHEHBAZ

THELYPODIEAE Prantl in Engler & Prantl, Nat. Pflanzenfam. III. 2: 155. 1891.

Herbaceous annuals [biennials, or perennials, very rarely shrubs], glabrous or with simple trichomes only [very rarely with furcate hairs]. Inflorescence a terminal raceme or corymb, laxly or densely flowered, often ebracteate. Sepals equal at base (infrequently strongly saccate), erect or spreading, rarely reflexed [or sometimes forming an urceolate, flask-shaped, or slightly bilabiate calyx]. Petals often differentiated into claw and blade [occasionally undifferentiated or attenuate to a clawlike base], usually crisped or channeled. Stamens long-exserted, sometimes slightly protruding [rarely included], equal in length or slightly tetradynamous, rarely in 3 pairs of unequal length; anthers often sagittate at base, linear [or occasionally oblong or ovate], usually coiling circinately after dehiscence; filaments not appendaged, free, or the median ones connate in pairs. Siliques dehiscent, linear, several to many times longer than broad, flattened parallel to the septum [or terete], often borne on a distinct gynophore, rarely subsessile. Styles obsolete or evident in fruit. Stigmas entire or slightly [to strongly] 2-lobed; lobes opposite the valves [or replum] in fruit. Seeds winged or wingless, not mucilaginous when wet; cotyledons accumbent [or incumbent]. Base chromosome numbers 10, 11, 12, 13, 14, 15. (Including Stanleyeae Rob-

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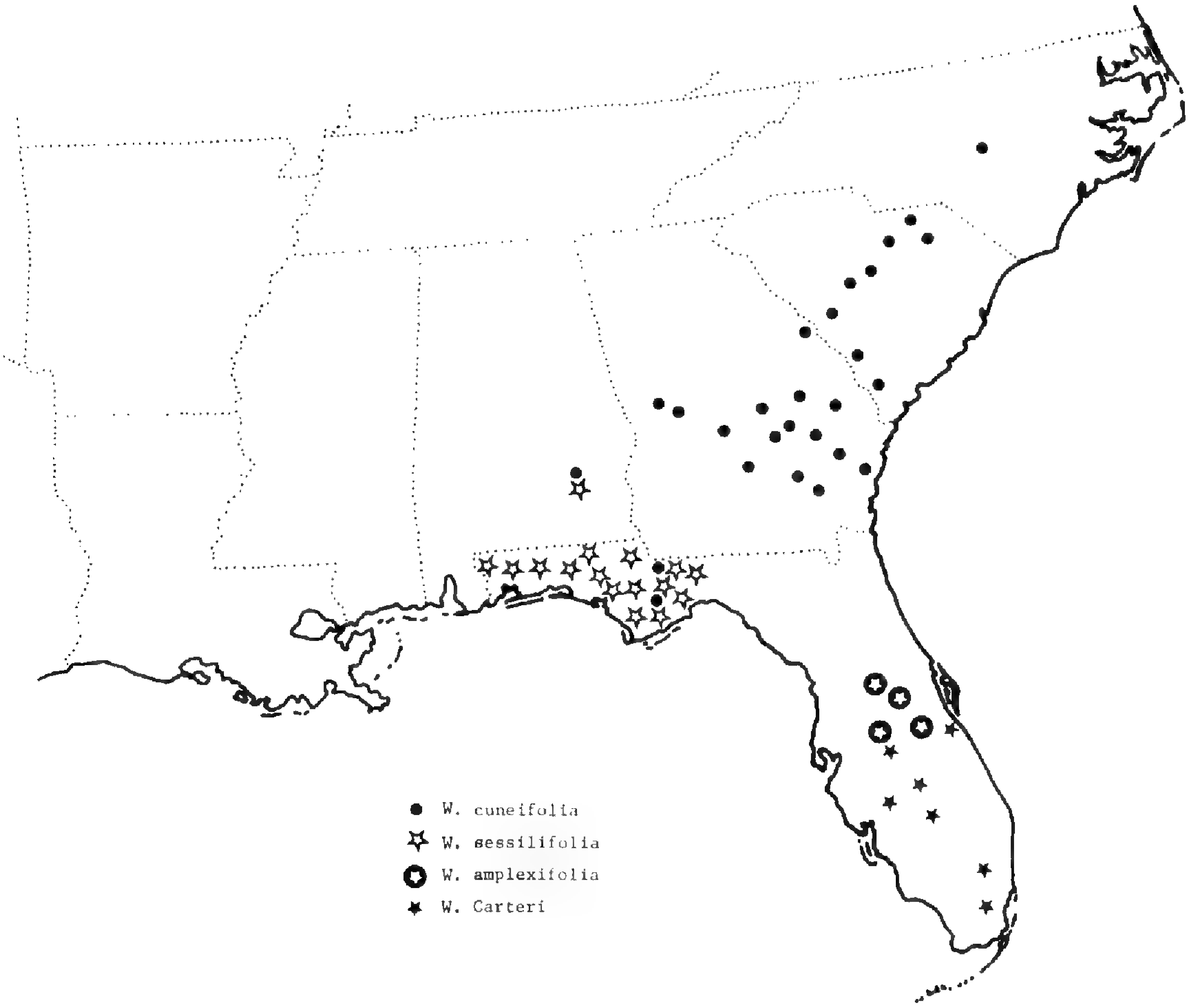
[1] Prepared for the Generic Flora of the Southeastern United States, a long-term project made possible by grants from the National Science Foundation and currently supported by BSR-8111520 (C. E. Wood, Jr., principal investigator), under which this research was done, and BSR-8303100 (N. G. Miller, principal investigator). This account, the 106th in the series, follows the format established in the first paper (Jour. Arnold Arb. **39**: 296–346. 1958) and continued to the present. The area covered by the Generic Flora includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with information about extraregional members of a family or genus in brackets [ ]. The reference that I have not verified is marked with an asterisk.

I am most indebted to Carroll Wood for his continuous guidance, help, and critical review of the present paper. Special appreciation is extended to Reed C. Rollins for his notes on the distribution of *Warea,* and to Norton G. Miller and George K. Rogers, as well as to Barbara Nimblett for the typing of the manuscript. I am grateful to Elizabeth B. Schmidt and Stephen A. Spongberg for their editorial advice.

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

Journal of the Arnold Arboretum **66**: 95–111. January, 1985.



The nine Southeastern States, showing distributions of species of *Warea*. Each symbol represents a county record.

inson, Romanschulzieae O. E. Schulz, Streptantheae O. E. Schulz.) TYPE GENUS: *Thelypodium* Endl.

A natural tribe of 11 genera and some 110 species, distributed primarily in North America from the Pacific States eastward to a line extending from North Dakota to Texas, occurring in all the Southeastern States except Tennessee and Mississippi, and from Mexico to Panama, but most numerous in California, Nevada, and Utah, where more than 60 species occur. *Macropodium* R. Br. (two species; Japan, Mongolia, and Siberia) is the only member of the tribe distributed outside North America. Nearly all of the typically tropical representatives of the Thelypodieae belong to *Romanschulzia* O. E. Schulz, the 14 species of which are found mainly at altitudes of 1200–3500 meters (4000–11,500 feet) in wet forests of Mexico (Nuevo León to Oaxaca), Guatemala, Costa Rica, and Panama. The tribe is represented in the southeastern United States by seven indigenous species of *Streptanthus* Nutt. and *Warea* Nutt. The latter is the only endemic genus of Cruciferae in our area (see MAP).

Members of the Thelypodieae can easily be distinguished from those of other tribes by a combination of the following characters: anthers usually exserted, sagittate at base, often linear, usually coiled after dehiscence; filaments equal in length, sometimes in 3 unequal pairs, or slightly tetradynamous; gynophore present, usually more than 1 mm long; petals crisped or channeled, usually with a distinct claw; and plants glabrous or with simple trichomes.

On the basis of similarities in floral morphology (particularly the presence of a gynophore, exserted stamens of equal length, obsolete styles, spreading parts, and equal sepals) and in several aspects of the fruit (dehiscent, 2-valved, much longer than broad, and many seeded), many authors have postulated that the subfamily Cleomoideae (Capparaceae) is the direct progenitor of the Cruciferae through the intermediate link Thelypodieae. The palynological evidence (Al-Shehbaz, 1973), however, does not support such a direct connection, and it is more likely that the two families evolved from a common ancestor. Any assumptions regarding the ties between the two families must account for members of the Thelypodieae. Some genera of the tribe undoubtedly possess characters more primitive than those found elsewhere in the family, but it is not entirely clear how the Thelypodieae relate to the rest of the Cruciferae. A few authors (Cronquist; Dvořák, 1973) have suggested that the most primitive extant Cruciferae probably occur in central Asia, an assumption apparently lacking a solid morphological foundation and most likely influenced by the hypothesis that the center of greatest taxon diversity and generic endemism represents the center of origin. The assumption has been based primarily on the presence of multicellular glands in some species of *Cleome* L. and the occurrence of their morphological equivalents in some genera of the Hesperideae. Glandular papillae are found on the inflorescences of all species of *Warea,* but whether or not these are anatomically similar to those of *Cleome* remains to be determined. Relict genera of the family are found throughout the world, but almost all of those listed by Hedge are undoubtedly advanced.

Except for two pairs of genera of Thelypodieae, the others are all morphologically well defined and can easily be separated by several characters. *Thelypodium* is very close to *Thelypodiopsis* Rydb. and is distinguished primarily by its entire stigmas (two-lobed in the latter genus). The boundaries between *Streptanthus* and *Caulanthus* S. Watson overlap, and the two are separable by a few characters that are sometimes continuous (see the treatment of *Streptanthus*). The relationships among members of the tribe have recently been studied by Hauser and Crovello (1982), who used phenetic and cladistic analyses. Their conclusions coincide in many ways with those reached earlier by Al-Shehbaz (1973), who defined the limits of the tribe primarily on the basis of the nearest sister relatives of its component genera.

Chromosome numbers have been reported for 46 species in nine genera (see Rollins, 1966; Rollins & Rüdenberg). The most common base number is 14, found in *Caulanthus, Stanleya* Nutt., *Streptanthella* Rydb., and *Streptanthus.* Other genera have $x = 10, 11, 12, 13$ (*Thelypodium*), and 15 (*Macropodium*). No cytological data are available for *Romanschulzia* or for *Chlorocrambe* Rydb., a monotypic genus endemic to Oregon and Utah.

The great diversity in floral morphology found among members of the Thelypodieae is not paralleled in any other tribe of the Cruciferae. Floral characters are very useful in distinguishing most of the genera. Although a wide range of variation in the shape, orientation, size, and color of floral parts can occasionally be found within some genera (e.g., *Streptanthus* and *Thelypodium*), unfortunately very little is known about the floral biology of either these genera or the rest of the tribe.

Nearly all of the Thelypodieae are herbaceous. A woody habit is known only in *Romanschulzia apetala* Rollins, a shrub to 3 m tall endemic to Costa Rica, and in *Stanleya pinnata* (Pursh) Britton, a subshrub of the western United States. Wood anatomy of the latter species was studied by Carlquist, who suggested that the woody habit may have evolved as an adaptation to warmer regions with long growing seasons.

Except for *Caulanthus lasiophyllus* (Hooker & Arnott) Payson and *Streptanthella longirostris* (S. Watson) Rydb., both of which have become weedy in the Pacific and Mountain states and in northern Mexico (Rollins, 1981), the tribe has no economic importance.

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KEY TO THE GENERA OF THELYPODIEAE IN THE SOUTHEASTERN UNITED STATES

Sepals reflexed, rarely spreading; floral buds clavate or pyriform; gynophore slender, (3–)5–14 mm long; petal claws slender, papillose or pubescent; stamens equal in length; fruiting pedicels deciduous from the rachis, often leaving elevated scars; seeds striate, wingless. . . . . 1. *Warea.*

Sepals erect or ascending; floral buds oval or lanceolate; gynophore stout, 1–2(–4) mm long; petal claws broad, flat, glabrous; stamens slightly tetradynamous or in 3 pairs of unequal length; fruiting pedicels persistent; seeds minutely reticulate, winged. . . . . 2. *Streptanthus.*

1. **Warea** Nuttall, Jour. Acad. Nat. Sci. Phila. **7:** 83. 1834.

Glabrous and occasionally glaucous annual herbs; stems slender, often branching above, leafless below. Lowermost leaves undescribed; middle and upper ones entire, short-petiolate or sessile. Inflorescence a short, ebracteate, corymbiform, terminal raceme, slightly elongating in fruit. Pedicels slender, sometimes filiform, straight, with 2 lateral, gland-tipped papillae at the base. Floral buds clavate or pyriform. Sepals linear to spatulate, not saccate at base, strongly reflexed and subappressed to pedicel, rarely widely spreading, green or same color as petals. Petals spreading, white, pink, or deep purple, clawed;

blades orbicular or obovate, equal or rarely slightly unequal, often abruptly narrowed to claw, sometimes cuneate or attenuate at base; claws minutely papillose to conspicuously pubescent, often slightly dilated at base. Glandular tissue subtending bases of all stamens, usually developed into 6 teeth alternating with filaments, the 4 teeth adjacent to the lateral stamens larger than the 2 alternating with the median ones. Stamens spreading, long-exserted, equal in length; filaments filiform, glabrous, often slightly dilated at base; anthers linear, sagittate at base, usually coiling circinately when fully dehisced. Ovary borne on a long gynophore; style obsolete; stigma entire. Fruiting pedicels often deciduous from the infructescence axis, usually leaving elevated, disclike scars. Siliques dehiscent, narrowly linear, glabrous, flattened parallel to the septum, horizontal or reflexed, straight or arcuate; valves with a prominent midnerve extending full length; gynophores slender, (3–)5–14 mm long. Seeds uniseriately arranged, wingless, brown, longitudinally striate, not mucilaginous when wet; cotyledons accumbent. TYPE SPECIES: *Stanleya amplexifolia* Nutt. = *W. amplexifolia* (Nutt.) Nutt.; see Payson, 1923. (Name commemorating Nathaniel A. Ware, 1789–1853, a teacher in South Carolina who traveled widely in the southeastern United States.)

A very well-defined genus of four species endemic to the southeastern United States in North and South Carolina, Georgia, Alabama, and Florida (see MAP). Species of *Warea* are restricted to the southeastern Coastal Plain, where they grow primarily on sandy soils in pinelands, dry open *Quercus* woods or scrub, and sandhills. Flowering and fruiting generally occur in the spring and summer, but under favorable conditions successive generations of a given species may be produced throughout the year. All four species are morphologically and geographically distinct. No infrageneric subdivisions are recognized.

The most widely distributed species of the genus is *Warea cuneifolia* (Muhl.) Nutt. (*Cleome cuneifolia* Muhl., *Stanleya gracilis* DC.), which occurs in certain counties of Florida (Liberty and Gadsden), Alabama (Pike), Georgia (Talbot, Ben Hill, Pierce, Montgomery, Richmond, Long, Taylor, Pulaski, Laurens, Wheeler, Bacon, Emanuel, Bulloch, Tattnall, and McIntosh), South Carolina (Jasper, Allendale, Aiken, Lexington, Richland, Kershaw, Darlington, and Chesterfield), and North Carolina (Harnett). The nearest relative of *W. cuneifolia* is *W. Carteri* Small, $2n = 24$, which is endemic to southern peninsular Florida (Brevard, Polk, Highlands, De Soto, Glades, Broward, and Dade counties). Both species have short-petiolate, cuneate, oblanceolate, or linear leaves and white flowers. The former is characterized by its glabrous or minutely papillose petal claws and by gynophores that are longer than the fruiting pedicels; the latter is easily recognized by its densely pubescent or somewhat fimbriate claws and by gynophores that are shorter than the fruiting pedicels. A few authors (e.g., Patman) have reduced *W. Carteri* to synonymy under *W. cuneifolia,* but such action is totally unwarranted, as is evidenced by the distinctive morphology and distribution of the two species.

Warea amplexifolia (Nutt.) Nutt. (*Stanleya amplexifolia* Nutt., *W. auriculata* Shinners) is a rare species confined to central peninsular Florida (Lake, Orange, Polk, and Osceola counties). It differs from the other species of *Warea* in having deeply auriculate and amplexicaul, ovate to lanceolate or oblong cauline leaves. Flower color is generally white changing to light purple.

Warea sessilifolia Nash is similar to *W. amplexifolia* in having sessile, ovate or lanceolate cauline leaves, but the leaves are not amplexicaul and are without auricles (or are rarely minutely auriculate), and the flowers are dark purple. It is distributed throughout the panhandle of Florida (from Leon and Wakulla counties westward through Escambia County) and in Alabama (Pike County). All reports of *W. amplexifolia* from areas outside central peninsular Florida are based on misidentifications of plants of *W. sessilifolia.*

Nuttall's original description of *Stanleya amplexifolia* was based on a fruiting specimen collected by Nathaniel Ware from "east" Florida (actually the central peninsular area). He transferred this species in 1834 to his new genus *Warea* after acquiring flowering material from "west" Florida (the panhandle area). Nuttall did not realize that he was dealing with two distinct entities, and that the flowering material and its illustration, which accompanied the original description of the genus, clearly belong to a different species (described later by Nash as *W. sessilifolia*). Without studying any of Nuttall's specimens, Shinners mishandled the nomenclature of both species, believing that Nuttall made a mistake in the locality (east vs. west), that both the flowering and fruiting specimens were collected from West Florida, and that Nuttall did not have a mixture of two species. Shinners reduced *W. sessilifolia* to synonymy under *W. amplexifolia* and redescribed the plants of central peninsular Florida as *W. auriculata.* (See Channell & James for further details.)

Warea is very well defined morphologically and is apparently without immediate relatives among the Thelypodieae. Both *Stanleya* Nutt. and *Romanschulzia* O. E. Schulz resemble it in several aspects of the flowers and fruits, but no close ties are found between any two of these genera (see Hauser & Crovello). Furthermore, it is highly unlikely that *Warea* is ancestral to *Streptanthus* Nutt., as was suggested by Hayek. The characters that in combination easily distinguish *Warea* from the other genera of the Cruciferae are corymbose inflorescences, clavate buds, spreading floral parts, slender and papillate or pubescent petal claws, long-exserted stamens of equal length, long gynophores, striate seeds, and fruiting pedicels that are deciduous from the rachis (see Al-Shehbaz, 1984, *fig. 2, a, b*).

Hardly anything is known about the chemistry, embryology, anatomy, genetics, or ecology of *Warea.* Chromosome counts (n = 12, $2n$ = 24) for *W. Carteri* are known from a single collection (Rollins & Rüdenberg, 1977). The adaptive value and the phylogenetic significance of the glandular papillae found in the inflorescence of all species of *Warea* are unknown. With the exception of *W. cuneifolia,* the species of the genus are listed as endangered or threatened in Florida and Alabama.

The genus has no economic value. *Warea sessilifolia* has very showy inflorescences and might well be used as an ornamental.

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2. **Streptanthus** Nuttall, Jour. Acad. Nat. Sci. Phila. **5:** 134. 1825.

Annual [biennial or perennial], often glaucous, glabrous or sparsely [to densely] hispid [or hirsute], taprooted herbs. Basal and lowermost cauline leaves usually absent in flowering specimens [rarely forming a definite rosette], petiolate or subsessile, thin [sometimes coriaceous or somewhat fleshy], dentate or pinnatifid to pinnatisect [runcinate or divided into linear or filiform segments]. Upper cauline leaves usually sessile, amplexicaul [or auriculate], sometimes short- [or long-]petiolate, linear, lanceolate, ovate, oblong [or of other shapes], entire or dentate. Inflorescence an ebracteate [very rarely bracteate], dense or lax, many- [or few-]flowered raceme [or panicle]; rachis straight [rarely flexuous], elongating in fruit; flowering pedicels ascending, divaricate, or reflexed [rarely secund]. Flowers actinomorphic or slightly [to strongly] zygomorphic, all fertile [occasionally the terminal cluster of flowers sterile, having larger and showier sepals than those of the fertile ones, and with other floral parts aborted or lacking]. Calyx regular [or irregular], campanulate, subcylindrical [or usually flask shaped, somewhat bilabiate, or urceolate], open [or closed] at apex; sepals equal or unequal at base, all or only the inner pair saccate, lanceolate to oblong [ovate or rarely orbicular], erect or ascending, separate [or connivent], herbaceous [or somewhat fleshy or membranaceous], acute or obtuse, cucullate [or not] at apex, usually scarious at margin, with straight or recurved tips, purple or green [white, yellow, red, or purplish black], glabrous or sparsely to densely hairy or setose [rarely with a subapical tuft of stiff hairs], round [or prominently keeled], uniform in size [or the adaxial (upper) sepal smaller than or markedly larger than and subtending the other 3]. Corolla cruciform, usually becoming slightly [to strongly] bilabiate by the divergence of petals in opposite pairs; petals always strongly differentiated into blade and claw, equal in size, shape, and color [or the adaxial pair smaller than or much larger than the abaxial one, or differing in color and/or shape], lavender or light to dark purple or magenta [green, yellow, white, brown, red, or purplish black]; blades broadly obovate, 2–4 times wider than the claw, or linear to oblanceolate or oblong [or spatulate] and as broad as or narrower than the claw, entire or partly [to wholly] undulate or crisped, usually reflexed, uniformly colored or with the center and/or veins darker; claws included, spatulate or oblanceolate, crisped, usually channeled. Stamens equal in length, somewhat tetradynamous, or in 3 unequal pairs (with the adaxial pair usually the longest), exserted to slightly protruding, or the outer pair [or all] included; filaments free, or those of 1 (the adaxial) or both median pairs partially to completely connate, straight or recurved; anthers linear or oblong, apiculate or obtuse, sagittate at base, all polliniferous, or those of the adaxial pair of stamens abortive and much shorter than the others. Glandular tissue flat, subtending the bases of all or only the lateral stamens. Siliques narrowly [to broadly] linear, somewhat [to very strongly] flattened parallel to the septum [very rarely subterete], 1–7 mm wide, smooth [or torulose], erect, divaricate [or pendent];

valves obscurely [to prominently] 1-nerved from base to apex, glabrous [hispid or setose]; style short or obsolete in fruit; stigma entire or 2-lobed, the lobes always opposite the valves; gynophore short [rarely exceeding 4 mm]; septum somewhat thick [or membranaceous and translucent]. Seeds oblong to orbicular, not mucilaginous when wet, usually minutely reticulate [or nearly smooth], brown, winged [rarely wingless]; wing narrow [or to 1–1.5 mm wide], completely surrounding the seed [or restricted to the distal end]; funiculus free or partially [to completely] adnate to the septum, slender or flattened; cotyledons accumbent or obliquely so. Base chromosome number 14. (Including *Agianthus* Greene, *Cartiera* Greene, *Disaccanthus* Greene, *Euklisia* (Nutt. ex Torrey & Gray) Rydb. ex Small, 1903 (*Euclisia* (Nutt. ex Torrey & Gray) Greene, 1904), *Icianthus* Greene, *Mesoreanthus* Greene, *Microsemia* Greene, *Mitophyllum* Greene, *Pleiocardia* Greene.) TYPE SPECIES: *S. maculatus* Nutt. (Name from Greek, *streptas*, twisted, and *anthos*, flower, in reference to the petals.) —TWIST-FLOWER, JEWEL FLOWER.

A genus of about 35 species in three subgenera and probably more than seven sections, distributed from Louisiana and Arkansas westward through Kansas and all the southwestern United States, the Mountain States (except Montana), and the Pacific States (except Washington), as well as in northern Mexico (Baja California, Chihuahua, and Coahuila). The great majority of the species (26) occur in California, and 14 of these are found in the western part of the state, particularly in the counties of the Coast Ranges north and south of San Francisco Bay. A few other species are endemic to the serpentine outcrops of the Sierra Nevada foothills from Shasta County to Fresno County. *Streptanthus cordatus* Nutt. is distributed in all the Mountain and Pacific states except Washington and Montana. Five species are endemic or primarily restricted to south-central or western Texas (Big Bend National Park and surrounding counties); one, *S. platycarpus* Gray, is localized in northern Mexico, and another, *S. carinatus* Wright, is widely distributed in New Mexico and Arizona. *Streptanthus* is represented in the southeastern United States by three species distributed in southwestern Arkansas and northwestern Louisiana, as well as in adjacent Texas, Oklahoma, and Kansas.

Infrageneric groups in *Streptanthus* have not been satisfactorily treated; formal sectional classification has been published only for subgenus EUCLISIA Nutt. ex Torrey & Gray (Kruckeberg & Morrison). Rodman and colleagues provided an informal provisional nomenclatural synopsis of *Streptanthus* in which they followed Jepson in reducing *Caulanthus* to two subgenera of *Streptanthus*. However, several authors (see Rollins, 1971; Al-Shehbaz; Rollins & Holmgren) have clearly demonstrated that, in order to obtain a workable classification in this group, both genera must be recognized. Strongly diverging from Jepson's position, Schulz recognized 11 genera (including *Caulanthus*) in this complex and retained only three species in *Streptanthus*. In this he followed Greene's splitting of the genus into nine segregates that are largely based on minor differences in the flower. Neither Schulz's nor Jepson's opposing generic concepts are practical, and they cannot be accepted.

Two species of *Streptanthus* occurring in the Southeast belong to subgenus

STREPTANTHUS (*Eustreptanthus* Endl.), a group of six or seven species distributed in Texas and its neighboring states and in northern Mexico. Plants of this subgenus are characterized by having petal blades usually broadly obovate and often more than twice the width of the claw; stamens free, tetradynamous or in three unequal pairs, with the anthers all fertile; stigmas strongly 2-lobed; siliques (2–)4–7 mm wide; flowers actinomorphic, rarely zygomorphic; and calyx usually regular, open at the apex. No sections have been proposed in subgenus STREPTANTHUS, but it is clear that at least two or probably three can be recognized.

Streptanthus maculatus Nutt. (*S. obtusifolius* Hooker, *Brassica Washitana* Muhl., *Stanleya Washitana* (Muhl.) DC.) is confined to rocky bluffs and moist woodlands in northeastern Texas, southeastern Oklahoma (McCurtain and Pushmataha counties), and southwestern and central Arkansas (Pike, Montgomery, Garland, Hot Springs, Saline, and Pulaski counties). With its broadly obovate, reflexed, purple petals of equal size, each with a central magenta spot, its glabrous and purplish sepals, its ovate or oblong, amplexicaul cauline leaves, and its divaricately ascending siliques that are 6–10 cm long and 2–2.5 mm wide, this is the most attractive and one of the most distinctive species in the genus.

A very close relative and a member of the same subgenus, *Streptanthus squamiformis* Goodman is endemic on sandstone and soft shale in *Pinus-Quercus-Carya* forests (see Kral for further details) of southeastern Oklahoma (McCurtain County) and southwestern Arkansas (Polk, Howard, and Sevier counties). The remarkable similarities between the two species in every respect except the pubescence and the sepals may support considering them as conspecific. The pedicels and sepals in *S. squamiformis* are characteristically pubescent with trichomes that are 1–2 mm long, thick, widely spreading, and (upon drying) scalelike; the sepals are generally long-cucullate. In *S. maculatus* the sepals are glabrous and not cucullate (or with only the outer pair bearing short cuculli). There is some variation in the amount of pubescence and in the thickness of trichomes on the sepals and pedicels of *S. squamiformis,* but in the absence of any field studies and crossing experiments between this and *S. maculatus,* the two are best treated as distinct species.

Streptanthus hyacinthoides Hooker (*Icianthus hyacinthoides* (Hooker) Greene, *Euklisia hyacinthoides* (Hooker) Small, *S. glabrifolius* Buckley, *I. glabrifolius* (Buckley) Greene) grows primarily on sand in *Pinus, Quercus,* or *Carya* woods, open areas, roadsides, grassy sandhills, and sand dunes in northwestern Louisiana (Winn, Caddo, and Bienville parishes), southwestern Arkansas (Nevada and Ouachita counties), eastern Texas, central and northwestern Oklahoma, and adjacent Kansas (Barber and Comanche counties). The linear-lanceolate, short-petiolate or subsessile cauline leaves, the pendent or horizontally spreading, deep-purple or magenta (rarely lavender) flowers, the open calyx, and the fused median filaments with aborted adaxial anthers serve to distinguish this species from all the others of the genus.

The subgeneric disposition of *Streptanthus hyacinthoides* is problematic. Earlier authors such as Gray and Watson (1871) placed it in subgenus EUCLISIA Nutt. ex Torrey & Gray, while Rodman and associates assigned it to subgenus

STREPTANTHUS. Subgenus EUCLISIA is characterized by zygomorphic flowers; reduced petal blades as wide as or narrower than the claw; three unequal pairs of stamens with the filaments of one or both pairs of the median stamens partially to completely connate; anthers of the upper (adaxial) stamens sterile; entire (rarely 2-lobed) stigmas; and narrow siliques 1–2 mm wide. All of these features are found in *S. hyacinthoides,* and they clearly support its placement in subgenus EUCLISIA. However, it clearly deviates from the 14 species of this subgenus, which are exclusively Californian and primarily serpentine endemics, by its open calyx that is regular and neither flask shaped nor urceolate. From members of subgenus STREPTANTHUS, *S. hyacinthoides* differs in having entire stigmas, narrow petal blades, connate median filaments, sterile adaxial anthers, and narrow siliques. Greene (1906a), who was the first to point out the differences between the typical members of *Euclisia* and *S. hyacinthoides,* proposed *Icianthus* to accommodate the species. Perhaps the best disposition for this species would be in a monotypic section, not yet proposed, of subgenus EUCLISIA.

Subgenus PLEIOCARDIA (Greene) Jepson, not represented in our area and primarily distributed in California, accommodates the remaining species of the genus. Members have slightly zygomorphic flowers, three usually unequal, free pairs of stamens with all anthers fertile, usually entire stigmas, and narrow petal blades often as wide as the claw.

The genera most closely related to *Streptanthus* are *Streptanthella* Rydb. and *Caulanthus* S. Watson. From these, *Streptanthus* is distinguished by its accumbent cotyledons, usually winged seeds, and flattened siliques. *Caulanthus* species usually have incumbent cotyledons, wingless seeds, and terete fruits. The line separating the last two genera, however, is not as well defined as it may seem, and there are few species that could be accommodated in either genus without drastically altering the generic limits. Nevertheless, a more practical taxonomy of the group can be achieved by maintaining both genera. Many other pairs of closely related genera with equally arbitrary boundaries are found in the Cruciferae. The monotypic *Streptanthella* is separated from *Streptanthus* by its incumbent cotyledons and its beaked siliques in which the valves remain undehisced in the beak area. Hauser and Crovello suggested that these two genera probably evolved from *Caulanthus.*

Several species of *Streptanthus* are highly polymorphic in flower color and pubescence. The most notable example is *S. glandulosus* Hooker, which has an enormous array of morphologically discrete forms that are apparently correlated with the spatial isolation of populations. As many as nine species have been described in this complex, but these were shown to be interfertile (Kruckeberg, 1957, 1958). Because of the importance of the flowers in the taxonomy of the genus, careful field notes should be made, particularly with respect to color, degree of irregularity, and petal size and orientation.

The remarkable diversity of the flowers of *Streptanthus* is certainly unparalleled in any genus of the Cruciferae. The specific epithets of *S. hyacinthoides* and *S. polygaloides* are indicative of the strong superficial resemblance of the flowers of these plants to those of the genera *Hyacinthus* L. (Liliaceae) and

Polygala L. (Polygalaceae). As shown in the generic description above, the calyx and corolla vary greatly in color, shape, size, orientation of parts, and symmetry. The androecium, too, is highly evolved and shows a wide range of variability, particularly with respect to the length, color, orientation, and degree of connation of the median stamens, and the fertility or sterility of the adaxial anthers. These patterns undoubtedly represent adaptations to certain pollinators, about which hardly anything is known. Kruckeberg (1957) observed bees, butterflies, beetles, and even hummingbirds visiting the flowers of *S. glandulosus,* but no attempt was made to identify the species of these pollinators.

Self-incompatibility and protandry were demonstrated in *Streptanthus carinatus* and *S. Cutleri* Cory (Rollins, 1963). In both species flower odor reaches its peak during anther dehiscence, while nectar secretion coincides with the maturation of the gynoecium. Both devices are nicely coordinated to fulfill the requirements for insect attraction. Selfing is reduced or prevented in many taxa of subgenus EUCLISIA by protandry and the curvature of the filaments away from the stigma during full anthesis. Data on the reproductive biology of the majority of species are needed.

A uniform haploid chromosome number of 14 has been reported for at least 18 species (Kruckeberg, 1958; Rollins, 1966; Rollins & Rüdenberg, 1977; Kruckeberg & Morrison). Earlier counts of $n = 12$ for *Streptanthus cordatus* may have been in error, or the species may have a deviant chromosomal race. No chromosome counts are available for the three species occurring in our area.

Extensive hybridization experiments have been conducted within sections EUCLISIA, INSIGNES Kruckeberg & Morrison, and HESPERIDES Kruckeberg & Morrison. In all cases species of a given section can be crossed, but the artificial hybrids either are inviable or suffer from reduced pollen fertility (Kruckeberg, 1957; Kruckeberg & Morrison). No visible meiotic irregularities during microsporogenesis were observed that explain the low degree of pollen viability. Natural hybridization in *Streptanthus* was first reported between two subspecies of *S. carinatus* (Kruckeberg *et al.*).

Forty species of *Streptanthus* and *Caulanthus* have been analyzed for their seed glucosinolates, and 26 compounds have been identified (Rodman *et al.*). In general, the glucosinolate profiles have been shown to be species specific, but the two genera are chemically indistinguishable. The serpentine endemics are apparently as complex and diverse in their glucosinolates as the nonserpentine taxa. Although infraspecific variability in these compounds is significant in six species, only *S. cordatus* shows a clear correlation, with morphological discontinuities corresponding to recognizable infraspecific taxa. Seeds of *S. hyacinthoides* contain two volatile compounds (3-butenyl as the major component and allyl glucosinolate in smaller concentrations) and two nonvolatiles, with 4-methylsulfinylbutyl as the major constituent and 2-hydroxy-3-butenyl glucosinolate as the minor. *Streptanthus maculatus* (listed as *S. orbicularis*), by contrast, contains two volatiles, with allyl glucosinolate as the dominant constituent and 3-butenyl glucosinolate as the minor one.

Of the 32 species of *Streptanthus* and *Caulanthus* analyzed for nickel content

(Reeves *et al.*), *S. polygaloides* is the first known hyperaccumulator in the New World, with values in the range of 3300–14,800 parts per million of dry weight. Other serpentine-tolerant species had nickel values of only 10–100 ppm. Greene (1904) established the monotypic genus *Microsemia* for this species on the basis of its very broad, bannerlike, adaxial sepal that subtends the other sepals in bud, a feature not encountered elsewhere in the Cruciferae. The nickel data may support Greene's position, but in floral and fruit morphology the species fits well in *Streptanthus*.

Edaphic factors probably play a major role in the localized distribution of most species of *Streptanthus*. Although many species are restricted to limestone, shale, sand, clay, and granite gravel and rocks, by far the narrowest endemism is shown by the serpentine inhabitants. Kruckeberg's pioneering studies on serpentine tolerance show that some species (such as *S. glandulosus, S. tortuosus* Kellogg, and *S. cordatus*) are broad generalists adapted to different soils, while others (at least 22 taxa of 15 species) are serpentine endemics. Ecotypic differentiation in the form of several serpentine-tolerant and intolerant races is now well documented in *S. glandulosus*. Kruckeberg believes that evolutionary diversification in *Streptanthus* may have resulted from the reduced gene flow between edaphic races accentuated by spatial and edaphic isolation, particularly in serpentine habitats, and that the serpentinophytes probably represent the end product of a process of biotype depletion in which the serpentine intolerants were eliminated by competition pressure, leaving only the serpentine obligates.

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THE GENUS MERYTA (ARALIACEAE) IN SAMOA

PAUL ALAN COX

THE GENUS MERYTA, a group of araliaceous trees of the islands of the southwestern Pacific, New Guinea, Micronesia, and Australia, was proposed by J. R. and G. Forster (1775) on the basis of a staminate collection made at an unspecified site during the second voyage of Captain Cook. According to Willis (1973), the genus includes 16 species; according to Harms (1937), it includes 38. Consisting of dioecious trees or shrubs with simple leaves and with flowers either solitary or borne in heads, the genus remains poorly understood and has yet to be monographed. Intrageneric relationships are particularly obscure, and limits between species are difficult to define.

The genus occurs in all of the major archipelagoes of Polynesia except Hawaii, although it is rare in Fiji, where prior to 1971 it was believed to be completely absent (Smith & Stone, 1968). At present, the Fijian species *Meryta tenuifolia* A. C. Smith is known only from the type collection from Viti Levu (Smith, 1971). The ecological and biogeographic factors responsible for the present distribution of the genus remain unknown.

It is hoped that a clarification of the status of the genus in Samoa will prove useful to those concerned with the Samoan flora, as well as to those dealing with the Araliaceae in general. Of the Araliaceae known to be extant in Samoa, species of *Reynoldsia* A. Gray, *Polyscias* J. R. & G. Forster, and *Schefflera* J. R. & G. Forster have been collected in addition to *Meryta.*

Two species, *Meryta macrophylla* (Rich ex A. Gray) Seemann and *M. capitata* Christoph., have been described from Samoa (Seemann, 1862; Christophersen, 1935). However, an analysis of the type specimens and descriptions, as well as of recent and old collections of *Meryta* from Samoa, reveals the existence of two additional taxa and some confusion concerning the two known taxa.

The first species of *Meryta* from Samoa was described as *Botryodendrum macrophyllum* Rich ex A. Gray, based on an unnumbered specimen collected at an unspecified site in Samoa by the U. S. Exploring Expedition. Gray's description (1854, p. 732) was characteristically brief ("B. foliis obovato-lanceolatis basi attenuatis membranaceis ad apicem ramorum confertis"), and it is apparent from his discussion (*ibid.*) that he regarded the specimen as inadequate: "This is said to be 'a simple shrub, from 10 to 25 feet high.' Whether it is really distinct from the preceding species *Botryodendrum taitense* cannot be satisfactorily determined from the present materials which consist of foliage, some badly preserved fertile flowers, a detached portion of male inflorescence (which perhaps belongs to *B. taitense*), and mature fruit."

Journal of the Arnold Arboretum **66**: 113–121. January, 1985.

All of the species in the genus *Botryodendrum* Endl. were transferred by Seemann (1862) to the genus *Meryta*. Subsequently, numerous specimens of a common species of *Meryta* in Samoa have been placed in *M. macrophylla*. However, examination reveals the type to have little in common with these specimens. The fruits of the type specimen are completely free or united only at the base, have sessile stigmas and prominent ridges, and do not exceed 1 cm in length. This contrasts greatly with the fruits of the common Samoan *Meryta*, which are fused to half of their length within the heads, lack prominent ridges, and exceed 1.5 cm in length. It is thus clear that although the most common species of *Meryta* in Samoa has been called *M. macrophylla*, it is actually an undescribed species. It is here designated *Meryta mauluulu* (described below).

The status of *Meryta macrophylla* remains uncertain because of the possibility, mentioned by Gray, that the type is a composite specimen. Only one of the *Meryta* specimens I have examined from Samoa (*Bristol 2118* (BISH), from Salamumu, Upolu) can possibly be ascribed to this species. I cannot exclude the possibility that the type specimen represents a very early developmental stage, although Gray's dissection led him to declare the fruit mature. Another specimen (*Setchell 1253* (BISH)), in which only one fruit per capitulum developed, shows ridges on the fruits similar to those of the U. S. Exploring Expedition specimen, although the fruits themselves are much larger.

Meryta mauluulu can readily be distinguished from the other common Samoan species, *M. capitata*: the fruits of the former species are fused along the lower half only, while those of the latter are completely fused. After periodic observation of several tagged trees in Upolu in 1978 and 1979, I am convinced that *M. capitata* and *M. mauluulu* are indeed different and not merely developmental stages of the same species. The similarity of the erect entomophilous terminal inflorescences of these two sympatric species raises interesting ecological questions concerning the nature of the isolating mechanisms. Perhaps *M. mauluulu* is a relatively recent introduction from Tonga or, alternatively, *M. mauluulu* spread to Tonga from Samoa but *M. capitata* did not. With regard to the latter possibility, it is of interest to note the occurrence of "leaky dioecy" (Baker & Cox, 1984) in *M. mauluulu*: *Christopherson 1254* has both staminate and pistillate flowers borne in different fascicles on the same inflorescence.

Meryta malietoa (described below) can easily be distinguished from the other Samoan species of *Meryta* by its greater degree of ramification, its fruits that are free or united only at the base, and its prominently exserted stigmas. It is apparently confined to the mountain forests of Savaii, although *Whistler 1047*, a specimen collected from Mt. Mariota in Upolu and lacking fruits, may be referable to *M. malietoa*. (In 1980, I climbed Mt. Mariota but did not find any plant similar to *M. malietoa*.)

The four Samoan species of *Meryta* are difficult to distinguish vegetatively. *Meryta malietoa* has a much greater degree of ramification than *M. capitata* or *M. mauluulu*, both of which appear to approximate Chamberlain's model (Hallé *et al.*, 1978). Obtaining decisive foliar characteristics is particularly problematic. Although laminas of *M. capitata* and *M. mauluulu* are somewhat

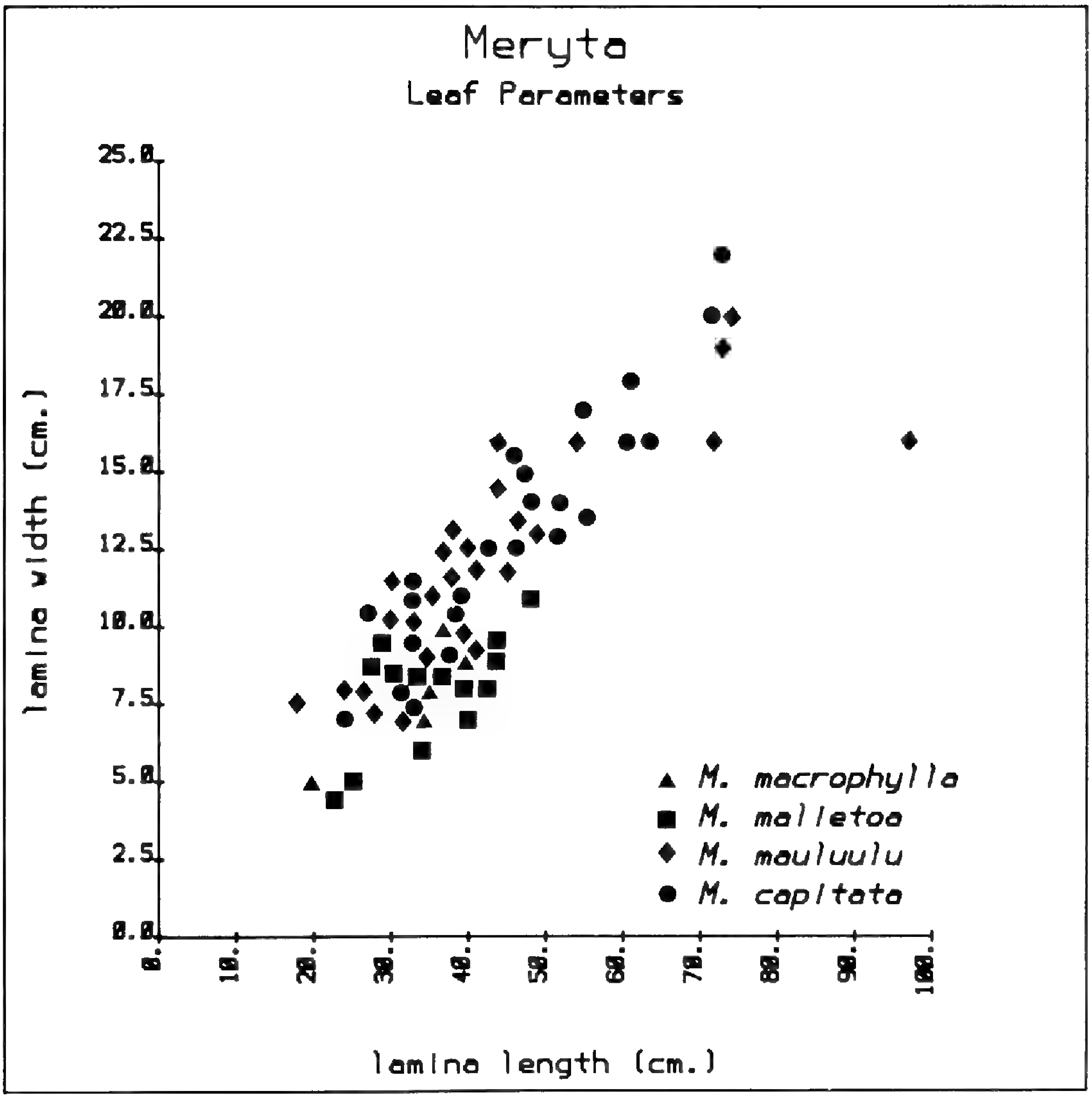

FIGURE 1. Lamina lengths plotted against lamina widths for species of *Meryta* in Samoa.

longer than those of *M. malietoa* or *M. macrophylla,* this character is highly variable (see TABLE 1). Leaves of *M. malietoa* and *M. macrophylla* do appear to be considerably narrower, however (see TABLE 1). A plot of lamina lengths and widths (FIGURE 1) effectively divides the four species into two separate groups, with *M. capitata* and *M. mauluulu* having identical length/width quotients of 3.5, and *M. malietoa* and *M. macrophylla* having quotients of 4.4 and 4.2, respectively (TABLE 1). Thus, while these four species are very similar vegetatively, my observation of tagged individuals over a one-year period leaves little doubt that they are distinct. There was no variation in fruit characters observed through time within any individual, and intermediate fruit character states have not been found. The overall vegetative similarities between these species is perhaps not surprising, given the climatic and relative ecological homogeneity of their habitats (with the exception of the montane *M. malietoa*). The ecological factors that maintain the integrity of these species

TABLE 1. **Leaf characteristics of Samoan species of Meryta.**

	SPECIES			
CHARACTERISTICS	**M. capitata** (N = 26)	**M. mauluulu** (N = 27)	**M. malietoa** (N = 19)	**M. macrophylla** (N = 6)
Mean lamina length (cm)/S.D.	46.9/13.2	43.1/17.2	34.1/6.7	33.8/6.4
Mean lamina width (cm)/S.D.	13.3/3.7	12.1/3.4	8.0/1.6	7.8/1.6
Lamina length-width quotient/S.D.	3.5/0.4	3.5/0.7	4.4/0.9	4.2/0.4
Mean petiole length (cm)/S.D.	8.5/4.9	9.2/4.3	11.8/3.9	7.6/1.2
Lamina length–petiole length quotient/S.D.	9.3/11.8	6.0/5.7	3.2/7.33	4.4/0.6

and the relationships of Samoan species to the rest of the genus await further study.

KEY TO THE SAMOAN SPECIES OF MERYTA

1. Fruits free or united only at base.
    2. Fruits less than 1 cm long; stigmas sessile. .... 2. *M. macrophylla.*
    2. Fruits greater than 1 cm long; stigmas prominently exserted. ... 3. *M. malietoa.*
1. Fruits completely or partially fused into heads.
    3. Fruits completely fused along entire length. .... 1. *M. capitata.*
    3. Fruits fused only along lower half, the upper half free. .... 4. *M. mauluulu.*

1. **Meryta capitata** Christoph. Bernice P. Bishop Mus. Bull. **128:** 161. 1935.

Few-branched tree 5 m high, with leaves inserted near ends of branches. Leaves with lamina oblanceolate, 20–80 by 6–25 cm, apex short acuminate, base decurrent, margin slightly undulate, glabrous. Infructescence terminal, racemose, with fruits borne in heads. Fruits sessile or short pedicellate, completely fused except for the 2- to 3-mm conical apex, green, with 8 to 12 persistent stigmas.

TYPE. Western Samoa, Savaii, edge of forest back of Vaipouli, 150 m alt., 7 July 1931, *Christophersen & Hume 1913* (holotype, BISH!; isotypes, A!, BISH!, US!).

SPECIMENS EXAMINED. **Western Samoa.** SAVAII: Falealupo, *Christophersen 2802* (BISH); Manase, *Christophersen 2369* (BISH); Taga, *Bristol 2219* (BISH, GH, US), *Christophersen 2839* (BISH, US); Patamea, 280 m alt., *Bristol 2365A* (BISH); Vaipouli, 75 m alt., *Christophersen & Hume 1837* (A, BISH); road to Papa, *Whistler 2184* (BISH); Fatuvalu, *Cox 10* (GH). UPOLU: Tapatapao, 700 m alt., *Cox 78* (GH). **American Samoa.** TAU: top of island, *Whistler 3204* (BISH); 100 m alt., *Yuncker 9162* (BISH); 600 ft alt., *Garber 622* (BISH). OFU: *Yuncker 9545* (BISH). OLOSEGA: 1700 ft alt., *Garber 622* (BISH).

A tree common throughout Samoa, called "lau fagufagu" in Samoan.

2. **Meryta macrophylla** (Rich ex A. Gray) Seemann, Bonplandia **10:** 294, 295. 1862.

"Small tree 10 to 25 feet high" (Gray, 1854, p. 732). Leaves with petiole 6–

10 cm long; lamina oblanceolate, 20–40 by 6–10 cm. Fruits free or united only at base, 0.8–1 cm long, with prominent longitudinal ridges, stigmas sessile.

TYPE. "Samoan or Navigator Islands, Herbarium of the U. S. Exploring Expedition, under the command of Captain Wilkes, U.S.N., 1838–1842" (US!).

SPECIMEN EXAMINED. **Western Samoa.** UPOLU: Lefaga-Salamumu, *Bristol 2118* (BISH).

3. **Meryta malietoa** P. A. Cox, sp. nov. FIGURE 2.

Infructescentia bracteata paniculata, fructibus parum pedicellatis vel sessilibus, solitariis vel in capitulis aggregatis. Fructus virides, discreti vel basi tantum conjuncti, diametro 1–1.2 cm, globosi vel ovoidei, cristis longitudinalibus prominentibus 5–8 instructi, baccati, pericarpio carnosulo 5–6 pyrenibus instructi; calyce, stylo, et stigmatibus persistentibus, stigmatibus 6–8, prominentibus, 3–5 mm longis, stylo 2 mm exserto.

Few-branched tree 6 m high, with leaves inserted near ends of branches. Leaves with petiole 10–20 cm long; lamina obovate to oblanceolate, 36–43 by 8–9 cm, apex short acuminate, base decurrent, margin slightly undulate particularly near apex, glabrous, coriaceous, with lateral nerves 25 to 30 on each side, prominent. Infructescence solitary, paniculate, bracteate, with fruits borne singly or aggregated into heads. Fruits short pedicellate or sessile, free or united only at base, baccate, globose to ovoid with 5 or 6 prominent longitudinal ridges, 1–1.2 cm in diameter, green, with calyx, style, and stigmas persistent (stigmas 6 to 8, prominent, 3–4 mm long, styles exserted 2 mm); pericarp fleshy; pyrenes 5 or 6, asymmetrically oblong, 11 by 6 by 1 mm, hard. Seed with 3 or 4 wings, 7 by 3 by 0.2 mm, testa soft, with circular red layer in transection; ovule solitary, pendulous, anatropous; endosperm copious.

TYPE. Western Samoa, Savaii Island, Mt. Silisili, Letui side, above salafa toward summit, 1800 m alt., in cloud forest, 27 June 1979, *Cox 279* (holotype, UC; isotypes, BISH, GH).

SPECIMENS EXAMINED. **Western Samoa.** SAVAII: above Matavanu, wet forest, 1400 m alt., *Christophersen & Hume 2199* (UC); W of Mt. Silili, 1600 m alt., *Whistler 2678* (US); Aopo west, Asau forestry, 300 m alt., *Whistler 1770* (US); inland from Asau, 500 m alt., *Whistler 1047* (US).

The specific epithet of *Meryta malietoa* comes from the chiefly title of His Highness, the Head of the State of Western Samoa, Malietoa Tanumafili II, and is used with his permission. It is hoped that the association of his kingly title with this plant will add impetus to the establishment of a national park in the interior forests of Savaii to which this plant is confined.

4. **Meryta mauluulu** Cox, sp. nov. FIGURE 3.

Fructus virides, infra conjuncti supra liberi, 5–7 mm alti, calyce persistenti, plerumque 8-partito, stigmatibus persistentibus, plerumque 8, sessilibus, papillosis, 1–1.6 mm longis. Fructus baccatus pericarpio carnosulo 8 pyrenibus instructus.

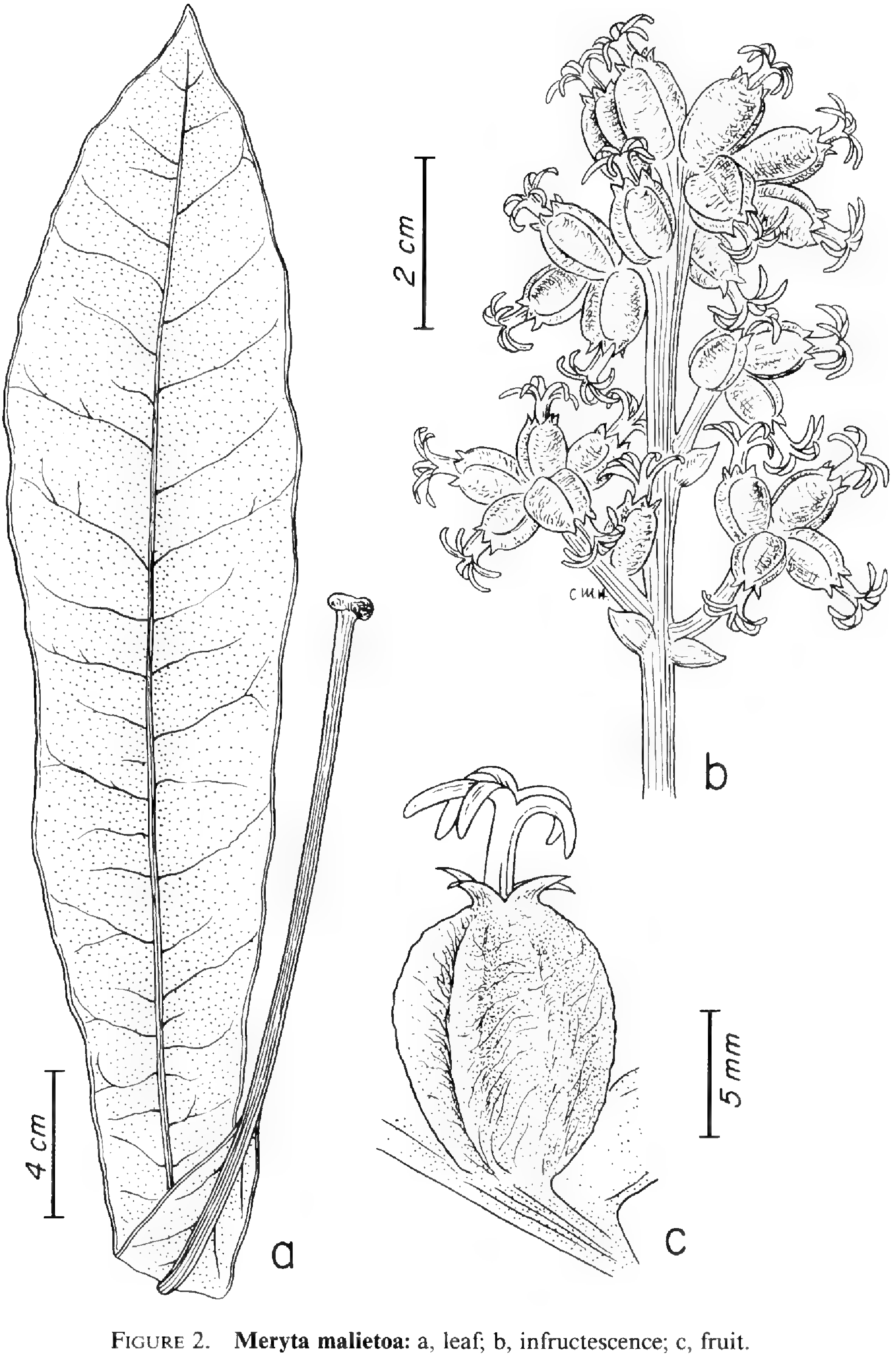

FIGURE 2. **Meryta malietoa:** a, leaf; b, infructescence; c, fruit.

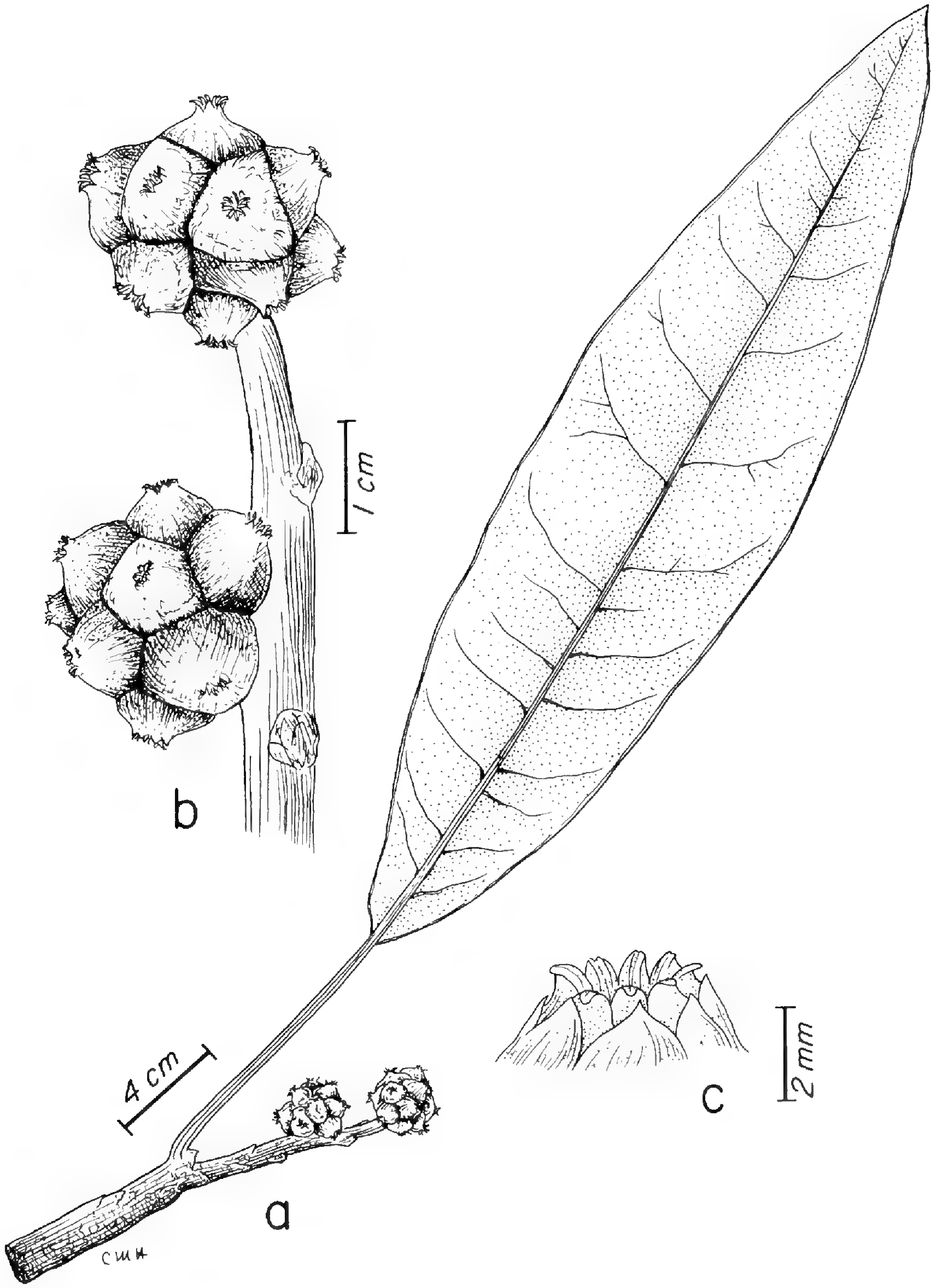

FIGURE 3. **Meryta mauluulu:** a, leaf; b, infructescence; c, apex of fruit.

Few-branched tree 8 m tall, with leaves inserted near ends of branches, apparent phyllotaxis 10/3. Leaves with petiole 9–11 cm long; lamina oblanceolate, 37–40 by 10–11 cm, apex short acuminate, base short decurrent, margin very slightly undulate, glabrous, chartaceous, with lateral nerves 24 to 28 on each side, prominent. Infructescence racemose, bracteate, unbranched, with fruits borne in heads; heads sessile, globose, 2.5–3 cm in diameter, with 12 to 16 fruits. Fruits sessile, united along lower half, free along upper half, slightly conical, 5–7 mm long, baccate, green, the calyx persistent, calyx members usually 8, the stigmas persistent, usually 8, sessile, 1–1.6 mm long, papillose; pericarp fleshy; pyrenes 8, asymmetrically oblong, 8 by 3 by 1 mm. Ovule solitary, pendulous, anatropous, oblong, 2.2 by 1 mm, smooth; endosperm copious.

TYPE. Western Samoa, Savaii Island, on road between Letui and Aopo in young forest, 24 June 1979, *Cox 252* (holotype, UC; isotypes, BISH, GH).

The specific epithet comes from the Samoan name given this plant by botanically adept Samoans resident in the type area. It is a cognate of "kulukulu," the Tongan name for this species as noted on several sheets from Tonga (*Yuncker 16050, Yuncker 16181, Setchell 15652, Parks 16231*), and "lutulutu," the Fijian name noted by Smith (1971) for the type specimen of *Meryta tenuifolia* (*M. J. Berry 97*). The leaves are used to wrap food for baking in stone ovens ("umu").

SPECIMENS EXAMINED. **Western Samoa.** UPOLU: Malolelei above Apia, 1600 ft alt., *Setchell 15667* (BISH); Mt. Vaea, 150 m alt., *Bryan 99* (BISH); Lefaga–Salamumu, *Bristol 2118* (BISH); Afiamalu, 600 m alt., *Whistler 806* (US); Mt. Mariota, 600 m alt., *Whistler 1269* (US); Tiavi, 700 m alt., *Whistler 715* (US), *Cox 5* (GH); Malolelei, 550 ft alt., *Christophersen 304* (BISH); Lepupupue, *Cox 166* (GH), *Teraoka & Kennedy 87* (US); *Teraoka & Whitaker 340* (US). SAVAII: Avao, *Vaupel 135* (BISH); between Letui and Aopo, *Cox 236* (GH, UC); E of Asau, *Cox 262* (GH); Asau, *Teraoka 342* (US), 300 m alt., *Whistler 962* (US). **American Samoa.** TUTUILA: ridge above Pagopago, *Garber 929* (BISH); Alava ridge, 400 m alt., *Christophersen 1130* (BISH, US); Papatele ridge, 300 m alt., *Christophersen 1006* (BISH, US); Pagopago ridge west, *Setchell 1253* (BISH). TAU: Amouli trail, 600 ft alt., *Garber 622* (A); central mountain, *Cox 312* (BISH, GH, US). **Tonga.** VAVAU: *Setchell 15652* (UC); 150 m alt., *Yuncker 16181* (GH). EUA: *Parks 16231* (US); Anovai Lake, 20 m alt., *Yuncker 16050* (GH).

ACKNOWLEDGMENTS

I thank Aumalosi, H. G. Baker, L. Constance, L. Dempster, F. R. Fosberg, L. Heckard, Samu, A. C. Smith, P. F. Stevens, F. Tauiliili, and A. Whistler for helpful advice at various stages; D. Betham and B. Cox for logistical support; and C. Hannan for artwork. I also thank the curators of the Gray Herbarium (GH), the Arnold Arboretum (A), the Bishop Museum (BISH), the U. S. National Herbarium (US), and the University of California Herbarium (UC) for workspace, loans, and numerous courtesies. During this study, I was funded by fellowships from the Danforth Foundation, the National Science Foundation, and the Miller Institute for Basic Research in Science, and grants from the National Science Foundation and the Fernald Fund of Harvard University.

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1. TITLE OF PUBLICATION THE ARNOLD ARBORETUM	A PUBLICATION NO	2. DATE OF FILING 9-26-84
3. FREQUENCY OF ISSUE Quarterly	A. NO. OF ISSUES PUBLISHED ANNUALLY 4	B. ANNUAL SUBSCRIPTION PRICE 50.00

4. COMPLETE MAILING ADDRESS OF KNOWN OFFICE OF PUBLICATION *(Street, City, County, State and ZIP Code) (Not printers)*
1041 New Hampshire St., Lawrence,(Douglas) KS 66044

5. COMPLETE MAILING ADDRESS OF THE HEADQUARTERS OR GENERAL BUSINESS OFFICES OF THE PUBLISHERS *(Not printers)*
Same as #4

6. FULL NAMES AND COMPLETE MAILING ADDRESS OF PUBLISHER, EDITOR, AND MANAGING EDITOR *(This item MUST NOT be blank)*

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Arnold Arboretum,Harvard University, 1041 New Hampshire St.,Lawrence,KS 66044

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(Page 1)

Journal of the Arnold Arboretum *January, 1985*

CONTENTS OF VOLUME 66, NUMBER 1

Volume 65, Number 4, including pages 429–592, was issued October 12, 1984.

JOURNAL OF THE
ARNOLD ARBORETUM

HARVARD UNIVERSITY VOLUME 66 NUMBER 2

ISSN 0004–2625

Journal of the Arnold Arboretum

The *Journal of the Arnold Arboretum* (ISSN 0004-2625) is published quarterly in January, April, July, and October for $50.00 per year, plus $5.00 postage for addresses outside of the United States, by the Arnold Arboretum of Harvard University. It is printed and distributed by the Allen Press, Inc., 1041 New Hampshire Street, Lawrence, Kansas 66044. Second-class postage paid at Lawrence, Kansas. POSTMASTER: send address changes to *Journal of the Arnold Arboretum,* % Allen Press, Inc., P. O. Box 368, Lawrence, Kansas 66044.

Subscriptions and remittances should be sent to *Journal of the Arnold Arboretum,* 1041 New Hampshire Street, Lawrence, Kansas 66044, U. S. A. Claims will not be accepted after six months from the date of issue.

Volumes 1–51, reprinted, and some back numbers of volumes 52–56 are available from the Kraus Reprint Corporation, Route 100, Millwood, New York 10546, U. S. A.

Printed at Allen Press, Inc., Lawrence, Kansas

COVER: The stylized design appearing on the Journal and the offprints was drawn by Karen Stoutsenberger.

JOURNAL
OF THE
ARNOLD ARBORETUM

VOLUME 66 APRIL 1985 NUMBER 2

THE SUBFAMILIES AND TRIBES OF GRAMINEAE (POACEAE) IN THE SOUTHEASTERN UNITED STATES[1]

CHRISTOPHER S. CAMPBELL

THE FAMILY GRAMINEAE (POACEAE), the fourth largest family of flowering plants, is represented in the southeastern United States by about 575 species, 130 genera, and 21 tribes assigned to five subfamilies. In number of genera it matches the Compositae (Asteraceae) almost exactly and exceeds both the Leguminosae (Fabaceae) (ca. 72 genera) and the Orchidaceae (ca. 50 genera) in this area of some 444,000 square miles (1.15 million square kilometers). The present account contains a comprehensive family description; general

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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-8111520 (C. E. Wood, Jr., principal investigator), under which a part of this research was done, and BSR-8303100 (N. G. Miller, principal investigator). This account, the 107th in the series, follows in general the format established in the first paper (Jour. Arnold Arb. **39**: 296–346. 1958) and continued to the present. It departs from this format in some respects, most notably in the APPENDIX (a data matrix) and in the single bibliography placed at the end of the paper, instead of a separate one under the family and each subfamily and tribe. Only references cited are included in the bibliography. In the interest of readability, dates of papers referred to in the text usually are given, as in other papers of the series, only when needed to identify the reference. 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 the family in brackets [ ].

I thank Carroll Wood for his support and guidance, his critical review of the manuscript, and his work on the nomenclature of the taxa in this paper. Mary E. Barkworth, David W. Hall, Walter S. Judd, Elizabeth A. Kellogg, John R. Reeder, Thomas R. Soderstrom, and John W. Thieret provided many helpful comments. I am grateful to Elizabeth B. Schmidt and to Stephen A. Spongberg for their editorial expertise.

FIGURE 1 was drawn by Donna Marino, and FIGURE 2 is by Scott E. Bergquist. FIGURES 3–11 were drawn by Karen Stoutsenberger in 1975, 1976, and 1977, largely under NSF Grant BMS-21469 (C. E. Wood, Jr., principal investigator); Carroll Wood or Kenneth R. Robertson and the author prepared the materials and supervised these illustrations. FIGURE 4 was based on living plants collected by Norton Miller near Chapel Hill, North Carolina, and grown by Carroll Wood in Cambridge, Massachusetts.

Journal of the Arnold Arboretum **66**: 123–199. April, 1985.

comments on the systematics, phylogeny, origin and distribution, reproductive biology, and economic importance of the family; a general diagnosis of the family followed by a key to the subfamilies and tribes; and brief diagnoses and discussions of the subfamilies and tribes. Fuller descriptions of these taxa are given in the APPENDIX (a data matrix based on 84 characters) at the end of the paper. Two pages of figures illustrate variations in leaf epidermis and internal leaf anatomy; four genera are illustrated as in other papers in the Generic Flora series; and five pages of drawings show details of spikelets, florets, and various other parts of representatives of 17 of the 21 tribes.

GRAMINEAE A. L. de Jussieu, Gen. Pl. 28. 1789.
Nom. alt. POACEAE Barnhart, Bull. Torrey Bot. Club **22**: 7. 1925.

(GRASS FAMILY)

Annual or perennial herbs or shrubs with stems to 7.6 m high [trees to over 40 m in height and 30 cm in diameter], occasionally aquatic [or climbing]; hardness of woody stems not from secondary growth but from caps of fibers on both sides of the vascular bundles, lignified ground tissue, and to a lesser extent, silicified epidermis. Cyanogenic glycosides and various fructosans often present; major flavonoids flavone C-glycoside and tricin. Nucleoli disintegrating before or after metaphase, either enclosed within a lumen during interphase or not. Vessel members with mostly simple perforation plates. Primary roots usually ephemeral, the mature root system adventitious and fibrous (FIGURES 4a, 6a, 10a); prop roots sometimes adventive from lower stem nodes; epidermal cells all equal in size or alternating long and short; root hairs perpendicular to or obliquely angled from the surface of the root; roots sometimes forming mycorrhizae. Corms and bulbs sometimes present. Shoot apex with 1 or 2 tunica layers. Stems jointed, terete to somewhat flattened, rarely quadrangular, erect, ascending, or prostrate; in some biennials and perennials forming sterile tufts of leaves (innovations) that later grow into fertile stems; branching absent or at the upper nodes, sometimes from dormant buds, and near the ground by tillering intravaginally, the plants then often caespitose (FIGURE 10a), or extravaginally and then often stoloniferous or rhizomatous (FIGURE 4a); all vegetative branches bearing 2-keeled prophylls proximal on the adaxial surface of the branch and perpendicular to the plane of distichy of succeeding leaves; internodes growing by basal intercalary meristems, hollow or solidly filled with parenchyma; vascular bundles scattered to more or less concentrated toward the periphery; nodes transversely septate [armed with spines or thorns].

Leaves distichous [phyllotaxis 3/8 in the Australian endemic *Micraira* F. Mueller], green or glaucous from 2-β-diketone-containing waxes, and usually consisting of sheath, ligule, and blade, the sheaths and blades growing by basal intercalary meristems. Sheaths tightly encircling and supporting the stem (FIGURE 4b), the margins overlapping or, less commonly, united to form a tube. Ligules consisting of a membranaceous flange or a fringe of hairs at adaxial apex of sheath (FIGURES 4b, 6b, 8b, 10d), rarely absent. Blades simple, 1–150 cm [5 m] long, entire, usually linear, less often lanceolate to ovate [sagittate or cordate], flat, involute, convolute, or terete, sometimes deciduous from the sheath, continuous with the sheath or petiolate [the petiole twisting], sometimes dimorphic (much reduced on the main stem and normal on the branches), usually absent from leaves on rhizomes; venation parallel, rarely pinnate, cross-veins absent to prominent; small basal auricles often present (FIGURE 6b). Leaf epidermis (FIGURE 1) composed predominantly of files of long (length considerably greater than width) and short (more or less isodiametric) cells; walls of long cells sinuous or straight, with or without small epidermal protrusions (papillae); short cells usually occurring over veins, often absent from between veins, arranged in files of 5 or more, mainly paired or solitary, in short rows, or in mixtures of 1's, 2's, and short rows, often containing cork bodies or silica bodies, sometimes modified into usually apically pointing hooks or prickles (the latter larger than the former) or microhairs; silica bodies sinuous or crenate, cross to dumbbell shaped or nodular, tall and narrow, saddle shaped, crescentic, or oryzoid; microhairs usually in or between stomatal rows, usually bicellular, rarely unicellular [3- or 4-celled], the apical cell spherical to linear; stomata paracytic, biperigynous (i.e., the subsidiary and guard cells not derived from the same meristematic cell), raised above or at the same level as surrounding epidermal cells, with parallel-sided to triangular subsidiary cells; macrohairs unicellular, rarely multicellular, intergrading with prickles; 2-celled salt glands found in some halophytes and their relatives. Transverse-sectional anatomy of leaves (FIGURE 2) either C_3 or C_4—see discussion below; midrib bundle(s) 1 or more than 1 and either arranged in an arc or not, conspicuous or inconspicuous; vascular-bundle sheaths usually 2, an inner, thick-walled, endodermal mestome sheath and an outer parenchyma sheath, less often only 1 sheath present, rarely 3; sclerenchyma associated with all or nearly all vascular bundles, or only with larger bundles, as girders connecting the bundle and epidermis or as strands not reaching the epidermis; "arm" or "ratchet" cells with invaginated walls and large, elongated "fusoid" cells present or absent; simple, fan-shaped groups of bulliform cells present or absent in the adaxial epidermis; colorless cells sometimes traversing the mesophyll or forming deeply penetrating fans, narrow groups penetrating into the mesophyll, or arches over small bundles; palisade parenchyma rarely present.

Primary inflorescence a spikelet (FIGURES 3–11) composed of an axis, the rachilla (FIGURES 3F2, G2; 4g; 5A2, B2, C2; 6j, k; 7D2, I2), bearing distichously [spirally] arranged and closely overlapping basal bracts (glumes) and florets; disarticulating above the glumes or as a unit and with or without other spikelets; dorsally compressed (perpendicular to the plane of distichy; FIGURE 10n) or laterally (parallel to the plane of distichy; FIGURE 4c); the base sometimes formed into a hard, often pointed and/or hairy callus (FIGURE 3A3); sometimes viviparous (containing bulbils or bearing germinating seeds while still attached to the plant) or proliferating (i.e., converted into a leafless shoot, usually by growth of the lemmas); rarely subterranean. Spikelets borne in terminal or terminal and lateral secondary inflorescences of various kinds: panicles (FIGURES 4a; 10b, c), false panicles, cymes, racemes, rames (FIGURE 8a, k), and spikes (FIGURE 6c) that mature either basipetally or acropetally and basipetally from the middle and that may or may not be associated with leaves or bladeless sheaths. Glumes proximal on the rachilla (FIGURE 4c), usually 2, equal (FIGURE 4d) or unequal (FIGURES 5A1, 10f) in size and appearance, sometimes 1 (FIGURE 5D2) (then usually the upper) or absent, awned or unawned, 0- to several-nerved, and subtending no axillary structures. Florets (FIGURES 3–11) maturing acropetally within a spikelet, made up of a bract (the lemma) subtending a flower and a bract (the palea) lying between the flower and the rachilla, 1–30 (–50) per spikelet; uppermost floret terminal or subterminal (with the rachilla therefore prolonged above it); base of florets sometimes formed into a hard, often hairy or pointed callus (FIGURES 4e, k; 5J3; 7C2). Lemmas similar or dissimilar to the glumes in texture or appearance, indurate or membranaceous, 0- to several-nerved; awn(s) 0, 1, or more, apical or abaxial, straight or hygroscopically sensitive and basally twisted and geniculate. Paleas with 2, infrequently 0, 1, or more than 2, nerves, often hyaline, sometimes absent, rarely awned, usually smaller than and more or less enclosed by the lemma.

Flowers (FIGURES 4i, 6h, 8h, 10h) small, perfect or imperfect (the plants then variously monoecious or dioecious), anemophilous, rarely entomophilous, mostly protandrous, greatly reduced relative to most other monocotyledons in the size and number of floral parts. Lodicules (the outermost floral parts) 2 and located adjacent to the lemma and opposite the palea, less often 3, rarely 1 [or more than 3], translucent, veined or veinless, glabrous or hairy, apically thick or thin, toothed, pointed or truncate, rarely adnate to palea. Stamens hypogynous, 6 in 2 whorls of 3 or, more commonly, only the 3 outer present, less often 1, 2, or 4 [to 30]; filaments slender, free or connate; anthers (FIGURES 4h, 6f, 8i) 4-sporangiate, 2-locular at anthesis, appearing versatile, dehiscing extrorsely (or in the stamen between the lodicules, introrsely) by longitudinal slits or terminal pores; anther wall formation of the monocotyledonous type; [staminodes present]. Pollen (FIGURES 6g, 8j) trinucleate when shed, monoporate, operculate, more or less spheroidal-ovoid, (14–)20–55(–130) μm in diameter, very ephemeral, the sexine granular. Gynoecium tricarpellate, syncarpous. Styles 2, less often 1 or 3, terminal or rarely subterminal, free or connate; stigmas (FIGURES 3C3; 4f, g, i, l; 6e, h, i, k; 7A2, A3; 8a, c, h; 9A1, A5, B5; 10e, h) dry, plumose, white or colored, free or connate. Ovary superior, unilocular, uniovular, smooth or hairy. Ovule anatropous, hemianatropous, campylotropous, or orthotropous, bitegmic, rarely the integuments 1 or none, pseudocrassinucellate or sometimes tenuinucellate; micropyle formed by the inner integument; megasporogenesis of the Polygonum (rarely Adoxa) type; antipodals proliferate (3).

Fruit (FIGURES 6n, 8m, 10j) a single-seeded caryopsis (grain), in which the pericarp is adnate to the seed, or when the pericarp is free, an achene or utricle [or berry], often associated with parts of the floret or spikelet for dispersal; hilum punctiform to linear and more than ½ the length of the fruit; endosperm (FIGURES 4m, 6m, 10k) present or absent, hard or milky, with or without lipids, its development nuclear; starch grains simple or compound. Embryogeny of the asterad type; embryo achlorophyllous, basal and lateral (FIGURES 4m, 6m, 10k), from $\frac{1}{10}$ of the length of the seed to equal to it; radicle ensheathed by the coleorhiza; plumule ensheathed by the coleoptile; scutellum large, flat, adjacent to the endosperm, haustorial, its base free from (FIGURES 8n, 10l) or adnate to

(FIGURE 4n) the coleorhiza; epiblast (a small, nonvascularized outgrowth opposite the scutellum; FIGURE 4n) present or absent; vascular bundles to scutellum and coleoptile separated by an internode (the embryo mesocotyl; FIGURES 8n, 10l) or not separated (FIGURE 4n); plumule leaves with many to few vascular bundles, margins either overlapping (FIGURES 8o, 10m) or not (FIGURE 4o). Seedlings (FIGURE 8p–r) with adventitious roots present or absent at scutellar and coleoptilar nodes; first several leaves above coleoptilar node with or without a well-developed blade; first well-developed blades either broad and horizontal to ascending or more or less narrow and erect. Chromosomes mostly with median to submedian centromeres, the base numbers primarily 7, 9, 10, and 12. (Including Agrostidaceae Burnett, Andropogonaceae Herter, Anomochloaceae Nakai, Arundinellaceae Herter, Avenaceae Burnett, Bambusaceae Burnett, Chloridaceae Herter, Eragrostidaceae Herter, Festucaceae Herter, Graminaceae Lindley, Hordeaceae Burnett, Lepturaceae Herter, Miliaceae Burnett, Oryzaceae Burnett, Panicaceae Herter, Parianaceae Nakai, Phalaridaceae Burnett, Saccharaceae Burnett, Spartinaceae Burnett, Sporobolaceae Herter, Stipaceae Burnett, and Streptochaetaceae Nakai.) TYPE GENUS: *Poa* L.

References used in family description: Anton & Astegiano; Arber (1925, 1934); Avdulov; Barnard; Beetle (1980); Bor; W. V. Brown (1958a, 1977); W. V. Brown, Harris, & Graham; W. V. Brown & Johnson; Burns; Calderón & Soderstrom (1973); Cheadle (1955); Clayton (1970, 1978); Clifford & Watson; Cronquist; Davis; Ellis (1976, 1979); Evans; Gibbs; Gould & Shaw; Hackel (1890); Harborne & Williams; Hitchcock; Hubbard (1973a); Jacques-Félix (1962); Lipschitz & Waisel; McClure (1973); Metcalfe (1960); Monod de Froideville; J. S. Page; Pohl; Reeder (1957); Roshevits; Row & Reeder; Soderstrom (1981a); Stapf; Stebbins (1982); Tulloch & Hoffman; Wagner; and Yakovlev & Zhukova.

A very natural family, the fourth largest in the flowering plants (about 600 genera and 10,000 species) and the foremost in ecological and economic importance. Species occur on all continents, in desert to freshwater and marine habitats, and at all but the highest elevations. Communities dominated by grasses (e.g., the North American prairie and plains, the South American pampas, the Eurasian steppes, and the African veld) account for about 24 percent of the earth's vegetation (Schantz). The grassland communities of the southeastern United States (e.g., the Pennyroyal area of Tennessee and the Black Belt of Alabama) occupy small areas, but grasses are major components of the flora, with 130 genera—about ten percent of the total number of angiosperm genera.

A division of the family into two major groups (the pooids and the panicoids) based on the structure of the spikelet, the basic unit of the inflorescence, and dating from Robert Brown (1810, 1814), was used in most floras through the first half of this century. Evidence from leaf and embryo anatomy, from chromosome number and size, and from a remarkably broad series of morphological, anatomical, physiological, chemical, cytological, and phenological studies has subsequently led to the recognition by most workers of from five to eight subfamilies and as many as 60 tribes. All five of the subfamilies recognized here (Bambusoideae, Arundinoideae, Pooideae, Chloridoideae, and Panicoideae) have indigenous members in the southeastern United States, and the 21 tribes that occur there include most of the major ones in the family.

Difficulties with grass taxonomy at all levels stem from a number of features. First, the great reduction in size and complexity of reproductive parts has limited the use of characters that are taxonomically useful in many other families (Stebbins, 1982). Second, parallelism is believed to be frequent in the family (Arber, 1934; Hubbard, 1948; Prat, 1960; Stebbins & Crampton; Decker; Phipps; Guédès & Dupuy; Renvoize, 1981; Estes & Tyrl). Third, two common aspects of the breeding system of grasses—hybridization, with the attendant phenomena of polyploidy and apomixis, and inbreeding—have obscured taxonomic boundaries and made the biological species concept difficult to apply to many grasses.

SYSTEMATICS, PAST AND PRESENT

In his sexual system of classification, Linnaeus recognized 38 genera of grasses in six groups. His knowledge of the morphology of grasses was as limited as his sytematic treatment, for he was not clear about the nature of the "spicula" (his term for the spikelet; see Jacques-Félix (1972) for a multilingual etymology of the parts of grass spikelets and flowers). Robert Brown (1814) interpreted the spikelet as a modified inflorescence consisting of an "outer envelope or gluma" (the latter term taken from Jussieu) and an "inner envelope" (the calyx of Jussieu, i.e., the lemma and palea). He considered the "inner valve" (the palea) to be homologous with two fused members of the "proper envelope" (outer perianth whorl) and the "squamae" (lodicules) to be derived from the inner perianth whorl. He defined (1810, 1814) the Paniceae (the Panicoideae of modern authors), a mostly tropical group bearing spikelets with two florets, of which the lower is imperfect, and the Poaceae (the Pooideae), a group mostly of temperate climates, the spikelets of which contain one to many florets, with the imperfect florets, if present, not basal. This remarkably perceptive taxonomic insight is supported by a wealth of data (see below), and it orders suprageneric studies in the family even to the present. The gradual accumulation of taxonomic knowledge of the tribes and genera of the family through the efforts of Palisot de Beauvois, Trinius (1820, 1824), Dumortier, Kunth, and others culminated in the cosmopolitan treatments of Bentham, Bentham & Hooker, and Hackel (1887). These classifications include a dozen or more tribes in two subfamilies corresponding to Brown's subdivisions.

The classifications of Bentham & Hooker and of Hackel rely almost exclusively on gross morphology, especially that of the inflorescences. At about the same time many workers were uncovering systematically useful variation in leaf anatomy (Duval-Jouve, T. Holm, Pée-Laby), in embryology (Van Tieghem), and in the nature of starch grains in the endosperm (Harz). In spite of the patent taxonomic value of these works, they were largely ignored, perhaps because of major incongruities with morphological classifications. The work of Avdulov (1931) on the size and base numbers of chromosomes and that of Prat (1932, 1936) on the leaf epidermis emphasized the synthesis of morphological and nonmorphological data in grass systematics. They initiated redefinition of the Pooideae by removing the chloridoid grasses. These had traditionally been grouped with the pooids because of spikelet characters, but new characters clearly showed them to be much closer to panicoids. Each also established an additional major subdivision, Avdulov's series Phragmitiformes and Prat's Bambusoideae.

The subsequent search for new taxonomic data and the use of these in establishing subfamilial relationships have been highly productive. While variation in some characters (e.g., pollen morphology (J. S. Page) and flavonoid chemistry (Harborne & Williams)) is small throughout the family, a diverse series of morphological, anatomical, physiological, chemical, cytological, and phenological features provides useful taxonomic information (see Reeder, 1957; Bor; Metcalfe, 1960; Prat, 1960; Tateoka, 1960; Stebbins & Crampton; Jacques-Félix, 1962; Auquier; Clifford & Watson; and Gould & Shaw for additional discussions of taxonomically useful variation). As a rule, this array of characters distinguishes not only the two extremes of the family, the panicoid and pooid groups, but also one or more of the other subfamilies recognized here.

The contrasts given in the paragraphs that follow are intended to show the breadth of characters separating the panicoids and pooids in the restricted, modern sense. The wider taxonomic use of each of these characters, if one exists, will be detailed later.

The pooids accumulate fructosans as the predominant reserve polysaccharide; panicoids accumulate starch (De Cugnac; D. Smith, 1968). Pooid caryopses contain consistently higher levels of alanine, methionine, and phenylalanine than do those of panicoids (Yeoh & Watson). Taira also pointed out differences in amino-acid composition of the two groups. Fairbrothers & Johnson and P. Smith demonstrated a clear serological distinction between pooid and panicoid grasses.

In pooids the nucleoli do not persist beyond metaphase and do not appear to lie within a lumen during interphase, but in panicoids they do persist and are surrounded by a lumen (Avdulov; Brown & Emery, 1957). Vessels tend to be more specialized in pooids than in panicoids (Cheadle, 1960). Pooid shoot apices mostly have two tunica layers, and panicoids one layer (Brown, Heimsch, & Emery). Goller established differences between pooid and panicoid anatomy of the cortex and stele of the root. Pooid root hairs are directed toward the root apex and come from relatively small epidermal cells alternating with larger cells, while panicoid root hairs tend to emerge at right angles from uniformly sized cells (Row & Reeder). Hitch & Sharman noted several differences in the vascular patterns of pooid and panicoid axes. Pooids tend to have a definite sheath pulvinus and no culm pulvinus; panicoids usually bear a culm pulvinus but a poorly developed sheath pulvinus (Brown, Pratt, & Mobley; Ebinger & Carlen). Brown, Harris, & Graham found that pooid stem internodes are mostly hollow, panicoid internodes mostly solid. On the basis of the nature of the vascular-bundle sheaths, De Wet (1960a) and Auquier & Somers set up groups that correspond well to those based on leaf transverse-sectional anatomy established by Brown (1958a, 1977) and Carolin and colleagues (see below). The second and third leaves of seedlings are less differentiated in pooids than in panicoids when the shoot breaks through the coleoptile (Stebbins & Crampton).

The absence of bicellular microhairs from the leaf epidermis of pooid grasses separates them from panicoids (Tateoka *et al.*; Johnston & Watson, 1977). Pooids generally have horizontally elongated or crenate silica bodies and sunken stomata bordered by parallel-sided subsidiary cells, while in panicoids the epidermis bears cross- or dumbbell-shaped or nodular silica bodies, and the stomata are flush with the rest of the epidermal cells and have triangular subsidiary cells (Prat, 1936; Clifford & Watson; Watson & Johnston). Pooid guard cells tend to be semicircular in cross-sectional outline, and the membrane is absent or rudimentary, while panicoid guard cells are angular and have a well-developed membrane (Brown & Johnson).

In addition to the spikelet differences upon which Robert Brown founded his two subdivisions, pooid spikelets tend to be compressed laterally, to disarticulate above the glumes, and to have the rachilla extending above the uppermost floret. In contrast, panicoid spikelets tend to be compressed dorsally, to disarticulate below the glumes, and to have the rachilla ending at the uppermost floret. They also tend to be viviparous less often than pooid spikelets (Beetle, 1980). Vasculature of the spikelets of the two groups differs (N. Chandra, 1962). In pooids the three or four nodes below the inflorescence do not bear branches, while in panicoids all but the uppermost node below the inflorescence bear branches or buds (Latting). The lemmas of pooids do not have germination flaps, while all panicoid lemmas studied so far have them (Johnston & Watson, 1981). Lodicules are thin, nonvascularized, and truncate in pooids and thick, heavily vascularized, and acute in panicoids (Decker; Tateoka, 1967; Jirásek & Jozífová).

The diffusible pollen-wall antigens of pooids and panicoids are immunologically distinguishable from each other (Wright & Clifford, Watson & Knox). Pooid ovules often have short outer integuments, no periclinal divisions in the nucellar epidermis, and laterally positioned antipodals. Long outer integuments, periclinal divisions, and chalazally positioned antipodals characterize panicoid ovules (N. Chandra, 1963). Numerous studies have shown that gametophytic apomixis in pooids is mostly (three out of four genera) diplosporous, and that the mature apomictic megagametophyte has the usual complement of nuclei. Apomictic panicoids are usually (18 out of 19 genera) aposporous, and their asexually derived megagametophytes contain only four nuclei (Brown & Emery, 1958; Reddy; Connor, 1979).

Reeder (1957, 1962) used four characteristics of the mature embryo to sort grasses into six groups (see below), including a pooid and a panicoid group. Genera with liquid or soft endosperm are found only among pooid grasses (Terrell). Starch grains are mostly smooth walled and either simple or compound in the pooids, and angular walled and usually simple in the panicoids (Harz; Tateoka, 1962). The germination of pooid seeds is inhibited more by isopropyl carbamate and low oxygen tensions than is that of panicoid seeds (Al-Aish & Brown). Pooid seedlings have narrow and erect or ascending leaves and often produce transitionary node roots. Panicoid seedling leaves are broad and horizontal and do not have transitionary node roots (Avdulov, Kuwabara, Hoshikawa).

Large chromosomes with a base number of seven characterize pooids, while small ones in multiples of nine or ten are found in panicoids (Avdulov; Tateoka, 1960). Different viruses and fungi attack pooid and panicoid hosts (Watson; Watson & Gibbs; Savile). Finally, Robert Brown's early observation about the different geographic distributions in pooid and panicoid grasses has been supported by more recent studies (Hartley, 1950; Clayton, 1975, 1981a; Cross).

There are numerous exceptions to these differences between pooid and panicoid grasses. In addition, many characters define groups distinct from the pooids and panicoids and corresponding to other suprageneric taxa. Furthermore, there is a strong congruence between the various groups established on the basis of these diverse characters. The most striking congruences come from leaf anatomy, embryo anatomy, and karyotypes.

Some of the best evidence for relationships at the subfamilial and tribal levels in grasses is from leaf anatomy. The abaxial epidermis of the blade provides two excellent diagnostic features. First, bicellular microhairs are generally found in all subfamilies except the Pooideae (FIGURE 1a), from which they are uniformly absent (Tateoka *et al.*; Johnston & Watson, 1977). Variation in the shape and wall thickness of the distal cell is useful in distinguishing the Chloridoideae (FIGURE 1d) from the Panicoideae (FIGURE 1c). Second, the shape and distribution of silica bodies often characterize tribes or subfamilies (Prat, 1932, 1936; Metcalfe, 1960; Clifford & Watson; see APPENDIX, characters 52–58). The shape of stomatal subsidiary cells is of secondary value.

Light- and electron-microscope studies of the transverse-sectional anatomy of leaves (Duval-Jouve; Brown, 1958a, 1975, 1977; Carolin *et al.*; Johnson & Brown) have established two extremes in grasses. At one extreme is the presence of a well-developed mestome sheath (presumably with endodermal functions) around the vascular bundles; a parenchyma sheath (outside the mestome sheath) with chloroplasts similar to those of the surrounding mesophyll cells; and irregularly arranged chlorenchyma cells in the mesophyll. At the other extreme the mestome sheath is either present or absent, and there are specialized, thick-walled photosynthetic cells located in bundle sheaths or rarely in the mesophyll. The chloroplasts of these specialized sheath cells are radially or tangentially arranged and are larger and more numerous than the chloroplasts in the mesophyll; there are many plasmodesmatal connections between the specialized cells and mesophyll; and the mesophyll cells are more or less radially arranged around the vascular bundles. The first extreme reflects the C_3 photosynthetic pathway and characterizes the Pooideae (FIGURE 2b), the Bambusoideae (FIGURE 2a), most of the Arundinoideae, and 20 percent of the Panicoideae. The other extreme, known as the "kranz syndrome,"[2] is associated with the C_4 pathway. It occurs uniformly in the Chloridoideae (FIGURE 2c), in most Panicoideae (FIGURE 2d), and in about 10 percent of the genera of the Arundinoideae. The best histological predictor of the photosynthetic pathway is the "one cell distant criterion" (Hattersley & Watson, 1975, 1976): in C_4 plants no chlorenchyma mesophyll cell is more than one cell away from the parenchyma sheath, while

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[2] "Kranz" is a German noun, meaning ring or wreath (W. V. Brown, 1977), and hence capitalized in German. In accounts in English, capitalization has been retained, as though of some significance. Since kranz is not a proper noun, lower case is used here to avoid possible confusion with the name of a person.

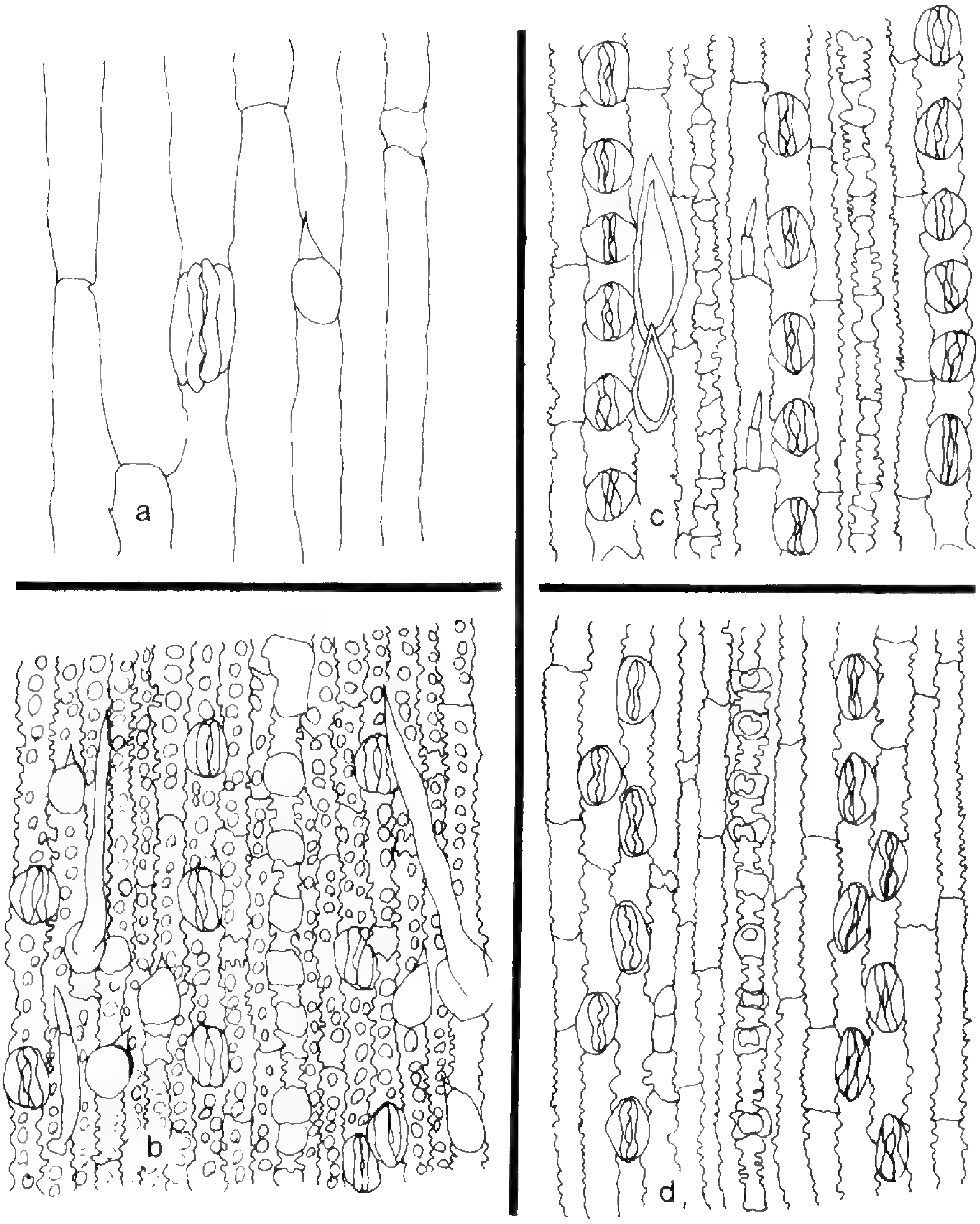

FIGURE 1. Camera-lucida drawings of abaxial leaf epidermises (leaf apex toward top) prepared according to hot-acids method of Steward and observed with phase-contrast microscopy, all × 130. a, *Elymus Hystrix* (*Hystrix patula*; Pooideae, Triticeae): note straight cell walls of long cells, parallel-sided stomatal subsidiary cells, and prickle hair. b, *Arundinaria gigantea* (Bambusoideae, Arundinarieae): note narrow distal cell of bicellular microhair, sinuous cell walls of long cells, papillae on long cells, nodular and more or less saddle-shaped silica bodies, dome-shaped stomatal subsidiary cells, and large macrohair. c, *Andropogon virginicus* (Panicoideae, Andropogoneae): note narrow distal cell of bicellular microhairs, sinuous cell walls of long cells, dumbbell-shaped to nodular silica bodies, more or less triangular stomatal subsidiary cells, and prickle hairs. d, *Tridens flavus* (Chloridoideae, Cynodonteae): note inflated distal cell of bicellular microhair, sinuous cell walls of long cells, dumbbell-shaped to nodular silica bodies alternating with cork cells, and more or less triangular stomatal subsidiary cells.

in C_3 plants some mesophyll cells are. All subfamilies, tribes, and genera (as circumscribed here) are uniformly either C_3 (non-kranz) or C_4 (kranz), except the Arundinoideae and Panicoideae (B. N. Smith & Brown; Brown, 1977; Renvoize, 1981), in which both pathways occur.

The kranz bundle-sheath of some C_4 grasses is derived from a mestome sheath (MS), and the chloroplasts are centrifugally positioned and contain either no grana or only small ones (Brown, 1977). In species with this MS subtype of kranz anatomy, the four-carbon compound transported into kranz cells is decarboxylated by NADP-malic enzyme (NADP-me). The kranz sheath of other C_4 grasses is derived from the parenchyma sheath (PS), and the four-carbon compound in this PS subtype of kranz anatomy is decarboxylated by one of two enzymes: PEP-carboxykinase (PCK or PEP-ck) is associated with a centrifugal position of the kranz bundle-sheath chloroplasts, NAD-malic enzyme (NAD-me) with a centripetal position. The significance of the difference between the PCK and NAD-me kinds of the PS subtype of kranz anatomy is not understood. There is, however, a clear association between systematics and variation in kranz anatomy (see discussion under the C_4 taxa and character 67 of the APPENDIX).

Plants with the C_3 pathway and those with the C_4 differ in numerous physiological ways: in the first intermediate into which atmospheric CO_2 is fixed, in carbon-isotope ratios, in light-saturation levels of photosynthesis, in temperature optima of photosynthesis, in photosynthetic translocation efficiency, and in CO_2 compensation point (Björkman & Berry; Brown, 1977; Ehleringer; Waller & Lewis). The C_4 pathway provides a high concentration of CO_2 in the parenchyma sheath and thereby allows higher photosynthetic rates in habitats with high light intensities and temperatures and low soil moisture (McWilliam & Mison). Low temperatures during growth offset the advantages of the C_4 pathway. Finally, the physiological differences between C_3 and C_4 grasses are associated with different geographic distributions. In North America the greatest relative abundance of C_4 species is found where the minimum temperature during the growing season is highest (Teeri & Stowe).

Other characters pertaining to transverse-sectional anatomy of the leaf have more or less unique states in certain subfamilies or tribes (Brown, 1958a; Clifford & Watson; also see below).

Reeder's (1957, 1962) embryological studies revealed four important characters, for each of which he determined two states, one found in the Panicoideae (designated "P") and the other in the Pooideae (designated "F" for Festucoideae, now a synonym of the Pooideae): presence (P) or absence (F) of an internode between the scutellar and coleoptilar nodes; presence (designated by a "+" and characteristic of the Pooideae) or absence (designated by a "−," the panicoid state) of a small flap, the epiblast, opposite the scutellar node; presence (P) or absence (F) of a cleft between the scutellum and the coleorhiza; and transverse section of the first embryonic leaf showing few vascular bundles and nonoverlapping margins (F) or many vascular bundles and overlapping margins (P). Hence the Pooideae are F + F F (FIGURE 4n, o) and the Panicoideae P − P P (FIGURES 8n, o; 10l, m). The five subfamilies in this paper have unique combinations of these four characters (see characters 38–41 in the APPENDIX). Five of the six embryological groups established by Reeder are the same as five of the six groups based on transverse leaf anatomy (Brown, 1958a; Carolin *et al.*).

The distribution of Avdulov's character states of chromosome size and base number divides the Gramineae into his three major subfamilial groups. His Sacchariferae have small chromosomes with base numbers of nine or ten. This group is basically the kranz subfamilies Panicoideae and Chloridoideae. His Poatae contain two "series": Festuciformes, with large chromosomes and base number usually seven, equivalent to the Pooideae; and Phragmitiformes, with small chromosomes in multiples of twelve, including the balance of the family.

While the works of Avdulov and Prat released grass systematics from the two-subfamily system, those of Reeder (1957, 1962) and Brown (1958a, 1977) have tended to stabilize formal classifications at five to eight subfamilies (Tateoka, 1957a; Prat, 1960; Parodi; Stebbins & Crampton; Clayton, 1978; Renvoize, 1981; Hilu & Wright; Gould & Shaw). Some agrostologists (Jacques-Félix, 1962; Clifford & Goodall; Hubbard, 1973b; Clifford & Watson), however, appreciating the taxonomic uncertainties at the highest subfamily levels, employ many more informal groupings.

The subfamilial classification used here consists of the Bambusoideae, Arundinoideae, Pooideae, Chloridoideae, and Panicoideae. Subfamily Bambusoideae is broadly conceived as encompassing the woody bamboos, the so-called herbaceous bambusoid grasses (e.g., the Phareae) (Tateoka, 1957a; Parodi; Clayton, 1978; Soderstrom & Calderón, 1979a; Renvoize, 1981; Hilu & Wright), and the oryzoid grasses (Jacques-Félix, 1955, 1962; Tateoka, 1957a; Clayton, 1981a; Renvoize, 1981). Since its conception as Avdulov's Phragmitiformes, subfam. Arundinoideae has encompassed a diverse assemblage of grasses united, not by the presence of specialized features, but by a general lack of specialization. As such, it presents both the greatest subfamilial taxonomic problem and the greatest potential source of insights regarding relationships at this level. Renvoize's (1981) concept of this subfamily, followed here, includes the Centotheceae (the Centothecoideae of Soderstrom (1981b)), the Aristideae, and the core tribe Arundineae, as well as other tribes not occurring in the southeastern United States. Subfamily Pooideae, a heterogeneous group even after the transfer of C_4 grasses to the Chloridoideae, has become more sharply defined by the removal of three traditionally pooid tribes, the Brachyelytreae, Diarrheneae, and Stipeae, by Macfarlane & Watson (1980, 1982). These three tribes do not fit well into any of the five subfamilies and are therefore treated here as unplaced. The composition of the Chloridoideae is similar to that of most systems of the past 30 years, but the tribal limits are broader here. The only major systematic question is the placement of tribe Aristideae. Some (Pilger; Parodi; Clayton, 1978; Hilu & Wright; Gould & Shaw) consider it to be chloridoid, but its closeness to *Danthonia* DC. and its relatives (Brown, 1977) argues for including it in the Arundinoideae, as Reeder (1957), Tateoka (1957a), Prat (1960), Stebbins & Crampton, Jacques-Félix (1962), and Renvoize (1981) did. Robert Brown's (1810, 1814) delimitation of the Panicoideae (as the Paniceae) persists with minor changes to the present.

The works of Butzin and of Clayton (1981c; in prep.) are important sources for answers to nomenclatural questions at the suprageneric level.

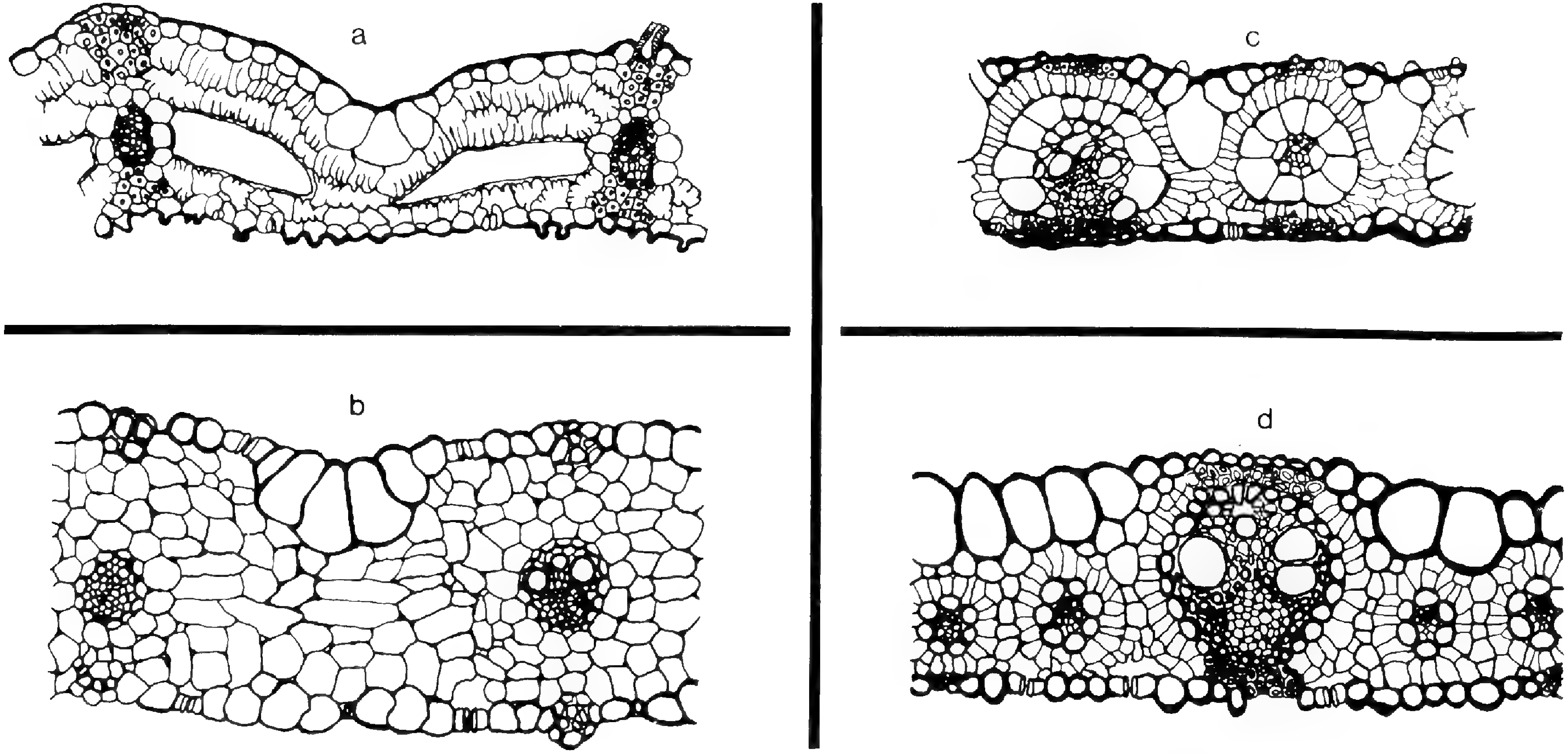

FIGURE 2. Drawings of portions of transverse sections of leaves. a, *Arundinaria variegata* (Bambusoideae, Arundinarieae; after Metcalfe (1960), *fig. XVIII, no. 3*): note numerous cells separating veins, indicating C_3 photosynthesis; large, elongated fusoid cells and arm or ratchet cells with invaginated cell walls; and sclerenchyma associated with vascular bundles. b, *Phalaris tuberosa* (Pooideae, Agrostideae; after Barnard, *fig. 4.22*): note numerous cells separating veins, indicating C_3 photosynthesis; 2 bundle sheaths; bulliform cells in upper epidermis; and stomata in both upper and lower epidermis. c, *Tragus racemosus* (Chloridoideae, Zoysieae; after Jacques-Félix (1962), *fig. 153B*): note short interveinal distance indicative of C_4 photosynthesis, large parenchyma sheath cells, bulliform cells, and thickened cuticle. d, *Andropogon Gerardii* (Panicoideae, Andropogoneae; after Barnard, *fig. 4.21*): note short interveinal distance indicative of C_4 photosynthesis, 2 bundle sheaths, sclerenchyma associated with vascular bundles, bulliform cells in upper epidermis, and stomata confined to lower epidermis.

PHYLOGENETIC RELATIONSHIPS

The presence of numerous unique features makes the family Gramineae readily distinguishable from all other monocotyledons. Only two of its genera, *Anomochloa* Brongn. and *Ochlandra* Thw., are questionably graminaceous (Arber, 1934; Hubbard, 1948; Clifford, 1961). The distinctive bicellular microhairs of grasses may be derived from the multicellular hairs found in many monocotyledons (Stebbins, 1982). The complex development of the inflorescence characteristic of many grasses is not known outside the family (Stebbins, 1972), nor are structures strictly equivalent to the grass spikelet and its glumes, lemmas, and paleas. The anatomy of the grass stigma is unique (Y. Heslop-Harrison & Shivanna). Grasses are exceptional in having both gametophytic self-incompatibility and tricellular pollen (J. Heslop-Harrison). Finally, the coleoptile, epiblast, coleorhiza, and scutellar and coleoptilar nodes are peculiar to the grass embryo. Questions about the homologies of these unique features are still not fully answered.

Most agrostologists agree that grass perianths are derived from a trimerous, biseriate state but disagree about what has happened to the perianth in the evolution of the grass flower. Hackel (1881) thought that the palea was a modified prophyll because of its position and two nerves. Holttum, Bor, Hubbard (1973a), Clifford & Watson, Clayton (1978), Soderstrom (1981a), and many others also take this view, but Bourreill (1969) regarded the palea as homologous with a leaf sheath. A sepaloid origin of the palea was first hypothesized by Robert Brown (1814) and was supported by Bentham, Schuster, Stebbins (1972, 1982), and Cronquist. Virginia Page studied the unusual spikelets of the bambusoid genus *Streptochaeta* Schrader, which has two large, basally fused "palea bracts" (her term designating the position of the structures and not necessarily their equivalence to the palea of other grasses). Although she confirmed earlier reports of the separateness of the two palea bracts and the presence of a primordium of a third bract in the same whorl, she neither verified nor falsified the sepaloid homology of the palea. She suggested that the palea bracts of *Streptochaeta* might instead be sterile bracts or lemmas, a view also taken by Soderstrom (1981a). Hackel (1881) apparently thought the perianth to be totally absent from grass flowers, for he saw the position of the lodicules (between the lemma and the androecium in grasses with two lodicules) as evidence of their being two halves of a bract that continues the distichy of the spikelet. Arber (1934) pointed out that lodicules surely must be modified perianth parts because intermediates between stamens and lodicules can be found. According to Guédès & Dupuy, the fundamentally peltate nature of the lodicules confirms their petaloid origin.

With respect to the embryo, the nature of the scutellum is involved in interpretations of other parts. Brown (1960a), who also reviewed the extensive literature on homologies of the parts of the grass embryo, postulated that neither the scutellum nor the coleoptile is foliar because they do not arise from the shoot apex. He considered them to be parts of the cotyledon separated by an intercalated meristem, the mesocotyl. Cocucci & Astegiano suggested that the scutellum, coleoptile, and epiblast are lamina, ligule, and sheath, respectively, of the foliar cotyledon. Shah & Sreekumari proposed that the scutellum, the coleoptile, and even the coleorhiza are parts of the cotyledon. The prevailing view holds that the scutellum and coleoptile are homologous with the cotyledon and first leaf of the shoot, respectively (Reeder, 1953, 1956; Guignard; Negbi & Koller; Guignard & Maestre). The formation of typical leaf hairs and chlorophyll in these structures supports this interpretation (Norstog). Because of the position of the epiblast opposite the scutellum, some (e.g., Negbi & Koller; see also Brown, 1960a) have seen it as a much-reduced second cotyledon. However, that the epiblast is actually an outgrowth of the coleorhiza is widely supported by observation (Brown, 1960a; Guignard; Soderstrom, 1981a) and experimentation (Foard & Haber). Apparently it is never vascularized (Reeder, pers. comm.). The predominant view of the coleorhiza is that it is homologous with the primary root or at least with the outer covering of the primary root (Guignard; Negbi & Koller; Guignard & Maestre).

In view of these specialized features, it is not surprising that the Gramineae are separated from other families by a large gap and that, as a result, their systematic relationships are poorly understood. The families most frequently considered as close relatives are the Cyperaceae, the Flagellariaceae, and the Palmae (Clifford, 1970; Dahlgren & Clifford). The resemblance in overall appearance and spikelet morphology of the Gramineae and the Cyperaceae has led to their union in various suprafamilial taxa. The two also have silica bodies in the leaf epidermis (Metcalfe, 1960, 1971), similar flavonoid patterns (Harborne & Williams), similar micropyles and ovules (Maze *et al.*), and nuclear endosperm formation (Dahlgren & Rasmussen). They are the only monocotyledonous families with C_4 species (Waller & Lewis). These similarities are, however, only superficial and may well represent parallel evolution (Metcalfe, 1971; Clayton, 1978). Many fundamental differences separate the two families. The bracts of the sedge spikelet are more often spirally than distichously arranged, and the similarity between sedge and grass spikelets is not close (Stebbins, 1982). Sedges also have differently shaped silica bodies (Metcalfe, 1971), pollen grains with more than one aperture (S. Chandra & Ghosh), simultaneous rather than successive microsporogenesis (Dahlgren & Rasmussen), embryos embedded in endosperm, several embryological features unlike those of grasses (Guignard; Clifford, 1970; Maze *et al.*; Maze & Bohm, 1973), lateral rather than terminal flowers, and diffuse centromeres. The Cyperaceae appear actually to lie closer to the Juncaceae (Takhtajan; Soo; Metcalfe, 1971; Stebbins, 1982; Dahlgren & Rasmussen), and the grasses share more features with the Flagellariaceae or the Joinvilleaceae, a segregate of the Flagellariaceae (Tomlinson & Smith). The Gramineae and Joinvilleaceae have both long and short epidermal cells that often have sinuous walls, similar stomata (Smithson), ulcerate pollen (S. Chandra & Ghosh), and some similar vegetative character states (Dahlgren & Clifford). Nevertheless, beyond its ties with this monogeneric family of Southeast Asia and the South Pacific, the Gramineae remain isolated.

By using the Joinvilleaceae (*sensu stricto*) or the monocotyledons in general as outgroups, it is possible to establish some evolutionary trends within characters of grasses and thereby some notions of evolution within the family. Stebbins (1982) used this outgroup criterion and four others to polarize the states of 36 anatomical and morphological characters and two karyotype characters. Some of these characters—for example, habit (perennial vs. annual), ligule morphology, presence or absence of rhizomes, and several inflorescence characters—are not very useful taxonomically at the subfamilial and tribal levels and hence cannot help in phylogenetic hypothesis formation. The lack of knowledge about homologous structures for an outgroup makes polarization uncertain in seedling morphology (but see Hoshikawa's postulated trends), several inflorescence characters, and embryo anatomy. The use of starch grains (Stebbins, 1982) and karyotypes (Avdulov; Tsvelev; Brown & Smith, 1972; Mehra *et al.*; Sharma; Stebbins, 1982) is limited by lack of information about the outgroup character state. These qualifications leave leaf anatomy and floral morphology as useful.

The contention that the presence of microhairs in the leaf epidermis is primitive rests on their homology with the multicellular hairs of *Joinvillea* Gaudichaud and other monocots (see also Prat, 1936). There seems to be little doubt that the anatomical and physiological adaptations of the kranz syndrome are derived from the non-kranz conditions; Brown (1977) pointed out that there is no good evidence for reversals from C_4 to C_3. Among kranz grasses, long parenchyma-sheath cells are considered primitive and short ones derived (Brown, 1974). If it is assumed that grasses arose from ancestors with characteristically trimerous monocotyledonous flowers, it is safe to define as primitive in grasses perfect flowers with three highly vascularized lodicules, six stamens, and three styles. Hubbard (1948), Dedecca, Auquier, Sharma, and Ghorai & Sharma also called these floral states ancestral.

On the basis of these assertions about character-state evolution, the subfamily Bambusoideae, which has the greatest number of primitive floral character states among the subfamilies, is usually thought of as containing the most primitive extant grasses (Bews; Prat, 1936; Beetle, 1955; Stebbins, 1956b; Tateoka, 1957a; De Wet, 1958; Clayton, 1975, 1981a; Soderstrom & Calderón, 1979a). Floral evolution involves reduction in the number of each of these floral parts. The prominence of these floral reductions perhaps prompted Brown and colleagues (1957) to generalize that specialization in grasses means reduction. The absence of microhairs from the Pooideae and the kranz syndrome of the Chloridoideae and Panicoideae mark them as more advanced than the remaining subfamilies.

ORIGIN AND GEOGRAPHIC DISTRIBUTIONS

There is really no clear evidence for a place of origin of grasses. Some specialists (Bews; Stebbins, 1972; Clayton, 1975, 1981a) have suggested that they originated in tropical forests or at their margins. From these forest dwellers, an early offshoot similar to the Arundinoideae (Brown & Smith, 1972; Clayton, 1975, 1981a; Renvoize, 1981) extended into savannas and gave rise to—and was partially replaced by—the photosynthetically more efficient kranz subfamilies in the tropics and the pooids in the North Temperate Zone. The pooids migrated successfully along mountains into South America following the joining of North and South America in the Pliocene. An alternate hypothesis (Tsvelev) calls for pooid-like prototypes bearing bambusoid flowers and originating in high mountains, with later movement to plains and temperate regions. This view finds some supporting evidence in the primitive nature of leaf and stem anatomy of pooids (Brown, 1958a; Auquier & Somers).

The meager fossil remains of grasses do little to resolve questions of the geologic age of the family, its relationships with other monocots, and evolution within the family. The oldest records of grass pollen are from the Paleocene (doubtful records from the Cretaceous) and, in North America, the uppermost Eocene (Muller). The first abundant grass pollen comes from Miocene deposits in Kansas and Nebraska. Caryopses of four species from England and oryzoid leaves from Germany, all from the Eocene, are among the first megafossil remains (Daghlian; Stebbins, 1981). Isolated florets (in which the flowers are not preserved) of the Stipeae and Paniceae from the Miocene in Kansas, and of the Oryzeae from the Miocene in Nebraska, provide the first extensive grass megafossils (Thomasson). The Miocene upsurge in grasses likely stems from their symbiotic relationship with the then newly evolved groups of grass-eating ungulates (Clayton, 1981a; Stebbins, 1981; De Wet, 1981).

Present distribution, in conjunction with past continental plate movement, can be used to infer the age of suprageneric grass taxa. Clayton (1975, 1981a) and Brown & Smith (1972) postulated that the subfamilies, tribes, and even some subtribes evolved by the end of the Cretaceous or the first half of the Tertiary before the continents were sufficiently separated to prevent dispersal between them. As a consequence, the continents now contain a full array of suprageneric taxa. The differentiation of many modern genera, however, followed the movement of continental plates beyond the dispersal range of most grasses, so that two-thirds of modern grass genera occur on single continents (Clayton, 1975, 1981a).

The subfamilies and larger tribes occupy all the world's tropical to temperate regions. Only the subfamily Pooideae has taken extensively to colder climates. Clayton (1975) recognized seven basic centers of distribution of grass genera (excluding those with worldwide ranges): Eurasia, North America, temperate South America, tropical America, Africa, India–Southeast Asia, and Australia. North America shares genera with only Eurasia (24 genera), temperate South America (ten), and Australia (one). Several disjunct distributions involve grass genera of the southeastern United States. Five genera—*Arundinaria, Brachyelytrum, Diarrhena, Schizachne,* and *Torreyochloa* (*Puccinellia*)—are found there, elsewhere in North America, and also in China or Japan (Koyama & Kawano). *Gymnopogon, Muhlenbergia,* and *Zizania* show a New World–Indian disjunction (Clayton, 1975). Temperature and rainfall strongly influence geographic distribution (Hartley, 1950, 1958a, 1958b, 1964, 1973; Hartley & Slater; Cross). These factors are discussed under the individual subfamilies and tribes.

Native grasslands develop where there are periodic droughts, level to gently rolling topography, frequent fires, and in some instances grazing and certain soil conditions (R. C. Anderson). Drought, fire, and grazing prevent invasion by woody plants, and the latter two may actually stimulate grassland productivity. Several factors may account for the competitive advantage of grasses in the presence of fire and grazing: basal tillering; intercalary meristems at the base of the internodes, sheaths, and blades; short internodes of nonflowering stems; and caespitose habit. The general success of grasses may be further attributed to the protection of flower and fruit within the spikelet and to the great diversity of habit, photosynthetic pathways, breeding systems, and dispersal mechanisms.

REPRODUCTIVE BIOLOGY

The vagility of the fruits has promoted the ubiquity and ecological hegemony of grasses. Caryopses rarely leave the parent plant free from the spikelet or one or more of its parts, for these parts are multifariously adapted for dispersal by animals, wind, or water (Roshevits; Monod de Froideville; Hubbard, 1973a; Van der Pijl). Spiny involucres (as in *Cenchrus*), barbs, bristles, teeth, gluelike glandular secretions, hairs, awns, and awnlike glumes and lemmas catch on animal hair or even, in the case of the awns of some Triticeae, penetrate the skin around the mouth of herbivores (Stebbins, 1972). Many grasses bear fruits specially adapted to attract herbivores, which can then disperse the seeds. Some species have elaiosomes, encouraging ant dispersal (Monod de Froideville). Some bamboos produce fleshy berries, and the hard lemmas of some oryzoids are thought to have evolved as a protection from digestive enzymes (Stebbins, 1972). Wind dispersal depends upon winglike developments on spikelet parts or, more commonly, plumes on various spikelet or secondary-inflorescence parts. All or part of the inflorescence may break free from the plant and disperse by tumbling (Roshevits; Rabinowitz & Rapp). Grasses have at least two presumed adaptations for self-sowing of the dispersal unit. Hygroscopically sensitive awns may force the dispersal unit into the soil (Clayton, 1969; Stebbins, 1972; Clifford & Watson). Spikelet and floret calluses may serve the same purpose, sometimes operating together with awns (Hackel, 1890; Jain & Pal).

Grass flowers have obvious characteristics for wind pollination: reduced perianth (the lodicules), small and smooth pollen grains, high pollen-ovule ratio, and feathery stigmas. Pollination by pollen-collecting insects is infrequently of secondary importance (see Adams *et al.* and references therein), and it is primary only in certain herbaceous bambusoid grasses of relatively windless forests (Soderstrom & Calderón, 1971). Adaptations associated with animal pollination—large pollen (Adams *et al.*), numerous closely placed, bright-yellow anthers (Soderstrom & Calderón, 1971), and perhaps the striking sexine pattern of the insect-pollinated *Pariana* Aublet (J. S. Page)—are found in these partially or entirely entomophilous grasses.

Anthesis in grasses is of short duration (usually minutes), and in many species it regularly occurs at a certain time of day or night (Jones & Brown, Evans). The critical events of grass anthesis are the rapid swelling of the lodicules, which forces open the florets, the rapid extension growth of the staminal filaments, and the spreading of the stigmatic branches. Grass pollen is viable for less than five minutes in some species, and for up to 24 hours in others. Gregarious flowering of numerous genera of woody bamboos at sometimes very long intervals is an astounding phenomenon that is very rare in angiosperms (Soderstrom & Calderón, 1979a). Frequent protandry and rare protogyny (Hackel, 1890; Stapf; Monod de Froideville) promote outcrossing. A two-locus, multi-allelic control of self-incompatibility has been demonstrated in numerous grasses (J. Heslop-Harrison). On the other hand, self-compatibility and self-fertilization through cleistogamy are common in grasses (East; Connor, 1979, 1981). In the majority of cases of cleistogamy in grasses, two conditions prevail: leaf sheaths or bracts confine the spikelets so that the lodicules cannot open the spikelet for chasmogamy, and the pollen-ovule ratio of cleistogamous flowers is lower than that of chasmogamous flowers of the same individual or species (Hackel, 1906; Campbell *et al.*, 1983).

Knobloch listed over 2400 hybrids in grasses. Hybridization is often associated with polyploidy, the doubling of chromosomes in a sterile hybrid restoring chromosome pairing and fertility. Of the 4000 grass species for which chromosome counts have been made, 2200 show a multiple of the base number of the genus (Goldblatt). If the uncounted species of obviously polyploid genera are included, this estimate jumps from 55 to 64 percent. Hybridization and polyploidy have undoubtedly played significant roles in grass evolution (for examples, see Myers; Stebbins, 1956b, 1975; McWilliam; Dewey; Waines *et al.*).

Apomixis, usually arising following hybridization or polyploidization or both, has been demonstrated in 33 grass genera (Connor, 1979). Most apomictic grasses are pseudogamous. The genus *Poa* contains aposporous, diplosporous, pseudogamous, and nonpseudogamous biotypes (Nygren).

As judged by the frequency of cleistogamy (reported from 82 genera from a broad tribal spectrum by Campbell *et al.*, 1983) and the more extensive occurrence of self-compatibility (East), inbreeding is common in grasses. Like apomixis, inbreeding generates populational phenomena that pose major systematic problems. Inbreeding has also apparently been an important factor in the colonizing success of many weeds (Allard).

Economic Importance

The economic importance of grasses lies in their paramount role as food: 70 percent of the world's farmland is planted in crop grasses, and over 50 percent of the world's calories come from grasses (Heiser). Man has cultivated the cereals for 10,000 years (De Wet, 1981). From the beginning of their domestication, wheat (*Triticum aestivum* L.), barley (*Hordeum vulgare* L.), and oats (*Avena sativa* L.) in the Near East, sorghum (*Sorghum bicolor* (L.) Moench) and pearl millet (*Pennisetum americanum* (L.) K. Schum.) in Africa, rice (*Oryza sativa* L.) in southeastern Asia, and maize (*Zea Mays* L.) in Meso-America have made possible the rise of civilizations. In terms of world production today, the first four crops are grasses: sugar cane (*Saccharum officinarum* L.), wheat, rice, and maize. Barley is seventh and sorghum eleventh. For an extensive review of the cultivation, breeding, and history of major grass crops, the reader is referred to volumes on sugar cane (Artschwager & Brandes), wheat (Quisenberry), rice (Grist), maize (Sprague), barley (Briggs), and sorghum (Hulse *et al.*).

Grasses are also used for livestock feed, erosion control, and turf production, and as a sugar source for the fermentation of many alcoholic beverages. Bamboos are an integral part of the economies of many tropical areas since they contribute young shoots for food, fiber for paper, pulp for rayon, strong stems for construction, and various items for numerous other uses (Soderstrom & Calderón, 1979a). In the southeastern United States the forage crop–ruminant livestock industry yields 40 percent as much in total sales as all row crops and close-grown field crops (Mays). Sugar cane, rice, maize, and sorghum are also grown commercially in this area.

The spread of civilization, commercial trade between the continents, and man's great nutritional dependence upon grasses have produced important, often weedy, adventive grass floras throughout the world (Hartley, 1964; De Wet, 1981). Species belonging to some 80 genera are cultivated as ornamentals in the United States (Bailey *et al.*).

KEY TO THE SUBFAMILIES AND TRIBES OF GRASSES IN THE SOUTHEASTERN UNITED STATES

General characters: *Annual or perennial herbs, rarely shrubs; roots fibrous; leaves distichous, made up of sheath, ligule, and usually linear blade; leaf epidermis dominated by long cells and short cells, the latter often modified into hooks, prickles, or bicellular microhairs, or containing cork or variously shaped silica bodies; transverse-sectional anatomy of leaves either kranz and characterized by specialized bundle sheaths with large chloroplasts or non-kranz; primary inflorescence a spikelet consisting of an axis (the rachilla) and 3 kinds of distichously arranged bracts—glumes (basal, usually 2), lemmas, and paleas; secondary inflorescence paniculate, cymose, racemose, or spicate; florets 1–30 per spikelet and comprising a lemma subtending a flower and a palea between the flower and the rachilla; flowers perfect or imperfect, anemophilous; the outermost floral parts, the lodicules, 2 (rarely 3), fleshy; stamens 3, sometimes 1, 2, or 6; ovary superior, unilocular and uniovular; stigmas 2 or 3 (1); fruit a caryopsis or less often an achene or utricle; embryo basal and lateral, with a large cotyledon, the scutellum; endosperm usually abundant.*

A. Plants with C_3 photosynthesis and non-kranz leaf anatomy (2 or more mesophyll cells separating adjacent vascular bundles, chloroplasts uniform and all starch forming); hilum usually linear; embryos small, less than ⅓ the length of the caryopsis; stomatal subsidiary cells mostly parallel sided or dome shaped.
  B. Arm and fusoid cells usually present (FIGURE 2a) (fusoid cells absent in some Oryzeae); stamens often more than 3; stigmas usually 3 (2 in Oryzeae); first seedling leaf without a blade, except in Phareae. .... Subfam. 1. BAMBUSOIDEAE.
    C. Stems woody; leaf blades disarticulating; fertile florets 6–12 per spikelet; glumes usually 2 per spikelet; flowers perfect; scutellar tail present. .... Tribe 1a. ARUNDINARIEAE.
    C. Stems herbaceous; leaf blades not disarticulating; fertile floret 1 per spikelet; glumes usually absent (rarely 1 or 2 and vestigial); flowers often imperfect (plants monoecious); scutellar tail rarely present.
      D. Transverse veins absent in leaf blades; spikelets solitary; stigmas 2; first seedling leaf without a blade; microhairs present; silica bodies oryzoid; vascular bundles in stem internodes in 1 or 2 rings. .... Tribe 1b. ORYZEAE.
      D. Transverse veins present in leaf blades; spikelets paired; stigmas 3; first

seedling leaf with a blade; microhairs absent; silica bodies cross to dumbbell shaped to nodular; vascular bundles in stem internodes scattered. . . . . Tribe 1c. PHAREAE.

- B. Arm and fusoid cells absent (FIGURE 2b–d) (arm cells present in some Arundineae); stamens 3 or fewer; stigmas 2; first seedling leaf with a blade.
  - E. Scutellar tail absent (present in Diarrheneae); embryo mesocotyl short; microhairs absent (present in some Stipeae).
    - F. Rachilla not prolonged above uppermost floret; lodicules 2 or 3; microhairs sometimes present; silica bodies saddle shaped and crescentic. . . . . Tribe 6c. STIPEAE.
    - F. Rachilla prolonged above uppermost floret; lodicules generally 2; microhairs absent; silica bodies elongated, sinuous or crenate (absent from Brachyelytreae).
      - G. Embryonic leaf margins overlapping; silica bodies cross to dumbbell shaped to nodular.
        - H. Floret 1 per spikelet; lemmas awned, equally as firm as the glumes; lodicules glabrous; ovary apex hairy; pericarp adnate to seed; endosperm soft, the starch grains all simple; epidermis papillate; silica bodies not elongated, sinuous or crenate; sclerenchyma accompanying the smallest vascular bundles absent; base chromosome number 11. . . . . Tribe 6a. BRACHYELYTREAE.
        - H. Florets 2–5 (rarely 1) per spikelet; lemmas awnless, firmer than the glumes; lodicules hairy; ovary apex glabrous; pericarp free from the seed; endosperm hard, at least some of the starch grains compound; epidermis not papillate; silica bodies elongated, sinuous or crenate; sclerenchyma accompanying at least some of the smallest vascular bundles present; base chromosome number 10. . . . . Tribe 6b. DIARRHENEAE.
      - G. Embryonic leaf margins not overlapping; cross- to dumbbell-shaped silica bodies absent, tall and narrow silica bodies present. . . . . Subfam. 3. POOIDEAE.
        - I. Leaf auricles often present; ovary apex hairy; epiblast absent (present in some Triticeae); starch grains simple; seedling transitionary node roots present (supertribe Triticanae).
          - J. Inflorescence a panicle (rarely a raceme); lodicules glabrous; ovary appendage present; caryopsis compressed laterally. . . . . Tribe 3e. BROMEAE.
          - J. Inflorescence a solitary spike (rarely with spiciform branches); lodicules hairy (rarely glabrous); ovary appendage absent; caryopsis usually compressed dorsiventrally. . . . . Tribe 3f. TRITICEAE.
        - I. Leaf auricles absent; ovary apex glabrous (hairy in some Aveneae); epiblast present; at least some starch grains compound (rarely all simple in some Agrostideae); seedling transitionary node roots absent (supertribe Poanae).
          - K. Lodicules often truncate, connate, distally fleshy and palpably vascularized; base chromosome number 9 or 10. . . . . Tribe 3c. MELICEAE.
          - K. Lodicules acute, free, distally membranaceous and without evident veins; base chromosome number mostly 7.
            - L. Crescentic silica bodies present; vernation folded (rarely rolled). . . . . Tribe 3d. POEAE.
            - L. Crescentic silica bodies absent; vernation rolled (rarely folded).

M. Florets usually 1 per spikelet; ovary apex glabrous (rarely hairy); hilum punctiform (rarely linear). .... Tribe 3a. AGROSTIDEAE.

M. Florets usually more than 1 per spikelet; ovary apex mostly hairy (rarely glabrous); hilum linear. .... Tribe 3b. AVENEAE.

E. Scutellar tail present; embryo mesocotyl long; microhairs present.

N. Spikelets usually dorsally compressed, disarticulating below the glumes, with 1 caryopsis-bearing floret; embryonic leaf margins overlapping (rarely not); base chromosome number generally 9 or 10. .... Tribe 5b. PANICEAE.

N. Spikelets laterally compressed or not compressed, disarticulating above the glumes, with more than 1 caryopsis-bearing floret; embryonic leaf margins not overlapping; base chromosome number 12. .... Subfam. 2. ARUNDINOIDEAE.

O. Rachilla prolonged above uppermost floret; hilum punctiform (rarely linear); epiblast absent; first seedling leaf curved; bulliform cell groups absent. .... Tribe 2b. ARUNDINEAE.

O. Rachilla not prolonged above uppermost floret; hilum linear; epiblast present; first seedling leaf supine; bulliform cell groups present. .... Tribe 2c. CENTOTHECEAE.

A. Plants with C_4 photosynthesis and kranz leaf anatomy (no more than 1 mesophyll cell separating adjacent vascular bundles, bundle sheaths starch forming); hilum mostly punctiform; embryos mostly large, more than ⅓ the length of the caryopsis; stomatal subsidiary cells dome shaped or triangular.

P. Stomatal subsidiary cells dome shaped. ..... Subfam. 2. ARUNDINOIDEAE.

Q. Floret 1 per spikelet; lemmas firmer than glumes; kranz bundle-sheaths 2; base chromosome number 11. .... Tribe 2a. ARISTIDEAE.

Q. Florets 6–9 per spikelet; glumes and lemmas equally firm; kranz bundle sheath 1; base chromosome number 12. ..... Tribe 2b. ARUNDINEAE (*Neyraudia*).

P. Stomatal subsidiary cells triangular.

R. Spikelets compressed dorsally; staminate or neuter floret proximal to the lowermost carpel-bearing floret; epiblast absent; embryonic leaf margins overlapping; microhair distal cell narrow; tall and narrow silica bodies and saddle-shaped silica bodies absent (rarely present); parenchyma sheath cells elongate, their chloroplasts centrifugally positioned and containing either small grana or none; sclerenchyma accompanying the smallest vascular bundles absent. .... Subfam. 5. PANICOIDEAE.

S. Glumes firmer than lemmas, the first glume longer than the spikelet; lemma nerves usually 3 or fewer. .... Tribe 5a. ANDROPOGONEAE.

S. Glumes softer than lemmas, the first glume usually much shorter than the spikelet; lemma nerves usually 3 or more. .... Tribe 5b. PANICEAE.

R. Spikelets compressed laterally (rarely dorsally) or not compressed; staminate or neuter florets usually distal to the lowermost carpel-bearing floret; epiblast present (rarely absent); embryonic leaf margins rarely overlapping; microhair distal cell inflated; tall and narrow silica bodies and saddle-shaped silica bodies present (rarely absent); parenchyma sheath cells short, their chloroplasts centripetally positioned and containing large grana; sclerenchyma accompanying the smallest vascular bundles present. .... Subfam. 4. CHLORIDOIDEAE.

T. Lemma nerves 7–11; silica bodies cross to dumbbell shaped; colorless cells traversing the leaf absent. .... Tribe 4c. UNIOLEAE.

T. Lemma nerves 7 or fewer; silica bodies saddle shaped; colorless cells traversing the leaf usually present.

U. Leaf blade disarticulation present; flowers imperfect, plants dioecious. .... Tribe 4a. AELUROPODEAE.

U. Leaf blade disarticulation usually absent; flowers usually perfect.
  V. Rachilla usually prolonged above uppermost floret; lodicules usually distally fleshy; combined adaxial and abaxial girders with an "anchor," "I," or "T" shape usually absent. .... Tribe 4b. CYNODONTEAE.
  V. Rachilla not prolonged above uppermost floret; lodicules distally membranaceous; combined adaxial and abaxial girders with an "anchor," "I," or "T" shape present. ...... Tribe 4d. ZOYSIEAE.

Subfamily 1. BAMBUSOIDEAE Ascherson & Graebner, Synop. Mitteleurop. Fl. **2:** 769. 1902.

Aquatic to terrestrial, often rhizomatous annuals, perennial herbs, or woody plants. Lodicules 2 or 3; stamens 6, sometimes fewer; stigmas 2 or more often 3. Hilum linear; embryo small, with an epiblast but without a mesocotyl. Seedling mesocotyl usually short; first seedling leaf blade generally absent. Papillae and microhairs with narrow distal cells present in the leaf epidermis (FIGURE 1b). Arm and fusoid cells often present in the mesophyll; midrib with 2 or more vascular bundles that are usually superposed; photosynthesis of the C_3 type (FIGURE 2a). Base chromosome number usually 12. (Including Oryzoideae Parodi ex Caro, Dominguezia **4:** 10. 1982.) TYPE GENUS: *Bambusa* Schreber. FIGURES 1b, 2a, 3A-D.

A widely distributed, almost cosmopolitan subfamily, especially in the tropics. Each of the three groups making up the subfamily is represented by an indigenous tribe in the southeastern United States: the bamboos by the Arundinarieae, the herbaceous bambusoid grasses by the Phareae, and the oryzoids by the Oryzeae. There are about ten genera and 13 species in our area.

The concept of the Bambusoideae has been expanded from comprising only the woody bamboos to include a group of tribes called (Soderstrom & Calderón, 1979a) the herbaceous bambusoid grasses (Jacques-Félix, 1955; Tateoka, 1957a; De Wet, 1958; Parodi; Clayton, 1978; Renvoize, 1981; Soderstrom, 1981a; Soderstrom & Calderón, 1974, 1979a, 1979b; Hilu & Wright; Gould & Shaw). Important similarities between the bambusoids in general and the oryzoids (Brown, 1950; De Winter, 1951; Tateoka, 1957a; Reeder, 1962; Clifford, 1965; Christopher & Abraham, 1971; Clayton, 1978, 1981a; Renvoize, 1981) warrant inclusion of rice and its relatives in this subfamily as well. The bamboos, herbaceous bambusoids, and oryzoids share character states in the flowers, bundle-sheath anatomy (Brown, 1958a; Auquier & Somers), and amino-acid composition of the caryopses (Yeoh & Watson). Two mesophyll cell types, arm and fusoid cells (FIGURE 2a), are almost unique to this subfamily (arm cells occur in *Phragmites* and some other arundinoids). Although these cells differ somewhat in bambusoids and oryzoids (Calderón & Soderstrom, 1973), their presence supports a monophyletic origin of this subfamily. Terrell & Robinson and Soderstrom (1981a) suggest that these cells may be adaptations for life in moist forests or aquatic habitats.

Because of the number of lodicules, stamens, and stigmas of many members of the Bambusoideae, the subfamily is generally considered to contain the most primitive extant grasses. On the other hand, woodiness, complex vegetative growth and inflorescence branching, various spikelet reductions, and perhaps the presence of arm and fusoid cells are presumably derived.

Tribe 1a. **Arundinarieae** Ascherson & Graebner, Synop. Mitteleurop. Fl. **2:** 770. 1902.

Stems woody. Leaf blades with transverse veins, disarticulating. Spikelets (FIGURE 3D) solitary, with 6–12 fertile florets and 2 glumes. Lemmas 11–17-nerved. Flowers perfect, with 3 lodicules, stamens, and stigmas. Embryos with a scutellar tail. Initial or first few seedling leaves without blades. Leaf epidermis (FIGURE 1b) with microhairs, cross- to dumbbell-shaped silica bodies, and saddle-shaped silica bodies, but without oryzoid silica bodies. TYPE GENUS: *Arundinaria* Michaux. FIGURES 1b, 2a, 3D.

A tribe of 61 genera extending from a center of distribution in tropical forests to 46°N and 47°S latitudes, to 4000 m elevation, and to regions with snowy winters (Soderstrom, 1981a). The major center of diversity of the group appears to be southeastern Asia. In the New World there are 17 genera. The one native bamboo in the southeastern United States, *Arundinaria gigantea* (Walter) Muhl., is the only New World member of this genus of over 100 species (McClure, 1973). This species, commonly called giant or switch cane, consists of three subspecies that grow in moist ground from southern Maryland and Ohio to Florida and Texas. Its rhizomatous growth produces extensive populations, sometimes called canebrakes, which are sought for cattle forage and as a source of materials for fishing rods, baskets, and other purposes (Hitchcock). Hall reported that various species of *Bambusa, Pseudosasa* Makino ex Nakai, and *Phyllostachys* Sieb. & Zucc. persist after cultivation in Florida.

Holttum's study of ovary anatomy and Grosser & Liese's study of rhizome and leaf anatomy generated four concordant groups. Nevertheless, tribal limits and interrelationships are not clear (McClure, 1966; Calderón & Soderstrom, 1980; Soderstrom & Calderón, 1979b), at least in part because bamboos grow primarily in the tropics where the flora is relatively poorly known, and more importantly, because it is difficult to make good herbarium specimens of the bulky stems and branches, the growth patterns of which are taxonomically important. Moreover, because the plants flower infrequently, they are often avoided by collectors and are not well represented in herbaria.

The infrequency of flowering is associated with flowering cycles of up to 120 years in many (perhaps the majority) of bamboos (Soderstrom & Calderón, 1979a). What makes the cyclical flowering all the more fascinating is that populations of a taxon tend to flower gregariously and, after fruiting, die. The functioning of the biological clock governing this rare phenomenon is unknown. Janzen hypothesized that this mast flowering oversaturates the food supply of fruit predators. The fruits of some bamboos may be as large as an avocado, and being poorly dispersed (at least by the wind), may accumulate in large numbers under the plants following a gregarious flowering (Soderstrom & Calderón, 1979a). Although *Arundinaria* may flower annually or remain sterile for many years, its aerial stems are monocarpic like those of most bamboos. Bamboos rely predominantly on vegetative reproduction by thick, extensively branched rhizomes (McClure, 1966, 1973). Reduced selection pressures for floral evolution may explain the primitiveness of bamboo flowers.

The bamboos are unique among grasses for their long-persistent aerial stems. Their woodiness comes not from cambial activity but from caps of fibers on both sides of the vascular bundles, thick-walled and lignified ground tissue, and to some extent, silicification of the epidermis (Soderstrom, 1981a). The two-stage growth pattern of bamboo stems is also unique. It consists of a relatively short period of apical dominance characterized by rapid internode elongation and suppression of lateral appendages, and then extensive lateral branching (Calderón & Soderstrom, 1980). Soderstrom (1981a) argued that competition with tropical trees for light brought about woodiness in bamboos, and that this woodiness and the polyploidy of bamboos are evidence for their derivation from the diploid herbaceous bambusoid grasses. Clayton (1981a, *fig. 1*) presented the same phylogeny.

Another unusual feature of bamboos, which is also found in herbaceous bambusoids, is leaf torsion or "sleep movement." Leaf-pulvinus activity serves either to orient all leaves of a branching system in one plane or to move leaves from a horizontal position during the day to a reflexed one at night (Calderón & Soderstrom, 1973). In addition to their unusual flowering cycles, growth pattern, and leaf torsion, the bamboos are parasitized by fungi generally distinct from those on other grasses (Savile).

Tribe 1b. **Oryzeae** Dumortier, Obs. Gram. Belg. 83. 1824.

Annual or perennial herbs. Stems and leaves more or less aerenchymatous. Leaf blades without transverse veins, not disarticulating. Spikelets (FIGURE 3A, B) solitary, with 1 fertile floret and glumes either small or absent. Lemmas 3–5(–7)-nerved. Flowers perfect, or more often plants monoecious; lodicules 2, stamens 6 (rarely as few as 1), stigmas 2. Embryos without a scutellar tail (except in *Zizania*). First seedling leaf without a blade. Leaf epidermis with microhairs and oryzoid silica bodies, but without cross- to dumbbell-shaped silica bodies or saddle-shaped silica bodies. TYPE GENUS: *Oryza* L. FIGURE 3A, B.

A tribe containing about ten genera (Hubbard, 1973a) and 100 species. It is best known for rice, both the Asian species, *Oryza sativa,* which occasionally escapes from cultivation in the southeastern United States, and the wild rice of North America, *Zizania aquatica* L. *Oryza,* and the four native genera that represent the tribe in our area, fall into three subtribes (Terrell & Robinson). The Oryzinae include the perfect-flowered *Oryza* and *Leersia* Sw. The monogeneric Zizaniinae Hitchc. are characterized by monoecy, the presence of a scutellar tail, the fusion of pericarp and seed coat, and a karyotype of relatively large chromosomes and base numbers of 15 or 17. *Luziola* Juss. (including *Hydrochloa caroliniensis* Beauv., of our area) and *Zizaniopsis* Doell & Ascherson, of the Luziolinae Terrell & Robinson, are also monoecious, but they lack a scutellar tail, the pericarp is free from the seed coat, and the chromosomes are small with a base number of 12.

The tribe Oryzeae has been regarded as an aquatic offshoot of the bambusoids (Ghorai & Sharma). The presence of stem and leaf aerenchyma, arm and fusoid cells (Terrell & Robinson), and the least specialized vessels of the family (Cheadle, 1960) may be associated with the predominantly moist or aquatic habitats

FIGURE 3. Spikelets or their parts, **Bambusoideae** and **Arundinoideae.** A, *Zizania aquatica* (Oryzeae): A1, 2 staminate spikelets slightly after anthesis, all anthers shed but 1 (note longitudinal dehiscence), no glumes, each spikelet 1-flowered, × 3; A2, carpellate spikelet at anthesis (note styles), with pedicel and portion of rachis (palea clasped by lemma), × 3; A3, base of carpellate spikelet disarticulated from pedicel to show callus,

of this tribe. The tribe is characterized by the oryzoid type of silica body, which is found elsewhere only sparingly in the genus *Aristida* (Watson & Dallwitz, 1981). The oryzoid silica body is basically dumbbell shaped, but unlike those of similarly shaped silica bodies of other grasses, its long axis is perpendicular to the long axis of the leaf. It seems best to recognize the affinities of this tribe by including it in the Bambusoideae rather than giving it subfamilial rank (Pilger; Parodi; Stebbins & Crampton; Hilu & Wright; Gould & Shaw) or treating it as a "series" (Jacques-Félix, 1962) or a "group" (Clifford & Watson).

Difficulty in assessing homology has beset the interpretation of the parts of the spikelets and florets of the Oryzeae. Hitchcock described the spikelet as one-flowered with reduced glumes, but most agrostologists consider Hitchcock's glumes to be actually the lemmas of sterile florets below the terminal, fertile floret (De Winter, 1951). The glumes form an inconspicuous cupular structure. In his review of the numerous ideas about the fertile floret, De Winter (1951) supported Pilger's concept of fusion of two florets, with the loss of paleas from both and of lodicules, androecium, and gynoecium from one. If this view is correct, then the three-or-more-nerved "palea" is actually a lemma and is the only remaining part of the terminal floret.

Tribe 1c. **Phareae** Stapf in Thiselton-Dyer, Fl. Capensis 7: 319. 1898.

Perennial herbs. Leaf blades with obliquely oriented main veins connected by transverse veins, not disarticulating. Spikelets paired (1 carpellate and 1 staminate), with 1 fertile floret and no glumes. Lemmas few nerved. Stamens 6; stigmas 3. Embryos mostly without a scutellar tail. First seedling leaf with a blade. Leaf epidermis with cross- to dumbbell-shaped silica bodies, but without microhairs, saddle-shaped silica bodies, or oryzoid silica bodies. TYPE GENUS: *Pharus* P. Br. FIGURE 3C.

The Phareae are made up of the African genus *Leptaspis* R. Br. and *Pharus*, a New World genus of eight species. *Pharus* has survived where other herbaceous bambusoids presumably have not because it is successful in disturbed sites and disperses well (Soderstrom, 1981a). The sole member of the tribe in our area, *P. parvifolius* Nash, is rare in northern and central Florida (Hall).

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lemma (to right) and palea partly separated, styles protruding (spikelet rotated 90° from position in A2), × 6. B, *Leersia oryzoides* (Oryzeae), spikelet (lemma and palea separated, glumes absent), × 6. C, *Pharus parvifolius* (Phareae): C1, staminate (pedicellate) and carpellate spikelets (sessile; note dense pubescence [individual uncinate hairs not visible at this scale]), × 4; C2, staminate spikelet, showing 4 of 6 stamens, × 6; C3, lemma of carpellate floret completely enclosing palea (note 3 protruding styles), × 4. D, *Arundinaria gigantea* (Arundinarieae): D1, spikelet, × 2; D2, floret (lemma clasping palea), × 3. E, *Danthonia spicata* (Arundineae): E1, spikelet, × 3; E2, floret (lemma awned; note rachilla segment), × 5. F, *Chasmanthium latifolium* (Centotheceae): F1, spikelet, × 1.5; F2, floret, × 3; F3, caryopsis, × 5. G, *Phragmites australis* (Arundineae): G1, spikelet (parts spread out and hairs omitted for clarity), × 4; G2, floret with villous rachilla segment, × 5. H, *Arundo Donax* (Arundineae): H1, spikelet, × 3; H2, floret (from adaxial side; note hairs along edge of lemma and glabrous rachilla segment), × 3.

The herbaceous bambusoid grasses as a group consist of eight tribes and 24 genera (Soderstrom, 1981a). Only five genera are native to the Old World, while 21 occur from Mexico to Argentina, especially between 10°N and 9°S latitudes, mostly below 850 m, and in forest shade or more open places (Soderstrom & Calderón, 1979b). In addition to the characters of the APPENDIX that separate them from the more evolutionarily advanced bamboos, the herbaceous bambusoids differ in being mostly diploid, rather than mostly tetraploid or hexaploid (Hunziker *et al.*), and in their much simpler stem branching. Otherwise the boundary between the two groups is not well marked.

Animal pollination has developed in herbaceous bambusoids in response to the relative lack of wind in their habitats (Soderstrom & Calderón, 1971). In *Eremitis* Doell cleistogamy in subterranean spikelets (Soderstrom & Calderón, 1974) may also be a compensation for lack of wind. The strongly twisted awns of *Streptochaeta* (Soderstrom, 1981a) and the short, hooked hairs of the persistent lemma of *Leptaspis* (Bor) and perhaps those of *Pharus* are evidently adaptations for catching on animal fur.

The regularly produced spikelets of herbaceous bamboos may be inconspicuously situated within leaf sheaths, behind broad leaves, or even under leaf litter (Calderón & Soderstrom, 1980). Hence these plants may be as neglected by collectors as the bamboos are. The herbaceous bamboos are, however, better understood taxonomically. The flower of *Streptochaeta* is solitary and subtended by numerous spirally arranged bracts (V. M. Page; Soderstrom, 1981a). These specialized structures, called pseudospikelets (McClure, 1966, 1973), are also found in some bamboos (Soderstrom, 1981a). Leaf torsion is also common to both groups.

Subfamily 2. ARUNDINOIDEAE Tateoka, Jour. Jap. Bot. **32**: 377. 1957, "Arundoideae."

Perennial (rarely annual) herbs (in *Phragmites* somewhat woody). Ligules fringed or of hairs. Embryo with a scutellar tail and a long mesocotyl. First seedling leaf blade curved or supine. Microhairs with a narrow distal cell. Photosynthesis mostly C_3 (C_4 in about 7 genera, including *Aristida* and probably *Neyraudia* of our area). Base chromosome number (11) 12. (Centothecoideae Soderstrom, Taxon **30**: 614. 1981, as "Centostecoideae." Phragmitoideae Parodi ex Caro, Dominguezia **4**: 13. 1982. Aristidoideae Caro, *ibid.* 16.) TYPE GENUS: *Arundo* L. FIGURES 3E–H, 7B.

A subfamily treated by Renvoize (1981) as comprising eight tribes and 72 genera. It is represented in the southeastern United States by three tribes, four genera, and about 30 species.

Subfamily Arundinoideae is the least sharply defined and the most undoubtedly polyphyletic of the subfamilies. The APPENDIX shows the variability in numerous characters that are taxonomically discriminating for other subfamilies—for example, hilum shape (character 35), embryo size (36), seedling morphology (43, 45), and some leaf-epidermal (59–62) and transverse-sectional characters (63, 67, 75, and 82). Internal diversity in leaf ultrastructure (Carolin *et al.*) and in amino-acid profiles (Taira) surpasses that of other subfamilies.

It is not surprising, then, that discussions of the subfamily focus on phrases such as "miscellaneous group" (De Wet, 1958), "less homogeneous" (Stebbins & Crampton), "unspecialised subfamily" (Clayton, 1978), and "loosely related genera" (Renvoize, 1981), or that Clayton's *fig. 1* (1981a) shows this subfamily, as defined by Renvoize, to be paraphyletic.

The taxonomic concept of this group varies from one considerably broader than Renvoize's to one separating one to all three of the tribes of our area into different subfamilies (Pilger; Parodi; Clayton, 1978), "series" (Jacques-Félix, 1962), or groups (Clifford & Watson). Prat (1960) and Stebbins & Crampton agreed with Renvoize at least in including the Aristideae, Arundineae, Centotheceae, and Danthonieae in the subfamily. The results of Renvoize's multivariate analysis illustrate arundinoid taxonomic complexity well. Of the 72 genera he included, only 43 formed an "arundinoid nucleus," and 29 were peripheral. This nucleus, except for *Lygeum* L. and a few peripheral genera, makes up his Arundineae. The taxonomic relationships of *Lygeum, Danthonia,* and *Neyraudia* of Renvoize's Arundineae, as well as of four of Renvoize's peripheral tribes (Aristideae, Centotheceae, Ehrharteae Link, and Micraireae Pilger) need further study. This diverse assemblage holds together because its members have slightly more similarity to each other than to other grasses.

That only four genera of arundinoids are native to the southeastern United States reflects the Old World, Southern Hemisphere, subtropical, and Gondwanaland distribution of the subfamily (Clayton, 1975; Cross). The wide geographic distribution hints at considerable age.

Tribe 2a. **Aristideae** C. E. Hubbard in Bor, Grasses Burma, Ceylon, India, Pakistan, 685. 1960.

Annuals or perennials. Spikelets 1-flowered, with a 3-awned lemma. Embryo without an epiblast. Two kranz bundle-sheaths present. Base chromosome number 11. TYPE GENUS: *Aristida* L. FIGURE 7B.

A tribe considered by De Winter (1965) to comprise the large, cosmopolitan, often xerophytic *Aristida* (330 species) and two primarily African genera, *Stipagrostis* L. and *Sartidia* De Winter. In our area there are about 20 species of *Aristida* (Hitchcock).

Depending upon what aspect of the plant one considers, the Aristideae resemble several other groups. The overall similarity of spikelets, caryopses, and base chromosome number to those of the Stipeae are countered by a wealth of differences in ligules (character 7 of the APPENDIX), lemma-awn and nerve numbers (20, 22), lodicule number (24), embryos (38–40), silica bodies (52), and leaf anatomy (66, 67, and 78). The Aristideae have often been associated with chloridoids on the bases of leaf-mesophyll anatomy (characters 67, 78) (Brown, 1958a; De Winter, 1965; Carolin *et al.*; Sutton) and amino-acid patterns of the caryopses (Yeoh & Watson). But again, there are more differences: lemma-awn number (20), lodicule texture (25), epiblasts (38), microhair distal-cell shape (49), silica-body type (52), and base chromosome number (84). The presence of microhairs with narrow distal cells and cross- to dumbbell-shaped silica bodies in the leaf epidermis unites the Aristideae and the Panicoideae.

Furthermore, in longitudinal sections of leaves, the parenchyma-sheath cells are longer than wide in both the Aristideae and the Paniceae (Brown, 1974, 1975). These cells are usually isodiametric in chloridoids. Nevertheless, there are important differences between the Aristideae and the Paniceae in lodicule texture (25), embryonic leaf margins (41), silica-body types (52, 56, 57), colorless cells traversing the leaf (78), and base chromosome number (84).

In a consideration of the systematic position of the Aristideae, an important character is the unique double kranz sheath of *Aristida.* In all other C_4 grasses, the kranz bundle-sheath has evolved either from the parenchyma sheath (most chloridoids, danthonioids, and some panicoids) or the mestome sheath (some panicoids) (Brown, 1977). In *Aristida* both sheaths are kranz, giving the cross-sectional anatomy of the leaves a distinctive double sheath (Lommasson; Brown, 1958a).

Brown (1977) viewed the Aristideae as specialized, single-floreted Danthonieae and argued that the Aristideae arose from some danthonioid ancestor, possibly in southern Africa. Bourreill (1969) claimed that the wide distribution of *Aristida* indicates a Cretaceous beginning for the genus. His hypothesis (1968) about intratribal phylogeny disagrees with Brown's (1977) and does not give enough weight to the probably derived double sheath of *Aristida.*

Tribe 2b. **Arundineae** Dumortier, Obs. Gram. Belg. 82. 1824, "Arundinaceae."

Perennials. Spikelets 2- to many-flowered (except in axillary cleistogamous spikelets of *Danthonia*). Rachilla prolonged above uppermost floret. Stamens 3. Embryo without an epiblast. Parenchyma sheaths with large vacuoles and no chloroplasts. Bulliform cell groups absent from leaves. Base chromosome number 12. (Elytrophoreae Jacques-Félix, Jour. Agr. Trop. Bot. Appl. **5:** 304. 1958. Cortaderieae Zotov, New Zealand Jour. Bot. **1:** 83. 1963. Danthonieae Zotov, *ibid.* 86. Molineae Jirásek, Preslia **38:** 33. 1966.) TYPE GENUS: *Arundo* L. FIGURE 3E, G, H.

According to Renvoize's (1981) circumscription, a tribe of 57 genera. Five genera, all posing taxonomic problems, grow in the southeastern United States. Both *Arundo,* with one Old World species (*A. Donax* L., the reed, FIGURE 3H), and *Phragmites* Adanson, whose single species in our area (*P. australis* (Cav.) Steudel (*P. communis* Trin.), FIGURE 3G) has the widest geographic distribution of any angiosperm (L. G. Holm *et al.*), are peripheral in the tribe. Their stomata are narrower than the intervening epidermal cells and dominate the intercostal zones. *Phragmites* is unusual in the invaginated walls of the mesophyll cells (see Decker's *fig. 3*), which resemble bambusoid arm cells.

Cortaderia Stapf, pampas grass, a genus of the Southern Hemisphere represented in our area by the frequently planted ornamental *C. Selloana* (Schultes) Ascherson & Graebner, is unique in the subfamily in that its vascular bundles are linked by sclerenchyma to the adaxial leaf surface only. It was one of the ungrouped genera of Renvoize's Arundineae. Zotov put it in its own tribe, the Cortaderieae. *Neyraudia* Hooker f. is a small Old World genus of the Southern Hemisphere, represented by *N. Reynaudiana* (Kunth) King & Hitchc., an escape in Florida (Hall). It was placed in the Eragrostideae (the Cynodonteae in this paper) because of its embryo anatomy (Decker) and its radially arranged mesophyll. Brown (1977) put it in the Tristegineae (Melinideae) of the Panicoideae because of its PS subtype of kranz leaf anatomy, but there is no biochemical evidence to verify its C_4 photosynthesis. Phillips suggested that the genus lies on the boundary between the Arundinoideae and the Chloridoideae. On the whole, morphological and anatomical data support placement of *Neyraudia* in the Arundinoideae (Tateoka, 1957a; Stebbins & Crampton; Jacques-Félix, 1962; Clifford & Watson; Renvoize, 1981).

Finally, *Danthonia* DC. in Lam. & DC. (FIGURE 3E), represented by only three species in the Southeast, is the largest genus of a primarily Southern Hemisphere group often recognized as the Danthonieae. Traditionally, it was grouped with the Aveneae because of its many-flowered, laterally compressed spikelets. However, Hubbard (1948), De Wet (1954, 1956), and Reeder (1957) pointed out numerous differences in spikelets, karyotypes, embryo anatomy, and leaf anatomy. Its intermediacy between the pooid and panicoid extremes of the family makes it a taxonomic problem. Since it fits quite well into Renvoize's arundinoid nucleus, he sank the Danthonieae into the older Arundineae. Nevertheless, the danthonioids remain a diverse group containing both C_3 genera, such as *Danthonia*, and C_4 genera, such as *Allochaete* Hubb., *Asthenatherum* Nevski, and *Pheidochloa* S. T. Blake. Further study of the group may elucidate some aspects of evolution in the family as a whole.

Many genera of the Arundineae are small and not dominant floristic elements—a situation that suggested to Renvoize (1979) that they are competitively inferior relative to the mainstream of grass evolution.

Tribe 2c. **Centotheceae** Ridley, Mater. Fl. Malay. Penin. **3**: 122. 1907.

Perennials. Spikelets awnless, few- to many-flowered (FIGURE 3F); rachilla not prolonged above uppermost floret. Stamen[s] 1 [generally 3 in other centothecoids]. Embryo without an epiblast. Parenchyma-sheath vacuoles not as large as those of the Arundineae. Bulliform cell groups prominent in leaves. Base chromosome number 12. TYPE GENUS: *Centotheca*[3] Desv. FIGURE 3F.

A group of nine genera and 26 species, represented in the southeastern United States by *Chasmanthium* Link. This endemic genus of five woodland species has its center of distribution in our area (Yates).

Many-flowered, laterally flattened spikelets made *Chasmanthium* an unquestioned member of the pooid alliance until Reeder (1957, 1962) demonstrated a unique embryo anatomy for this and related genera. Jacques-Félix (1962), Reeder (1962), and Decker established a centothecoid group on the basis of the transversely veined (tessellate) and pseudopetiolate leaves, truncate and heavily vascularized lodicules, distinctive embryo, narrow distal cell of the microhairs, dumbbell-shaped silica bodies, prominent bulliform cell groups in the leaves, and base chromosome number of 12. In addition, the plants of

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[3] Reeder (Taxon **30**: 348, 349. 1981) has proposed the conservation of this spelling over *Centosteca*, an orthographic error.

this group grow in moist, often tropical forests, in contrast to the various habitats of the largely temperate pooids.

Jacques-Félix (1962) put his centothecoid series on an evolutionary line defined by embryo type between bamboos and chloridoids, but not far from the arundinoid series (see his *figs. 32* and *33*). Brown (1958a), Brown & Smith (1974), Clayton (1978), Ghorai & Sharma, and Renvoize (1981) mentioned ill-defined relationships with the bamboos. Soderstrom & Decker (1973), however, outlined numerous differences between the groups in leaf anatomy, lodicule morphology, caryopsis compression, and hilum shape. There are similarities to panicoids in amino-acid patterns (Taira) and smut pathogens (Watson), and to oryzoids in seedlings (Hoshikawa) and karyotypes (De Wet, 1960b). Tribe Centotheceae or its genera have either been placed in the Arundinoideae or its equivalent (Tateoka, 1957a; Prat, 1960; Parodi; Stebbins & Crampton; Yates; Renvoize, 1981) or been given the status of subfamily (Clayton, 1978; Soderstrom, 1981b; Gould & Shaw) or an informal, high-level group (Clifford & Watson). Whatever the rank, there is now a consensus about the composition of the group (Clayton, 1978; Renvoize, 1981; Soderstrom, 1981b). It fits into Renvoize's broad definition of the Arundinoideae, and differences from arundinoids in the palisade layer of the mesophyll, in nucleolus persistence (Brown & Emery, 1957), and in seedlings (Hoshikawa) do not warrant separation of the two groups at the level of subfamily.

The inclusion of *Chasmanthium* in *Uniola* L. by most authors prior to Yates's work reflects a striking example of convergent evolution in spikelet morphology. The Unioleae are a monogeneric tribe of the Chloridoideae (q.v.). *Chasmanthium* differs from other centothecoids in not having transversely veined and strongly pseudopetiolate leaves and in some aspects of leaf anatomy (Decker). In leaf cross-section it resembles some members of the Arundineae. In general, however, it is unquestionably centothecoid.

Subfamily 3. POOIDEAE [A. Braun in Ascherson, Fl. Prov. Brandenb. 32, 810. 1864, "Poëideae"].

Ligules membranaceous. Spikelet disarticulation usually above the glumes; rachilla prolonged above the uppermost floret. Staminate or neuter florets usually distal to lowermost carpel-bearing floret; lemmas usually with 3 or more nerves. Lodicules distally membranaceous, weakly vascularized. Hilum generally linear. Embryos small; epiblast present or absent, scutellar tail absent,

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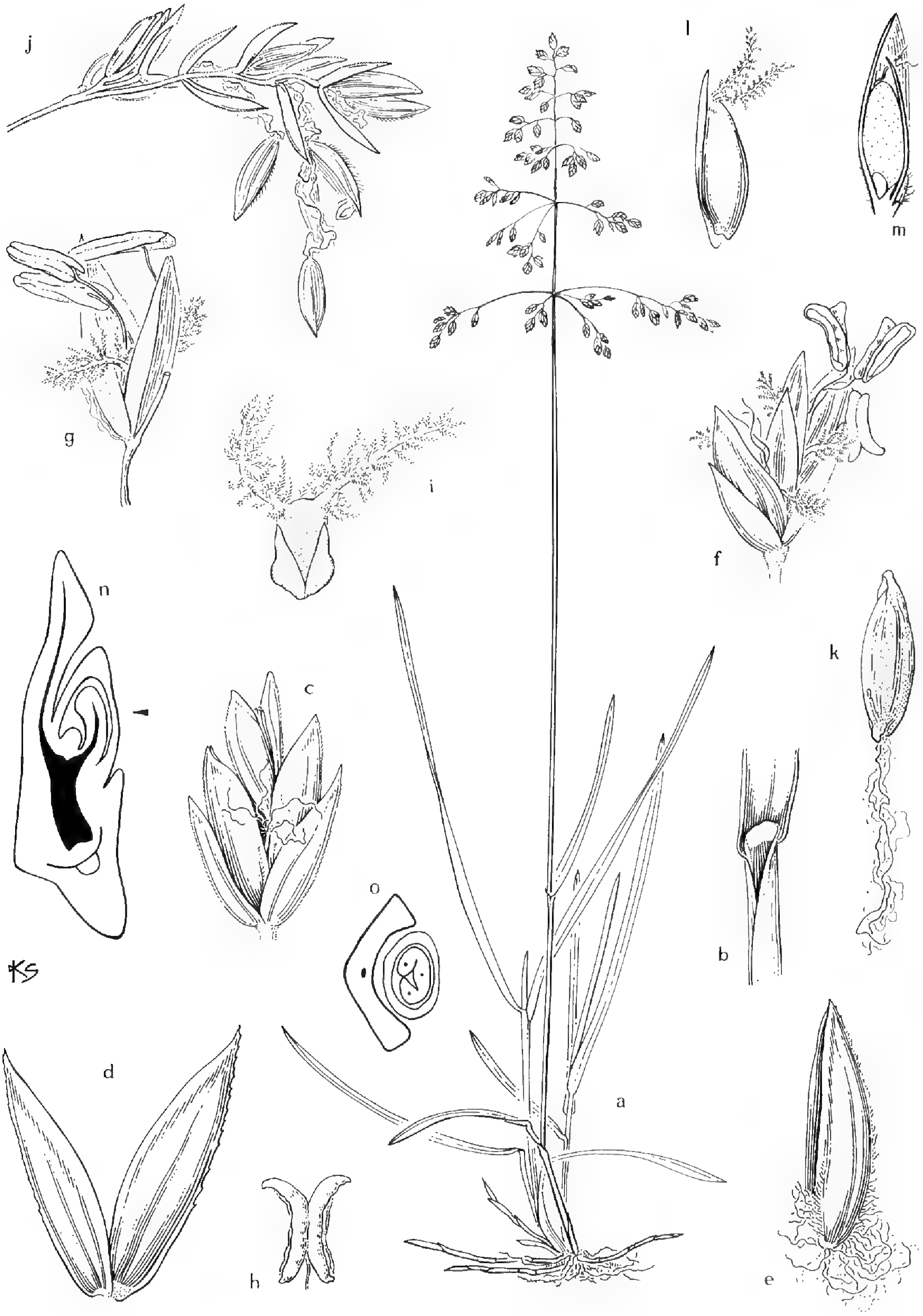
FIGURE 4. **Poa** (Pooideae, Poeae). a–o, *P. pratensis*: a, flowering plant with lateral stolons at base, × ½; b, apex of leaf sheath, ligule, and base of blade, × 3; c, spikelet, × 12; d, glumes, first glume to left, × 20; e, floret before anthesis, the lemma long-pubescent below, × 12; f, spikelet with lower flower open and stigmas receptive, the second floret open, anthers dehisced, × 12; g, floret at anthesis, lemma to left, palea and rachilla to right, × 12; h, dehisced anther with 2 locules, × 12; i, turgid lodicules and gynoecium with receptive stigmas, removed from open floret, × 15; j, portion of inflorescence with mature fruits, 2 florets falling from spikelets, disarticulation occurring above glumes and between florets, × 6; k, floret in fruit (note pubescent lemma), × 12; l, caryopsis, lemma removed, palea to left, × 12; m, caryopsis in diagrammatic longitudinal section, lemma to left, palea to right, endosperm stippled, embryo unshaded,



× 12; n, embryo in diagrammatic longitudinal section (scutellum to left, coleoptile and coleorhiza to right, vascular tissue in black), showing no internode between scutellar and coleoptilar nodes, epiblast (small flaplike structure opposite scutellum), and no cleft between base of scutellum and coleorhiza; o, diagrammatic transverse section of embryo through scutellum, coleoptile, and first embryonic leaf at level of arrow in "n," showing few vascular bundles in leaf, margins of which meet but do not overlap ("n" and "o" redrawn after Reeder, 1957, *fig. 2*).

mesocotyl short, embryonic leaf margins not overlapping. First seedling leaf usually narrow and erect. Microhairs absent; elongated, sinuous or crenate silica bodies present; subsidiary cells parallel sided. Photosynthesis exclusively of the C_3 type. Base chromosome number most commonly 7. (Festucoideae Rouy, Fl. France **14:** 28. 1913.) TYPE GENUS: *Poa* L. FIGURES 1a; 2b; 4; 5A–C, E–I; 6.

A subfamily of about 155 genera in eight tribes and two subtribes (Macfarlane & Watson, 1982). Six tribes are represented in the southeastern United States by about 40 genera and 132 species.

The center of distribution of the Pooideae is the Mediterranean area (Cross). The not-nearly-as-diverse North American pooid component may represent immigrants from Europe before the separation of North America and Europe in the Eocene (Clayton, 1975). Today members of the Pooideae characteristically grow at high latitudes, especially in the Northern Hemisphere (Hartley, 1950, 1973; Cross). Past dispersal along tropical mountains presumably took members of the subfamily to the Southern Hemisphere.

Robert Brown's (1814) perceptions of spikelet morphology clearly defined the panicoids but left other grasses in one heterogeneous group, the pooids. The use of other character suites by Avdulov, Prat (1932, 1936), Reeder (1957, 1962), and Brown (1958a) led to the removal of major groups such as the bambusoids, arundinoids, and chloridoids from the Brownian Poeae. Decker and Macfarlane & Watson (1980, 1982) sharpened the limits of the subfamily even further and produced a reasonably homogeneous taxon, although there is no unique character state holding all pooids together. As a result of Macfarlane & Watson's thorough studies, three traditionally pooid tribes (Brachyelytreae, Diarrheneae, and Stipeae) have been removed from the subfamily. Until more is known about these tribes it seems best to leave them unplaced (see tribes 6a–c).

In supertribe Poanae there are five tribes: the Agrostideae, Aveneae, Meliceae, and Poeae, in our area; and the Seslerieae, a small tribe in the Mediterranean region. Supertribe Triticanae Macfarlane & Watson contains tribes Bromeae and Triticeae, which occur in our area, and the monogeneric Brachypodieae of tropical mountains. The two supertribes differ in numerous ways: presence or absence of auricles, number of nerves in the lemma awns, spikelet and caryopsis length (Macfarlane & Watson, 1982), lodicule and ovary-apex hairiness (characters 26 and 29 of the APPENDIX), presence of an epiblast (38), seedling mesocotyls (43; Harberd), and transitionary node roots (Hoshikawa). For most of these characters, considerable variability in one or more of the tribes produces overlap between the two supertribes. In addition, chemical differences exist in chain length of the starch fructosan (D. Smith, 1973), redundant DNA sequences (Bendich & McCarthy), enzyme kinetics of RuBP carboxylase (Yeoh *et al.*), pollen antigens (Watson & Knox), and the kinds of caryopsis glycosides (De Cugnac), globulins (P. Smith), and amino acids (Yeoh & Watson). Starch grains (character 42 of the APPENDIX) are simple or compound in the Poanae and always simple in the Triticanae. With the exception of this difference in starch grains, these chemical features are like the morphological characters in not being entirely definitive. The great number of these divergent tendencies, however, supports recognition of the two groups.

Tribe 3a. **Agrostideae** Dumortier, Obs. Gram. Belg. 83. 1824.

Spikelets usually 1-flowered. Ovary apex usually glabrous. Hilum usually punctiform. Embryo with an epiblast. At least some starch grains compound. (Phalarideae Dumort. Anal. Fam. Pl. 64. 1829. Milieae Endl. Fl. Posoniensis, 109. 1830. Anthoxantheae Endl. *ibid.* 113.) TYPE GENUS: *Agrostis* L. FIGURES 2b, 5G.

The Agrostideae, as delimited by Macfarlane & Watson (1982), are the largest tribe in the Pooideae. Its 55 genera are most abundant relative to other grasses north of a line between 52° and 62°N latitude, with southern extensions in eastern and western North America (Hartley, 1973). Nineteen genera and about 50 species occur in the southeastern United States. Thirteen of the genera (*Agrostis, Alopecurus* L., *Ammophila* Host, *Calamagrostis* Adanson, *Cinna* L., *Deschampsia* Beauv., *Hierochloë* R. Br., *Koeleria* Pers., *Limnodea* L. H. Dewey, *Milium* L., *Phalaris* L., *Sphenopholis* Scribner, and *Trisetum* Pers.) have indigenous species. Six genera (*Aira* L., *Anthoxanthum* L., *Holcus* L., *Lagurus* L., *Phleum* L., and *Polypogon* Desv.) indigenous mostly to Europe are represented in our area by one or more adventive species.

The Agrostideae are most closely related to the Aveneae; the relationship between the two tribes is discussed under the latter. Both tribes also appear to be close to the Poeae serologically (P. Smith), in enzyme kinetics of RuBP carboxylase (Yeoh *et al.*), and in being the only tribes of grasses in which the endosperm is liquid in some species (Terrell; Macfarlane & Watson, 1982). These three tribes may form a "reticulate biological unit" (Hilu & Wright).

The tribe Phalarideae has been recognized on the basis of the presence of reduced structures between the glumes and the single, perfect terminal floret of spikelets in its three genera (*Anthoxanthum, Hierochloë,* and *Phalaris*). These reduced structures, often thought to be sterile lemmas (Hitchcock), are not necessarily homologous between genera. Barnard considered the spikelet of *Anthoxanthum* to consist of four sterile glumes and two lemmas, each of which subtends a single stamen. The gynoecium forms directly from the apex of the spikelet axis. Since nothing else sets these genera off from agrostoid or avenoid grasses, the Phalarideae have been lumped either with the Agrostideae (Macfarlane & Watson, 1982) or the Aveneae (Clayton, 1978), or with the combined Agrostideae and Aveneae (Tateoka, 1957a; Stebbins & Crampton; Hilu & Wright).

Tribe 3b. **Aveneae** Dumortier, Obs. Gram. Belg. 82. 1824, "Avenaceae."

Spikelets usually 2–7-flowered. Ovary apex usually hairy. Hilum linear. Embryo with an epiblast. At least some starch grains compound. TYPE GENUS: *Avena* L.

Macfarlane & Watson (1982) included eight genera in the Aveneae. Four are confined to the Old World, one to the New, with three occurring in both. In our area the tribe is represented by three adventive species in three genera, *Avena* (*A. fatua* L.), *Amphibromus* Nees (*A. scabrivalvis* (Trin.) Swallen), and *Arrhenatherum* Beauv. (*A. elatius* (L.) Mert. & Koch).

This tribe is so similar to the Agrostideae that many workers (Pilger; Tateoka, 1957a; Stebbins & Crampton; Watson; Hilu & Wright) have united the two. On the basis of rather small samples, it seems that the two tribes are not distinct serologically (P. Smith), embryologically (Maze & Bohm, 1974), or in terms of enzyme kinetics of RuBP carboxylase (Yeoh *et al.*). In contrast, immunology (Watson & Knox) and amino-acid complements (Yeoh & Watson) appear to separate the two tribes, but sample sizes here were also small. Macfarlane & Watson (1982), who have made the most recent and thorough study of the two groups, maintain them as tribes. In addition to noting differences in the number of florets per spikelet, hairiness of the ovary apex, and hilum shape (see characters 15, 29, and 35 in the APPENDIX), they pointed out tendencies for the Aveneae to bear longer spikelets, awns from terminal notches (rather than abaxially), and lower glumes with more than one vein (rather than usually a single vein).

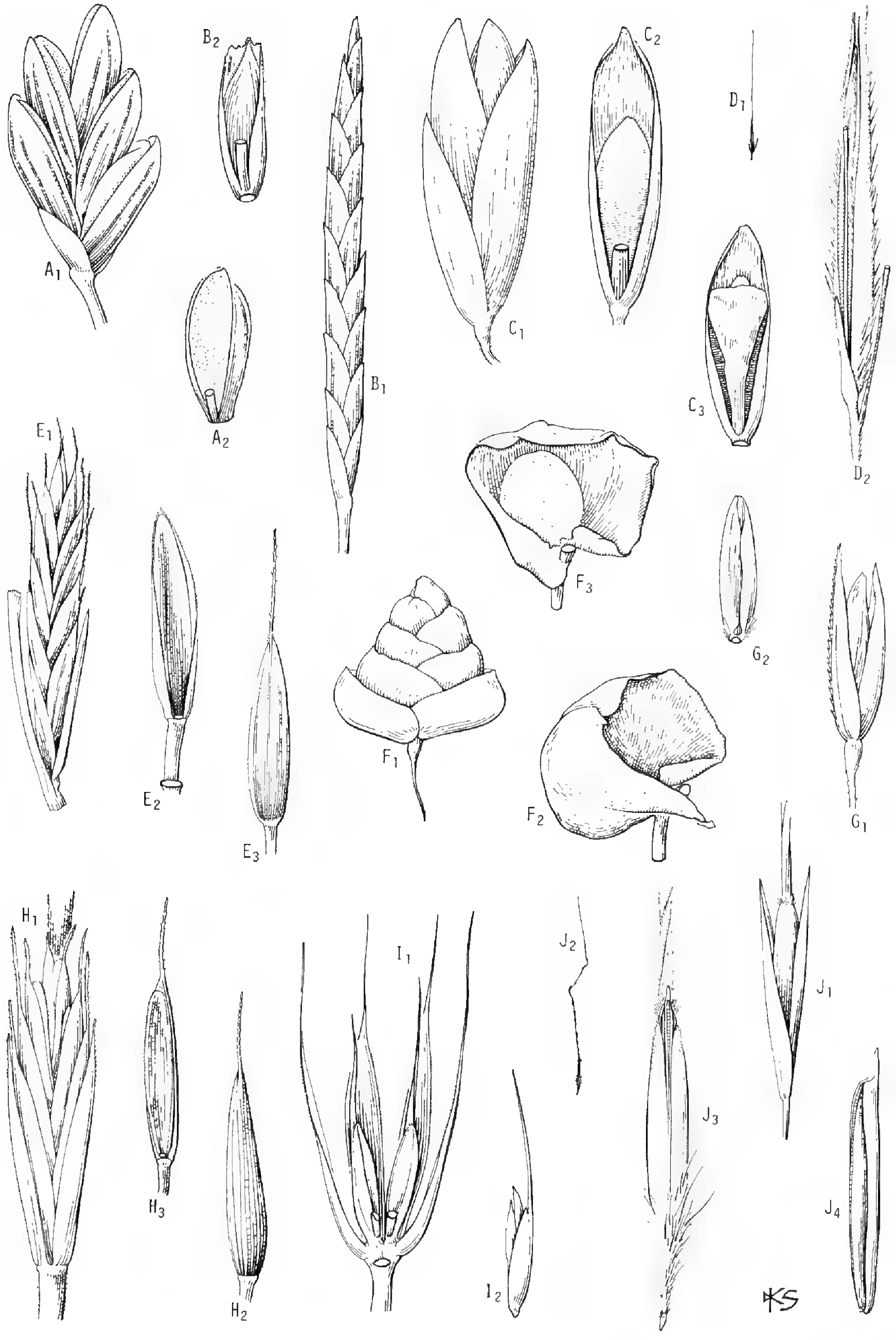
Tribe 3c. **Meliceae** Reichenbach, Consp. Reg. Veg. 53. 1828, "Melicaceae."

Lodicules usually connate, truncate, and distally fleshy. Ovary apex glabrous. Leaf-sheath margins more or less connate. Embryo with an epiblast. Base chromosome number 9 or 10. TYPE GENUS: *Melica* L. FIGURE 5A–C.

A tribe of nine genera that do not form a closely interrelated group (Hilu & Wright; Macfarlane & Watson, 1982). Three genera, *Glyceria* R. Br., *Melica*, and *Schizachne* Hackel, with about 12 species, occur in our area.

The Meliceae are distinguished from other pooids by unusual lodicules and relatively small chromosomes with base numbers atypical for the subfamily.

FIGURE 5. Spikelets and their parts, **Pooideae, Stipeae,** and **Brachyelytreae.** A, *Glyceria striata* (Meliceae), × 12: A1, spikelet; A2, floret with portion of rachilla. B, *Glyceria septentrionalis:* B1, spikelet, × 3; B2, floret with portion of rachilla, × 6. C, *Melica mutica* (Meliceae), × 5: C1, spikelet; C2, fertile floret with segment of rachilla; C3, upper fertile floret with knoblike cluster of empty lemmas. D, *Brachyelytrum erectum* (Brachyelytreae): D1, spikelet with long-awned lemma, × ½; D2, spikelet, showing second glume (first glume absent), fertile floret with lemma and palea (lemma awn not shown), and rachilla extending upward as bristle against palea, segment of rachis to right of spikelet, × 5. E, *Lolium perenne* (Poeae): E1, spikelet with portion of rachis, × 3; E2, second floret from base of spikelet, lemma without awn, palea toward viewer, × 5; E3, awned lemma of fertile floret, palea hidden from view, × 5. F, *Briza minor* (Poeae): F1, spikelet, × 6; F2, floret with rachilla segment, palea not visible, × 12; F3, same, seen from axis, palea visible within lemma, × 12. G, *Agrostis hiemalis* (Agrostideae), × 12: G1, spikelet, showing glumes and single floret; G2, floret (lemma) enclosing caryopsis, palea absent. H, *Elymus repens* (*Agropyron repens*) (Triticeae), × 3: H1, spikelet with part of rachis behind it (contrast with E1); H2, floret from near base of spikelet, showing back of awned lemma; H3, same, showing palea. I, *Elymus canadensis* (Triticeae), × 2: I1, section of rachis with a pair of spikelets, each with 2 glumes and 1 floret; I2, upper florets of a



spikelet, lateral view showing awned lemma. J, *Piptochaetium avenaceum* (*Stipa avenacea*) (Stipeae): J1, spikelet with single floret (only base of lemma awn shown), × 2; J2, floret, to show relative length of hygroscopic lemma awn, × ½; J3, floret, note hairy base of lemma and rachilla forming bearded, sharp-pointed callus, lemma clasping pointed palea (only base of lemma awn shown), × 5; J4, palea, × 5.

The tribe is also serologically distinct (on the basis of *Melica* alone—Fairbrothers & Johnson, P. Smith) and is unusual among pooids for its sometimes abundantly papillose leaf epidermis, uniformly thickened walls of the inner bundle sheath (Decker), and scarcity of silica bodies in the leaf epidermis (Stebbins & Crampton). Although in most characters the tribe certainly belongs in the supertribe Poanae, its similarity to the supertribe Triticanae in disaccharides and oligosaccharides in the seeds (MacLeod & McCorquodale), amino-acid patterns of the caryopses (Yeoh & Watson), and enzyme kinetics of RuBP carboxylase (Yeoh *et al.*) hints that it may be intermediate between the two supertribes.

Tribe 3d. **Poeae** [R. Brown in Flinders, Voy. Terra Austral. **2:** 583. 1814].

Leaf vernation often folded. Ovary apex glabrous. (Festuceae Dumortier, Obs. Gram. Belg. 82. 1824. Including Monermeae C. E. Hubb. in Hutchinson, Brit. Fl. Pl. 332. 1948.) TYPE GENUS: *Poa* L. FIGURES 4; 5E, F.

A tribe of 50 genera (Macfarlane & Watson, 1982), primarily north-temperate in distribution. According to Hartley (1950), they are most abundant relative to other grasses north of the 50°F isotherm for mean temperature of the mid-winter month. Four (*Festuca* L., *Poa, Puccinellia* Parl., and *Vulpia* K. C. Gmelin) of the ten genera found in the southeastern United States are represented by native species. The other genera, *Briza* L., *Catapodium* Link, *Cynosurus* L., *Dactylis* L., *Lolium* L., and *Parapholis* C. E. Hubb., are mostly natives of Europe. In all, there are approximately 37 species of this tribe in our area. The Monermeae, containing the genus *Parapholis* of our area, have been included in the Poeae by Macfarlane & Watson (1982).

The group is rather heterogeneous morphologically, serologically (P. Smith), and in the composition of seed carbohydrates (MacLeod & McCorquodale) and fructosans (D. Smith, 1968, 1973). The only pooid tribe with more multistate characters in the APPENDIX is also the only larger tribe, the Agrostideae. The Poeae are morphologically very close to both the Agrostideae and the Aveneae (see discussion under Agrostideae). The Poeae differ from the other two tribes in having folded, rather than rolled, vernation (character 6 of the APPENDIX) and in the presence of crescentic silica bodies in the leaf epidermis (56). They differ further from the Agrostideae in the number of florets per spikelet (15), and from the Aveneae in the lodicule apex (27) and ovary apex (29).

Tribe 3e. **Bromeae** Dumortier, Obs. Gram. Belg. 82. 1824, "Bromaceae."

Stem leaf sheaths united into a tube. Lemma awns abaxial or from a terminal notch. Ovary appendage hairy, terminal; styles laterally positioned. Embryo without an epiblast. Starch grains all simple. TYPE GENUS: *Bromus* L.

The genus *Bromus* (about 50 species) is distributed in cooler regions throughout the world. It is usually either isolated as a monogeneric tribe (Clayton, 1978; Hilu & Wright; Macfarlane & Watson, 1982) or grouped with *Boissiera* Hochst. & Steudel (Bor). About 15 species of *Bromus,* two-thirds of them adventive, occur in the southeastern United States.

Inflorescence and spikelet morphology alone dictate placement of *Bromus* in the Poeae, and it has often been placed there (e.g., Hitchcock; Pilger; Prat, 1960; Parodi; Jacques-Félix, 1962; Decker; Hubbard, 1973a; Gould & Shaw). Hubbard (1948) and Stebbins & Crampton, while maintaining *Bromus* in the Poeae, pointed out that its starch grains are all simple (first noted by Harz) and never compound like those of members of the Poeae.

Both Avdulov and Hubbard (1948) noted the similarity of *Bromus* and the Triticeae in their starch grains and hairy ovary apices. In addition, the Bromeae and Triticeae share numerous morphological, anatomical, and other character states (see discussion of subfam. Pooideae). The two tribes are clearly distinct from one another, however, in secondary-inflorescence form (character 10 of the APPENDIX), lemma-awn position (21), lodicule hairiness (26), and ovary appendage (30). The Bromeae also differ from the Triticeae in amino-acid composition of the caryopses (Yeoh & Watson). The Bromeae have been considered to be a linking group between the Triticeae and other pooids (P. Smith; Clayton, 1978).

Tribe 3f. **Triticeae** Dumortier, Obs. Gram. Belg. 82. 1824.

Inflorescence a solitary spike. Lemma awns apical. Lodicules hairy. Ovary apex hairy. Embryo with or without an epiblast. Starch grains all simple. (Hordeae Spenner, Fl. Friburg. **1:** 155. 1825. Secaleae Reichenb. Consp. Reg. Veg. 48. 1828. Brachypodieae Harz, Linnaea **43:** 15. 1880. Frumenteae Krause, Verh. Nat. Ver. Preuss. Rheinl. **59:** 172. 1903.) TYPE GENUS: *Triticum* L. FIGURES 1a; 5H, I; 6.

The Triticeae are not a prominent tribe in our area, for there are only about nine indigenous species in three genera (*Agropyron* Gaertner, *Elymus* L. [including *Hystrix* Moench], and *Hordeum* L.). About seven species in five genera (*Aegilops* L., *Agropyron, Hordeum, Secale* L., and *Triticum*) are adventive, mostly from Eurasia. In North America the tribe is more common at latitudes north of 35°N (Dewey). Worldwide, it is most frequent relative to other grasses in low-lying areas in and near Asia Minor, Iraq, the Caspian Sea, and to a lesser extent, the western United States (Hartley, 1973).

The Triticeae, easily recognized by the spicate inflorescences, form a close-knit group (Macfarlane & Watson, 1982) most closely related to the Bromeae (see discussion under the latter tribe). Within the tribe, however, there have been widely differing opinions about generic limits, ranging from a monogeneric concept (Stebbins, 1956a) to the most generally accepted circumscription of 15 to 30 genera (Baum, 1982a, 1982b, 1983; Dewey). Taxonomic problems persist in the group, although the economic importance of some of its members as cereals (wheat, barley, and rye [*Secale cereale* L.]) and as forage and range grasses (*Agropyron* and *Elymus*) has motivated extensive research.

The Triticeae are remarkable for the great extent of intergeneric hybridization. For the 28 genera Baum (1982a) recognizes, he records 65 intergeneric crosses or about 17 percent of all possible intergeneric hybrids. Only five genera do not hybridize with others, while *Agropyron* and *Hordeum* each cross with 14 other triticoid genera. It is therefore not surprising that the taxonomy of this tribe at both generic and specific levels is difficult and that polyploidy

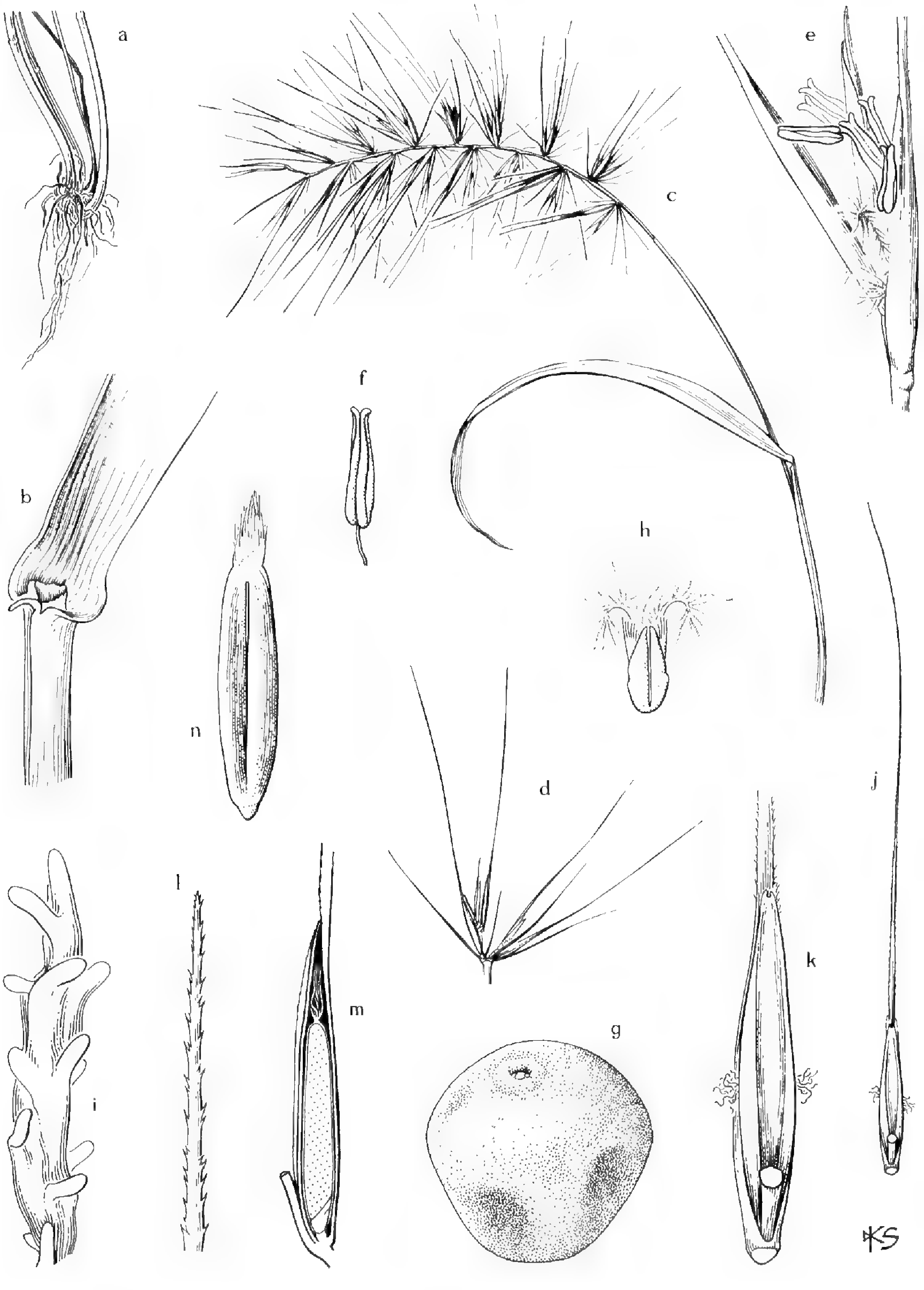


FIGURE 6. **Elymus** (*Hystrix*) (Pooideae, Triticeae). a–n, *E. Hystrix* (*H. patula*): a, base of plant, × ½; b, junction of leaf sheath and leaf blade (note ligule), × 6; c, inflorescence, × 1; d, paired spikelets from near base of inflorescence (note 2 glumes subtending each spikelet), × 1; e, spikelet with 1 floret at anthesis (lemma awn not shown), × 4; f, longitudinally dehiscent basifixed anther, × 6; g, pollen with single germination pore, × 750; h, gynoecium and turgid lodicules, × 6; i, tip of stigmatic branch, × 500; j, floret in fruit, × 2; k, base of same to show palea and rachilla, × 5; l, tip of lemma awn, × 25; m, base of floret in fruit, vertical section (rotated 90° from floret in "k"), endosperm stippled, embryo unshaded, × 5; n, adaxial side of caryopsis, × 6.

predominates: only two of the approximately 50 species occurring in North America are diploid. Hybridization has been important in the development of agriculturally desirable taxa such as triticale (*Triticum* × *Secale*) and the bread wheats.

Subfamily 4. CHLORIDOIDEAE Rouy, Fl. France **14:** 2. 1913, "Chloridineae."

Ligules often fringed. Spikelets often laterally flattened; staminate or neuter florets usually distal to the lowermost carpel-bearing floret; lemma nerves often 3 or fewer. Lodicules usually fleshy distally. Hilum punctiform. Embryo with an epiblast and a long mesocotyl, usually with a scutellar tail; embryonic leaf margins not overlapping. First seedling leaf usually broad. Microhair distal cell usually inflated; both tall and narrow silica bodies and saddle-shaped silica bodies usually present; subsidiary cells generally triangular. Photosynthesis of the C_4 type; mesophyll cells radially arranged. Sclerenchyma accompanying the smallest vascular bundles usually present. Base chromosome number usually 10. (Eragrostoideae Pilger, Nat. Pflanzenfam. ed. 2. **14d:** 167. 1956.) TYPE GENUS: *Chloris* Sw. FIGURES 1d; 2c; 7A, C–I.

A subfamily of about five tribes, 90 genera, and 900 species. In the southeastern United States, the 26 genera, six of which are represented only by adventive species, are divided into four tribes. The boundaries between some of the traditionally recognized tribes (e.g., Eragrostideae and Cynodonteae (Chlorideae); Eragrostideae and Sporoboleae) are arbitrary (Hubbard, 1973a; Christopher & Abraham, 1974; Clayton, 1978; Hilu & Wright; Phillips). A broad tribal concept is therefore used here.

The Chloridoideae, perhaps the most homogeneous grass subfamily, are clearly defined by leaf anatomy. The distal cell of the microhairs is inflated (character 49 of the APPENDIX); the parenchyma sheath is kranz, and its chloroplasts are in most cases centripetally positioned (Brown, 1960b, 1975, 1977; Sutton); and salt glands are known in 17 chloridoid genera but in none outside this subfamily (Lipschitz & Waisel).

The subfamily is apparently most closely related to the Arundinoideae (Clifford *et al.*; Clayton, 1981a; Phillips) and may be evolutionarily derived from ancestral stock of that subfamily. Some affinities with the Paniceae have also been suggested (Watson), and the two groups do share a center of distribution in Africa (Clayton, 1981a). They differ, however, in numerous ways (see discussion under the Panicoideae).

The abundance (in terms of number of taxa and endemics) of chloridoids in tropical Africa led Hartley & Slater to propose an African origin for the group. Their association of high speciation with arid climates was challenged by Cross, who characterized chloridoids as savanna grasses primarily of Africa and Australia. Clayton (1981a), noting the conspicuously large number of chloridoids in North America, suggested that they are filling a gap created by the "evolutionary lethargy" of the pooids there.

Tribe 4a. **Aeluropodeae** Nevski ex Bor, Oesterr. Bot. Zeitschr. **112:** 184. 1965.

FIGURE 7. Spikelets and their parts, **Chloridoideae** and **Aristideae.** A, *Monanthochloë littoralis* (Aeluropodeae), × 5: A1, staminate spikelet at anthesis, 3 stamens visible; A2, carpellate spikelet at tip of branch with 4 leaves; A3, carpellate floret (glumes absent). B, *Aristida longispica* (Aristideae): B1, spikelet with glumes spread apart, × 6; B2, floret with mature caryopsis, 3-awned lemma completely enclosing palea and caryopsis, × 6; B3, caryopsis, × 6; B4, palea, × 12 (note palea drawn twice as large as lemma in B2).

Rhizomatous or stoloniferous. Leaf blades disarticulating. Plants usually dioecious. Lemma nerves 7 or more. Embryo without a scutellar tail. Starch grains all simple. Short cells over the veins solitary or in short rows. TYPE GENUS: *Aeluropus* Trin. FIGURE 7A.

A small tribe of about seven genera including 25–30 species. They are rhizomatous or stoloniferous, often dioecious halophytes, mostly with narrow distributions in the New World. The largest genus, *Distichlis* Raf., is represented by *D. spicata* (L.) Greene in the southeastern United States. The only other species in our area comes from the monotypic genus *Monanthochloë* Engelm. (*M. littoralis* Engelm.), which is found elsewhere only in the West Indies.

The Aeluropodeae are close to the Cynodonteae but are distinguished by several features uncommon in the subfamily: short, pungent leaves; abundant epidermal papillae; small, rounded, often sunken microhairs; and many-nerved lemmas (Stebbins & Crampton; Decker; Soderstrom & Decker, 1964).

Tribe 4b. **Cynodonteae** Dumortier, Obs. Gram. Belg. 83. 1824, "Cynodoneae."

Inflorescence usually paniculate or of spiciform branches. Spikelets disarticulating above the glumes. Cross- to dumbbell-shaped silica bodies present. (Chlorideae Reichenb. Consp. Reg. Veg. 48. 1848. Spartineae Gren. & Godron, Fl. France **3:** 434. 1855. Sporoboleae Stapf in Thiselton-Dyer, Fl. Capensis **7:** 315. 1898. Eragrostideae Stapf, *ibid.* 316. Perotideae C. E. Hubb. in Bor, Grasses Burma, Ceylon, India, Pakistan, 686. 1960.) TYPE GENUS: *Cynodon* Rich. FIGURES 1d; 7C–E, G–I.

A broadly defined tribe, here including four traditionally recognized tribes: Cynodonteae (Chlorideae), Eragrostideae, Spartineae, and Sporoboleae. The first two contain many genera; the third, only *Spartina* Schreber; and the last, only *Calamovilfa* (A. Gray) Scribner, *Muhlenbergia* Schreber and *Sporobolus* R. Br. Twenty-one genera of this enlarged tribe occur in the southeastern United States: *Bouteloua* Lag., *Buchloë* Engelm., *Calamovilfa, Chloris, Crypsis* Aiton,

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C, *Ctenium aromaticum* (Cynodonteae), × 6: C1, transverse section of rachis (unshaded) with 2 spikelets (spikelets in 2 rows), the first spikelet shaded (note small first glume, stoutly awned second glume; first 2 florets sterile and with long awns, third floret fertile); C2, fertile (third) floret, showing hairy lemma, palea, and hairy callus. D, *Cynodon dactylon* (Cynodonteae): D1, portion of rachis, showing sessile spikelets in 2 rows, each spikelet 1-flowered, × 6; D2, floret, lemma to left, rachilla prolonged behind palea, × 12. E, *Eustachys* (*Chloris*) *petraea* (Cynodonteae): E1, portion of rachis, showing spikelets in 2 rows, × 10; E2, spikelet, × 12; E3, spikelet with glumes removed, fertile floret to left, rudimentary floret to right (stippled), × 12; E4, fertile floret, turned to show part of palea within lemma, × 12. F, *Uniola paniculata* (Unioleae): F1, spikelet, lower florets sterile, × 1.5; F2, fertile floret, palea to left, × 12. G, *Muhlenbergia Schreberi* (Cynodonteae), × 12: G1, spikelet, from side, showing glumes, lemma (to right), and palea; G2, lemma from back. H, *Muhlenbergia capillaris* (Cynodonteae): H1, spikelet at anthesis, stigmas protruding, 1 anther visible, × 6; H2, spikelet, showing long pedicel of this species, × 3. I, *Eragrostis Elliottii* (Cynodonteae): I1, spikelet, × 5; I2, floret with segment of rachilla, × 12; I3, caryopsis, palea persistent on rachilla, and mature floret, × 12.

Ctenium Panzer, *Cynodon, Dactyloctenium* Willd., *Diplachne* Beauv., *Eleusine* Gaertner, *Eragrostis* Wolf, *Eustachys* Desv., *Gymnopogon* Beauv., *Leptochloa* Beauv., *Muhlenbergia, Opizia* Raf., *Schedonnardus* Steudel, *Spartina, Sporobolus, Tridens* Roemer & Schultes, and *Triplasis* Beauv. Clayton (1967), D. E. Anderson, and Phillips have discussed numerous problems in defining generic limits in the Cynodonteae.

The four tribes combined here are based upon inconsistent inflorescence characters: the Cynodonteae and Spartineae bear one-sided, spiciform secondary inflorescences of one-flowered spikelets; the Eragrostideae, panicles of several-flowered spikelets; and the Sporoboleae, panicles of one-flowered spikelets. Hilu & Wright pointed out that certain genera (e.g., *Dactyloctenium, Eleusine,* and *Leptochloa*) bear the spiciform inflorescences of the Cynodonteae, but their spikelets are eragrostoid in having several florets. The Eragrostideae may rarely have one-flowered spikelets like the Sporoboleae (Phillips). Furthermore, at least for the Cynodonteae and Eragrostideae, there are no other significant distinguishing characters, and the two groups should either be given subtribal status (Hilu & Wright) or merged entirely. The Sporoboleae, on the other hand, differ from eragrostoids in lacking a culm pulvinus (Brown *et al.,* 1959b) and in the centrifugal position of the parenchyma-sheath plastids of some of the species of *Muhlenbergia* and *Sporobolus* (Brown, 1960b). That these differences do not hold all the time, however, underscores the artificiality of the Sporoboleae. Phillips considered the tribe to be "clearly no more than an offshoot of the Eragrostideae," and Stebbins & Crampton, Sutton, and Gould & Shaw lumped it with the Eragrostideae. *Spartina* does not differ from the Cynodonteae sufficiently to warrant tribal status (Mobberley; Hitchcock; Reeder & Singh; Hubbard, 1973a).

The broadly circumscribed Cynodonteae make up most of the Chloridoideae, and hence the discussion of the distribution of the subfamily applies well to this dominant tribe.

Tribe 4c. **Unioleae** (Clayton) Roshevits ex C. S. Campbell, stat. nov.

Lemma nerves 7–11. Microhair distal cell narrowly dome shaped; cross- to dumbbell-shaped silica bodies absent; cork-silica pairs absent; short cells over the veins in rows of 5 or more. Midrib bundles more than 1 and arranged in an arc. (Subtribe Uniolinae Clayton, Kew Bull. **37:** 417. 1982. Tribe Unioleae Roshevits, Zlaki, 244. 1937, nomen invalidum sine descriptione latine.) TYPE GENUS: *Uniola* L. FIGURE 7F.

The tribe contains only *Uniola,* comprising two species of sea beach grasses. *Uniola Pittieri* Hackel ranges from Mexico to Ecuador, and *U. paniculata* L., commonly called sea oats, occurs from Virginia to Texas and in the Caribbean and Mexico. Spikelets of *Uniola* strongly resemble the many-flowered, laterally compressed spikelets of many non-chloridoid grasses, but Yates clearly demonstrated that leaf and embryo anatomy and chromosome number show *Uniola* to be chloridoid. It differs from other chloridoids in the lemma nerves and in several characters of the leaf epidermis (see diagnosis above).

Tribe 4d. **Zoysieae** Bentham, Jour. Linn. Soc. Bot. **19:** 29. 1881.

Floret 1 per spikelet; disarticulation below the glumes; rachillas not prolonged above the floret. Tall and narrow silica bodies absent. (Nazieae Hitchc. Gen. Grasses U. S. 15. 1920. Trageae Hitchc. Contr. U. S. Natl. Herb. **24:** 599. 1927.) TYPE GENUS: *Zoysia* Willd. FIGURE 2c.

Clayton & Richardson considered this tribe of 12 genera to be entirely Old World in distribution and closely related to the Cynodonteae. One species of *Tragus* Haller, *T. racemosus* (L.) All., is occasionally adventive in our area, and a few species of *Zoysia* used in lawns escape from cultivation (Hitchcock).

Subfamily 5. PANICOIDEAE A. Braun in Ascherson, Fl. Prov. Brandenb. 32, 799. 1864.

Spikelets (FIGURES 8–11) compressed dorsally, with 1 carpel-bearing floret per spikelet, the staminate or neuter florets proximal to the carpel-bearing one. Lodicules distally fleshy (FIGURES 8h, 10h). Embryo with a scutellar tail, without an epiblast, the mesocotyl long (FIGURES 8n, 10l), embryonic leaf margins overlapping (FIGURES 8o, 10m). First seedling leaf blade broad. Microhair distal cell narrow; cross- to dumbbell-shaped silica bodies present (FIGURE 1c); guard cells overlapped by interstomatals. C_3- or C_4-type photosynthesis (FIGURE 2d); sclerenchyma not accompanying the smallest vascular bundles. Base chromosome number mostly 9 and 10. (Saccharoideae Reichenb. Repert. Herb. 37. 1841. Andropogonoideae Ridley, Mat. Fl. Malay. Penin. **3:** 120. 1907.) TYPE GENUS: *Panicum* L. FIGURES 1c, 2d, 8–11.

Because of its distinctive spikelets, the subfamily Panicoideae was circumscribed early (R. Brown, 1810, 1814). This is the largest subfamily in terms of genera (about 200) and species (about 2800), most of which fall into two large tribes, the Andropogoneae and Paniceae. Up to ten other tribes, all with fewer than seven genera, are recognized by some agrostologists, but the three small panicoid tribes represented in the southeastern United States—Anthephoreae, Maydeae, and Tristegineae (Melinideae)—are here included in the two large tribes. In our area there are about 46 genera and 275 species.

Clayton (1981a) considered subfamily Arundinoideae to have provided the ancestral stock for the Panicoideae. Of the other subfamilies it resembles the Chloridoideae in C_4 photosynthesis, chromosome base number (mostly 10), and broadly tropical distribution. These two subfamilies differ in numerous ways, however: spikelets (APPENDIX, characters 12, 15, and 18), embryos (38, 41), microhair distal-cell shape (49), and silica bodies (53–55). In photosynthetic pathway (67), 20 percent of the genera of Panicoideae are non-kranz; of the kranz genera, 89 percent are of the mestome-sheath (MS) subtype of kranz anatomy (Brown, 1977). Chloridoids, on the other hand, uniformly have the parenchyma-sheath (PS) subtype. The caryopses of the Panicoideae contain lower levels of glutamine and methionine and higher levels of proline, alanine, and leucine than the Chloridoideae (Yeoh & Watson). The levels of proline and glycine in the Paniceae are intermediate between the levels in subfam. Chloridoideae and in tribe Andropogoneae.

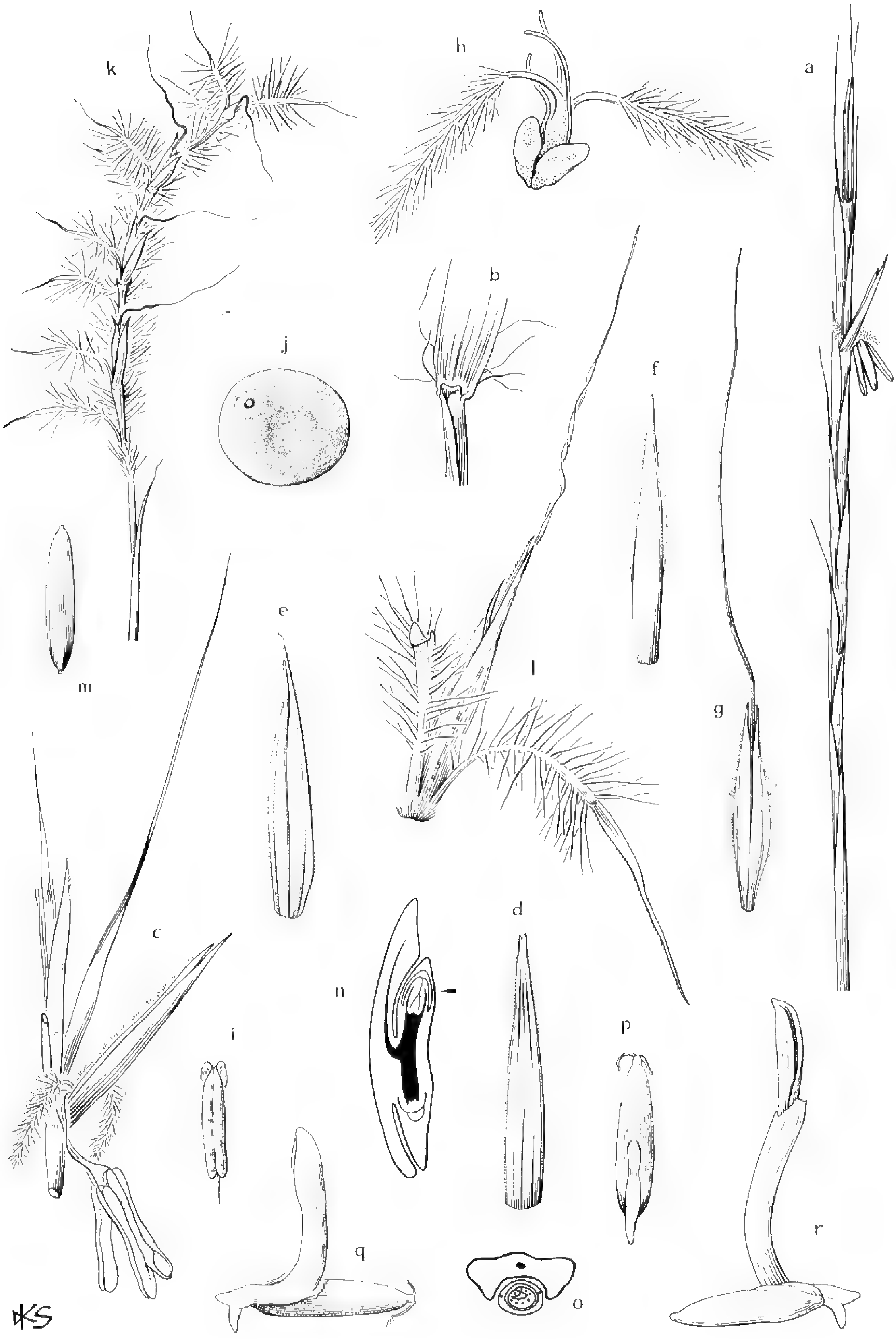

FIGURE 8. **Schizachyrium** (Panicoideae, Andropogoneae). a–r, *S. scoparium* (*Andropogon scoparius*): a, solitary inflorescence with 1 spikelet at anthesis, × 2; b, apex of leaf sheath, ligule, and base of blade, × 3; c, spikelet pair, sterile spikelet to upper left and behind, fertile spikelet at anthesis, × 6; d, first glume (abaxial side), × 6; e, second glume (abaxial side), × 6; f, sterile lemma, × 6; g, fertile lemma with long awn (palea absent),

More chromosome base numbers have been reported in the Panicoideae than in any other subfamily (character 84 of the APPENDIX). Base numbers are mostly nine or ten, but five (Christopher & Abraham, 1976) and four (Celarier & Paliwal) have also been reported.

Tribe 5a. **Andropogoneae** Dumortier, Obs. Gram. Belg. 84. 1824, "Andropogineae."

Spikelets often paired, with 1 sessile, perfect or carpellate, and 1 pedicellate, staminate or neuter (FIGURES 8, 9); glumes usually firmer than the lemmas and with 3 or fewer nerves; lemmas of fertile floret awned (FIGURE 8g) or unawned. Photosynthesis type kranz, subtype MS. (Saccharineae Dumortier, *op. cit.* 83, 141. Maydeae Dumortier, *op. cit.* 84, 142. Zeae Reichenb. Consp. Reg. Veg. 55. 1828. Ophiureae Dumortier, Anal. Fam. 64. 1829. Imperateae Gren. & Godron, Fl. France **3:** 471. 1855. Coiceae Nakai, Ord. Fam. etc. Append. 223. 1943. Euchlaeneae Nakai, *ibid.* Tripsaceae Nakai, *ibid.*) TYPE GENUS: *Andropogon* L. FIGURES 1c, 2d, 8, 9.

The approximately 85 genera of the Andropogoneae form one of the most easily recognized and clearly monophyletic large taxa in the family. Clayton (1972, 1973, 1981b, and in prep.) recognized about 12 subtribes, eight of which occur in our area: Andropogoninae Presl (*Andropogon* and *Schizachyrium* Nees); Anthistirriinae Presl (*Heteropogon* Pers., *Hyparrhenia* Fourn., and *Themeda* Forskål); Coicinae Reichenb. (*Coix* L.); Dimeriinae Hackel (*Arthraxon* Beauv.); Rottboelliinae Presl (*Coelorachis* Brongn. [*Manisuris* L., in part], *Elionurus* Willd., *Eremochloa* Buese, *Hackelochloa* Kuntze, and *Hemarthia* R. Br. [*Manisuris*, in part]); Saccharinae Griseb. (*Erianthus* Michaux, *Imperata* Cyr., and *Microstegium* Nees); Sorghinae Stapf (*Bothriochloa* Kuntze, *Chrysopogon* Trin., *Sorghastrum* Nash, *Sorghum* Moench, and *Vetiveria* Bory); and Tripsacinae Dumort. (*Tripsacum* L.). The last was long recognized as the tribe Maydeae, but this group is closely tied to the Andropogoneae through the Rottboelliinae. These 21 genera contain about 57 species in our area.

All species studied so far are C_4 and have the MS subtype of kranz anatomy (Carolin *et al.*; Johnson & Brown; Brown, 1977). Epidermal and transverse-sectional anatomy of leaves (Renvoize, 1982), base chromosome number (Celarier), host distribution of smuts (Watson), overall morphology (Hackel, 1889; Keng), and perhaps the nature of the spikelets (Grassl) emphasize the uniformity of the tribe and its distinctness from other tribes.

× 6; h, floret (lemma removed), showing turgid lodicules, receptive stigmas, and staminal filaments (anthers fallen), × 12; i, dehisced anther with apical slits, × 6; j, pollen with 1 germination pore, × 500; k, solitary inflorescence, × 2; l, spikelet pair in fruit, vestigial sterile spikelet recurved to right, × 6; m, caryopsis, × 6; n, embryo in diagrammatic longitudinal section (scutellum to left, coleoptile and coleorhiza to right, vascular tissue in black), showing internode between scutellar and coleoptilar nodes, no epiblast, and cleft between base of scutellum and coleorhiza; o, diagrammatic transverse section of embryo through scutellum, coleoptile, and first embryonic leaf at level of arrow in "n," showing numerous vascular bundles and overlapping margins of leaf ("n" and "o" after Reeder, 1957, *fig. 16*).

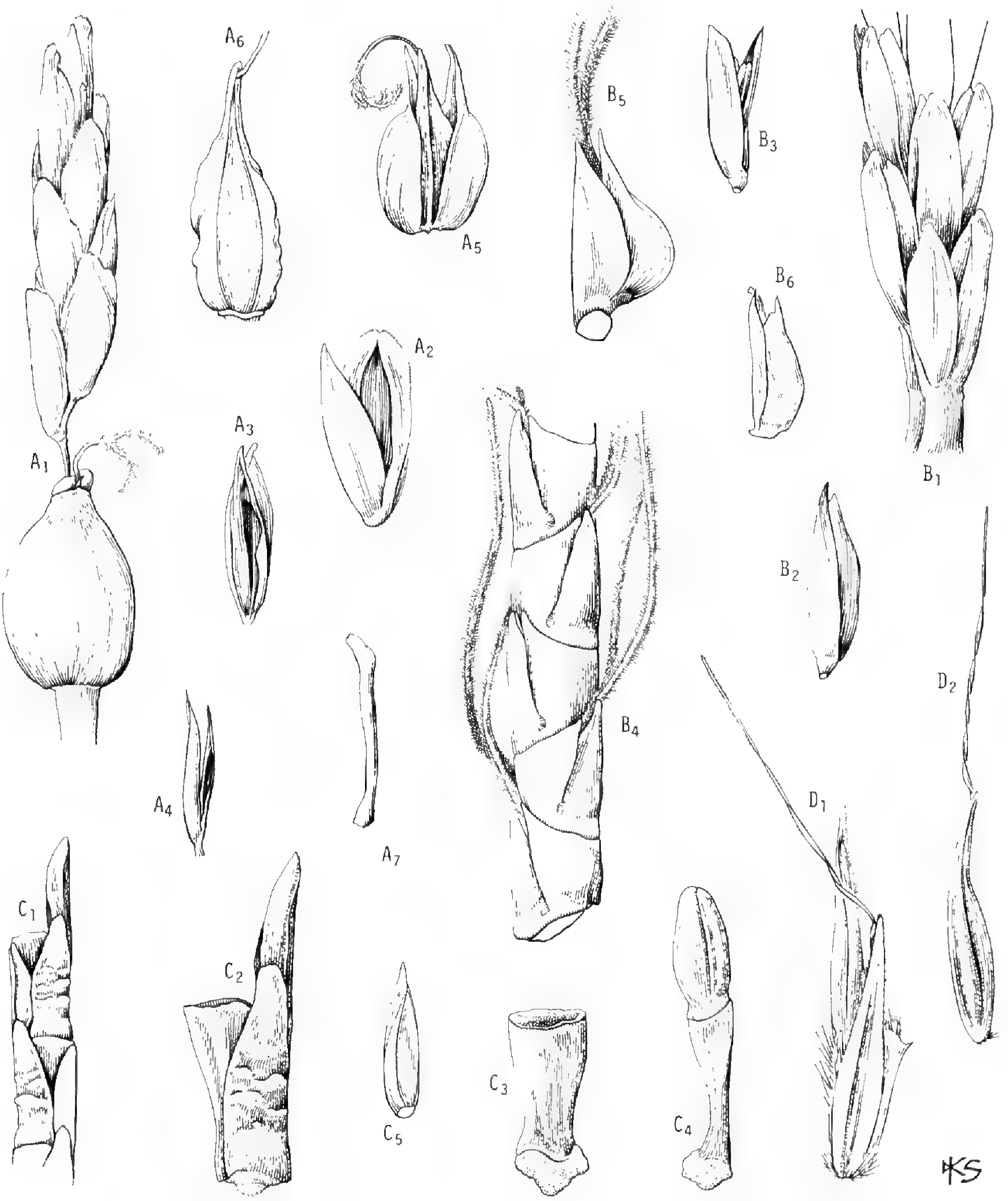

FIGURE 9. **Inflorescences, spikelets, and their parts, Andropogoneae (Panicoideae).** A, *Coix Lacryma-Jobi*: A1, inflorescence, staminate spikelets above, carpellate spikelet enclosed in bony involucre below, style of fertile spikelet and tips of 2 sterile spikelets protruding, × 2; A2, glumes of staminate spikelet, × 3; A3, fertile staminate floret, palea facing viewer, lemma behind, × 3; A4, sterile staminate floret, × 3; A5, carpellate spikelet removed from involucre, glumes separated to show fertile floret, sterile florets removed from both sides of central ridge on fertile floret, × 2; A6, fertile floret seen from side opposite that in A5, delicate lemma overlapping thin palea, × 3; A7, sterile carpellate floret, × 2. B, *Tripsacum dactyloides*: B1, portion of inflorescence with staminate spikelets, × 2; B2, staminate spikelet seen from side, showing glumes, × 3; B3, staminate floret, anthers partly visible (before anthesis), × 3; B4, portion of carpellate inflorescence at anthesis, styles omitted from third floret from bottom, × 2; B5, carpellate spikelet removed from rachis, outer glume to left, × 3; B6, carpellate floret, gynoecium removed, × 3. C, *Coelorachis rugosa* (*Manisuris rugosa*): C1, portion of inflorescence, showing 2 fertile spikelets (outer glume rugose) and their pedicellate sterile spikelets, × 3; C2, joint

The andropogonoid spikelet pairs are often grouped into a linear structure (FIGURES 8a, k; 9B1, B4) traditionally called a raceme but perhaps deserving a separate term such as rame (Pohl). At maturity this linear structure breaks up into dispersal units (FIGURES 8l, 9D1) consisting of an internode, a sessile spikelet, a pedicel, and the pedicelled spikelet if it has not already senesced and fallen.

The Andropogoneae presumably arose in the Old World (Hartley, 1950, 1958a; but see Cross) from a kranz panicoid ancestor (Brown & Smith, 1972; Johnson & Brown) probably resembling members of the small tribe Arundinelleae (Clayton, 1981a). The andropogonoids reached North America by way of southern Europe before the separation of the continents beyond dispersal range in the Tertiary (Brown & Smith, 1972). Now they range broadly in the tropics and subtropics, with centers of diversity in savannas of Indochina and southwestern Africa (Hartley, 1950, 1958; Cross).

In addition to the differences between the Andropogoneae and Paniceae given in the diagnoses, the Andropogoneae have higher levels of proline and glycine in their caryopses (Yeoh & Watson) and more numerous and longer mesocotylar roots in their seedlings (Hoshikawa). They may also be a younger group (Brown, 1958b).

Tribe 5b. **Paniceae** R. Brown in Flinders, Voy. Terra Austral. **2:** 582. 1814.

Spikelets usually solitary; glumes usually less firm than lemmas and with 3 or more nerves; lemmas usually awned. Photosynthesis types non-kranz and kranz, subtypes MS and PS (both NAD-me and PCK). (Tristegineae Link ex Nees in Hooker & Arnott, Bot. Voy. Beechey, 237. 1836. Melinideae Link, Hort. Bot. Berol. **1:** 270. 1827, nomen invalidum; see Clayton, 1981c. Anthephoreae Pilger ex Potztal, Willdenowia **1:** 771. 1957.) TYPE GENUS: *Panicum*. FIGURES 10, 11.

A large, widely distributed tribe represented in the southeastern United States by about 26 genera and 230 species. Cross documented the wide distribution of the Paniceae in the tropics and their prominence in the grass flora of the East African savanna. Hartley (1950, 1958b) pointed out the prominence of the tribe in the moist New World tropics, especially northeastern South America. The tribe does appear to be better developed in the New World than the andropogonoids. Brown (1958b) recorded a geographic distribution of panicoid apomictic taxa more widespread and uniform than that of andropogonoid apomicts. If, as he assumed, apomicts are more poorly dispersed than sexually reproducing taxa, then the distributional difference between panicoid and andropogonoid apomicts might indicate a greater age for the former group. The relatively frequent occurrence of apomicts in the Paniceae may be linked to

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of rachis, with fertile spikelet to right and pedicellate sterile spikelet above and behind fertile spikelet, × 5; C3, joint of rachis, × 5; C4, sterile spikelet and pedicel, × 5; C5, fertile floret, lemma to left, × 5. D, *Andropogon Gerardii,* × 4: D1, spikelet pair, joint of rachis to right behind fertile spikelet, pedicellate spikelet above and behind awn, with slight notch at left marking limit of spikelet (sterile); D2, fertile floret.

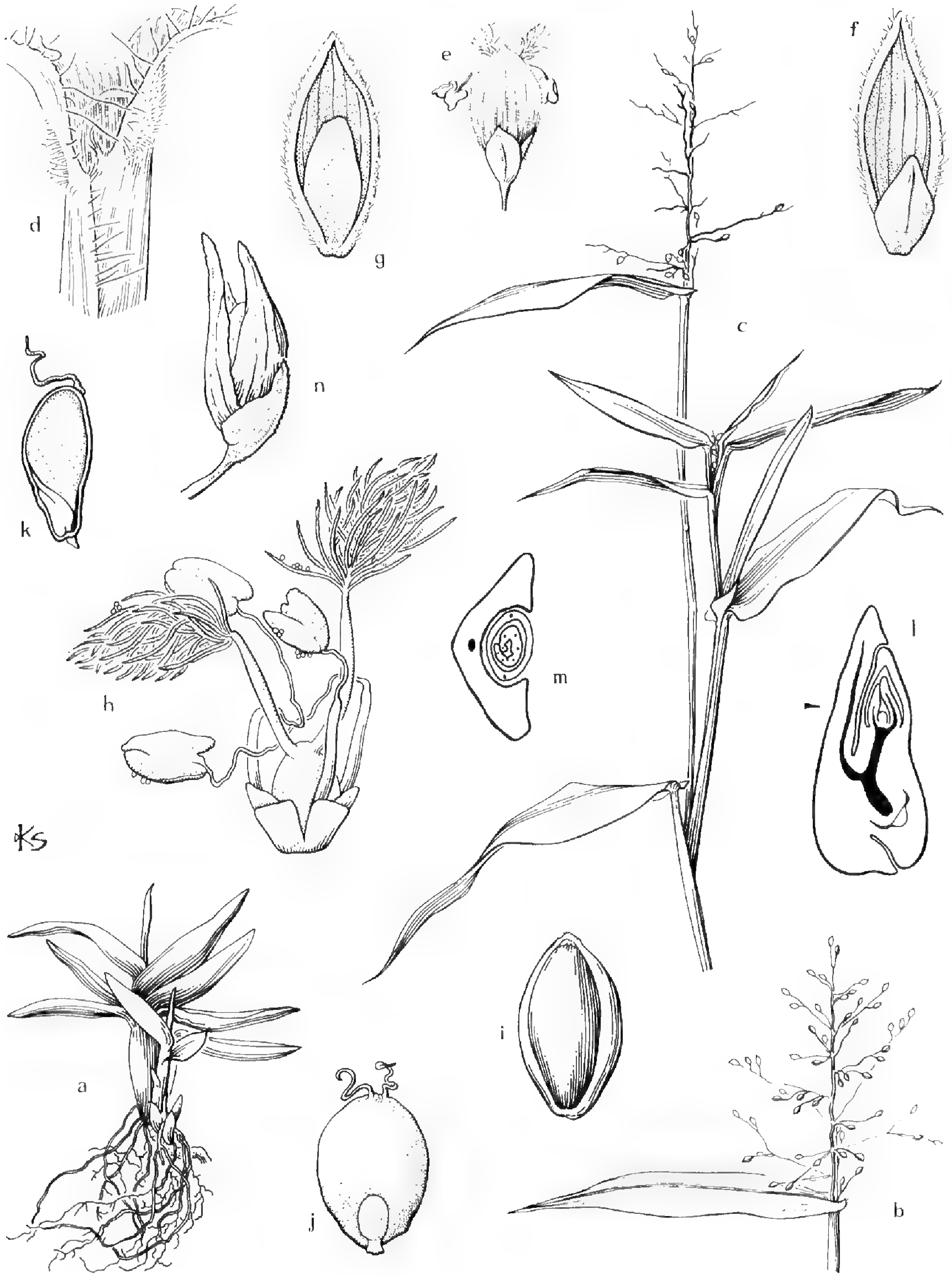

FIGURE 10. **Panicum** (Panicoideae, Paniceae). a–m, *P. clandestinum* (*Dichanthelium clandestinum*): a, part of winter rosette of leaves, × ½; b, inflorescence of chasmogamous spikelets, × ½; , c, upper part of plant, chasmogamous spikelets in fruit or shed from inflorescence, inflorescence of cleistogamous spikelets below, × ½; d, detail of upper part of leaf sheath, base of blade, and ligule, × 6; e, chasmogamous spikelet at anthesis, pollen already shed from anthers, 1 stamen not visible, × 6; f, small first and larger second glume, × 10; g, sterile lemma (pubescent) and sterile palea, × 10; h, flower of cleistogamous spikelet (note shriveled staminal filaments, pollen on stigmas, and lodicules), × 20; i, fertile lemma (behind) and palea enclosing mature caryopsis, × 10; j, mature caryopsis, adaxial surface (note shriveled styles and hilum), × 12; k, diagrammatic longitudinal

the high frequency (77 percent) of polyploidy estimated by Christopher & Abraham (1976) for this tribe.

Unlike the Andropogoneae, the Paniceae are not sharply defined in leaf anatomy (Carolin *et al.*) or photosynthetic pathway (Brown, 1977). Thirty-one genera are characterized by C_3 photosynthesis; 44 have the MS subtype of kranz anatomy, 13 the PS subtype; and two (*Panicum* and *Alloteropsis* Presl) contain both C_3 and C_4 taxa. Both PCK and NAD-me types have been reported among the PS taxa. Brown (1975) postulated two origins of kranz anatomy in the Paniceae, one involving the mestome sheath for most of the kranz taxa, and the other the parenchyma sheath.

Up to about eight small tribes are more or less closely related to the Paniceae. Two of these, the Anthephoreae and the Tristegineae (Melinideae), are represented in our area by adventive taxa. They are close enough to the Paniceae to be included (Stebbins & Crampton), although they are also arguably separable (Pilger; Brown, 1977). The Anthephoreae include *Anthephora* Schreber (about 20 species), which resembles the Paniceae in all respects except two. First, while the genus as a whole shows the MS subtype of kranz anatomy, some species also have "distinctive cells"—kranz cells not associated with a vascular bundle. That these unusual cells uniquely characterize the Anthephoreae and three other small panicoid tribes (Arthropogoneae Pilger, Garnotieae Tateoka, Arundinelleae Stapf) has suggested to some (Johnson & Brown; Brown, 1977) that these taxa should be amalgamated. Second, the spikelets of *Anthephora* are partially fused into groups of four. The Tristegineae are mostly African, with two species from two genera, *Melinis* (*M. minutiflora* Beauv.) and *Rhynchelytrum* Nees (*R. repens* (Willd.) Hubb.), adventive in the southeastern United States. This tribe is characterized by the PS subtype of kranz anatomy, known elsewhere in the Paniceae only in the subtribe Brachiariinae Butzin (see below) and in *Panicum* subgenus *Panicum*. The small panicoid tribes are important to an understanding of phylogeny within the subfamily. The Anthephoreae may share a common ancestor with the Andropogoneae, since both have MS anatomy, delicate and often awned fertile lemmas, and a base chromosome number of 10. Clayton (1981a) considered the Arundinelleae to be ancestral to the Andropogoneae; both he and Brown (1977) considered another small tribe, the Isachneae Bentham, to have been ancestral to the Paniceae.

Brown (1977) divided the Paniceae (*sensu stricto*) into four groups. All genera with the MS subtype of kranz anatomy fall into his informal group, subtribe 1. Thirteen of these genera occur in our area: *Athaenantia* Beauv., *Axonopus*

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section of caryopsis, embryo to left, adaxial side to right, hilum to right of embryo, aleurone layers densely stippled, endosperm lightly stippled, × 12; l, embryo in diagrammatic longitudinal section (scutellum to left, coleoptile and coleorhiza to right, vascular tissue in black), showing internode between scutellar and coleoptilar nodes, no epiblast, and cleft between base of scutellum and coleorhiza; m, diagrammatic transverse section of embryo through scutellum, coleoptile, and first embryonic leaf at level of arrow in "l," showing numerous vascular bundles and overlapping margins of leaf. n, *P. anceps*: spikelet in fruit, first glume to lower right, second glume to left, sterile lemma and tip of fertile lemma visible, × 10. (Diagrammatic sections "l" and "m" after Reeder, 1957, *fig. 12.*)

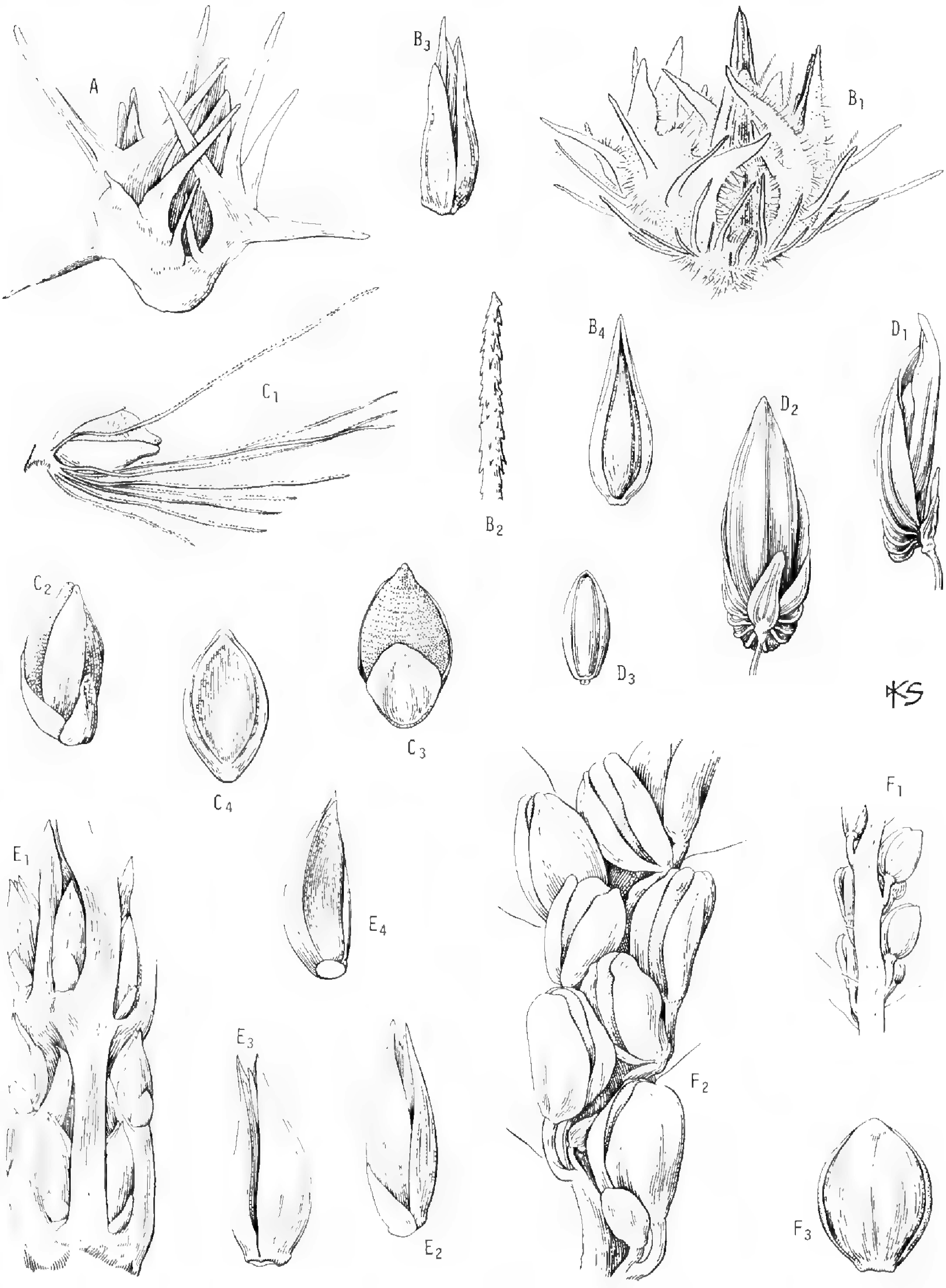

FIGURE 11. Inflorescences, spikelets, and their parts, **Paniceae (Panicoideae)**. A, *Cenchrus gracillimus*: involucre with spikelets, × 5. B, *Cenchrus echinata*: B1, involucre with spikelets, × 5; B2, tip of spine from involucre, × 25; B3, spikelet, × 5; B4, floret, palea to front, lemma behind, × 5. C, *Setaria geniculata*: C1, spikelet with subtending bristles, × 5; C2, spikelet, showing 2 glumes, sterile lemma to right, fertile lemma to left (slightly rugose), × 10; C3, spikelet, showing second glume and slightly rugose indurated lemma of fertile floret, × 10; C4, fertile floret, lemma clasping palea, × 10. D, *Sacciolepis striata*, × 10: D1, spikelet, showing 2 glumes and lemma of sterile floret; D2, same, turned 90° to show shape of sterile lemma and glumes; D3, fertile floret, showing lemma

Beauv., *Cenchrus* L., *Digitaria* Heister, *Echinochloa* Beauv., *Leptoloma* Chase, *Paspalidium* Stapf, *Paspalum* L., *Pennisetum* L., *Reimaria* Fluegge, *Setaria* Beauv., *Stenotaphrum* Trin., and *Trichachne* Nees. Brown's subtribe 2 contains the non-kranz genera, which both his (1977) and Hsu's data support as the most primitive in the tribe. Seven genera are found in our area: *Amphicarpum* Kunth, *Hymenachne* Beauv., *Lasiacis* (Griseb.) Hitchc., *Panicum* subgenus *Dichanthelium* Hitchc. & Chase, *Oplismenus* Beauv., *Sacciolepis* Nash, and *Steinchisma* Raf. Brown's third group, the Brachiariinae, has the PS, PCK subtype of kranz anatomy. It contains three genera in the Southeast: *Brachiaria* Griseb., *Coridochloa* Nees, and *Eriochloa* Kunth. The last group, the Panicinae Stapf, consists of *Panicum* species related to the type species, *P. miliaceum* L., the broomcorn millet. Some common species of this subtribe found in the southeastern United States are *P. capillare* L., *P. flexile* (Gatt.) Scribner, and *P. virgatum* L.

UNPLACED TRIBES

Three small tribes, all with C_3 photosynthesis and mostly temperate in distribution and therefore traditionally assigned to the Pooideae, are not well accommodated in that subfamily (Macfarlane & Watson, 1980). All three share several character states with the Bambusoideae as defined here, but none of them fits well in either that subfamily or any other. Hence they are left unplaced pending further study.

Tribe 6a. **Brachyelytreae** Ohwi, Bot. Mag. Tokyo **55:** 361. 1941.

Stem internodes solid. Transverse veins sometimes present in the leaves. Rachillas prolonged; spikelets (FIGURE 6D) 1-flowered; glumes very small; ovary with a short-hairy apex below the styles, forming a persistent beak on the caryopsis. Embryo with or without a scutellar tail; embryonic leaf margins overlapping. Microhairs absent; papillae present; dumbbell-shaped silica bodies present but elongated, sinuous or crenate silica bodies and tall and narrow silica bodies absent. Sclerenchyma not accompanying the smallest vascular bundles; vascular bundles without both adaxial and abaxial girders. Base chromosome number 11. TYPE GENUS: *Brachyelytrum* Beauv. FIGURE 5D.

A monogeneric tribe; *Brachyelytrum* contains one species (*B. erectum* (Schreber) Beauv.) found in moist woodlands of eastern Canada, the United States, Japan, Korea, and China. The Asian populations have been considered distinct at the varietal or specific level. The genus has most often been placed in the Pooideae, either in the Agrostideae (Bentham; Hitchcock; Prat, 1960; Stebbins

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clasping palea. E, *Stenotaphrum secundatum*: E1, section of flattened, thickened rachis, showing partially embedded spikelets, × 3; E2, spikelet, first glume to left, × 6; E3, spikelet with glumes removed, fertile (upper) floret to right, sterile floret to left, × 6; E4, fertile floret, showing lemma to left, × 12. F, *Paspalum floridanum*: F1, section of rachis, × 2; F2, section of rachis from other side, showing spikelets in pairs, 1 spikelet of each of 2 lowest pairs aborted, × 5; F3, fertile floret, lemma behind, inrolled margins clasping palea, × 5.

& Crampton), the Poeae (Pilger), or the Stipeae (Hackel, 1887; Brown, 1950; Clifford, 1965) or in its own tribe and near the Stipeae (Tateoka, 1957b) or the Bromeae (Ohwi).

Reeder (1957) and Macfarlane & Watson (1980) noted the similarity of the embryos of *Brachyelytrum* to those of *Oryza* and *Leersia.* There are other character states shared by *Brachyelytrum* and the Bambusoideae. Brown (1958a) put *Brachyelytrum* and the bambusoids together because of their somewhat specialized, thick-walled parenchyma sheath cells, and because transverse veins (character 4 of the APPENDIX), papillae (51), and cross- to dumbbell-shaped to nodular silica bodies (53) are found in both taxa. Among C_3 grasses, a base chromosome number of 11 is known in the Stipeae and some herbaceous bambusoids (Calderón & Soderstrom, 1980). Campbell and colleagues (in preparation) present evidence for bambusoid affinities of *Brachyelytrum* in seedling morphology and leaf ultrastructure. Like the seedlings of herbaceous and woody bamboos (Hoshikawa; Soderstrom, 1981a), that of *Brachyelytrum* has a very short mesocotyl and no adventitious roots at the first two seedling nodes or in the internode connecting them. In terms of leaf ultrastructure, *Brachyelytrum* and the few bamboos studied by Carolin and co-workers, unlike pooids, have few or no osmophilic granules in the mestome sheath and numerous thylakoids and large grana in the mesophyll plastids.

There are, however, numerous fundamental differences between *Brachyelytrum* and the Bambusoideae in number of floral parts (characters 24, 28, and 31 of the APPENDIX), ovary apex (29, 30), first seedling leaf blade (44), microhairs (47), stomatal subsidiary-cell shape (60), and leaf anatomy (69, 70). The inclusion of *Brachyelytrum* in the Bambusoideae would greatly loosen the circumscription of the subfamily.

Tribe 6b. **Diarrheneae** (Ohwi) Tateoka ex C. S. Campbell, stat. nov.[2]

Rachis prolonged above uppermost floret; spikelets with 2–5 florets. Lodicules hairy; ovary appendage yellowish or whitish, hard and glossy. Pericarp free from the seed coat. Embryo with a scutellar tail; embryonic leaf margins overlapping. Microhairs absent; elongated, sinuous or crenate silica bodies and cross- to dumbbell-shaped to nodular silica bodies present; tall and narrow silica bodies absent. Some vascular bundles with both adaxial and abaxial girders. Base chromosome number 11. TYPE GENUS: *Diarrhena* Beauv.

Like *Brachyelytrum, Diarrhena* is a small genus of broad-leaved, rhizomatous, woodland herbs with appendaged ovaries and a distributional disjunction between the eastern United States (*D. americana* Beauv.) and eastern Asia (several species). None of the subfamily positions suggested in the past—Pooideae (Stebbins & Crampton; Decker; Gould & Shaw), Arundinoideae (Tateoka, 1957a, 1957c), and Eragrostoideae (Schwab)—is defensible (Macfarlane & Watson, 1980). Hilu & Wright recommended a possible new subfamily, the Nardoideae, composed of *Diarrhena, Nardus* L., and *Lygeum* and intermediate between oryzoids and pooids. From embryo anatomy, Macfarlane & Watson (1980) concluded that this odd genus might have some connection with oryzoids or bambusoids.

[2] See note on page 188.

Tribe 6c. **Stipeae** Dumortier, Obs. Gram. Belg. 83. 1824, "Stipaceae."

Rachillas not prolonged above uppermost floret; spikelets with 1 floret; lemma awns terminal, often basally twisted. Lodicules 2 or 3 per flower. Microhairs present or absent; epidermal papilla 1 per cell; elongated, sinuous or crenate silica bodies absent, saddle-shaped silica bodies and crescentic silica bodies present. Some vascular bundles with both adaxial and abaxial girders. Base chromosome numbers 9, 10, 11, 12. TYPE GENUS: *Stipa* L. FIGURE 5J.

The Stipeae comprise about nine genera and 380 species, most of which belong to the genus *Stipa*. The tribe occurs primarily in dry grasslands of temperate latitudes and especially in the Caspian Sea region, Australia, and the Andes (Hartley, 1973). It is noteworthy for its rather extensive fossil record (Thomasson, Muller). In the southeastern United States the tribe is represented only by *Stipa leucotricha* Trin. & Rupr. and two species of *Piptochaetium* Presl: *P. avenaceum* (L.) Parodi (*Stipa avenacea* L.) and *P. avenacioides* (Nash) Valencia & Costas (*S. avenacioides* Nash).

There is abundant and eclectic evidence that the Stipeae are not closely related to pooid grasses (Macfarlane & Watson; Barkworth). Rachillas are not prolonged and lodicules are two or three in stipoids. Pooids and stipoids also differ in silica-body complements (APPENDIX, characters 52, 53, 55, 56). Johnston & Watson (1977) reported microhairs from the adaxial leaf surface of several species of *Stipa*. The two groups differ serologically (P. Smith), in terms of amino-acid complements (Semikhov; Yeoh & Watson), in the rusts and smuts parasitizing them (Watson, Savile), and in their germination response to IPC (Al-Aish & Brown). The stipoid embryo bears a distinctively long epiblast and a sharply bent primary root (Reeder, 1957). Finally, the extensive aneuploid series of chromosome numbers based on 11 and 12 (Reeder & Reeder) is quite unlike pooid karyotypes.

Suggested taxonomic affinities with the Aristideae (see discussion under this tribe), the Arundinoideae (Tateoka, 1957a; Johnston & Watson, 1977; Savile), or the Bambusoideae (Brown, 1958a; Auquier & Somers; Yeoh & Watson) do not appear to be convincingly strong.

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NOTE ADDED IN PROOF

In 1941 Ohwi established subtribe Diarrheninae to accommodate *Diarrhena,* and much later Tateoka (Canad. Jour. Bot. **38:** 963. 1960) suggested that the establishment of a separate tribe might be "the best way to arrange *Diarrhena* into the grass system." However, because further studies seemed desirable, Tateoka confined himself to pointing out the peculiarities of the genus. It seems appropriate at this point to raise the subtribe formally to the rank of tribe and to attribute the new status to Tateoka. The tribal name is then Diarrheneae (Ohwi) Tateoka ex C. S. Campbell and is based upon subtribe Diarrheninae Ohwi (Acta Phytotax. Geobot. **10:** 134. 1941), with the type genus *Diarrhena* Beauv.

APPENDIX. **Data matrix of grass subfamilies and tribes.**

CHARACTER TAXON	1	2	3	4	5	6	7	8	9	10	11
BAMBUSOIDEAE	a(b)	var	var	pr(ab)	(pr)ab	(a)	a(b)	a/b	b	d/e	a(b)
ARUNDINARIEAE	b	b	var	pr	pr	NC	var	a	b	d/e	a
ORYZEAE	a	(a)b	var	ab	ab	(a)	a	(a)b	b	d/e	a
PHAREAE	a	a	pr	pr	ab	NC	a	b	b	e	b
ARUNDINOIDEAE	a(b)	var	ab	ab	(pr)ab	var	b	a(c)	b	(a/b)e	a
ARISTIDEAE	a	var	ab	ab	ab	a	b	a	b	a/e	a
ARUNDINEAE	a(b)	var	ab	ab	var	var	b	a(c)	b	e	a
CENTOTHECEAE	a	b	ab	ab	ab	NC	b	a	b	b	a
POOIDEAE	a	(a)b	ab	(pr)ab	ab	a(b)	a	a	b	(a/b/d)e	a(c)
AGROSTIDEAE	a	b	ab	ab	ab	a(b)	a	a	b	e	a
AVENEAE	a	b	ab	ab	ab	a	a	a	b	e	a
MELICEAE	a	b	ab	(pr)ab	ab	var	a	a	b	(d)e	a
POEAE	a	(a)b	ab	ab	ab	(a)b	a	a	b	(a)e	a
BROMEAE	a	b	ab	ab	ab	a	a	a	b	(d)e	a
TRITICEAE	a	(a)b	ab	ab	ab	a	a	a	b	a(b)	a(c)
CHLORIDOIDEAE	a	var	(pr)ab	ab	var	a(b)	(a)b	a(b/c)	(a)b	(a/b/c/d)e(f)	a
AELUROPODEAE	a	a	ab	ab	pr	a	b	(a/b)c	b	d/e/f	a
CYNODONTEAE	a	var	(pr)ab	ab	(pr)ab	var	(a)b	a(b/c)	(a)b	(a)b(c/d)e	a
UNIOLEAE	a	b	ab	ab	NC	NC	b?	a	b	e	a
ZOYSIEAE	a	a	ab	ab	ab	a	b	a	b	a/c/d	a
PANICOIDEAE	a(b)	var	(pr)ab	(pr)ab	(pr)ab	var	var	a(b)	var	(a)b(c)e(f)	var
ANDROPOGONEAE	a(b)	a(b)	(pr)ab	ab	ab	var	(a)b	a(b)	var	(a)b/e(f)	a/b(c)
PANICEAE	a(b)	var	(pr)ab	(pr)ab	(pr)ab	a(b)	var	a	(a)b	b(c)e	var
UNPLACED											
BRACHYELYTREAE	a	a	ab	var	ab	a	a	a	b	e	a
DIARRHENEAE	a	NC	ab	ab	ab	NC	a(b)	a	b	e	a
STIPEAE	a(b)	var	ab	ab	ab	var	a(b)	a	b	e	a

APPENDIX (*continued*).

CHARACTER / TAXON	12	13	14	15	16	17	18	19	20
BAMBUSOIDEAE	a/c	var	b	1(6-12)	0(1/2/3)	ab/NA	b/NA	b/NA	a/b
ARUNDINARIEAE	a	a	b	6-12	(1)2(3)	ab	b	b	a/b
ORYZEAE	a/c	var	b	1	0(2)	NA	NA	NA	a/b
PHAREAE	c	NA	b	1	0	NA	NA	b	a
ARUNDINOIDEAE	a(b/c)	a	a(b)	1-20	2	(pr)ab	a(b)NA	(a/b)c	var
ARISTIDEAE	a(b)	a	a	1	2	var	NA	b	b/c
ARUNDINEAE	a/c	a	a	2-20	2	ab	var	a/c	var
CENTOTHECEAE	a	a	b	3-12	2	ab	a	c	a
POOIDEAE	a(b)c	a(b)	a(b)	1-30	(0/1)2	(pr)ab	(a)b/NA	var	a/b(c)
AGROSTIDEAE	a(b)c	a(b)	a(b)	1(2-12)	2	(pr)ab	a/b/NA	var	a/b(c)
AVENEAE	a/c	a	a	(1)2-7(10)	2	ab	a/b/NA	b(c)	b
MELICEAE	a/c	a(b)	a	(1)3-7(16)	2	ab	b	b	a/b
POEAE	a/c	a	a	(1)2-10(22)	2	var	b	var	a/b
BROMEAE	a/c	a	a	(1/2)3-30	2	ab	b	c	a/b
TRITICEAE	a/c	a/b	a	(1)2-7(12)	(0/1)2	var	b/NA	var	(a)b(c)
CHLORIDOIDEAE	a(b)/c	a(b)NA	var	1-45	(0)2	(pr)ab	(a)b(c)	var	a(b/c)
AELUROPODEAE	a/c	a/NA	a	(2)3-12(20)	0/2	ab	b	NC	a
CYNODONTEAE	a(b)/c	a(b)NA	a(b)	1-5(45)	(0)2	var	b/NA	(var)	a(b/c)
UNIOLEAE	a/c	a	a	3-13	2	ab	a/c	a/c	a
ZOYSIEAE	var	b/NA	b	1	2	ab	NA	a	a
PANICOIDEAE	(a)b(c)	(a)b/NA	(a)b	1	(0/1)2	(pr)ab	a/NA	a/b(c)	a/b
ANDROPOGONEAE	(a)b(c)	b	b	1	2	(pr)ab	a/NA	a	a/b
PANICEAE	(a)b(c)	(a)b/NA	(a)b	1	(0/1)2	(pr)ab	a	(a)b(c)	a
UNPLACED									
BRACHYELYTREAE	b/c	a	a	1	1/2	ab	NA	c	b
DIARRHENEAE	a/c	a	a	(1)2-5	2	ab	b	b	a
STIPEAE	a/c	a	b	1	2	ab	NA	b/c	b

TAXON \ CHARACTER	21	22	23	24	25	26	27	28	29	30
BAMBUSOIDEAE	a/NA	3-17	2 or more	2/3	(b)	var	var	(1-)3/6	b	ab
ARUNDINARIEAE	a	11-17	2	3	NC	var	b	3	b	ab
ORYZEAE	a/NA	3-5(7)	(2)3 or more	2	b	b	var	(1-)6	b	ab
PHAREAE	NA	NC	NC	NC	NC	NC	NC	6	NC	NC
ARUNDINOIDEAE	a(b)NA	1-15	0-2	(0)2	var	(a)b	(a)b	1(2)3	b	ab
ARISTIDEAE	a	1-3	0-2	0/2	b	b	b	1-3	b	ab
ARUNDINEAE	a/b	1-15	2(var)	2	a(b)	var	NC	3	b	ab
CENTOTHECEAE	NA	5-15	2	2	a	b	var	1	b	ab
POOIDEAE	(a)b/c	(1)3-15	(0/1)2(4)	2	(a)b	(a)b	var	(1/2)3	var	(pr)ab
AGROSTIDEAE	b/c	(1)3-5(7)	(0/1)2(4)	2	b	(a)b	var	(1-)3	(a)b	ab
AVENEAE	c	3-15	2	2	b	b	(a)b	3	a(b)	ab
MELICEAE	b/c	5-15	2	2	a	b	(var)	3	b	ab
POEAE	var	3-15	2	2	b	b	a(b)	(1-)3	(a)b	ab
BROMEAE	b/c	5-15	2	2	var	b	b	2/3	a	pr
TRITICEAE	a(b)	(3)5-7(11)	2	2	b	a(b)	var	3	a	ab
CHLORIDOIDEAE	var/NA	1-11	(0/1)2	(0)2	a(b)	b	(a/b)	(1-)3	b	ab
AELUROPODEAE	NA	3-7	2	2	var	b	a	3	b	ab
CYNODONTEAE	a/b	1-7	2	2	a(b)	b	(var)	3	b	ab
UNIOLEAE	NA	7-11	2	2	a	NC	NC	1/3	b	ab
ZOYSIEAE	NA	1/3	0/1/2	2	b	b	a	2/3	b	ab
PANICOIDEAE	a/b(c)NA	(0)1-6(11)	0/2/NA	(0/1)2	a(b)	(a)b	b	(1-)3	b	ab
ANDROPOGONEAE	a/b(c)	(0)1-3(5)	0/2/NA	(0)2	a(b)	(a)b	b	(1-)3	b	ab
PANICEAE	NA	(0)3-6(11)	2	(0/1)2	a(b)	b	b	3	b	ab
UNPLACED										
BRACHYELYTREAE	a	5	2	2	b	b	b	3	a	pr
DIARRHENEAE	NA	3-5	2	2	b	a	var	(1)2/3	b	ab
STIPEAE	a/b	3-7	1/2	2/3	var	b	b	(1)3	b	ab

APPENDIX (*continued*).

CHARACTER TAXON	31	32	33	34	35	36	37	38	39	40	41
BAMBUSOIDEAE	(2)3	(a/b)	pr(ab)	b/c	a	b	b	pr	var	b	a(b)
ARUNDINARIEAE	3	NC	pr	c	a	b	b	pr	pr	b	a
ORYZEAE	2	a/b	(ab)	b/c	a	b	b	pr	(pr)ab	b	a/b
PHAREAE	3	NC	NC	NC	NC	NC	NC	pr	(pr)ab	b	a
ARUNDINOIDEAE	2	b	(pr)ab	var	var	var	b	(pr)ab	pr	a	b
ARISTIDEAE	2	b	ab	b	a/b	a	b	ab	pr	a	b
ARUNDINEAE	2	b	var	a/b	(a)b	var	b	(pr)ab	pr	a	b
CENTOTHECEAE	2	b	ab	b	b	b	b	pr	pr	a	b
POOIDEAE	2	b	var	var	a(b)	(a)b	(a)b	pr(ab)	ab	b	b
AGROSTIDEAE	2	b	var	var	(a)b	(a)b	var	pr	ab	b	b
AVENEAE	2	b	var	var	a	b	(a)b	pr	ab	b	b
MELICEAE	2	b	pr	a/c	a	b	b	pr	ab	b	b
POEAE	2	b	var	a(b)	var	b	(a)b	pr	ab	b	b
BROMEAE	2	b	pr	b	a	b	b	ab	ab	b	b
TRITICEAE	2	b	pr	a(b/c)	a	b	b	var	ab	b	b
CHLORIDOIDEAE	2	(a)b	ab	var	b	a(b)	b	pr(ab)	pr(ab)	a(b)	(a)b
AELUROPODEAE	2	NC	NC	NC	b	NC	b	pr	ab	a	b
CYNODONTEAE	2	(a)b	ab	var	b	a(b)	b	pr	var	a(b)	(a)b
UNIOLEAE	2	b	NC	NC	b	a	NC	pr	pr	a	b
ZOYSIEAE	2	b	ab	var	b	a	b	pr	pr	a	b
PANICOIDEAE	2	b	ab	var	(a)b	a(b)	b	ab	pr	a	a(b)
ANDROPOGONEAE	2	b	ab	var	b	a(b)	b	ab	pr	a	a(b)
PANICEAE	2	b	ab	a(b/c)	(a)b	a(b)	b	ab	pr	a	a
UNPLACED											
BRACHYELYTREAE	2	b	pr	a/c	a	b	b	pr	pr/ab	b	a
DIARRHENEAE	2	a	NC	c	var	b	b	pr	pr	b	a
STIPEAE	2	b	ab	a/c	a	b	b	pr	ab	b	b

CHARACTER TAXON	42	43	44	45	46	47	48	49	50	51	52	53
BAMBUSOIDEAE	(b)	b	ab(pr)	a(b)	(a)c	pr(ab)	2	a/NA	a	pr	ab	pr(ab)
ARUNDINARIEAE	NC	b	ab	NA	NA	pr	2	a	a	pr	ab	pr
ORYZEAE	b	var	ab	NA	NA	pr	2	a	a	pr	ab	ab
PHAREAE	NC	b	pr	a	c	ab	NA	NA	a	NC	ab	pr
ARUNDINOIDEAE	b	var	pr	var	b(c)	pr(ab)	2	a	a	ab	(pr)ab	pr
ARISTIDEAE	b	b	pr	b	b	pr	2	a	a	ab	pr	pr
ARUNDINEAE	b	var	pr	var	b	pr(ab)	2	a	a	ab	ab	pr
CENTOTHECEAE	NC	a	pr	a	c	pr	2	a	a	NC	ab	pr
POOIDEAE	(a)b	var	pr	var	a	ab	NA	NA	var	(pr)ab	pr	(pr)ab
AGROSTIDEAE	(a)b	a(b)	pr	(a)b	a	ab	NA	NA	var	ab	pr	(pr)
AVENEAE	b	a	pr	(var)	(a)	ab	NA	NA	(a)b	ab	pr	ab
MELICEAE	b	a	(pr)	(var)	(a)	ab	NA	NA	var	pr/ab	pr	(pr)
POEAE	b	a(b)	pr	(a)b	a	ab	NA	NA	var	(pr)ab	pr	ab
BROMEAE	a	var	pr	b	a	ab	NA	NA	b	ab	pr	ab
TRITICEAE	a	(a)b	pr	b	a	ab	NA	NA	var	ab	pr	ab
CHLORIDOIDEAE	(a)b	a(b)	pr	a(b)	(var)	pr(ab)	1/2	(a)b	a(b)	var	(pr)ab	var
AELUROPODEAE	a	NC	NC	NC	NC	var	1/2	b	a	var	ab	ab
CYNODONTEAE	b	(a)	(pr)	(a/b)	(a/b)	pr	1/2	(a)b	a(b)	var	(pr)	(pr/ab)
UNIOLEAE	NC	NC	NC	NC	NC	pr	2	a	a	ab	ab	pr
ZOYSIEAE	b	a/b	pr	a	a/c	pr(ab)	2	b	a	var	ab	ab
PANICOIDEAE	var	a(b)	pr	a	var	pr	(1)2	a(b)	a(b)	var	ab	pr
ANDROPOGONEAE	var	a	(pr)	(a)	(var)	pr	2	a(b)	a(b)	var	ab	pr
PANICEAE	a(b)	a(b)	pr	a	(a)b(c)	pr	(1)2	a(b)	a(b)	(pr)ab	ab	pr
UNPLACED												
BRACHYELYTREAE	a	b	pr	b	var	ab	NA	NA	a	pr	ab	pr
DIARRHENEAE	b	NC	NC	NC	NC	ab	NA	NA	a	ab	pr	pr
STIPEAE	var	var	pr	b	a	var	2	a	a	var	ab	pr

APPENDIX (*continued*).

CHARACTER TAXON	54	55	56	57	58	59	60	61	62	63
BAMBUSOIDEAE	ab	(pr)ab	(pr)ab	(pr)ab	ab	(b)	(a)c	(var)	var	b
ARUNDINARIEAE	ab	pr	ab	ab	ab	NC	c	NC	b(a)	b
ORYZEAE	ab	ab	(pr)	pr	ab	b	a	var	var	b
PHAREAE	ab	ab	ab	ab	ab	NC	c	NC	a	b
ARUNDINOIDEAE	pr(ab)	pr(ab)	pr(ab)	(pr)ab	ab	var	var	var	var	(a)b
ARISTIDEAE	pr	pr	pr	var	ab	var	a(b)	var	a/c	a
ARUNDINEAE	(pr)	(pr)	(pr)	ab	ab	var	var	var	var	(a)b
CENTOTHECEAE	ab	ab	ab	ab	ab	NC	a	pr	var	b
POOIDEAE	pr(ab)	(pr)ab	(pr)ab	ab	(pr)ab	a(b)	b	var	(a)b/c	b
AGROSTIDEAE	(pr)	(pr)	ab	ab	(pr)	a(b)	b	var	(a/b)c	b
AVENEAE	ab	ab	ab	ab	ab	a(b)	b	ab	b/c	b
MELICEAE	ab	ab	ab	ab	ab	NC	b	var	(a/b)c	b
POEAE	(pr)	ab	pr	ab	ab	a(b)	b	var	(a/b)c	b
BROMEAE	pr	ab	pr	ab	ab	a	b	ab	var	b
TRITICEAE	pr	(pr)	pr	ab	ab	a	b	var	b/c	b
CHLORIDOIDEAE	pr(ab)	pr(ab)	var	ab	ab	(a)b	a(b/c)	pr(ab)	var	a
AELUROPODEAE	pr	pr	ab	ab	ab	var	a	pr	c	a
CYNODONTEAE	(pr)	pr(ab)	(pr/ab)	ab	ab	var	a(b/c)	var	a(b/c)	a
UNIOLEAE	ab	ab	ab	ab	ab	NC	a	ab	a	a
ZOYSIEAE	ab	pr	pr	ab	ab	var	a	pr	var	a
PANICOIDEAE	(pr)ab	(pr)ab	ab	ab	(pr)ab	(a)b	a	var	a(b/c)	a(b)
ANDROPOGONEAE	ab	ab	ab	ab	ab	b	a	var	a(b/c)	a
PANICEAE	(pr)	(pr)	ab	ab	(pr)	(a)b	a	var	a(b/c)	a(b)
UNPLACED										
BRACHYELYTREAE	ab	ab	ab	ab	ab	var	b	ab	a	b
DIARRHENEAE	ab	ab	ab	ab	ab	a	var	ab	a/c	b
STIPEAE	pr	pr	pr	ab	ab	var	var	ab	var	b

CHARACTER TAXON	64	65	66	67	68	69	70	71	72	73	74
BAMBUSOIDEAE	ab	(ab)	ab	a	(a)b	pr	pr(ab)	(a)b	pr	var	(var)
ARUNDINARIEAE	ab	NC	ab	a	b	pr	pr	b	NC	pr	NC
ORYZEAE	ab	ab	ab	a	b	pr	var	(a)b	(pr)	var	var
PHAREAE	NC	NC	ab	NC	a	pr	pr	b	pr	NC	NC
ARUNDINOIDEAE	(ab)	ab	var	a(b)	b	(pr)ab	ab	a(c)	(pr)ab	var	var
ARISTIDEAE	ab	ab	pr	b	b	ab	ab	a	ab	var	var
ARUNDINEAE	NC	ab	var	a	b	(pr)ab	ab	a/c	ab	var	ab
CENTOTHECEAE	NC	NC	ab	a	b	ab	ab	NC	pr	NC	NC
POOIDEAE	(ab)	ab	(pr)ab	a	b	ab	ab	a(c)	(pr)	var	var
AGROSTIDEAE	(ab)	ab	(pr)ab	a	b	ab	ab	a(c)	(pr)	var	(pr)ab
AVENEAE	NC	ab	ab	a	NC	ab	ab	a	NC	(pr)ab	var
MELICEAE	ab	ab	ab	a	NC	ab	ab	a	(pr)	(pr)ab	(pr)ab
POEAE	NC	ab	ab	a	b	ab	ab	a	NC	var	(pr)ab
BROMEAE	NC	ab	ab	a	b	ab	ab	a	NC	var	ab
TRITICEAE	NC	ab	ab	a	b	ab	ab	a(c)	NC	var	(pr)ab
CHLORIDOIDEAE	(ab)	ab	pr(ab)	a	(a)b	ab	ab	a/c	(pr)	var	var
AELUROPODEAE	NC	ab	pr	a	b	ab	ab	a	NC	ab	ab
CYNODONTEAE	(ab)	ab	pr(ab)	a	(b)	ab	ab	a(c)	(pr)	(pr)ab	pr(ab)
UNIOLEAE	ab	ab	pr	a	NC	ab	ab	c	pr	pr	NC
ZOYSIEAE	NC	ab	pr	a	var	ab	ab	a	NC	var	var
PANICOIDEAE	(pr)ab	(pr)ab	pr(ab)	var	var	ab	ab	a/c	(var)	var	var
ANDROPOGONEAE	(ab)	ab	pr(ab)	b	a(b)	ab	ab	(a)c	NC	var	var
PANICEAE	(pr)ab	(pr)ab	pr(ab)	var	var	ab	ab	a/c	(var)	var	var
UNPLACED											
BRACHYELYTREAE	ab	ab	ab	a	b	ab	ab	a	pr	pr	ab
DIARRHENEAE	ab	ab	ab	a	NC	ab	ab	a	pr	pr	ab
STIPEAE	NC	ab	ab	a	b	ab	ab	a/c	pr	pr	ab

APPENDIX (*continued*).

TAXON \ CHARACTER	75	76	77	78	79	80	81	82	83	84
BAMBUSOIDEAE	(ab)	(ab)	(var)	(var)	(pr)	pr	pr	(ab)	a/c	12
ARUNDINARIEAE	NC	NC	NC	NC	NC	pr	pr	NC	NC	12
ORYZEAE	ab	ab	var	var	pr	pr	(pr)	ab	a	12(15/17)
PHAREAE	NC	NC	NC	NC	NC	pr	NC	NC	c	12
ARUNDINOIDEAE	var	ab	ab	var	pr	pr	var	var	a/b(c)	(11)12
ARISTIDEAE	ab	ab	ab	pr	pr	pr	ab	pr	b/c	11
ARUNDINEAE	var	ab	ab	ab	pr	pr	var	var	a/b	12
CENTOTHECEAE	NC	NC	NC	NC	NC	pr	NC	NC	a/b	12
POOIDEAE	ab	ab	ab	(pr)ab	pr(ab)	var	var	(pr)ab	a/b	(var)
AGROSTIDEAE	ab	ab	ab	ab	pr(ab)	pr(ab)	(pr)ab	(pr)ab	a(b)	(4/5)7(9/13)
AVENEAE	ab	ab	ab	(pr)ab	pr	pr(ab)	ab	(pr)ab	a	7
MELICEAE	ab	ab	ab	ab	pr	pr(ab)	var	ab	(a)	9/10
POEAE	ab	ab	ab	ab	pr(ab)	var	(pr)ab	(pr)ab	(a)	(5)7(13/19)
BROMEAE	ab	ab	ab	ab	var	pr	var	ab	a	7
TRITICEAE	ab	ab	ab	ab	pr(ab)	pr(ab)	(pr)ab	ab	a	7
CHLORIDOIDEAE	ab	ab	(pr)ab	var	pr(ab)	pr(ab)	var	ab	a(b)	(7/9)10(12)
AELUROPODEAE	ab	ab	ab	pr	pr	pr	pr	ab	NC	10
CYNODONTEAE	ab	ab	(pr)ab	pr(ab)	pr(ab)	pr(ab)	(pr)ab	ab	var	(7)10(9/12)
UNIOLEAE	ab	ab	NC	ab	pr	NC	NC	ab	a	10
ZOYSIEAE	ab	ab	ab	var	pr	pr	pr	ab	a	10
PANICOIDEAE	ab	(pr)ab	var	(pr)ab	(pr)ab	pr(ab)	var	(pr)ab	var	5/9/10(var)
ANDROPOGONEAE	ab	(pr)ab	var	(pr)ab	(pr)ab	pr(ab)	var	(pr)ab	var	5/10(var)
PANICEAE	ab	(pr)ab	var	(pr)ab	(pr)ab	pr(ab)	(pr)ab	ab	var	9/10(var)
UNPLACED										
BRACHYELYTREAE	ab	ab	ab	ab	ab	ab	ab	ab	NC	11
DIARRHENEAE	ab	ab	ab	ab	pr	pr	var	ab	NC	10
STIPEAE	ab	ab	ab	ab	pr	pr	pr	var	a	9-12

Data for this table are based on the character states found in the genera of the southeastern United States that make up the tribes and subfamilies. Data come both from the literature (Hitchcock; Johnston & Watson, 1977; McClure, 1973; Reeder, 1957, 1962; Metcalfe, 1960; Yates, 1966; Terrell; Macfarlane & Watson, 1980, 1982; Soderstrom, 1981a; Watson & Dallwitz, 1981, 1982) and from examination of living material or herbarium specimens (A, GH, NY, and US). The characters and their states in this table are defined below. Two or more characters occurring with roughly equal frequency are separated by a slash, while "var," meaning variable, indicates that all character states occur with roughly equal frequency. Character states enclosed in parentheses are rare, occurring in a third or fewer of the taxa (genera of tribes or tribes of subfamilies). When data are available for a minority of the genera of a tribe or tribes of a subfamily, the recorded character state or states are also enclosed in parentheses. "NA" indicates not applicable and "NC" no data available. The presence or absence of a character is indicated by "pr" or "ab," respectively.

CHARACTERS AND THEIR STATES AS USED ABOVE

1. Stems: (a) herbaceous, (b) woody
2. Stem internodes: (a) solid, (b) hollow
3. Pseudopetioles: pr/ab
4. Transverse veins: pr/ab
5. Leaf blade disarticulation: pr/ab
6. Vernation: (a) rolled, (b) folded
7. Ligules: (a) membranaceous, (b) of hairs or fringed
8. Sex distribution: (a) some perfect flowers present, (b) plants monoecious, (c) plants dioecious
9. Inflorescences: (a) leafy, (b) not leafy
10. Inflorescence form: (a) solitary spike, (b) spiciform branches, (c) glomerule, (d) raceme, (e) panicle, (f) other
11. Spikelets: (a) solitary, (b) paired, (c) in 3's
12. Spikelet compression: (a) lateral, (b) dorsal, (c) absent
13. Spikelet disarticulation: (a) above glumes, (b) below glumes (NA indicates disarticulation of axis at some point below the spikelet)
14. Rachilla: (a) prolonged above uppermost floret, (b) not prolonged above uppermost floret
15. Carpellate and/or perfect florets/spikelet
16. Glumes/spikelet
17. Glume awns: pr/ab
18. Staminate or neuter florets: (a) proximal to lowermost carpel-bearing floret, (b) distal to lowermost carpel-bearing floret, (c) both proximal and distal to lowermost carpel-bearing floret
19. Relative glume/lemma firmness: (a) glumes firmer, (b) lemmas firmer, (c) equal
20. Lemma-awn number: (a) 0, (b) 1, (c) more than 1
21. Lemma-awn position: (a) apical, (b) apical notch, (c) dorsal
22. Lemma-nerve number
23. Palea-nerve number

24. Lodicules/flower
25. Lodicules: (a) distally fleshy, (b) distally membranaceous
26. Lodicules: (a) hairy, (b) glabrous
27. Lodicules: (a) toothed, (b) entire
28. Stamens/flower
29. Ovary apex: (a) hairy, (b) glabrous
30. Ovary appendage: pr/ab
31. Stigmas/gynoecium
32. Pericarp: (a) free, (b) adnate to seed
33. Caryopsis groove: pr/ab
34. Caryopsis compression: (a) dorsiventral, (b) lateral, (c) none
35. Hilum: (a) linear, (b) punctiform
36. Embryo length: (a) more than one third of caryopsis, (b) less than one third of caryopsis
37. Endosperm: (a) liquid or soft, (b) hard
38. Epiblast: pr/ab
39. Scutellar tail: pr/ab
40. Embryo mesocotyl: (a) long, (b) short
41. Embryonic leaf margins: (a) overlapping, (b) not overlapping
42. Starch grains: (a) all simple, (b) at least some compound
43. Seedling mesocotyl: (a) long, (b) short
44. First seedling leaf blade: pr/ab
45. First seedling leaf blade; (a) broad, (b) narrow
46. First seedling leaf blade: (a) erect, (b) curved, (c) supine
47. Microhairs: pr/ab
48. Microhair cell number
49. Microhair distal cell: (a) narrow, (b) inflated
50. Long cell wall: (a) sinuous, (b) more or less straight
51. Papillae: pr/ab
52. Elongated, sinuous or crenate silica bodies: pr/ab
53. Cross- to dumbbell-shaped to nodular silica bodies: pr/ab
54. Tall and narrow silica bodies: pr/ab
55. Saddle-shaped silica bodies: pr/ab
56. Crescentic silica bodies: pr/ab
57. Oryzoid silica bodies: pr/ab
58. Acutely angled silica bodies: pr/ab

59. Guard cells: (a) overlapped by interstomatal cells, (b) not overlapped by interstomatal cells

60. Subsidiary cells: (a) triangular, (b) parallel sided, (c) dome shaped

61. Cork-silica cell pairs: pr/ab

62. Short cells over the veins mostly: (a) in rows of five or more, (b) paired, (c) solitary or in short rows

63. Maximum cell interveinal distance count: (a) one (indicates C_4 photosynthesis), (b) two or more (indicates C_3 photosynthesis)

64. *Isachne*-type mesophyll: pr/ab

65. Circular cells in mesophyll: pr/ab

66. Radially arranged mesophyll: pr/ab

67. Whether $XyMS^+$ or $XyMS^-$: (a) $XyMS^+$ (indicates C_3 photosynthesis or C_4 type PCK or NAD-me), (b) $XyMS^-$ (indicates C_4 photosynthesis type NADP-me)

68. Bundle sheath number: (a) one, (b) at least some veins with two or three

69. Arm cells: pr/ab

70. Fusoid cells: pr/ab

71. Midrib bundle number: (a) one, (b) more than one and not arranged in an arc, (c) more than one and arranged in an arc

72. Bulliform cell groups: pr/ab

73. Simple fans of bulliform cells without colorless cells: pr/ab

74. Deeply penetrating fans of bulliform and colorless cells: pr/ab

75. Narrow, penetrating groups of bulliform and colorless cells: pr/ab

76. Arches of bulliform and colorless cells over small bundles: pr/ab

77. Colorless cells comprising adaxial half of mesophyll over midrib or of middle part of leaf: pr/ab

78. Colorless cells traversing leaf: pr/ab

79. Sclerenchyma accompanying smallest vascular bundles: pr/ab

80. Some vascular bundles with both adaxial and abaxial girders: pr/ab

81. Combined adaxial and abaxial girders with an "anchor," "I," or "T" shape: pr/ab

82. Nonbundle leaf sclerenchyma: pr/ab

83. Vascular bundles in stem internodes: (a) in one or two rings, (b) in three or more rings, (c) scattered

84. Base chromosome number

A BIOSYSTEMATIC STUDY OF THE POA SECUNDA COMPLEX

ELIZABETH ANNE KELLOGG

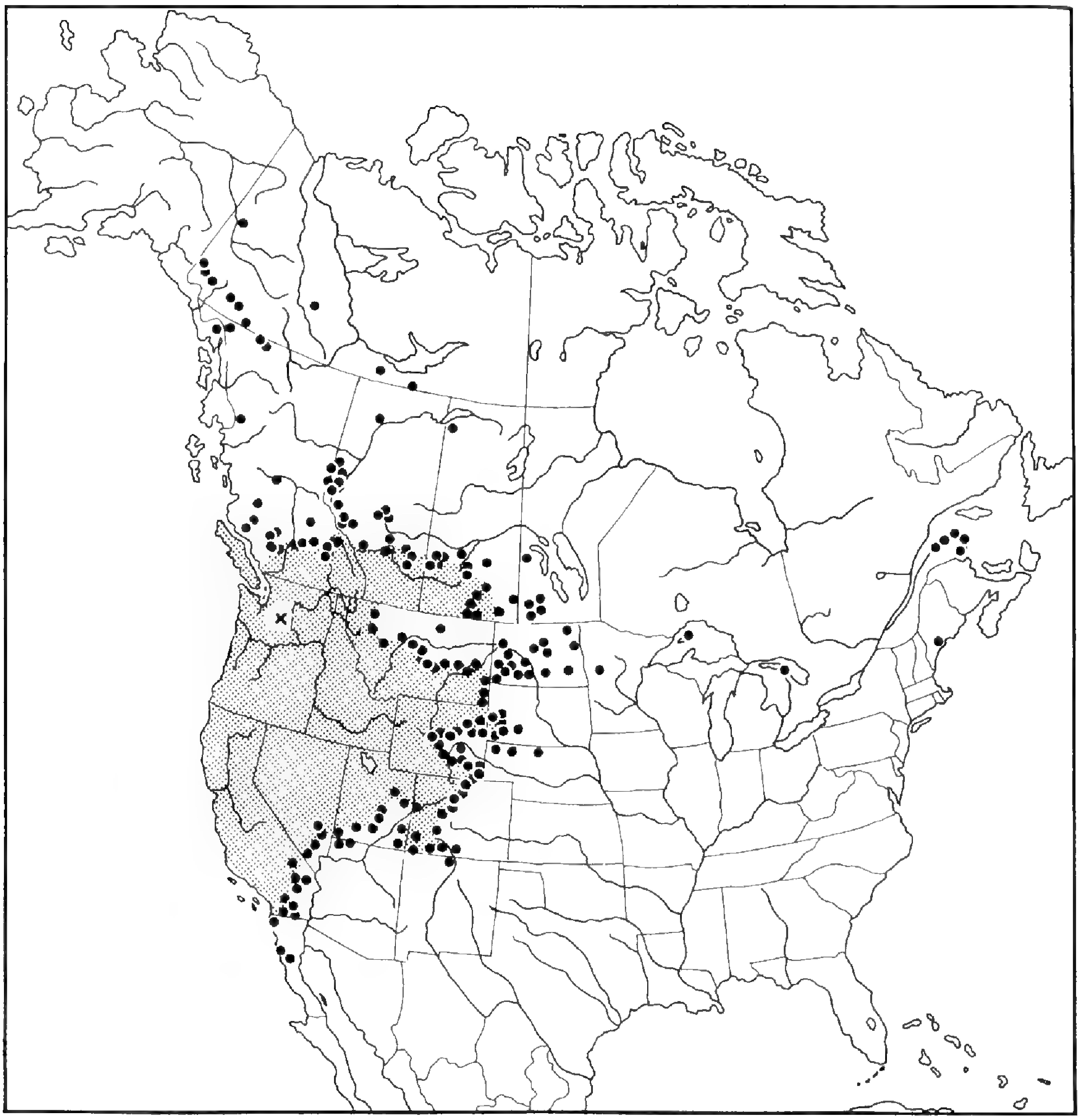
THE GENUS *Poa* L. comprises taxa with extraordinary ecological diversity and highly varied reproductive biology, yet with equally unusual morphological uniformity. It has a worldwide distribution, occurring mostly in temperate areas in both hemispheres and on all continents except Antarctica. It probably includes more than 200 species, about a quarter of which occur in the Pamirs and Himalayas; other centers of diversity are Alaska, Iceland, and Kamchatka (Hartley, 1961). Habitats range from moist meadows to warm deserts, from sea level to nearly 4000 m, and from the arctic to equatorial regions. Some species are fully sexual, whereas others are partial or obligate apomicts; both inbreeding and fully outbreeding and dioecious species also occur (Clausen, 1961).

Most workers have attempted to divide the genus into subgenera and/or sections, but the resulting classifications have not been similar (Bentham & Hooker, 1883; Hackel, 1887; A. S. Hitchcock, 1950; Marsh, 1952; Edmondson, 1978). Some of these classifications are compared in TABLE 1. In general there are few reliable characters on which to base such classifications; the ones that have been used most often are habit, size and pubescence of various plant parts, and sex of flowers. Habit is a reflection of mode of branching (extra- or intravaginal), and this character can also be used to delimit large groups of species. However, size and pubescence characters are quite unreliable in some groups, often varying widely with environment or even within a single plant. Mode of apomictic embryo-sac formation, whether aposporous or diplosporous, may be useful for creating a subgeneric classification; however, this character has not been studied for most species and would in any case only be applicable to those that are apomictic. There seem to be fertility barriers among some groups of species (see Hiesey & Nobs, 1982).

The *Poa secunda* Presl complex (also known as the *P. sandbergii* Vasey complex; see next section) is a widespread, difficult group; it is distributed over most of western North America, with disjunct populations in the Gaspé Peninsula of Quebec and others in Chile (MAP 1). The plants occur in a wide range of habitats, from low deserts to high alpine areas in the Sierra Nevada and the Rocky Mountains; most grow in relatively dry sites, but some occur in wet meadows or in damp gorges. There are currently 45 epithets in the group, and these have historically been included in from one to 11 species.

The results of Heidel and colleagues (1982) and Gilmartin and coworkers (unpubl. MS) illustrate the nature of the taxonomic problem. Both groups

Journal of the Arnold Arboretum **66**: 201–242. April, 1985.



MAP 1. Distribution of *Poa secunda* complex in North America. Cross shows distribution of *P. curtifolia*. Within shaded area collections too numerous to show individually.

looked at sets of vegetative and floral characters, comparing variation within and between several populations of *Poa secunda* in eastern Washington. They found that for the vegetative characters the ratio of inter- to intra-populational variance was similar to that of other unrelated grass species; for the floral characters, however, variance within populations was unusually low compared to that between populations. With respect to floral characters, in other words, populations of *Poa secunda* are more differentiated than those of other grasses, although my own data show that this differentiation never leads to complete discontinuity. Faced with this low but perceptible differentiation, some taxonomists have recognized the "units" taxonomically.

The complex is commonly distinguished from the rest of the genus by the lack of a prominent keel on the lemma. I have examined lemma cross sections of 15 different species of *Poa* to determine the anatomical basis of this character,

TABLE 1. **A comparison of five classifications of the genus Poa.***

HACKEL (1887)	BENTHAM AND HOOKER (1883)	EDMONDSON (1978)	HITCHCOCK (1950)	MARSH (1952)
Subg. *Dioicopoa*	Subg. *Dioicopoa*	Subg. *Dioicopoa*		Subg. *Dioecia*
				Subg. *Pistillata*
Subg. *Eupoa*	Subg. *Eupoa*	Subg. *Poa*		
		Sect. *Ochlopoa*	Sect. *Annuae*	
		Sect. *Coenopoa*	Sect. *Palustres*	
		Sect. *Stenopoa*		
		Sect. *Bolbophorum*	Sect. *Alpinae*	
		Sect. *Poa*	Sect. *Pratenses*	
		Sect. *Tichopoa*		
		Sect. *Homalopoa*	Sect. *Homalopoae*	
		Sect. *Cenisia*		
		Sect. *Macropoa*		
		Sect. *Leptophyllae*		
		Sect. *Oreinos*		
		Sect. *Abbreviatae*		
		Sect. *Nanopoa*		
			Sect. *Epiles*	
			Sect. *Scabrellae*	Subg. *Secundae*
			Sect. *Nevadenses*	
Subg. *Poidium*	Subg. *Poidium*			
Subg. *Pseudopoa*	Subg. *Pseudopoa*			
	Subg. *Leucopoa*			

*The first two classifications include the entire genus, the third only attempts to classify the European species, and the fourth and fifth include only North American species. Corresponding sections in Edmondson's and Hitchcock's classifications overlap only in part.

and I have found no appreciable difference in cross section between the *P. secunda* complex and other members of the genus. All species examined have two or three layers of sclerenchyma on the abaxial side of the middle vascular bundle, and these layers taper evenly to a single layer on both sides of the vein. Because the keel has no anatomical basis, and because specimens cannot easily be determined as keeled or nonkeeled, it may be an unreliable taxonomic character.

More consistently useful distinguishing characters are the lengths of the rachilla internodes (0.6–1.9 mm, vs. < 0.5 mm for most other members of the genus) and the spikelets. Anthers are long (1–4.2 mm), whereas those of many other bluegrasses are less than 1 mm. The plants are perennial and caespitose, with intravaginal branching; the panicles are mostly narrow, and the flowers are perfect, although frequently pollen sterile. Although there is often a tuft of hairs on the callus, the long, tangled, cobwebby hairs characteristic of many other species of *Poa* are lacking.

Spikelet shape and rachilla-internode length are the most distinctive characters of the *Poa secunda* group in comparison to the rest of the genus; most other bluegrasses have more or less ovoid spikelets with a very short internode between the first two florets. Intravaginal branching distinguishes all the caespitose bluegrasses from A. S. Hitchcock's sections *Homalopoae, Palustres,* and *Pratenses.* The lack of a prominent cobweb at the base of the lemma also distinguishes the *P. secunda* group from most members of the latter two sections. The perennial habit distinguishes it from section *Annuae,* which is made up entirely of annuals.

The *Poa secunda* complex is defined more by exclusion than by inclusion; there is thus no evidence that the group is strictly monophyletic (i.e., including only and all the descendants of a single ancestor). The long rachilla internodes and elongate spikelets might be considered apomorphies (unique, derived features) characterizing the group, but then such imperfect-flowered species as *P. cusickii* Vasey and *P. epilis* Scribner would have to be included as well. These latter two species may, in fact, prove to be obligately apomictic descendants of *P. secunda,* but this is only speculation at the moment. The whole notion of apomorphy, however, is difficult to apply in a genus in which there is probable hybridization. In such a group cladistic analysis is not appropriate, since it is based entirely on an assumption of branching evolution (but see Fink, 1982, for discussion of cladistic treatment of hybrids).

Sister groups might be sought in Hitchcock's (1950) sects. *Alpinae* or *Epiles,* as was suggested by Clausen and Hiesey (1958). The taxa in these sections are, like *Poa secunda,* mostly caespitose; they are alpine or arctic in distribution. They all lack a cobweb on the lemma. Such evidence does not allow inference of phylogeny but at least permits elimination of some possible sister groups. Because there are fertility barriers and differences in branching, embryo-sac formation, and spikelet size and shape, *P. secunda* is probably not closely allied to *P. nemoralis* L., *P. sylvestris* Gray, *P. autumnalis* Muhl., or *P. palustris* L. or other members of sect. *Palustres* (Kellogg, 1983; see also Hiesey & Nobs, 1982).

This study had three major goals: to analyze the pattern of morphological variation in the *Poa secunda* complex (and to assess the level at which taxonomic characters varied, whether within the individual, within a population, or between populations); to decide how many taxa the complex represented; and to investigate the reproductive biology of the group and its role in producing the pattern of morphological variation.

HISTORY OF SYSTEMATIC TREATMENTS

The type specimen of *Poa secunda* was collected by Thaddeus Haenke "in cordilleris Chilensibus" probably sometime between 1790 and 1794 and was described by Presl in *Reliquiae Haenkeanae* in 1830, making this the oldest valid name in the group. Later in the century, collectors in the western United States, particularly Vasey, Piper, Scribner, and Rydberg, found and described many of the other species included in the *P. secunda* complex, beginning with Sandberg's collection near Lewiston, Idaho, in 1892 of the plant that bears his name. Names proliferated, often without much justification. A case in point is Scribner's (1883, p. 66) description of *P. nevadensis,* in which he stated "The characters of the grass agree in many points with those of *Atropis scabrella,* Thurber, in Bot. Calif. ii, p. 310, but whether it be the same I am unable to say, having never seen any authentic specimens of that species." He then went on to publish the name *Poa nevadensis* as a new species.

By 1935 more than 40 names had been published. Jones (1912) had proposed an extensive synonymy, but it had not been accepted. In 1935 A. S. Hitchcock finally resolved some of the chaos by dividing the group into two sections, *Scabrellae* and *Nevadenses,* each with four species. Most other works since Hitchcock's *Manual of the Grasses of the United States* have followed his classification, recognizing similar—if not identical—groups of species.

Hitchcock's (1935) keys and descriptions were soon seen to be a poor reflection of the variation observed in nature. C. L. Hitchcock and colleagues (1969) stated that the range of variation in the complex is so continuous that were the populations freely interbreeding, the group should be regarded as a single polymorphic taxon. Cronquist and co-workers (1977) concluded that the distinction between sects. *Scabrellae* and *Nevadenses* is quite artificial—useful for keying purposes but tending to belie the close relationship among all the species. Marsh (1952) simply synonymized all the members of the group, recognizing only the single species *Poa secunda*; his treatment, however, has not been followed.

Authors have also disagreed on the relationship between the South American *Poa secunda* and the North American *P. sandbergii*; for a detailed review of the literature on the question, see Arnow (1981). Arnow compared North and South American populations both morphologically and ecologically, concluding that there is no reason to separate them and therefore that *P. secunda* is the appropriate name for the species. My observations support her conclusion.

METHODS

As noted below, taxa in *Poa* are recognized primarily on the bases of the size of parts and the presence or absence of trichomes and scabrosities on various parts of the plant. The core of any taxonomic revision within the genus must therefore involve a detailed analysis of variation in these characters.

PLANTS AND CHARACTERS: PRODUCTION OF THE DATA MATRIX

The analysis of character variation was done on two separate sets of plants. The first set consisted of 95 plants chosen to represent the full range of geographic and morphological variation (see APPENDIX 1). At least one plant was chosen from each of the states or provinces in which the species occurs, with additional plants taken from some states to include the extremes of morphological variation. The second set was chosen to evaluate variation within populations ("population" is defined here as plants growing in close proximity to each other, with no implication about the extent of interbreeding). Such an evaluation was necessarily limited by the collections available. Most of these populations were my own collections and included groups of plants that had been growing within a few meters of each other. For some of the "populations," however, I had to use herbarium collections with the same or sequential collection numbers from the same locality. All plants are listed in APPENDIX 2. Each of the populations could be placed in one of four broad morphological groups: large plants with short ligules, those with open panicles, those characteristic of *Poa curtifolia,* and "ordinary" *P. secunda.*

Plants were scored for the following 60 characters:

Nonvarying or nearly so

1. habit of plant
2. scabrousness of ligules
3. decurrence of ligules
4. ciliate nature of ligule margins
5. scabrousness of leaf margins
6. scabrousness of panicle branches
7. scabrousness of rachis
8. scabrousness of glume keels
9. ciliate nature of glume margins
10. shape of glume apexes
11. shape of lemma apexes
12. ciliate nature of lemma margins
13. no. of lemma nerves

Environmentally controlled

14. color of culms
15. involution of leaves
16. glaucousness of leaves

Varying as much within a clone as within the complex

17. no. of nerves in 1st glumes
18. no. of nerves in 2nd glumes
19. scabrousness of glumes next to keel
20. scabrousness of leaf midveins

Varying as much within a population as within the complex

21. scabrousness of culms
22. width of culms
23. scabrousness of sheaths
24. scabrousness of abaxial side of leaves
25. scabrousness of adaxial side of leaves
26. no. of branches at 1st panicle nodes
27. no. of branches at 2nd panicle nodes
28. no. of branches at 3rd panicle nodes
29. pubescence of rachillas
30. tuft of hairs on calluses
31. scabrousness of lemmas
32. length of pubescence on 1st lemmas
33. distribution of pubescence on lemmas
34. length of hairs on lemmas
35. length of pubescence on 1st paleas
36. hairs or teeth on palea keels
37. pubescence of paleas
38. shape of lodicules

Ranges of variation overlapping among populations

39. height of plant
40. height of flag leaves
41. length of flag leaves
42. length of basal leaves

43. shape of panicles
44. length of panicles
45. distance from 1st to 2nd panicle nodes
46. distance from 2nd to 3rd panicle nodes
47. width of leaves
48. shape of ligules
49. length of ligules
50. no. of florets per spikelet
51. length of 1st rachilla internodes
52. length of spikelets
53. length of 1st glumes
54. length of 2nd glumes
55. width of 1st glumes
56. width of 2nd glumes
57. length of lemmas
58. length of paleas
59. length of anthers
60. length of lodicules

This list includes all characters used in earlier keys, as well as many others suggested by close inspection of the specimens. For all quantitative characters five measurements were taken from each specimen and averaged. The mean was used in the final data matrices unless only integral values were possible (e.g., number of branches per panicle node), in which case the mode was used.

After scoring and recording character values for each plant, I could remove from the analysis those characters that were invariant, those that varied as much within as between individuals, those that varied as much within as between populations, and those that were clearly under environmental control (character weighting; see also Davis, 1983).

For assessment of variation among the offspring of self-pollinated plants, seeds from plants that I had self-pollinated in 1981 were stratified and planted in the greenhouse in early autumn. Percentage of germination was comparatively low in all cases, but two plants (*Kellogg 29,* from Nez Perce Co., Idaho, and *Kellogg 122* from Morrow Co., Oregon, both corresponding to *Poa canbyi*) produced a large number of surviving offspring; I will refer to these as families 29 and 122, respectively. Fourteen plants in family 29 and 17 in family 122 bloomed in the spring of 1983. The plants of each family were measured for height of plant, length of panicles, length of basal leaves, height and length of flag leaves, width of leaves, length of ligules, distances from the first to the second and from the second to the third panicle nodes, number of florets per spikelet, length of spikelets, length of first and second glumes, length of lemmas, paleas, and anthers, length of first-rachilla internodes, and extent of lemma pubescence (all from the fifth section of the character list).

NUMERICAL TAXONOMY: ANALYSIS OF THE DATA MATRIX

The analysis of the data matrix in taxonomy is simply a search for pattern, where pattern is defined as sets of correlated characters (see, for example, Sneath & Sokal, 1973). This correlation is not linear, however, but rather what Farris (1969) has called hierarchical. Because Farris's term uses neither the word hierarchical nor the word correlation in the usual sense, I will refer to such characters as concordant—i.e., producing a taxonomically useful pattern. Groups of concordant characters allow us to recognize groups of organisms; in such groups of characters, certain combinations of values do not occur, leaving "gaps" in the distribution of points. The distinction between concordant and

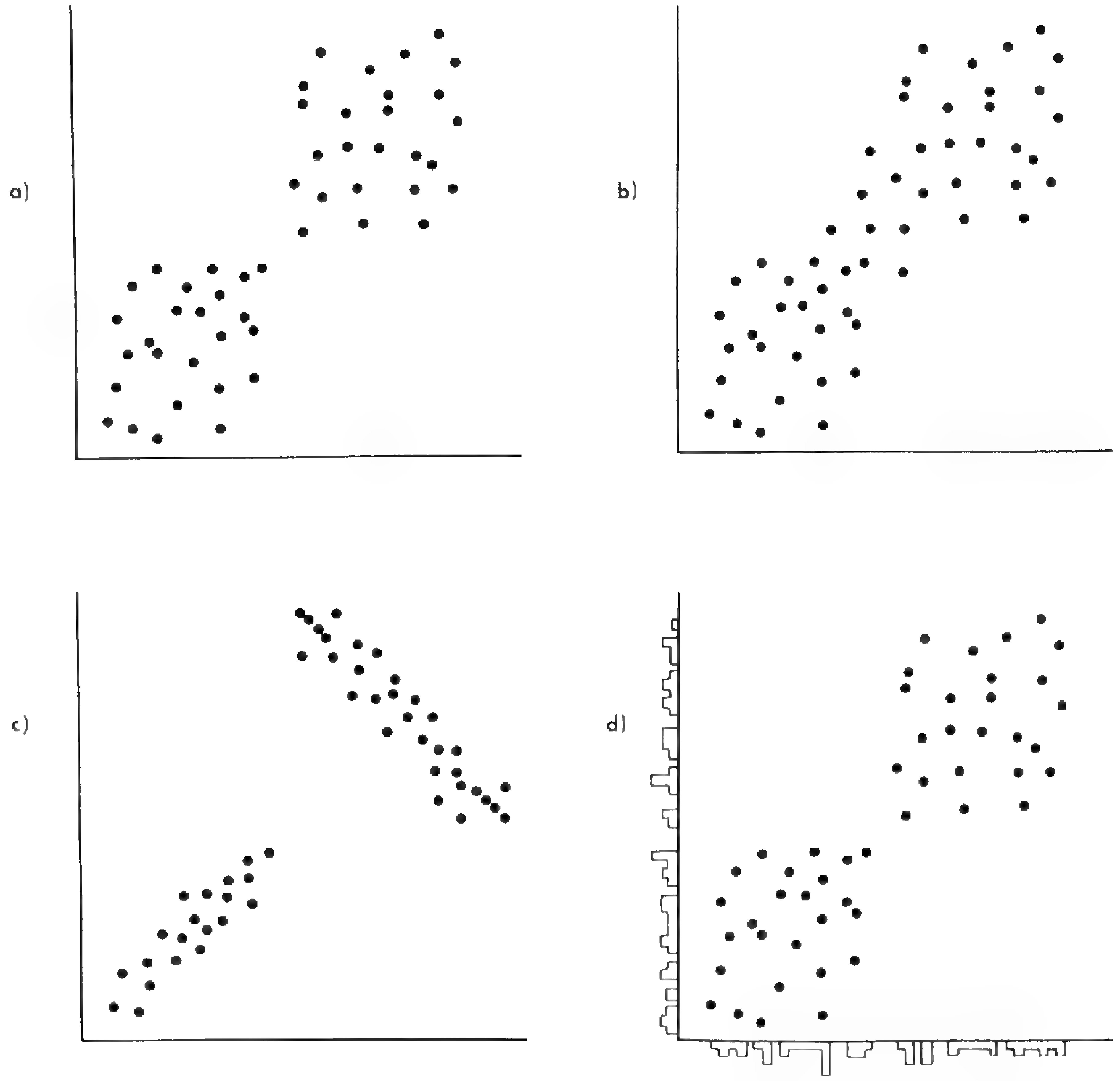


FIGURE 1. Distinction between correlated and concordant characters: a, characters linearly correlated ($r = 0.83$) and concordant; b, characters linearly correlated but not concordant ($r = 0.82$); c, characters less well correlated but concordant ($r = 0.65$); d, same data set as a, but with histograms for each character displayed on axes, characters almost continuously distributed but still concordant. Axes = values of a continuously varying morphological character, points = organisms.

linearly correlated characters is shown by comparison of FIGURE 1a–d. In FIGURE 1a the overall linear correlation coefficient (r) is 0.83; here the two characters are both linearly correlated and concordant in that they define two nonoverlapping sets of organisms. FIGURE 1b, on the other hand, shows two characters that have a similar linear correlation ($r = 0.82$) but no possibility of hierarchy since the characters do not define discrete sets of points. Finally, in FIGURE 1c, the characters are concordant but linear correlation is reduced ($r = 0.65$). FIGURE 1d shows histograms projected onto the axes of the same graph as 1a, showing that the univariate distribution of points is not dramatically bimodal; clearly, though, the lack of points in the lower right and upper left corners creates both the high correlation coefficient and the gaps that allow us to partition the points into two groups.

I began my search for pattern by using univariate, bivariate, and multivariate statistical techniques to examine various combinations of characters; I looked for concordance among the characters and for nonoverlapping sets of organisms.

Multivariate techniques have been applied to many groups of grasses in the past (Morishima & Oka, 1960; Goodman, 1968; Phipps, 1970; Clayton, 1971; Baum, 1974; Barkworth, 1978; Williamson & Killick, 1978; Doebley & Iltis, 1980). I chose to begin with principal-component analysis, a multivariate method that considers each plant as a point in multidimensional space, where each dimension is a taxonomic character. It is possible to visualize the relative positions of the plants on axes that are combinations of characters by mathematically reducing the dimensionality of the hyperspace. Plotting of the OTUs (operational taxonomic units—individual plants in this case) against pairwise combinations of the factors may make discontinuities between the clusters detectable (see, for example, McNeill, 1975). Each axis (factor) is a linear combination of several taxonomic characters; these characters are said to be "loaded" on that axis. By examining the factor loadings, one can determine which characters are responsible for explaining most of the variance in the data matrix. I performed a variety of principal-component analyses on different sets of plants and characters (see TABLE 2).

There are three major problems with the use of principal-component analysis. First, because it assumes multivariate normality, binary or multistate characters may be weighted disproportionately by the algorithm. I therefore ran one analysis with only the quantitative characters. Second, this type of analysis is strongly affected by outliers. I therefore did another analysis excluding all the representatives of *Poa curtifolia.* Third, principal-component analysis will pick out only the most distinct groups in a set of OTUs, partly because it is designed to find linear correlations among characters that, as shown earlier, may or may not be taxonomically concordant. The results thus have one-sided implications: if a group is found to be discrete, then it probably really is quite distinct, but the converse does not hold.

Discriminant analysis is useful for comparison with principal-component analysis in that it allows one to compare variation within populations to overall variation in the data matrix. Although discriminant analysis could be used to test the validity of previously described taxa, there is an element of circularity in using it in this way. Because such analyses attempt to minimize variance within groups relative to that between them, they effectively assume that the groups to which the OTUs are assigned are somehow real entities. Furthermore, by assigning plants to groups *a priori,* the taxonomist can only test whether those particular groups are nonrandom—very different from testing whether they in fact represent sets of concordant characters. If there are discrete groups in the complex that are quite different from the ones being tested, they may easily go undetected in a discriminant analysis. To minimize prejudice in the analysis, I therefore used populations as the groups. Cluster analysis is also commonly utilized in studies of this sort, but because this imposes a hierarchical structure on the data (Gower, 1967), it would be circular to use it to test for the presence of such structure (and inappropriate to use it in a hybridizing group).

Because of the difficulty of obtaining adequate population samples, I had to restrict the discriminant analyses to two populations of *Poa curtifolia,* five populations of large plants with short ligules, and three populations of open-panicled plants, with the rest being plants from southern California and the Gaspé Peninsula. Such a sample is clearly highly biased toward recognizing discrete groups; it thus has one-sided implications opposite those of principal-component analysis. Nondiscrimination of groups convincingly shows their morphological indistinctness, but discrimination does not prove that groups are discrete.

RESULTS

CHARACTERS STUDIED

All members of the complex have a caespitose habit (1).[1] The only exception is *Poa curtifolia,* which sometimes produces short rhizomes, although it maintains the intravaginal branching characteristic of the rest of the group.

Many plants, particularly those on dry sites, become red with age (14). As Arnow (pers. comm.) has also observed, this character varies within a site. Plants that are red in their native habitat are often green when grown the next season in the garden, and all plants are green when grown in the greenhouse. This character is thus environmentally controlled. Members of the complex are frequently glaucous (16), with a waxy coating on the leaves, but this also depends on the environment in which the plants are grown. The one exception to this is *Poa curtifolia,* which is glaucous in any environment, although the extent to which the culms become red varies among individual plants. In general, larger plants are more likely to be strikingly glaucous, whereas smaller ones are more likely to become red during development. Because these characters are not consistently expressed, however, they cannot be used as reliable taxonomic characters, except to distinguish *P. curtifolia.* Such characters can be used to reinforce an existing classification but not to establish it.

Height of plants (39) (greater vs. less than 3 dm) has been used as a specific character in previous classifications. This character varies considerably with environment, among members of a population, and within a clone. Some relative differences in size persist in the garden, so this character may still help distinguish groups within the complex. The range of variation is great within populations, however, and there is considerable overlap between them (FIGURE 2).

All members of the complex have a conspicuous tuft of more or less erect basal leaves; these sometimes become more lax when the plants occur on very wet sites (such as the open-panicled plants growing near Multnomah Falls, Oregon, in wet canyons). The length of the basal leaves (42) varies within and among populations (see FIGURE 3). The flag leaf (the uppermost leaf on the

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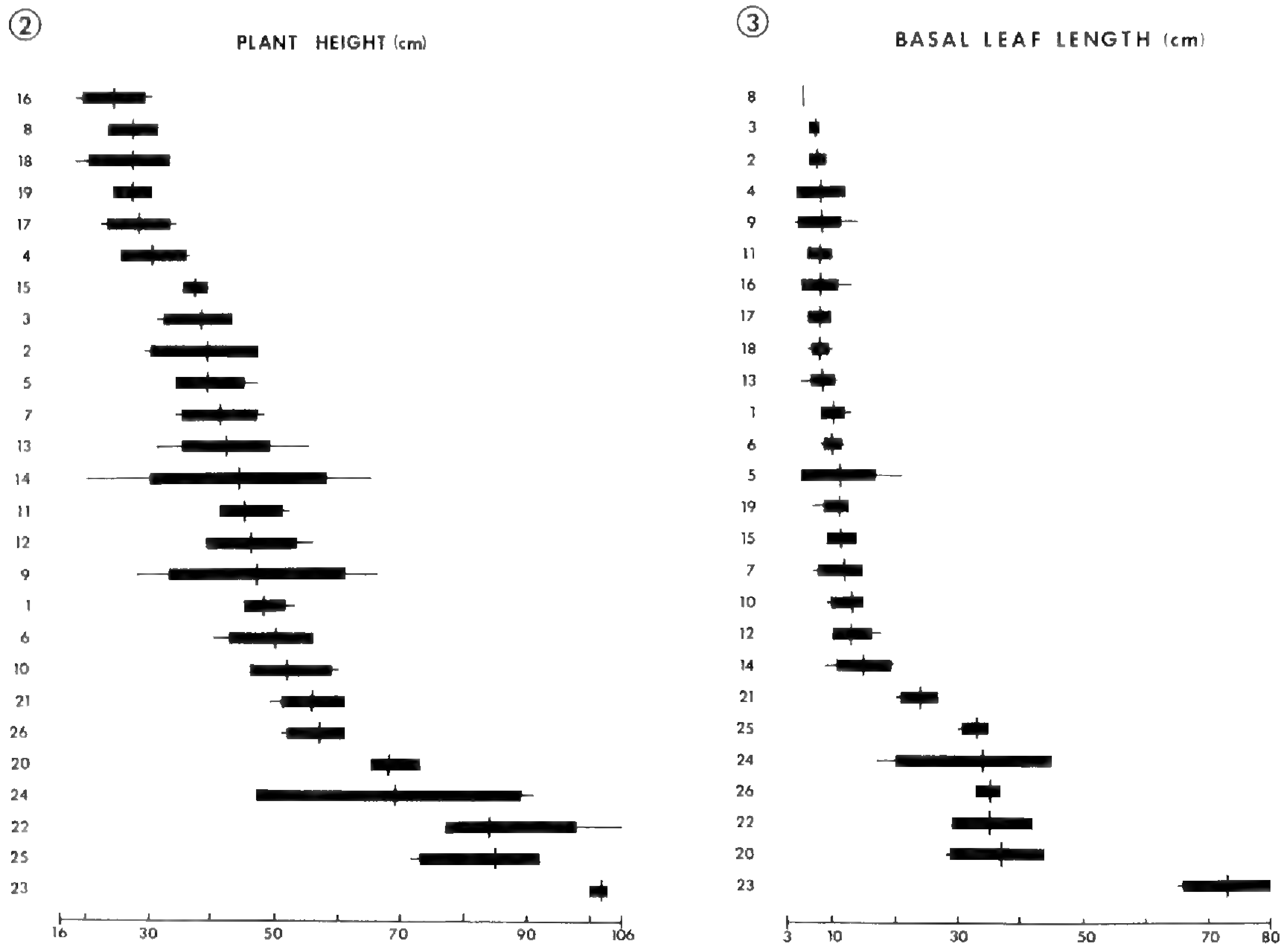
[1] Numbers in parentheses refer to character numbers in the list of characters.

TABLE 2. **Summary of multivariate analyses.**

ANALYSIS	PLANTS INCLUDED	CHARACTERS USED	ILLUSTRATION (figure no.)	CUMULATIVE PERCENT OF VARIANCE			CANONICAL CORRELATIONS			AXES WITH EIGENVALUES > 1
				A1	A2	A3	A1	A2	A3	
Principal-component	All in Appendix 1	15, 22, 23, 32, 40, 42, 43, 47, 48	—	39	44	68				3
	All in Appendix 1 except *Poa curtifolia*	15, 22, 23, 32, 40, 42, 43, 47, 48	16	38	56	69				3
	All in Appendix 1	1–60	17, 18	17	29	38				16
	All in Appendix 1	2–8, 16, 19, 21–37, 39–60	—	20	32	43				13
	All in Appendix 1	17, 18, 26–28, 32, 34, 35, 39–42, 44–47, 49–60	—	28	48	56				7
	All in Appendix 1 except *Poa curtifolia*	1–60	19	24	36	44				11
Discriminant	All in Appendix 2	23, 32, 39–44, 47–50, 52–54, 57, 59	20	58	71	81	.98	.95	.95	7
	All in Appendix 2 except population 23	23, 32, 39–44, 47–50, 52–54, 57, 59	21	52	66	79	.98	.95	.95	7
	All in Appendix 2	23, 32, 39–41, 43, 44, 47–50, 52–54, 57, 59	—	48	64	77	.98	.95	.94	7
	All in Appendix 2 except population 23	23, 32, 39–41, 43, 44, 47–50, 52–54, 57, 59	—	45	62	77	.97	.94	.94	6



FIGURES 2, 3. Range of variation compared within and among populations: 2, plant height; 3, basal-leaf length. Each bar = separate population. Only 1 population of *Poa curtifolia* (26) shown. Numbers refer to population numbers as listed in APPENDIX 2. Narrow horizontal line = range of values for that population, broad horizontal bar extends 1 standard deviation on both sides of mean, narrow vertical line = mean. Horizontal scale = full range of variation in complex.

culm) is rarely borne much above midpoint on the culm (40) and varies considerably in length (41). The margins of the leaves are scabrous (5). The midvein is frequently scabrous (20) as well, particularly near the tip on the abaxial side of the leaf, but this character varies within an individual, some leaves being scabrous and others not. On some plants leaves are scabrous on either the abaxial (24) or the adaxial (25) side or both, but I have never found a population that was not polymorphic for this character.

Leaf width varies from 0.4 to 4 mm (47; FIGURE 4). Although some basal leaves tend to be somewhat wider than culm leaves, the difference is neither consistent nor, when present, significant. I therefore did not separate leaf width into basal and culm leaf components.

Among herbarium specimens there is considerable variation as to whether the leaves are rolled or flat (15), and this has been widely used as a specific character to distinguish *Poa juncifolia* Scribner from *P. ampla* Merr., and *P. sandbergii* from *P. incurva* Scribner & Williams. However, all plants, if given enough water, have flat leaves. Furthermore, few plants can be found with truly involute leaves. If the leaves are 1.5 mm or less in width, they will tend to appear involute on drying but are actually merely folded.

The ligule of all members of the complex is nonciliate (4), decurrent (3), and more or less scabrous (2), but almost never glabrous. Variation in length (49; FIGURE 5) and shape (48) is almost continuous from short (0.5 mm) and truncate to long (6 mm) and acuminate. Plants with scabrous sheaths (23) are not found in pure populations; they are always mixed with glabrous-sheathed plants. This character has been used in the past to distinguish *Poa scabrella* (Thurber) Bentham from the rest of the complex, but the pattern of variation suggests that it is simply a population-level polymorphism.

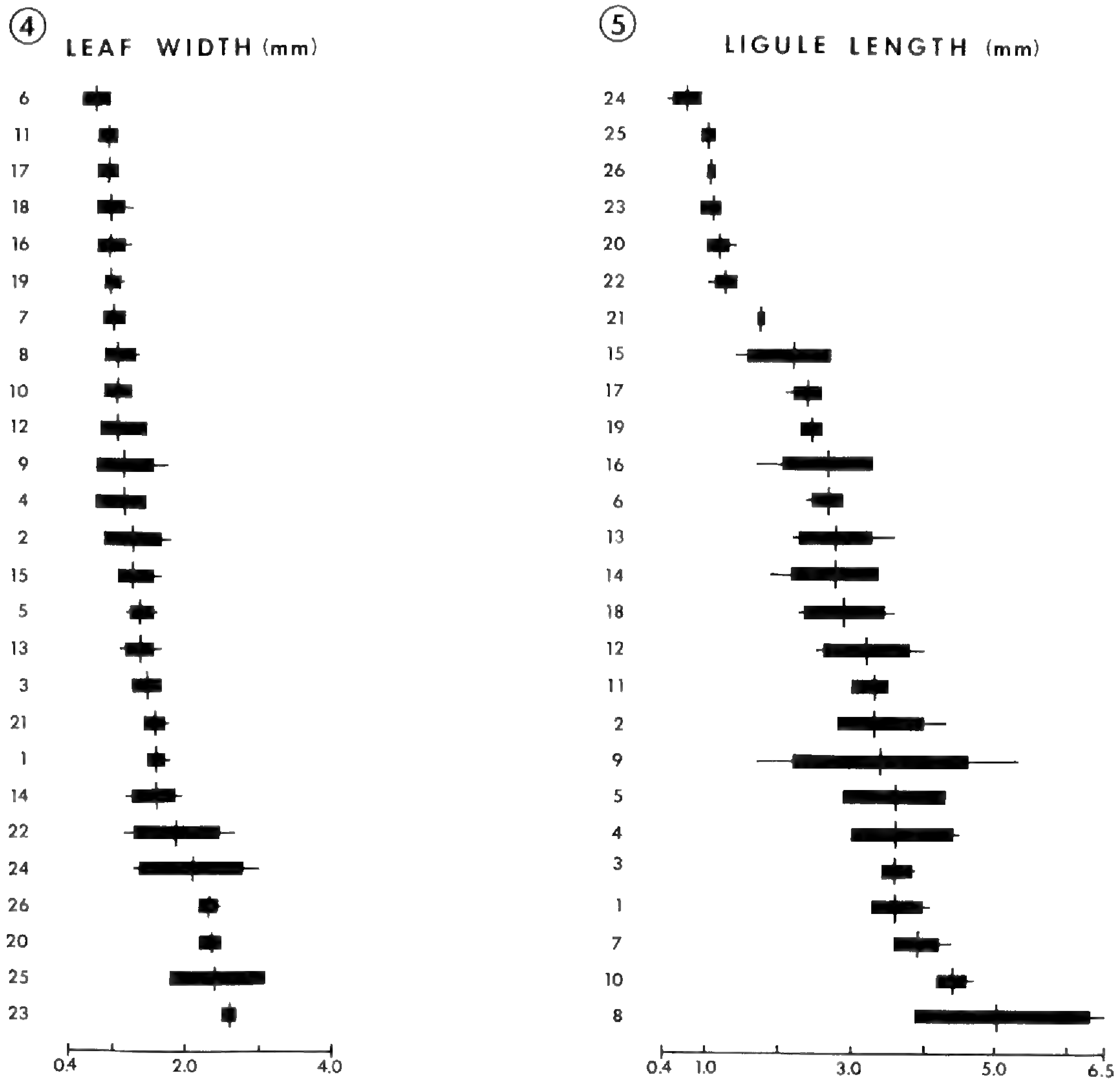
Inflorescences are either contracted or open panicles (43); plants with open panicles are usually referred to *Poa gracillima* Vasey. However, panicles of all plants become open for about a week at anthesis, contracting again afterward in most. Those plants with persistently open panicles occur mainly in montane habitats in the Rocky and Cascade mountains and the Sierra Nevada, and a few are known from Chile (Arnow, 1981). They frequently grow in cracks in granite outcrops but are not restricted to such sites. The open panicle of these plants persists in the garden.

The panicle branches and rachis are scabrous (6, 7) on nearly all specimens. There is considerable variation in culm width (22) just below the inflorescence, in distance between the first and second (45) and the second and third panicle nodes (46), and in number of branches at each of the first three nodes (26–28). Panicle length (44) also varies widely within populations, and the ranges of variation overlap (FIGURE 6).

Spikelets have from two (rarely one) to eight florets (50) and vary greatly in length (52; FIGURE 7). As noted above, the first rachilla internode (51) is relatively long for *Poa* species, varying from 0.6 to 1.9 mm, but variation is continuous among populations. The rachilla may be pubescent, scabrous, or glabrous (29), but this too varies within populations.

Glume and lemma apices are similar in shape (10, 11), mostly acute to nearly obtuse; there is no striking variation within the complex. The upper parts of the margins of both glumes and lemmas are finely ciliate (9, 12), and glume keels are consistently scabrous, at least toward the apex (8). The glumes of most plants each have three nerves (17, 18), although within a clone occasional glumes with one or five nerves can be found. Lemmas are consistently 5-nerved (13). Some glumes within a clone may also be scabrous next to the keel (19), but this character is rarely consistent within a population. Glume width (55, 56) varies almost as much within populations as within the entire complex, and the range of variation in length of the first (53; FIGURE 8) and second (54) glumes overlaps considerably among populations.

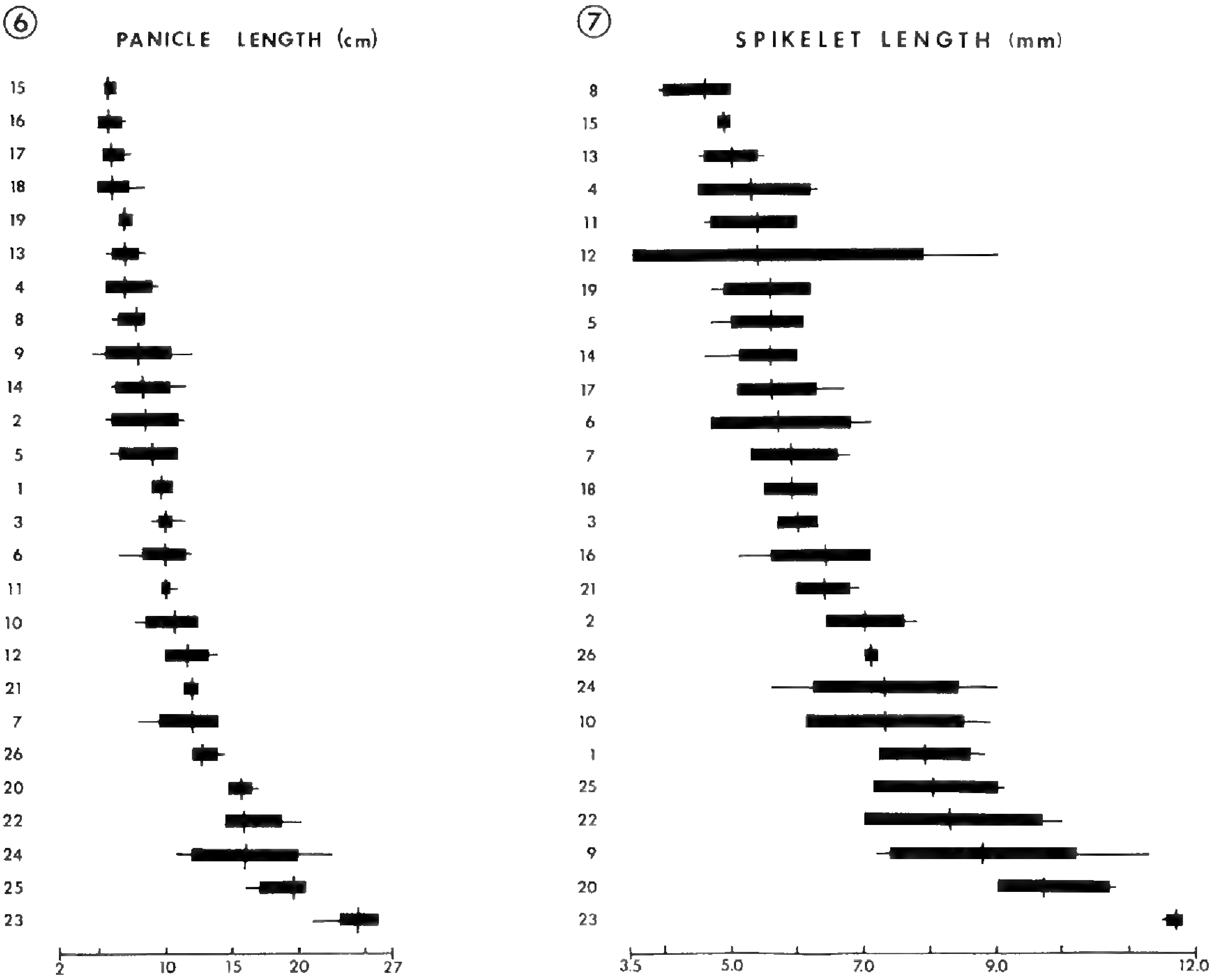
Lemma pubescence (32) is a major character in all classifications of *Poa* and has been heavily relied on in the *P. secunda* complex. *Poa ampla, P. juncifolia, P. nevadensis,* and *P. curtifolia* have been distinguished from other members of the complex on the basis of their scabrous to glabrous lemmas, and A. S. Hitchcock (1950) put them in a separate section, *Nevadenses,* on this basis. I have found, however, that this character commonly varies within populations, in some cases nearly as much as in the complex as a whole (FIGURE 9). Pubescence can extend up to nearly three-quarters the length of the lemma, but



FIGURES 4, 5. Ranges of variation compared within and among populations: 4, leaf width; 5, ligule length. Format same as in FIGURES 2, 3.

the character varies continuously. In this group lemma pubescence is thus of doubtful taxonomic utility. The lemma may or may not be scabrous above the area where there is pubescence (31); there may also be a small tuft of hairs on the callus (30). The pubescence may be distributed evenly, it may extend somewhat higher on the marginal nerves and keel (33), or it may rarely be confined only to the keel and margins, not occurring between; the trichomes may be as much as 0.3 mm long (34). All these characters vary at the population level. Lemma length (57) is relatively less variable within populations, but the ranges of variation overlap between populations (FIGURE 10).

Palea pubescence (37) has been useful in separating other species of *Poa* (e.g., *P. reflexa* Vasey & Scribner and *P. leptocoma* Trin.; Soreng & Hatch, 1983), but it is too variable to be of help in *P. secunda*. Paleas may be pubescent, scabrous, or glabrous, but all character states occur in almost every population studied. The palea keels may have either hairs or teeth (36), but this too varies



FIGURES 6, 7. Ranges of variation compared within and among populations: 6, panicle length; 7, spikelet length. Format same as in FIGURES 2, 3.

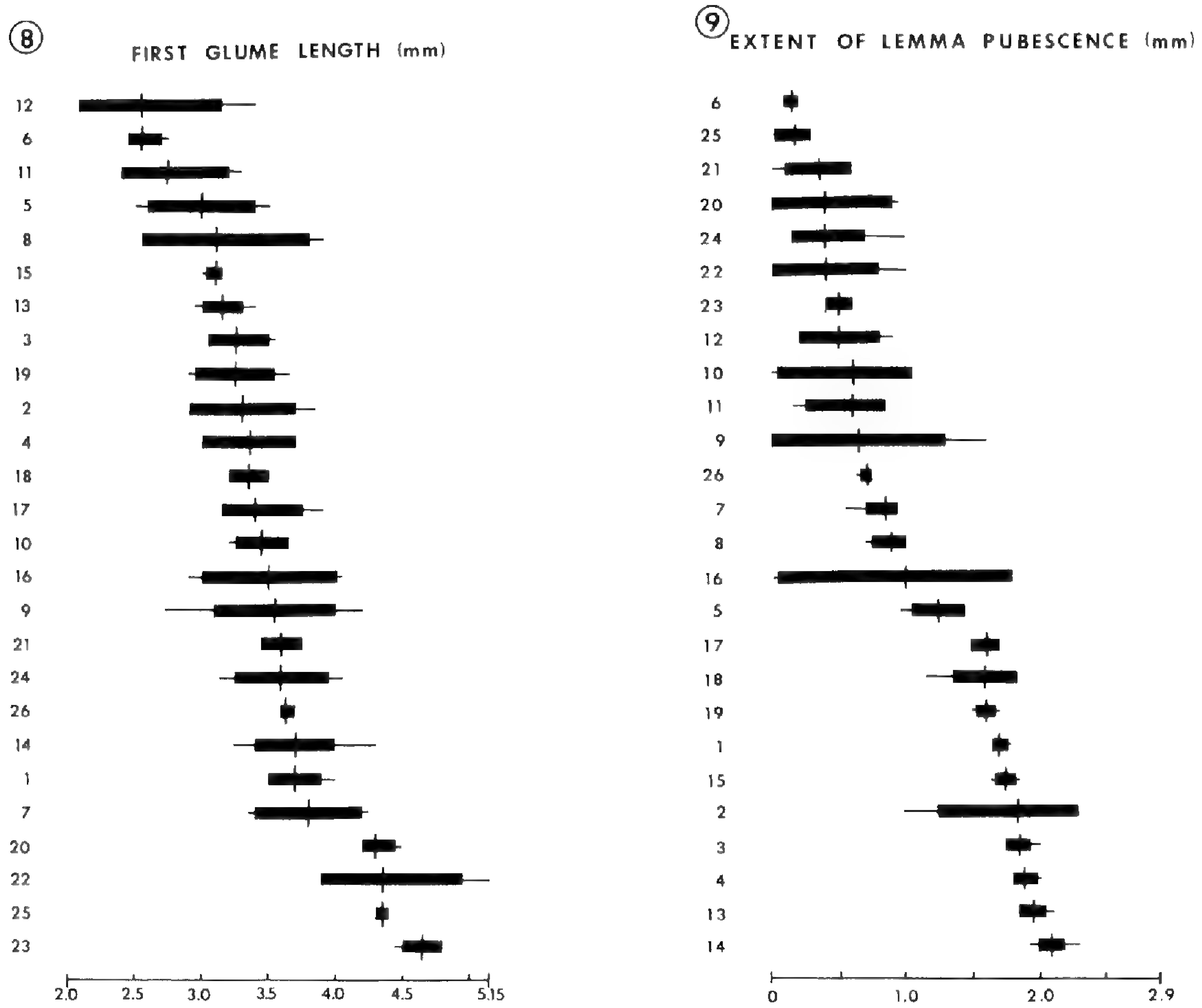
within populations. The length of the hairs (35) is variable: long hairs near the bottom of the palea nerves frequently grade into stiff teeth nearer the top. Again, the only remaining character is palea length (58), which shows considerable overlap among populations.

Lodicule shape (38), like lodicule length (60), varies as much within as between populations. Anther length (59) also varies within and between populations (FIGURE 11).

VARIATION AMONG OFFSPRING OF SELF-POLLINATED PLANTS

The offspring of plants I self-pollinated showed substantial variation within each family. I gave a set of the offspring and a traditional key (C. L. Hitchcock & Cronquist, 1973) to taxonomists not familiar with the group; they identified the offspring of each family as a mixture of *Poa scabrella, P. nevadensis,* and *P. gracillima.* Individual plants were generally identified differently by different taxonomists.

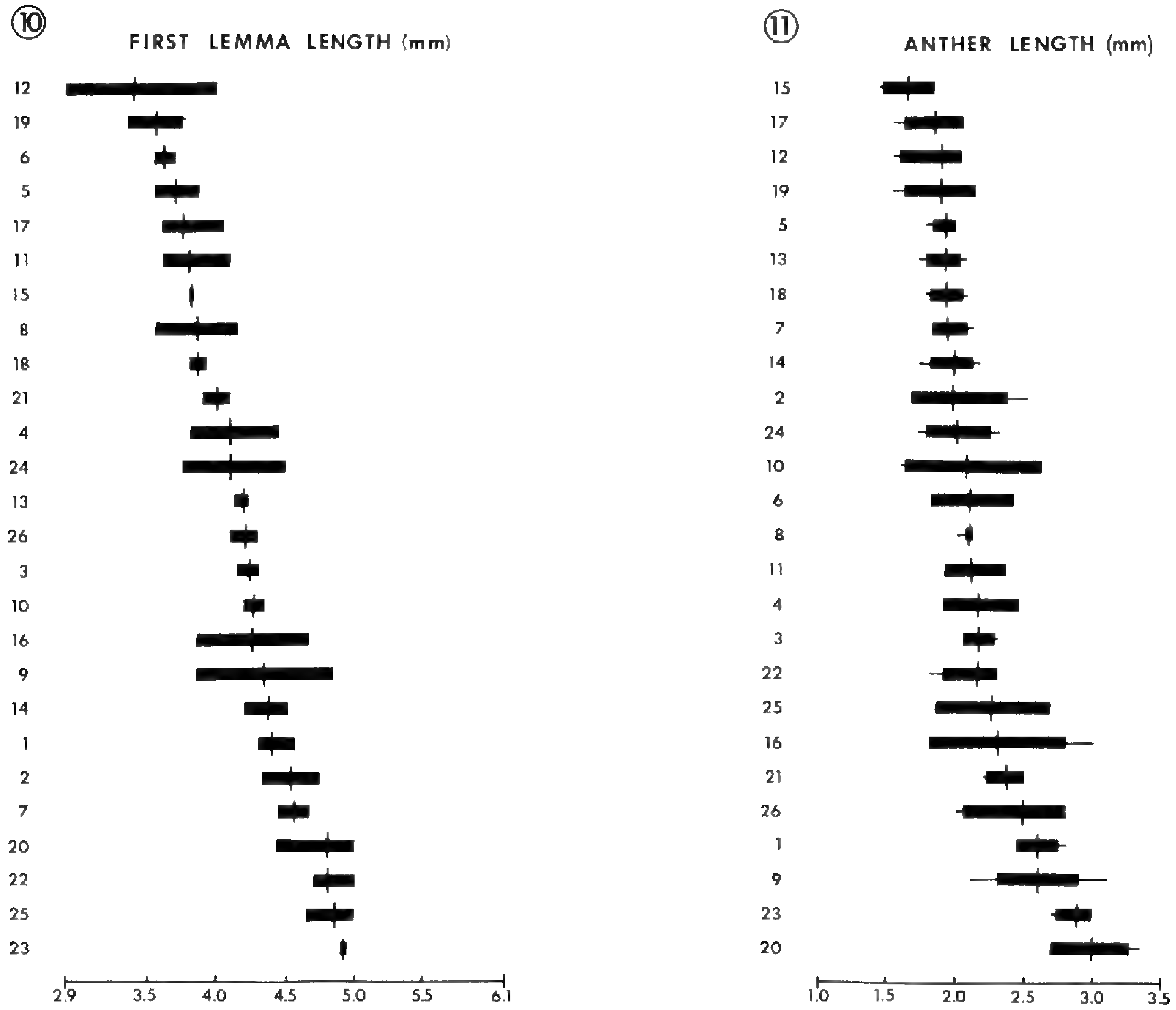
Histograms for some of the quantitative characters measured are shown in FIGURE 12. Comparison of these with FIGURES 2–11 shows that the range of



FIGURES 8, 9. Ranges of variation compared within and among populations: 8, first-glume length; 9, extent of lemma pubescence. Format same as in FIGURES 2, 3.

variation within each family is very high relative to the range of variation in the complex as a whole. For plant height the range within family 29 is 78 percent of that in the entire complex. The range for distance between the second and third panicle nodes is actually greater than that observed in the rest of the complex (1.5–6 cm vs. 0.6–3.6 cm). For many of the other characters, the range is between 38 and 62 percent of that of the whole complex. More important than the range of variation, though, is the distribution of values. Comparison of the ranges of values in the histograms of FIGURE 12 with those in the appropriate bar graphs of FIGURES 2–11 shows that the range of values in either family 29 or family 122 crosses most of the apparent breaks in distribution in the bar graphs. This is particularly true with such characters as extent of lemma pubescence (FIGURES 9, 12g), often considered to be of high taxonomic value in the genus.

Variation in each family could be entirely phenotypic, entirely genotypic, or some combination of the two. If all the plants were apomictically produced, they would be genetically identical, assuming no autosegregation or mitotic crossing-over. Although all the plants were greenhouse grown, the experiment was not controlled for small differences in environment. At the other extreme



FIGURES 10, 11. Ranges of variation compared within and among populations: 10, first-lemma length; 11, anther length. Format same as in FIGURES 2, 3.

the variation could be all genetic. If all the seeds were sexually produced, then they could all be genetically different. To sort out the phenotypic plasticity of these characters would require careful factorial experiments like those done by Davis (1983) in his study of *Puccinellia.* No matter how the variation is explained, however, it is still high enough to suggest that the characters are of minimal taxonomic value.

Could it be that, quite by accident, I happened on two unusually variable plants? Although possible, this seems unlikely. Plant 29 was collected from a crumbling basalt outcrop in northern Idaho, and plant 122 in a grassy meadow in north-central Oregon, both common habitats for *Poa secunda*; neither was part of an unusually variable population. Both plants were collected in 1978 and grown in a common garden for three years before being moved into the greenhouse early in 1981. The patterns of variation for many of the characters are strikingly similar for the two plants. Neither is consistently more variable from stem to stem than the other for all characters, and for such characters as spikelet and glume lengths, the ranges are virtually identical. It seems unlikely, therefore, that these results are simply accidental. The numerical analyses in the next section amplify and further support this conclusion.

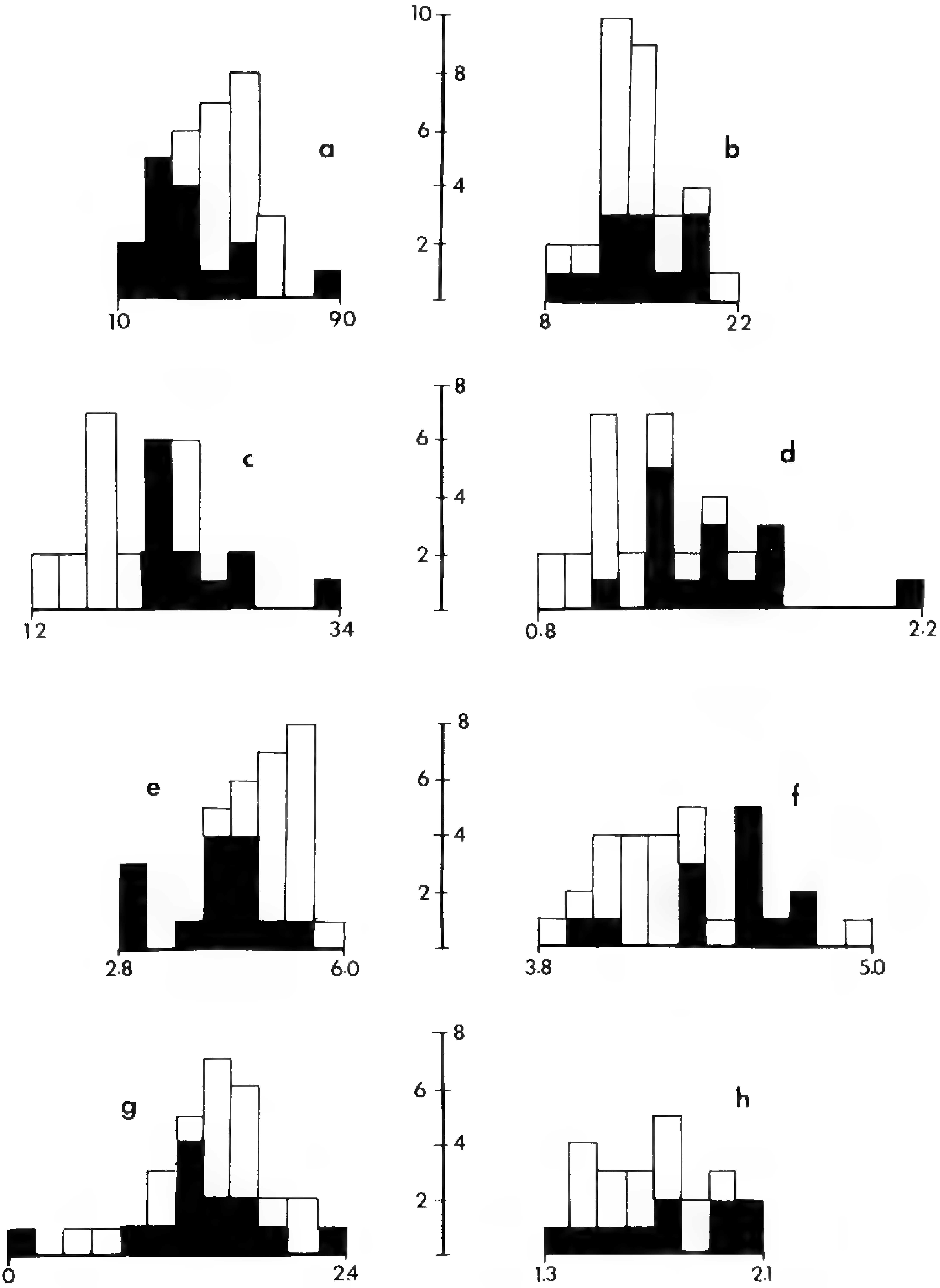


FIGURE 12. Histograms for 8 quantitative characters measured on 31 offspring of 2 self-pollinated plants: a, plant height (bar width = 10 cm); b, panicle length (bar width = 4 cm); c, basal-leaf length (bar width = 4 cm); d, leaf width (bar width = 0.1 mm); e, ligule length (bar width = 0.4 mm); f, first-lemma length (bar width = 0.1 mm); g, extent of lemma pubescence (bar width = 0.1 mm); h, anther length (bar width = 0.1 mm). Black bars = offspring of *Kellogg 29*, white bars = offspring of *Kellogg 122*; vertical scale = number of plants.

NUMERICAL TAXONOMY

Removal of all characters except those in which the range of variation is greater among than within populations leaves only 21 characters, the ranges of which still overlap among populations. The data described in the previous section suggest that many of these characters themselves are of questionable taxonomic value. Most of the key characters have been eliminated. Ligule decurrence is constant throughout the group. Sheath scabrousness and lemma pubescence vary as much within as between populations. Date of blooming (see next section), culm color, leaf involution and glaucousness, and—to a certain extent—plant height are all under environmental control. Of Hitchcock's eight original key characters, only panicle shape, ligule length and shape, and gross differences in height remain. There are 17 additional, non-key characters that are not automatically filtered out because of their variation pattern. This suggests three possible ways to describe and classify the complex: 1) four entities corresponding roughly to open-panicled plants, large plants, *Poa curtifolia,* and everything else, distinguished on the basis of combinations of the four characters mentioned above; 2) more than four entities, distinguished on the basis of characters other than those used in the past; or 3) one or more entities, none of which corresponds to previously recognized taxa.

UNIVARIATE STATISTICS. Both histograms and bar graphs show that no single character can be used to divide the complex. Histograms of the quantitative variables are mostly unimodal and approach normality, although a few are highly skewed; none is strongly bimodal. Four representative histograms, for all plants listed in APPENDIXES 1 and 2, are shown in FIGURE 13. Plants with extreme values for one character do not necessarily have extreme values for others. On the other hand, occasional aberrant individuals appear in which many of the parts are unusually large. When compared with many of the other plants, these stand out as strikingly different.

This pattern of variation also appears in the population samples illustrated in FIGURES 2–11. The order of populations, from lowest to highest mean values for each character, is not always the same. Furthermore, populations that are highly variable for one character are not highly variable in others, again suggesting noncorrelation of characters. The only exception is population 23, collected by C. V. Piper in the Grand Coulee, Washington, in 1900. This population is represented by three herbarium specimens that are all extremely large for most of the characters measured. However, because this "population" is a group of herbarium specimens with the same number, and because the range of variation in most characters is quite narrow, it may represent a single clump divided into three parts. Hence its extreme position should be treated cautiously (see also below).

BIVARIATE STATISTICS. Bivariate plots (see FIGURES 14, 15) show similar continua. Lemma pubescence and ligule length are two characters that have often been used in the taxonomy of the complex; they show, however, no perceptible groups. Other combinations of characters are similar. Although some characters such as plant height and panicle length are linearly correlated ($r = 0.8$), they

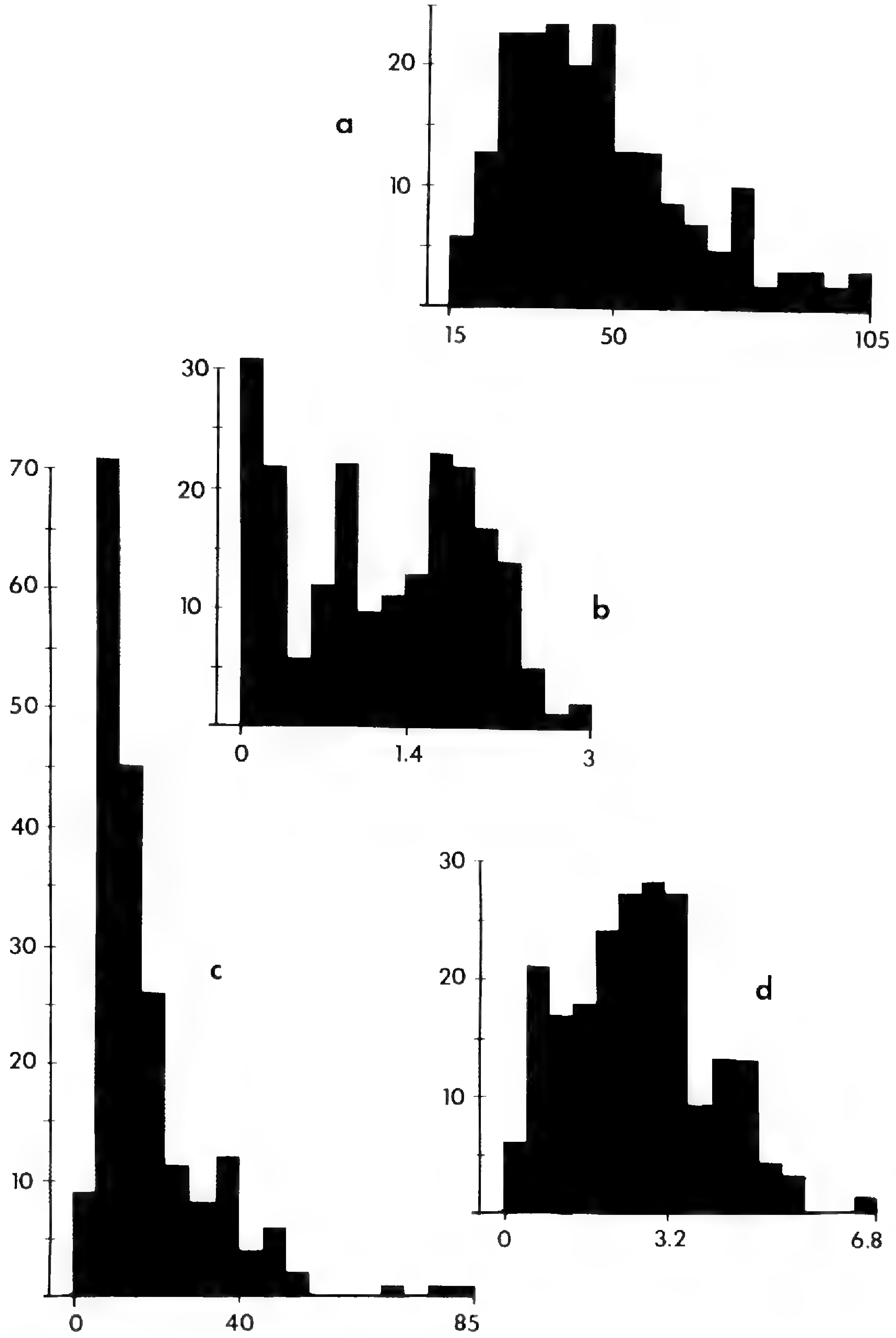
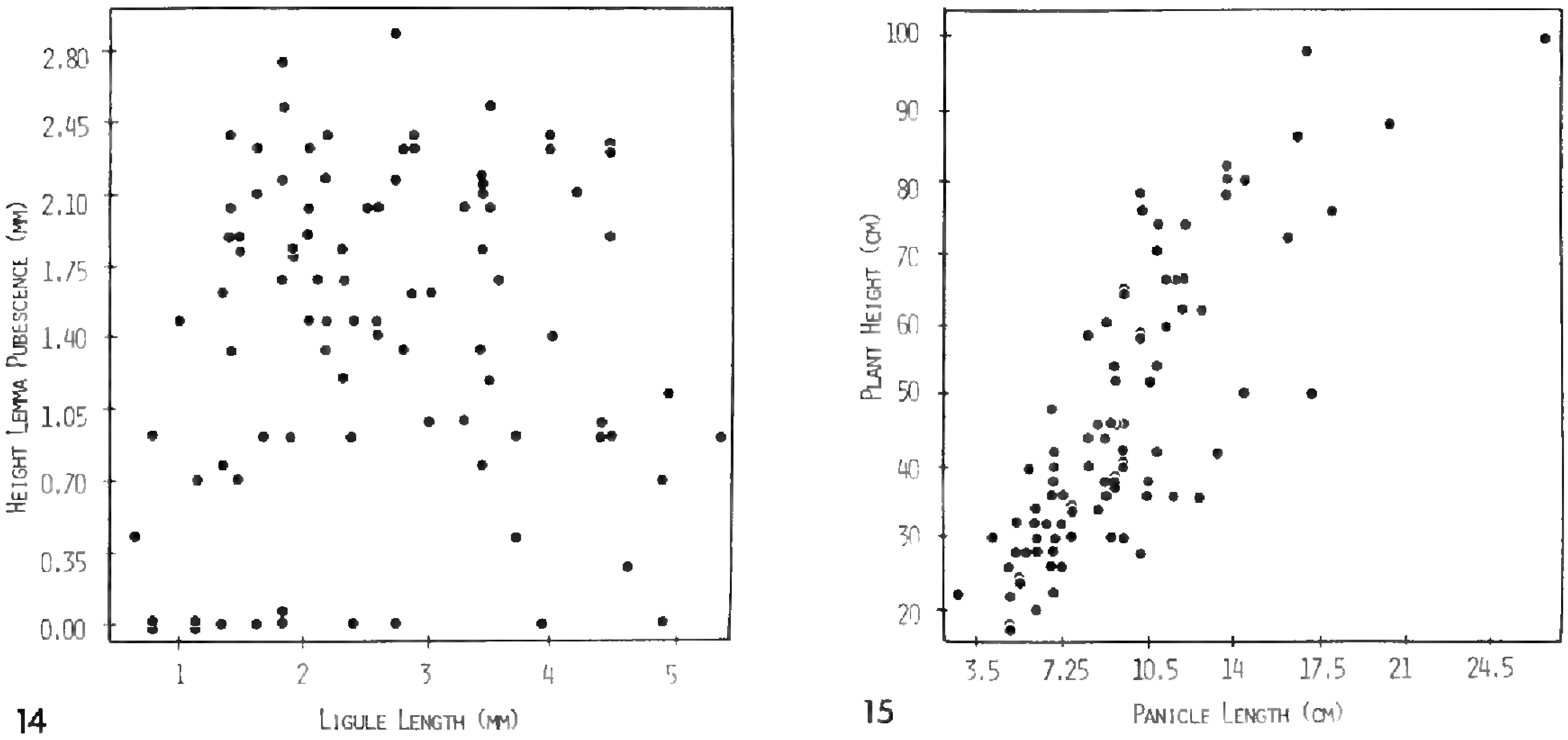


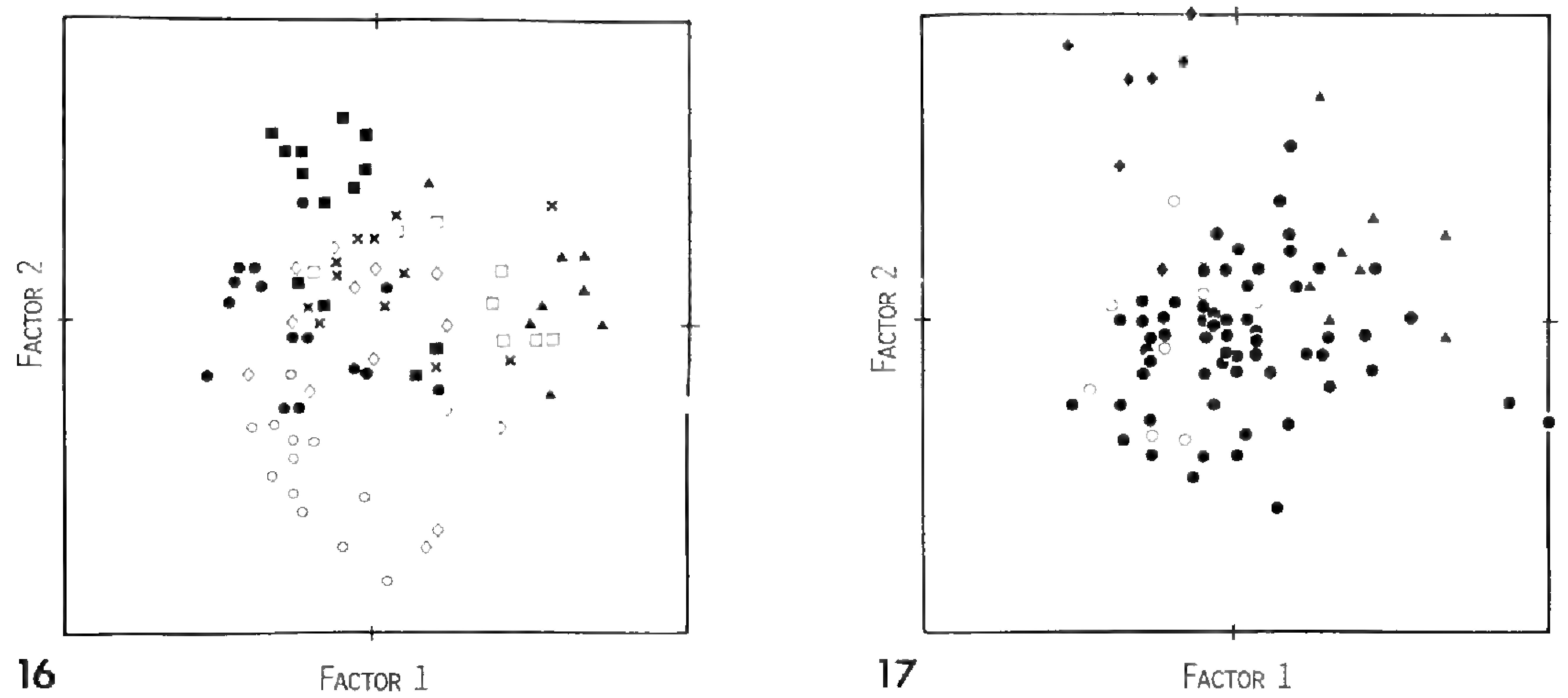
FIGURE 13. Histograms for 4 representative morphological characters measured on all plants in APPENDIXES 1 and 2: a, plant height (bar width = 5 cm); b, extent of lemma pubescence (bar width = 0.2 mm); c, basal-leaf length (bar width = 5 cm); d, lemma length (bar width = 0.4 mm). Vertical scale = number of plants.



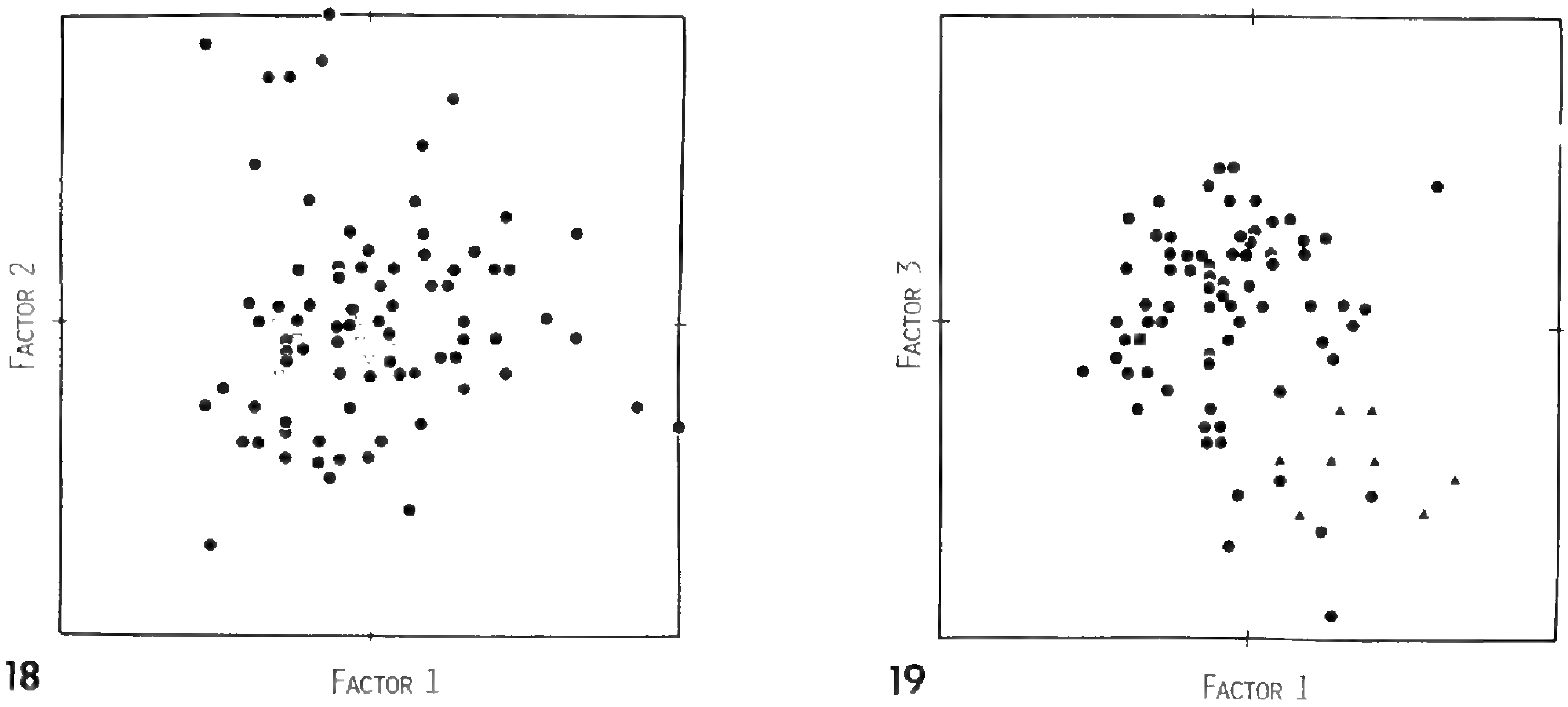
FIGURES 14, 15. Bivariate plots for plants listed in APPENDIX 1: 14, lemma pubescence vs. ligule length ($r = 0.087$); 15, plant height vs. panicle length ($r = 0.806$).

are not concordant and do not suggest any infrastructure for the group. It is more likely that the high linear correlation represents genetic linkage or similar developmental trajectories for the two characters.

PRINCIPAL-COMPONENT ANALYSES. A principal-component analysis on only the characters used by A. S. Hitchcock (FIGURE 16) shows that his taxa intergrade and that the single characters he used to define his species do not correlate with any other characters. The analysis using all 60 characters produced four notable results.



FIGURES 16, 17. Principal-component analyses: 16, A. S. Hitchcock's characters only (solid squares = *Poa scabrella,* open squares = *P. nevadensis,* solid circles = *P. sandbergii,* open circles = *P. gracillima,* open diamonds = *P. canbyi,* crosses = *P. juncifolia,* triangles = *P. ampla*); 17, all 60 characters (diamonds = *Poa curtifolia,* open circles = open-panicled plants, triangles = large plants with short ligules, solid circles = all other plants). Each axis = 6 standard deviations.



FIGURES 18, 19. Principal-component analyses: 18, all 60 characters (open triangles = separate culms of *Kellogg 56* scored as if separate plants, solid circles = all other plants); 19, all 60 characters, eliminating *Poa curtifolia* (triangles = large plants with short ligules, open squares = large plants with long ligules, solid circles = all other plants). Each axis = 6 standard deviations.

First, *Poa curtifolia* formed a more or less distinct cluster in the Factor 1 × 2 plot, separate from the other plants (FIGURE 17). This result is particularly interesting in that the characters most distinctive of this species—leaf succulence and a white leaf margin—were not included in the data set. (See the following section for a discussion of leaf anatomy).

Second, the first three factors mainly represent size of vegetative features (characters 22, 39–42, 44–47), size of spikelet parts (characters 20, 52–59), and amount and distribution of trichomes (characters 14, 32, 33, 35). The first factor in particular thus probably includes a large environmental component. This is borne out by the fact that garden-grown plants tend not to cluster with field-grown plants from the same population.

Third, the individuals marked by open triangles in FIGURE 18 are actually separate culms of the same plant (*Kellogg 56*) scored as if they were separate individuals. They are scattered over about one and a half standard deviations in character space in most factor combinations, suggesting that variation within a single clone is large relative to that in the whole group.

Fourth, sixteen factors have eigenvalues greater than one, and the first three factors together explain only 39 percent of the variance. This is what one would expect if there were no definite groups and the OTUs all formed a nearly hyperspherical constellation in multidimensional space. Examination of the first three principal-component axes on the three-dimensional visual display created by Huber and his graduate students (see Kolata, 1982) shows that the constellation of points is actually more or less L- or T-shaped. Most of the plants form a dense cloud that is the bar of the T; individuals classified as *Poa curtifolia* plus the plants with extremely large values in several characters form a more diffuse "tail." Some of the large plants fall as far from the dense part of the cloud as do members of *P. curtifolia.*

I examined plots of all possible two-way combinations of the first ten factors and found no pattern any more interpretable than those shown. The open-panicled plants are closest together in the plot of factor 1 vs. factor 5, but even so they do not form a discrete group.

Eliminating the characters that vary within the plant and those that are clearly under environmental control reduces the total number of characters to 48—29 quantitative and 19 qualitative. This changes the results only slightly. The first three factors now explain 43 percent of the variance. The relationships of most plants to each other remains similar, although *Poa curtifolia* is somewhat more distinct. The results of the analysis with quantitative characters only are also similar to those in the other analyses.

When *Poa curtifolia* is eliminated from the analysis, the first three factors explain 45 percent of the variance and some weak groups appear in the plot of Factor 1 × 3 (FIGURE 19). The group in the lower right corner of the graph includes mostly large plants with relatively short ligules. Factor loadings remain similar to those in the other analyses. The two plants in the upper right corner, shown by open squares, appear together in all analyses and are always distant from the rest of the group. These plants both have extremely large panicles on very long culms. Reference to the bivariate plot of plant height vs. panicle length (FIGURE 15) shows that the two plants (the rightmost points) are indeed extreme and may have slightly unusual proportions of those parts. Although the two plants are morphologically quite similar, they were collected nearly 600 miles apart and on very different sites, one near Reno, Nevada, the other in the Wasatch Mountains of Utah. Again, this suggests that the very largest plants are simply isolated extreme forms.

DISCRIMINANT ANALYSES. In the first of these analyses (shown in FIGURE 20), plants of population 23 (from eastern Washington—far left) appear radically different from the large plants in populations 21, 22, 24, and 25 (center), which are in turn distinct from the rest of the group. *Poa curtifolia* (populations 29 and 30) is less well separated than by the principal-component analysis. The open-panicled populations, the Gaspé populations, and the California group all cluster together. The greatest discrimination is provided by the first canonical variable, which is primarily a function of basal-leaf length, flag-leaf length and height, leaf width, and ligule shape. Characters loading on axis II are length of the flag leaves, the panicles, the first glumes, the lemmas, and the anthers, width of the leaves, and extent of pubescence on the lemmas.

As noted earlier, population 23 is an outlier in terms of most characters; furthermore, it may represent not a population but a single clump (clone). Removing it from the analysis produces the picture shown in FIGURE 21. Again the large plants of populations 21, 22, 24, and 25 are distinct, although not as dramatically so as in the first analysis. *Poa curtifolia* is now clearly separate. The other populations in the right-hand group overlap; the jackknife procedure[2]

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[2] A procedure whereby an OTU is removed from the data matrix and the discriminant functions are recalculated. The OTU is then entered into the new discriminant functions and is classified accordingly. This is done for each OTU in turn. If the group to which the OTU was initially assigned is discrete from the other groups, then the OTU will be reassigned to the group from which it came.

produces frequent misclassifications, suggesting little discrimination among them. Thus, in a procedure designed to maximize distances among populations, there are only three clear groups formed: *P. curtifolia,* large plants, and everything else.

The cloud of points in FIGURE 21 is roughly T-shaped, with the large plants forming a more or less diffuse tail. Virtually all discrimination is on the first canonical axis, which—like the first principal-component axis—represents size of vegetative parts. The variables with the highest F-values are the lengths of both basal and flag leaves. Removal of these from the analysis produces essentially the same picture, with the large plants now being distinguished on the basis of the short ligule. Because of the bias in the sample, these results are good evidence for the conclusions that panicle shape is not concordant with any other character, and that plants with open panicles do not form a discrete group. The same bias, however, means that this analysis does not provide good evidence for formal recognition of large plants with short ligules; large plants with long ligules were not included in the analysis. Thus, principal-component analyses give a weak argument for lumping these large plants with the rest of the complex, while discriminant analyses provide an equally weak argument for maintaining them as distinct. Other data on population structure and distribution give no rationale for recognizing them as a separate taxon.

OTHER CHARACTERS

Extensive analyses of gross morphology have shown that the *Poa secunda* complex is made up of only two taxa. This conclusion is supported by data on phenology, leaf anatomy, and ecology.

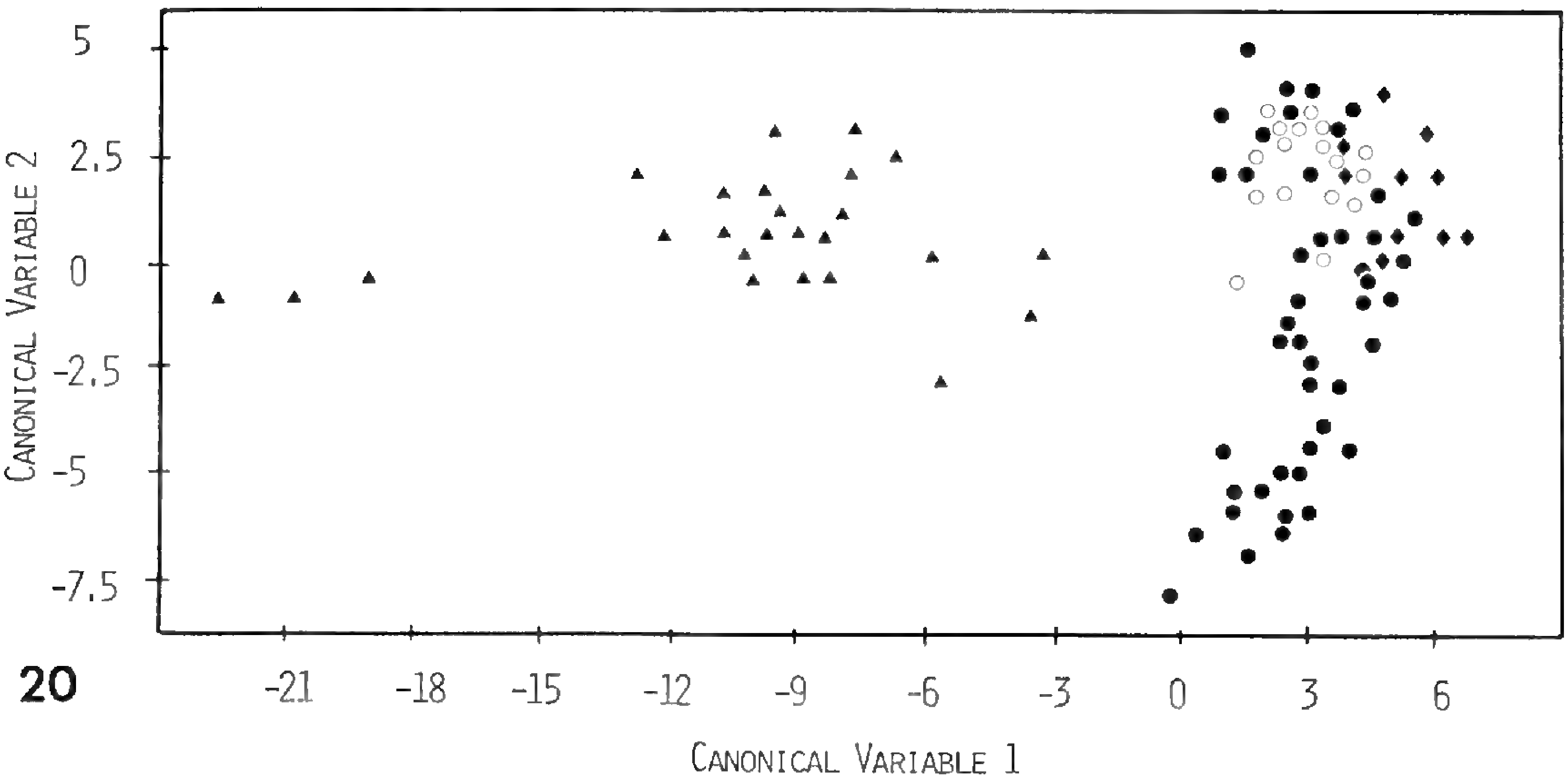
PHENOLOGY

Both C. L. Hitchcock and co-workers (1969) and Cronquist and colleagues (1977) have used phenology as a taxonomic character, separating species into those that bloom in April, May, or June vs. those that bloom in July or August. Date of blooming in the wild, however, appears to correlate more with altitude and habitat than with morphology: plants consistently bloom in the early part of the growing season and then become dormant.

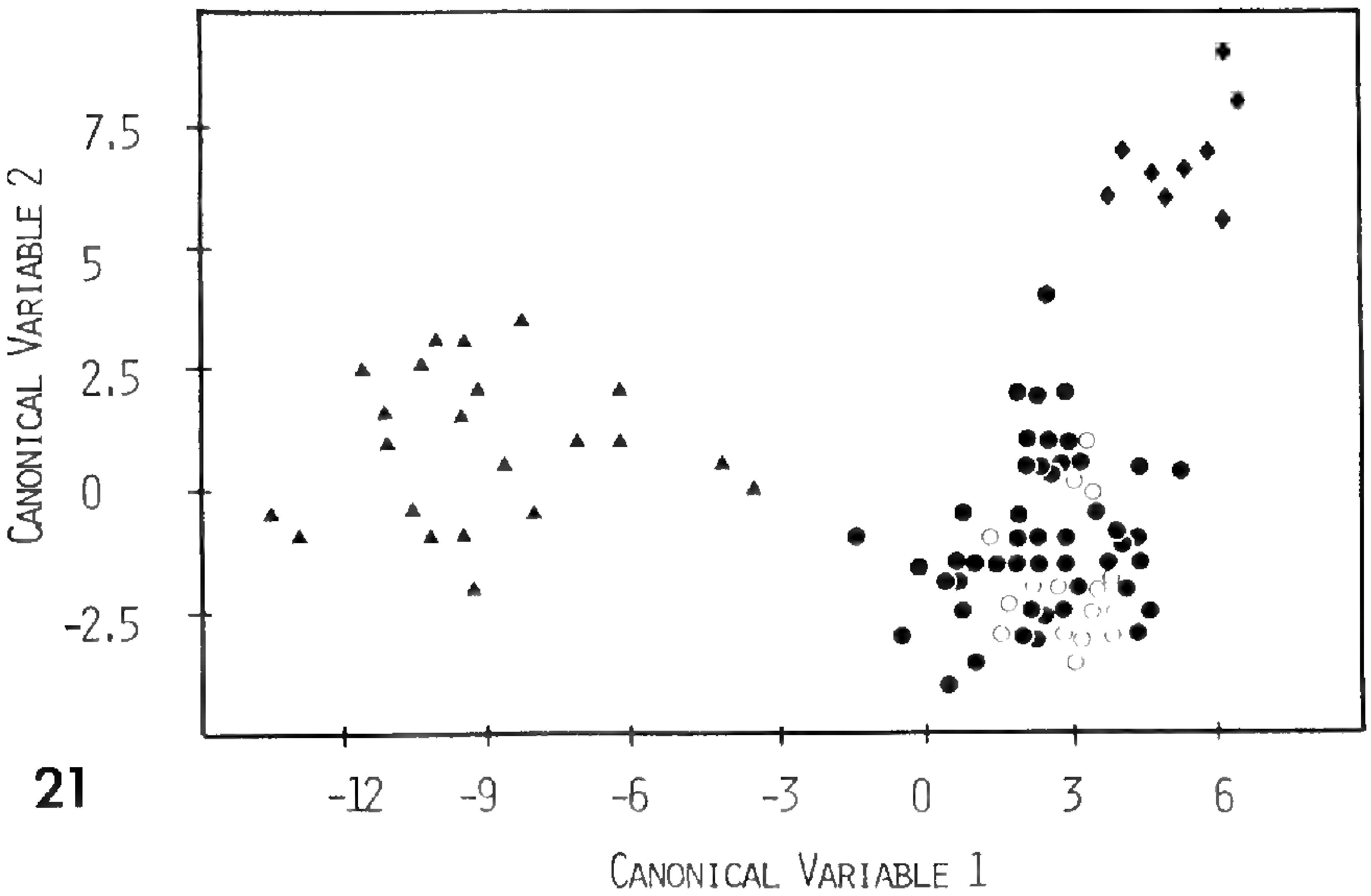
I followed marked plants in two natural populations near Moscow, Idaho, and observed two apparent peaks of blooming time, about three to five days apart, with each totaling about ten days. The early-blooming plants seemed to be somewhat smaller and to have smaller, narrower leaves than the later ones. Unfortunately, the numbers of plants observed were too small for any statistical tests of these observations.

Plants from a variety of provenances, when grown in the experimental garden, bloom within a period of 17 days; plants forced in the greenhouse bloom within four weeks of being brought indoors. Blooming time is thus not a good diagnostic character. In general, in both garden and greenhouse, specimens of *Poa curtifolia* are some of the earliest plants to reach anthesis, and the large plants that traditionally would have been assigned to *P. ampla* are among the latest.

20



21



FIGURES 20, 21. Discriminant analyses: 20, 18 characters and all plants listed in APPENDIX 2; 21, 18 characters and all plants listed in APPENDIX 2 except population 23 (diamonds = *Poa curtifolia,* open circles = open-panicled plants, triangles = large plants with short ligules, solid circles = all other plants).

If plants are assigned to Hitchcock's taxa and time to anthesis is compared among all taxa by analysis of variance, the earliest species is found to be significantly earlier than the latest. Because this represents the average time to anthesis, however, and because there is still considerable overlap among all the ranges, statistical significance may not indicate biological significance. The weak tendency for time of anthesis to correlate with plant size is shown in FIGURE 22.

ANATOMY

Cross sections of leaves show that members of the complex are anatomically variable (FIGURE 23). All plants have double bundle sheaths and a row of

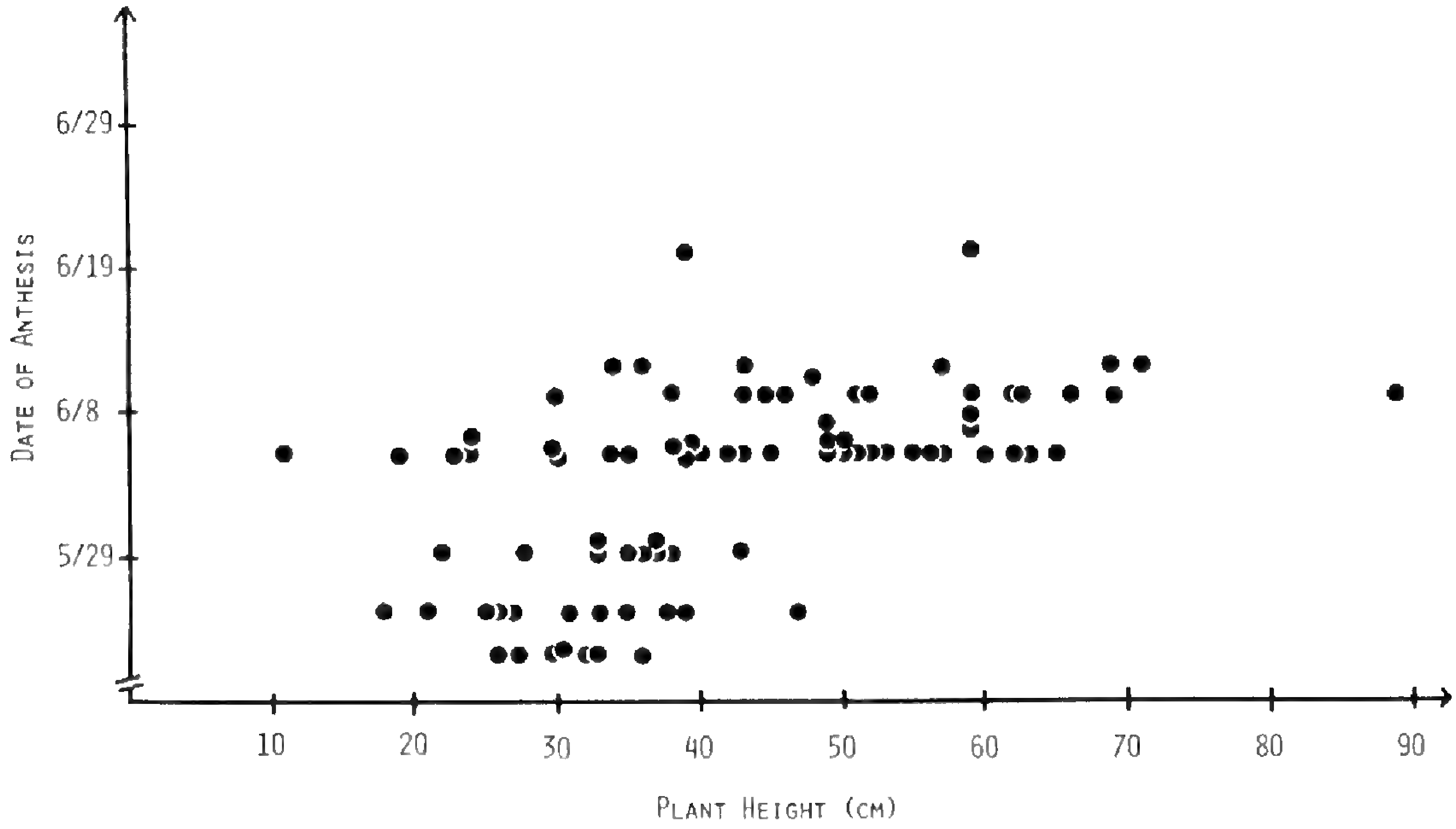


FIGURE 22. Bivariate plot of date of anthesis vs. plant height ($r = 0.45$).

bulliform cells on both sides of the midrib. Plants differ primarily in the amount of sclerenchyma and in the shape of the epidermal cells. Although many plants have the major vascular bundles fully embedded in sclerenchyma, others have sclerenchyma not connected to the vascular bundles, and some have the sclerenchymatous region reduced to only a few cells. The amount of sclerenchyma seems to correlate with the moisture level of the site, being much greater in plants grown on drier sites. Relative amount also varies when plants are moved from field to experimental garden, which also suggests environmental influence. The epidermal cells may be somewhat flattened in cross section, in which case there is generally a thick cuticle, or they may be more rounded and irregular with a thinner cuticle. In some plants the adaxial surface has rounded epidermal cells and the abaxial epidermis has flattened ones. Epidermal peels from a sample of 20 plants were all similar, with sinuous-sided silica bodies and parallel-sided subsidiary cells. Leaf anatomy thus conforms to the standard festucoid pattern (as described in Gould & Shaw, 1983), and the variation that occurs does not correlate with other characters.

SUBSTRATE

Members of the complex grow on a variety of substrates, generally on neutral to strongly alkaline soils, sometimes with high amounts of soluble salts. Plants

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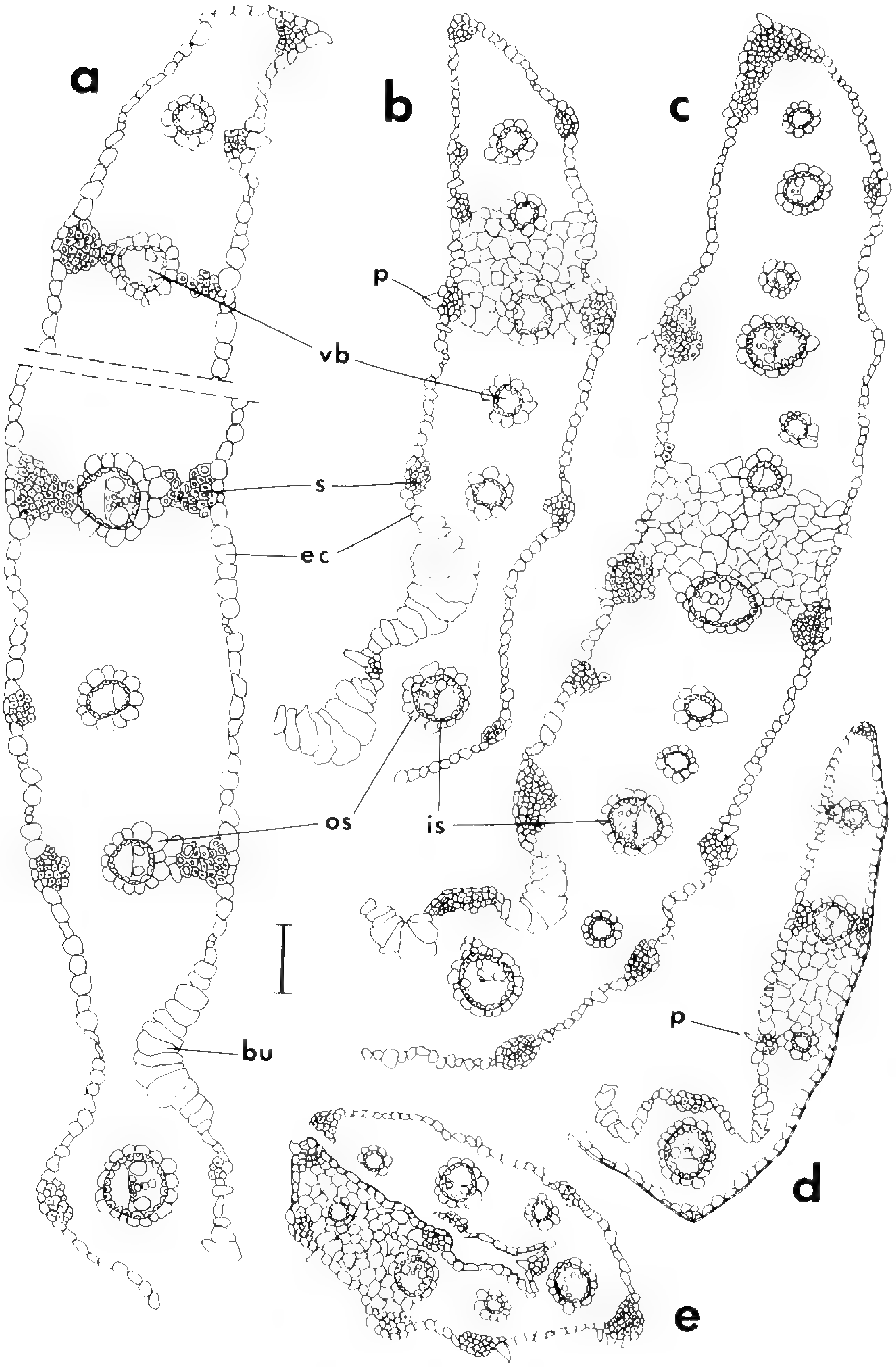
FIGURE 23. Cross sections of leaves showing range of variation in complex: a, *Kellogg 154* (Oregon; large plant with short ligules and nearly glabrous lemmas, greenhouse grown); b, *Kellogg 226* (central Idaho, open-panicled plant with long ligules, greenhouse grown); c, *Kellogg 227* (*Poa curtifolia*, central Washington); d, *Kellogg 263* (Oregon,



open-panicled plant with short ligules); e, *Kellogg 210* (Idaho, alpine plant with long ligules and pubescent lemmas). Scale = 0.1 mm; s = sclerenchyma; vb = vascular bundle; os = outer bundle sheath; is = inner (mestome) sheath; bu = bulliform cells; ec = epidermal cells; p = prickle hair.

with open panicles and short ligules occur only on the walls of wet, mossy gorges near Multnomah Falls above the Columbia River in Oregon; those with open panicles and long ligules are montane and usually grow in crevices in granite. Large, glaucous plants are often but not always found in apparently saline basins. These generalizations about ecology do not hold up to close inspection, however. To see if any edaphic characters correlated with morphology, I ran three multiple regressions of seven soil characteristics against basal-leaf length, ligule length, and lemma length (three characters shown by numerical taxonomy to be important in describing the total variation in the group). R^2 values are 0.092, 0.296, and 0.127, respectively, for all combinations of soil characters with the three morphological characters. Edaphic factors are thus taxonomically uninformative.

Poa curtifolia is the one exception, being restricted to serpentine soils in the Wenatchee Mountains of central Washington. Other members of the *P. secunda* complex are also found on serpentine soils, but they are not morphologically distinct.

REPRODUCTIVE BIOLOGY

The *Poa secunda* complex has long been known to be apomictic (Nygren, 1951), and apomixis has been widely used to explain morphological variability in the group. Early in my studies of the reproductive biology of the group, I developed a hypothesis, based on some sketchy preliminary data, that some of the more distinctive morphs (like the large, short-liguled plants) were more highly apomictic than the other members of the complex. This hypothesis not only proved to be wrong but also was based on a logical flaw that I will discuss briefly below.

Bagging experiments showed that pollen is necessary for seed set; apomixis, when it occurs, must be pseudogamous. All plants set seed when self-pollinated. From 2721 attempted crosses I produced 4 apparent hybrids; other offspring were morphologically indistinguishable from the maternal parent and so were presumed to be apomictic. The parents of the hybrids were very different morphologically. This suggests that if there are fertility barriers, they are not between forms that are highly morphologically differentiated. These results are confirmed by the much larger studies of Hiesey and Nobs (1982). Thus, sexual reproduction can and presumably does occur even between very different morphs.

To determine the extent of apomixis in individual plants, I cleared ovules in Herr's solution and observed them with Nomarski optics (see Kellogg, 1983; Greene, 1984). In each of 25 plants, I scored up to 50 ovules as being sexual or potentially apomictic. The percentage of apomictic ovules varied from 25 to 100. It varied as much as 40 percent among plants collected from the same locality, and percentages from the same plant in subsequent years are also quite different. Percent apomixis in parent plants did not correlate with that in the offspring. This variation in percent apomixis does not reflect variation in pollen stainability; although highly apomictic plants are usually mostly pollen sterile, pollen-fertile plants may exhibit any amount of apomixis. Like percent apomixis, percent pollen stainability varies widely with the environment. It is not correlated with regularity of meiosis.

Chromosome number is likewise variable. *Poa curtifolia* has $2n = 42$. Other members of the complex have numbers varying from $2n = 44$ to $2n = 106$ (Hartung, 1946). Many of the largest plants are 9-ploid, but some have higher or lower numbers, and not all 9-ploids are large. Thus, chromosome number is not associated with morphological variants.

Were they morphological characters, the aspects of reproductive biology that I have investigated would be ruled out as taxonomically unimportant. Some, such as interfertility, do not vary within the group. Others, such as percent apomixis and percent pollen stainability, are highly variable depending on the environment, but even if they were stable, they would be of no use in explaining the morphological variation since they do not correlate with any aspect of morphology. Because of this lack of correlation, there is no way in which I can conclude that the morphological complexities exist *because of* apomixis. My initial hypothesis of the unusual morphs being more highly apomictic than the more widespread ones has thus proved to be wrong, but even had it been correct, it would have been an inadequate explanation for the morphological variation. The only way apomixis can maintain a particular form is if it is obligate. If there is any recombination at all (and the production of a small number of hybrids suggests that there is), then the plants are effectively sexual in terms of their ability to generate variation. In the case of facultative apomixis, the process of recombination is slowed but by no means stopped (see discussions by Marshall & Weir, 1979, and Lynch & Gabriel, 1983).

DISCUSSION AND CONCLUSIONS

In general, my work suggests that much of the presently accepted taxonomy of the genus *Poa* is suspect. The amount of population-level variability in the *P. secunda* complex is not unique in the genus. The genus contains several widespread polymorphic taxa, including *P. pratensis, P. alpina, P. arctica,* and *P. glauca,* in which one to many species are commonly recognized. All include numerous entities that have been given specific status at some time in the past, and all are circumboreal, apomictic, and with aneuploid chromosome numbers suggesting some ancestral hybridization. Although characters that are variable in one part of the genus may still be taxonomically useful in another, such characters, once shown to be unreliable, should not be used blindly. Overreliance on one or a few gross morphological characters may have caused unnecessary splitting, producing artificial morphological entities rather than biological ones. Studies of other bluegrasses must consider the possibility that many traditionally used characters are unreliable. Lemma pubescence is heavily relied upon to separate species or sections throughout the genus. However, the amount of lemma pubescence often varies greatly within populations in *P. secunda* and among the offspring of a single self-pollinated plant; it also varies in populations of *P. curtifolia,* a narrowly endemic species. This character must thus be used carefully. Similarly, I have shown leaf folding to be controlled by soil moisture, yet a number of bluegrass species are distinguished by such features as folded or involute leaves. In other groups the value of this character can only be verified by common garden studies.

Included in the first multivariate analyses were several plants from species outside of the complex. On the basis of the characters used in the analyses, however, they did not appear distinct from other members of the group. This suggests that other taxa in the genus may prove, on closer examination, to be poorly delimited and, like the members of the *Poa secunda* complex, part of a continuum of variation.

Panicle shape has no taxonomic value in this complex. Plants with panicles that remain open after anthesis were formerly known as *Poa gracillima.* They often occur in granite outcrops, frequently at high altitude, in the northern Rocky Mountains and the Sierra Nevada, as well as in Chile (Arnow, 1981). The character state persists even in garden-grown plants. The preceding analyses have shown, however, that this character state does not correlate with any others. Open-panicled plants are shown by triangles in the scatter diagrams; it is obvious that they intergrade completely with other members of the complex on the basis of all characters but this one.

Several hybrids were produced in crosses of open-panicled plants with narrow-panicled ones. The F_1s had panicles that were narrow at the top, but the bottom two branches remained at an angle of about 30° to the rachis after anthesis. Such a plant would be classed by most taxonomists as having a narrow panicle, and its morphological intermediacy would probably go undetected. Thus, populations comprising plants with genes for both open and narrow panicles may not be recognized.

Poa curtifolia is morphologically distinct, based on the characters used in the numerical analyses. Not included, however, were the facts that it has thick, almost succulent leaves often with a prominently white margin, it is restricted to serpentine soils in the Wenatchee Mountains of Washington, and its chromosome number is $2n = 42$, with good pairing at meiosis. It should therefore continue to be recognized as a species distinct from the rest of the complex.

Many of the very largest plants are separated from the rest of the complex because of gaps in relative sizes of parts. These unusually large plants are geographically isolated from each other, with neither distinct ecological requirements nor a discrete range. I have never found them growing in pure stands. Either they grow with smaller members of the complex, or they occur as isolated plants in ditches or on cut-banks. What these forms represent biologically is still an unanswered question. Because sexual reproduction can and presumably does occur in the group (Kellogg, 1983), they may be simply unusual segregants that happen to be particularly vigorous on extreme sites. This contention is supported by the data presented under Results: among the offspring of a single self-pollinated plant, some had extreme values for certain characters. Unusually large plants may thus be produced fairly commonly.

In their most striking form these large plants, most of which would traditionally be put into *Poa ampla,* have short ligules, little lemma pubescence, and very glaucous foliage, but their most distinctive character is their long leaves. In FIGURE 3, which represents a univariate display of basal-leaf length, there is a break at about 20 cm separating the large plants. The histogram for this character (FIGURE 13C), however, shows little reason to define groups in this way. Also, the histogram in FIGURE 12C shows that the offspring of a single self-pollinated plant vary across the apparent break. Increasing the sample size obscures even the univariate pattern.

Some taxonomists might still prefer formal recognition of these plants at the varietal level at least. Such plants are most valuable as forage grasses, which sets them apart from the other members of the complex that are largely ignored by cattle. Cattle graze by wrapping their tongues around the leaves of the plants they eat and so prefer plants with long basal leaves. Cows can therefore "recognize" *Poa ampla* as distinct from the rest of *P. secunda* because of the leaf length, a character with a nearly continuous distribution. Formal recognition of *P. ampla* would thus be arbitrarily dividing the continuum of basal-leaf length so as to create a special-purpose classification reflecting the mouthparts of cattle. Continuity of variation makes it unjustifiable to recognize these forms taxonomically.

The *Poa secunda* complex is made up of many fewer taxa than previously described. In this study I have defined a species as a group of plants with similar morphology and with no obvious morphological gaps in sets of concordant characters. Only *P. secunda* and *P. curtifolia* adequately fit this definition. Such taxa as *P. sandbergii, P. canbyi, P. scabrella,* and *P. incurva* can be confidently placed in synonymy. The characters on which they were based either vary at the level of the clone or population or are almost completely under environmental control. Furthermore, no other characters were found that distinguish groups within this part of the complex. The search for taxonomically useful patterns in *P. secunda* has shown that no characters are concordant—i.e., that no characters define nonoverlapping sets of plants. In other words, a species is a cluster of points in taxonomic hyperspace, where the dimensions of the space are broadly defined to be any set of characters; in this case the characters are predominantly morphological ones. *Poa secunda* can be described as a sort of minimal species; at the very least we can make generalizations of the form "plants with character X will also have character Y." This is the rationale for not considering *P. gracillima* as a separate species even though it can be discriminated on the single axis representing open vs. closed panicles. Knowing that the plants have open panicles still does not allow even very trivial generalizations.

Such a conclusion also means that, at our current level of knowledge, we can make no claims about evolution within *Poa secunda.* Because there are no characters that can serve as evolutionary "markers," we cannot evaluate the various processes that might have generated the pattern. Hypotheses of fusion of disparate lineages by hybridization, although appealing, are merely plausible suggestions, not subject to test. The roles of polyploidy and apomixis cannot be evaluated. The pattern of variation, in other words, does not illuminate the historical pattern of microevolutionary processes.

FIGURE 24. *Poa curtifolia* and *P. secunda*. a, *P. curtifolia,* habit (*Kellogg 227*), × 0.35. b–m, *Poa secunda*. b, habit (*Kellogg 56*), × 0.35. c–f, variation in lemma size and pubescence, all × 3.5: c, *Stevens 1208* (DAO); d, *Hitchcock 11301* (US); e, *Ward 488* (US); f, *Maguire 13874* (DAO). g, open panicle (*Kellogg 226*), × 0.35. h–m, variation in ligule size and shape, all × 3.5: h, *Kellogg 214*; i, *Kellogg 114*; j, *Kellogg 222*; k, *Kellogg 36*; 1, *Kellogg 274*; m, *Kellogg 101*. Complete specimen citation in APPENDIX 1.

Poa secunda has been delimited on phenetic, not cladistic, grounds. Although it can be distinguished from other members of the genus by a combination of characters, there is no reason to believe that any of these characters is uniquely derived. As noted at the outset, the only possible apomorphies for the group are shape of the spikelet and length of the first rachilla internode, and even these are not unique to *P. secunda.* Other characters, such as caespitose habit and perfect flowers, may be plesiomorphic and therefore not indicative of phylogenetic relationship. Still others, such as lack of a lemma web, may be either plesiomorphic or convergent. The group is thus not demonstrably monophyletic *sensu* Hennig; monophyly could only be determined in the context of a phylogeny for the entire genus. Quite possibly other species should be included in a group united by long spikelets and rachilla internodes; *P. secunda* may thus be paraphyletic. To try to define a species within the complex as the smallest strictly monophyletic unit (see Mishler & Donoghue, 1982) seems unworkable, given the distribution of characters. The basic model of cladistics does not apply to hybridizing groups; the apomorphies of the parental lines become hopelessly blended, lineages cannot be identified, and the application of concepts of strict monophyly seems inappropriate. The definition I have used for a species, therefore, not only prevents analysis of evolution within *P. secunda,* but also analysis of evolution between *P. secunda* and other parts of the genus.

I have thus chosen to recognize formally only morphological units within which all characters vary and covary continuously. There are no gaps in the distribution of the characters, and most are uncorrelated. Such units do not reflect anything about phylogeny. Given the current state of classification and knowledge of characters in *Poa,* such a species concept may be the only one that can be applied with any consistency.

The foregoing points all lead to the conclusion that there is only one defensible taxonomic treatment for the group: to recognize *Poa curtifolia* and to include everything else in *P. secunda.* Variation in many characters is indeed complex, both at the level of the species (*P. secunda*) and also apparently at other levels. To impose any taxonomic structure would obscure, rather than illuminate, the pattern.

TAXONOMIC TREATMENT

Poa curtifolia Scribner, Circ. U. S. Div. Agrost. **16:** 3. 1899. TYPE: Washington, Kittitas Co., Cascades, Mt. Stuart, Aug. 1878, *Elmer 1148* (holotype, US!). FIGURE 24a.

Plants 2–5 dm, caespitose to short-rhizomatous, glaucous; branching intravaginal; culms 0.5–0.8 mm thick below inflorescences, sometimes becoming red with age. Basal leaves 3–8 cm × 0.5–2.5 mm, the blades extending almost at right angles from sheath, flat, more or less fleshy, with prominent white marginal vein, scabrous on margin only. Flag leaves 0.5–2 cm × 0.2–2.6 mm, borne well below midpoints of culms. Sheaths open, glabrous. Ligules 2–6 mm, acute to acuminate, strongly decurrent, entire, sparsely scabrous abaxially. Panicles narrow, 5–10 cm, spreading at anthesis, branches 2 to 4 per node; spikelets 2- to 5-flowered, 7–10.5 mm, generally at least 4 times as long as wide except at anthesis, more or less terete; glumes somewhat unequal (first 3.8–5.5 × 1.4–1.9 mm, second 4.5–6.7 × 1.8–2.3 mm), acute, 3-nerved, scabrous on upper ⅓–½ of keel; lemmas 4.6–6.6 mm, rounded, acute, with erose upper margin, 5-nerved, glabrous to pubescent along lower ⅓ of keel and marginal nerves, hairs to 0.3 mm; paleas 4–5.8 mm, slightly shorter than lemmas, glabrous; rachilla internodes 0.9–1.9 mm, glabrous; anthers 2.5–4.2 mm, yellow; lodicules 0.6–1.1 mm. Chromosome number $2n = 42$.

DISTRIBUTION. Wenatchee Mountains, central Washington; serpentine soils.

REPRESENTATIVE SPECIMENS. See APPENDIXES 1 and 2.

Poa secunda Presl, Reliq. Haenk. **1:** 271. 1830; not Roemer & Schultes, Syst. Veg. **2:** 697. 1817, *nomen nudum.* TYPE: ex Cordille[r]a de "Chili," 1790, *Haenke* (holotype, PR!; isotypes, GH!, MO). FIGURE 24b–m.

Aira brevifolia Pursh, Fl. Amer. Sept. **1:** 76. 1814. *Airopsis brevifolia* (Pursh) Roemer & Schultes, Syst. Veg. **2:** 578. 1817; not *Poa brevifolia* DC. 1806. TYPE: in the plains of Missouri, *M. Lewis s.n.* (PH). The specimen in the Lewis and Clark herbarium at PH bears the label: "The most common grass through the plains of Columbia R. 10 June 1806." It is probably therefore not the holotype.

Sclerochloa californica Munro ex Bentham, Pl. Hartweg. 342. 1857, *nomen nudum. Atropis californica* Munro ex Thurber *in* S. Watson, Bot. Calif. **2:** 309. 1880; *Eragrostis fendleri* Steudel and *Poa andina* Nutt. as synonyms. *Poa californica* (Munro ex Thurber) J. M. Coulter, Manual Bot. Rocky Mtn. Region, 420. 1885; not Steudel, 1854. SYNTYPES: California, San Francisco, *Bolander s.n.*; California, ["in valle Sacremento,"] *Hartweg 2035* (GH!).

Poa tenuifolia Buckley, Proc. Acad. Nat. Sci. Philadelphia, **1862:** 96. 1863; not A. Rich. 1851. *Poa buckleyana* Nash, Bull. Torrey Bot. Club **22:** 465, *nomen novum. Atropis tenuifolia* (Buckley) Thurber *in* S. Watson, Bot. Calif. **2:** 310. 1880. *Panicularia nuttaliana* Kuntze, Rev. Gen. Pl. **2:** 783. 1891. TYPE: Columbia R., *Nuttall s.n.* (holotype, PH!; isotypes, GH!, NY!).

Poa tenuifolia Nutt. ex S. Watson *in* King, Rep. Geol. Expl. 40th Parallel **5:** 387. 1871; neither A. Rich. 1851, nor Buckley, 1863. SYNTYPES: Nevada, E. Humboldt Mtns., alt. 8000 ft, Aug. 1868, and Diamond Mtns., alt. 6500 ft, July 1868, *Watson 1318* (GH!, NY!, US!; specimens mounted together, lectotypification not attempted here). Also numbered *1318*: Nevada, Virginia Mtns., alt. 6000 ft, Aug. 1867 (GH!, US!); Nevada, Pah-Ute Mtns., alt. 5000 ft, June 1868 (GH!, US!).

Poa tenuifolia Nutt. ex S. Watson var. *elongata* Vasey *in* Rothrock *in* Wheeler, Rep. U. S. Geogr. Survey W. 100th Meridian **6:** 290. 1878. *Poa buckleyana* Nash var. *elongata* (Vasey) M. E. Jones, Contr. W. Bot. **14:** 14. 1912. TYPE: Colorado, Twin Lakes, 1873, *Wolf 1141* (holotype, US!).

Poa tenuifolia Nutt. ex S. Watson var. *rigida* Vasey *in* Rothrock *in* Wheeler, Rep. U. S. Geogr. Survey W. 100th Meridian **6:** 290. 1878, *nomen nudum.*

Poa andina Nutt. ex S. Watson *in* King, Rep. Geol. Expl. 40th Parallel **5:** 387. 1897; not Trin. 1835–36. TYPE: Colorado, Trinity Mtns., alt. 5000 ft, May 1868, *Watson 1319* (holotype, US!; isotype, NY!). Also numbered *1319*: Colorado, E. & W. Humboldt Mtns. (NY!); Nevada, Clover Mtns. (NY!, US!).

Poa andina Nutt. ex S. Watson var. *spicata* Vasey *in* Rothrock *in* Wheeler, Rep. U. S. Geogr. Survey W. 100th Meridian **6:** 290. 1878. SYNTYPES: Colorado, 1873, *Wolf 1135, 1136, 1137* (US, not seen).

Poa andina Nutt. ex S. Watson var. *major* Vasey *in* Rothrock *in* Wheeler, Rep. U. S. Geogr. Survey W. 100th Meridian **6:** 290. 1878. SYNTYPES: Arizona, 1872, *Wolf 1133* (US, not seen); Colorado, 1873, *Wolf 1134* (US, not seen).

Atropis pauciflora Thurber *in* S. Watson, Bot. Calif. **2:** 310. 1880. *Poa pauciflora* (Thurber) Bentham ex Vasey, Grasses U. S. 42. 1883; not Roemer & Schultes, 1817. *Panicularia thurberiana* Kuntze, Rev. Gen. Pl. **2:** 783. 1891, *nomen illegit. Poa thurberiana* (Kuntze) Vasey, U. S. D. A. Div. Bot. Bull. **13:** *pl. 84.* 1893, *nomen illegit.* Type: California, Sierra Valley, 1871, *Lemmon s.n.* (holotype, NY!).

Atropis scabrella Thurber *in* S. Watson, Bot. Calif. **2:** 310. 1880. *Poa scabrella* (Thurber) Bentham ex Vasey, Grasses U. S. 42. 1883. *Panicularia scabrella* (Thurber) Kuntze, Rev. Gen. Pl. **2:** 783. 1891. *Puccinellia scabrella* (Thurber) Ponert, Feddes Repert. **84:** 740. 1974. Type: California, Oakland, *Bolander s.n.* (holotype, NY!).

Poa nevadensis Vasey ex Scribner, Bull. Torrey Bot. Club **10:** 66. 1883. *Atropis nevadensis* (Vasey ex Scribner) Beal, Grasses N. Amer. **2:** 577. 1896. *Puccinellia nevadensis* (Vasey ex Scribner) Ponert, Feddes Repert. **84:** 740. 1974. Type: S. Utah, N. Arizona, etc., 1877, *Palmer 474* (NY!). The label data on the specimen at NY agree with those originally cited, and this is an isotype. However, the specimen at US, "Austin, Nevada, M. E. Jones 1882," is sometimes cited as the type. It bears the following note signed "AC [Agnes Chase] Aug. 1951": "Specimen in Nat. Herb. named 'Poa nevadensis Vasey' *in Vasey script* is 'Austin Nevada ME Jones 1882.' Since Vasey is given as author by Scribner his specimen was taken as type by ASH."

Poa tenuifolia Nutt. ex S. Watson var. *scabra* Vasey ex Scribner, Bull. Torrey Bot. Club **10:** 66. 1883, *nomen nudum.*

Glyceria canbyi Scribner, Bull. Torrey Bot. Club **10:** 77. *figs. 1–4.* 1883. *Atropis canbyi* (Scribner) Beal, Grasses N. Amer. **2:** 580. 1896. *Poa canbyi* (Scribner) Howell, Fl. NW. Amer. **1:** 764. 1903. *Puccinellia canbyi* (Scribner) Ponert, Feddes Repert. **84:** 739. 1974. Type: Cascade Mtns., Washington Terr., Aug. 1882, *Tweedy & Brandegee s.n.* (holotype, US?, not seen).

Poa orcuttiana Vasey, W. Amer. Sci. **3:** 165. 1887. Type: California, near San Diego, Chollas Valley, 26 May 1884, *Orcutt 1070* (holotype, US!).

Poa filifolia Vasey, Contr. U. S. Natl. Herb. **1:** 271. 1893. Type: Idaho, Nez Perce Co., on rocky banks of Hatwai Creek, 1892, *Sandberg 138* (holotype, US?, not seen; isotypes, GH!, NY!, PH!).

Poa gracillima Vasey, Contr. U. S. Natl. Herb. **1:** 272. 1893; not Rendle, 1904. *Poa gracillima* Vasey, Grasses U. S. 42. 1883, *nomen nudum.* Type: Washington Terr., Mt. Paddo, *Suksdorf s.n.* (holotype, US!; isotypes, NY!, PH!).

Festuca spaniantha Philippi, Anal. Univ. Chile **94:** 174. 1896. Type: *sine loco, Anonymous s.n.* (SGO, not seen, *fide* Arnow, Syst. Bot. **6:** 418. 1981).

Festuca patagonica Philippi, Anal. Univ. Chile **94:** 174. 1896. Type: [Chile,] ad lacuna Pinto in Patagonia australi, *Ibar s.n.* (SGO, not seen, *fide* Piper, Proc. Biol. Soc. Wash. **18:** 147. 1905).

Poa laevis Vasey, Contr. U. S. Natl. Herb. **1:** 273. 1893; neither Borbás, 1877, nor R. Br. 1810. *Atropis laevis* (Vasey) Beal, Grasses N. Amer. **2:** 577. 1896. *Puccinellia laevis* (Vasey) Ponert, Feddes Repert. **84:** 739. 1974. Type: Montana, North Fork Smith R., 19 July 1883, *Scribner s.n.* (holotype, US!; isotype, NY!).

Poa laevigata Scribner, Bull. U. S. Div. Agrost. **5:** 31. 1897. *Poa nevadensis* var. *laevigata* (Scribner) M. E. Jones, Contr. W. Bot. **14:** 14. 1912. Type: Wyoming, Green R., 25 June 1896, *Scribner 2039* (holotype, US?, not seen).

Atropis laevis (Vasey) Beal var. *rigida* Beal, Grasses N. Amer. **2:** 578. 1896. Type: Utah, Lake Point, 19 July 1879, *M. Jones 1021* (holotype, MSC!).

Poa lucida Vasey, Contr. U. S. Natl. Herb. **1:** 274. 1893. Type: Colorado, on mountain sides near Georgetown, [Clear Creek Co.,] 3 July 1885, *Patterson 73* (holotype, US!). At PH are two specimens bearing the same number collected at Georgetown, Colorado, 18 July 1892.

Poa sandbergii Vasey, Contr. U. S. Natl. Herb. **1:** 276. 1893. *Poa buckleyana* var. *sandbergii* (Vasey) M. E. Jones, Contr. W. Bot. **14:** 14. 1912. *Paneion sandbergii*

(Vasey) Lunell, Amer. Midl. Naturalist **4:** 223. 1915. TYPE: Idaho, near Lewiston, 1892, *Sandberg 164* (holotype, US!; isotypes, GH!, NY!).

Atropis tenuifolia (Buckley) Thurber var. *stenophylla* Vasey ex Beal, Grasses N. Amer. **2:** 580. 1896 (as *stenophyla*). *Poa buckleyana* var. *stenophylla* (Vasey) M. E. Jones, Contr. W. Bot. **14:** 14. 1912. TYPE: Oregon, 1887, *Howell s.n.* (not seen).

Poa capillaris Scribner, Bull. U. S. Div. Agrost. **11:** 51. *fig. 11.* 1898; not L. 1753. *Poa nudata* Scribner, Circ. U. S. Div. Agrost. **9:** 1. 1898, *nomen novum.* TYPE: California, Portero, 9 April 1892, *Anonymous s.n.* (holotype, US!).

Poa juncifolia Scribner, Bull. U. S. Div. Agrost. **11:** 52. *pl. VIII.* 1898. *Poa fendleriana* var. *juncifolia* (Scribner) M. E. Jones, Contr. W. Bot. **14:** 14. 1912. TYPE: Wyoming, Sweetwater Co., Black Rock Springs, Point of Rocks, 13 July 1897, *Nelson 3721* (holotype, US!; isotypes, GH!, NY!).

Poa wyomingensis Scribner ex Pammel, Proc. Davenport Acad. Nat. Sci. **7:** 242. 1899. TYPE: Wyoming, Sheridan Co., Big Horn, July 1897, *Pammel 192* (holotype, US!).

Poa saxatilis Scribner & Williams, Circ. U. S. Div. Agrost. **9:** 1. 1899. *Poa gracillima* Vasey var. *saxatilis* (Scribner & Williams) Hackel, Allg. Bot. Zeitschr. **21:** 79. 1915. TYPE: Washington, Mt. Rainier, on rock cliffs, alt. 7000 ft, Aug. 1895, *Piper 1964* (holotype, US!).

Poa leckenbyi Scribner, Circ. U. S. Div. Agrost. **9:** 2. 1899. *Poa nevadensis* Vasey ex Scribner var. *leckenbyi* (Scribner) M. E. Jones, Contr. W. Bot. **14:** 14. 1912. TYPE: Washington, Klickitat Co., Scott, 5 June 1898, *Leckenby s.n.* (holotype, US!).

Poa acutiglumis Scribner, Circ. U. S. Div. Agrost. **9:** 4. 1899. TYPE: Oregon, Grave Creek, 21 May 1884, *Howell s.n.* (holotype, US!; isotype, GH!).

Poa tenerrima Scribner, Circ. U. S. Div. Agrost. **9:** 4. 1899. TYPE: ex Calif. Acad. Sci. Herb. 26, *sine loco, Anonymous s.n.* (holotype, US!).

Poa limosa Scribner & Williams, Circ. U. S. Div. Agrost. **9:** 5. 1899. TYPE: California, Mono Lake, 1866, *Bolander s.n.* (holotype, US!).

Poa invaginata Scribner & Williams, Circ. U. S. Div. Agrost. **9:** 6. 1899. TYPE: [California,] Sierra Nevada, Summit Camp, 10 July 1870, *Scribner 20* (holotype, US!).

Poa incurva Scribner & Williams, Circ. U. S. Div. Agrost. **9:** 6. 1899. TYPE: Washington, Olympic Natl. Park, moraine of Duckaboose Glacier, alt. 7000 ft, Aug. 1895, *Piper 1989* (holotype, US!).

Poa ampla Merr. Rhodora **4:** 145. 1902. TYPE: Washington, Steptoe, 3 July 1901, *Vasey 3009* (holotype, US!).

Poa laeviculmis Williams, Bot. Gaz. (Crawfordsville) **36:** 55. 1903. TYPE: Washington, Steptoe, 25 June 1900, *Vasey 3026* (holotype, US!; isotype, NY!).

Poa confusa Rydb. Bull. Torrey Bot. Club **32:** 607. 1905. TYPE: Wyoming, Albany Co., Medicine Bow Mtns., 28 July 1900, *Nelson 7787* (holotype, NY!; isotype, US!).

Poa truncata Rydb. Bull. Torrey Bot. Club **32:** 607. 1905. TYPE: Colorado, Summit Co., Dillon, 26 Aug. 1896, *Clements 373* (holotype, NY!; isotype, GH!).

Sporobolus bolanderi Vasey, Bot. Gaz. (Crawfordsville) **11:** 337. 1886; not *Poa bolanderi* Vasey, 1882. TYPE: Oregon, Multnomah Falls, *Bolander s.n.* (holotype, US?, not seen; isotype, GH!).

Poa multnomae Piper, Bull. Torrey Bot. Club **32:** 435. 1905. *Poa gracillima* var. *multnomae* (Piper) C. Hitchc. Vasc. Pls. Pacific Northw. **1:** 661. 1969. TYPE: Oregon, Multnomah Falls, 25 June 1904, *Piper 6459* (holotype, US!; isotype, NY!).

Poa alcea Piper, Bull. Torrey Bot. Club **32:** 436. 1905. TYPE: Oregon, on Elk Rock near Portland, 3 June 1904, *Piper 6463* (holotype, US!; isotype, NY!).

Poa brachyglossa Piper, Proc. Biol. Soc. Wash. **18:** 145. 1905. TYPE: Washington, Douglas Co., alt. 1300 ft, 22 June 1893, *Sandberg & Leiberg 267* (holotype, US!; isotype, NY!).

Poa helleri Rydb. Bull. Torrey Bot. Club **36:** 534. 1909. TYPE: Idaho, Nez Perce Co., Lake Waha, alt. 2000–3500 ft, 20 June 1896, *Heller & Heller 3274* (holotype, US!; isotypes, DS!, NY!).

Poa englishii St. John & Hardin, Mazama **11:** 64. 1929. TYPE: Washington, Whatcom Co., Mt. Baker Natl. Forest, Bagley Lake, 14 Aug. 1928, *Hardin & English 1391* (holotype, WSU!; isotype, US!).

Poa juncifolia Scribner subsp. *porteri* Keck ex Porter, Fl. Wyoming **3:** 24. 1964. TYPE: Wyoming, Albany Co., Pole Mtn. region, 6 July 1943, *Porter 3249* (holotype, NY!; isotypes, CI, RM).

Plants caespitose, 1.5–11 dm, sometimes glaucous, frequently becoming red later in season; branching intravaginal; culms 0.3–1.4 mm thick just below inflorescence. Basal leaves 3–80 cm × 0.4–3(–4) mm, usually much shorter than culms, sometimes so narrow as to appear involute, flat or becoming folded on drying, tip often drying early, scabrous on abaxial midvein and usually on margin (especially near tip), occasionally scabrous throughout. Flag leaves 0.2–22 cm × 0.4–4 mm, borne near midpoints of culms. Sheaths open, or closed only ca. ⅛ of length, glabrous or scabrous on margin or throughout. Ligules 0.5–6.5 mm, occasionally obtuse to truncate to more often acuminate, decurrent, entire, becoming erose or laciniate with age, generally sparsely scabrous abaxially. Panicles narrow, 2–27 cm, spreading at anthesis (and remaining open in some plants), the branches 2 to 8 per node, most commonly 3 or 4, some floriferous only near tip, others nearly to base; spikelets 1- to 6-flowered, 3.5–12 mm, generally 4 times as long as wide except at anthesis, more or less terete; glumes somewhat unequal (first 2–5 × 0.7–1.8 mm, second 2.5–6 × 1–2.3 mm), acute, more or less erose at margins, 3- (to 5-)nerved, scabrous on upper ⅓–½ of keel, sometimes also scabrous next to keel; lemmas 2.9–6.1 mm, not conspicuously keeled, acute at apex, with erose upper margin, 5-nerved, scabrous throughout, entirely glabrous, or pubescent up to ⅔ of lower part of lemma, with hairs evenly distributed or extending higher on keel and marginal nerves, to 0.3 mm long, then scabrous above; calluses often with tuft of hairs; paleas 2.5–5.6 mm, equaling or slightly shorter than lemmas, scabrous to pubescent the length of marginal nerves, glabrous to scabrous or pubescent between nerves; rachilla internodes 0.6–1.9 mm, often remaining attached to floret below, glabrous to scabrous or pubescent; anthers 1–3.8 mm, yellow or purple or both; lodicules 0.3–1 mm. Chromosome number $2n = 44$, 56, 61–66, 68, 70–72, 78, 81–106.

DISTRIBUTION AND ECOLOGY. *Poa secunda* is distributed throughout western North America from the Yukon to northern Mexico, and it extends eastward across the northern Great Plains to a few isolated populations north of the Great Lakes and on the Gaspé Peninsula (MAP 1). In addition, there are several disjunct populations in Chile; these are described in detail by Arnow (1981). The Gaspé representatives of *P. secunda* occur in isolated populations on limestone outcrops and seem not to colonize all available habitats. These populations are small (generally fewer than 50 plants), and seed set and plant vigor appear to be low.

The members of the complex grow on a variety of substrates—generally neutral to strongly alkaline soils, which sometimes contain high amounts of soluble salts. Plants with open panicles and short ligules occur only on the walls of wet, mossy gorges near Multnomah Falls above the Columbia River in Oregon. Those with open panicles but long, acuminate ligules are montane and are found most frequently in crevices in granite. Large, glaucous plants are often found in saline basins, although they are by no means restricted to such areas. The remaining forms in the complex are widespread from sea level to alpine areas up to 4000 m, growing on sites that dry out early in the season. Blooming time is early in the growing season, varying from April to July depending on latitude and altitude.

REPRESENTATIVE SPECIMENS. See APPENDIXES 1 and 2. A full list of specimens examined is on file in the library of the Arnold Arboretum and Gray Herbarium.

NOMINA EXCLUDENDA

These names have been included in the *Poa secunda* complex by some previous workers, but the affinities of the plants to which they refer appear to lie elsewhere for the reasons cited.

Poa cottonii Piper, Proc. Biol. Soc. Wash. **18:** 146. 1905, as *cottoni*. TYPE: Washington, Yakima Co., Rattlesnake Mtns., 7 May 1902, *Cotton 557* (holotype, US!; isotype, NY!). Excluded because the spikelets are large relative to the size of the plant, making it look more similar to *P. cusickii* (for a discussion of which, see introduction).

Poa macroclada Rydb. Bull. Torrey Bot. Club **32:** 604. 1905. TYPE: Colorado, Gunnison Watershed, Roger's, elev. 9000 ft, 14 Aug. 1901, *Baker 802* (holotype, NY!). Excluded because of the small spikelets and the diffuse panicle that suggest affinities with *P. interior*.

Poa fibrata Swallen, J. Wash. Acad. Sci. **30:** 210. 1940. TYPE: California, Siskiyou Co., 3 mi S of Grenada, Shasta Valley, alt. 2600 ft, 30 June 1935, *Wheeler 3629* (holotype, US!; isotype, NY!). Excluded because of extravaginal branching.

Poa napensis Beetle, Leafl. West. Bot. **4:** 289. 1946. TYPE: California, Napa Co., 2 mi N of Calistoga at Myrtledale Hot Springs, 7 May 1946, *Beetle 4256* (holotype, UC!; isotype, NY!). Excluded because of the unusually short rachilla internodes and the more nearly ovate glumes.

ACKNOWLEDGMENTS

For direction and criticism of this work, I thank M. J. Donoghue, C. W. Greene, D. M. Henderson, P. F. Stevens, E. L. Taylor, and C. E. Wood. For help with illustrations, many thanks are due to A. C. Kellogg. This study formed part of a doctoral dissertation submitted to the Department of Organismic and Evolutionary Biology, Harvard University, and was supported in part by a National Science Foundation Dissertation Improvement Grant. Specimens were kindly loaned by CAS, DAO, KANU, and US. Thanks are also extended to A. J. Gilmartin and J. Davis for their detailed comments on the manuscript, and to C. S. Campbell and L. Wagner for their critical reviews.

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APPENDIX 1. **Specimens measured for evaluation of morphological variation using principal-component analyses.**

Canada. YUKON TERRITORY: vic. of Mackintosh (mi 1022, Alaska Hwy.), *Schofield & Crum 7475* (DS); Canol Rd., mi 95, Upper Rose R. valley, elev. 3600 ft, *Porsild & Breitung 10345* (GH). BRITISH COLUMBIA: Allies Mine, Tranquille, 4000 ft, *Dominion Range Exp. Sta. 86* (US); on ridges between Baldy Mtn. and Dunn Peak ca. 7 mi ENE of Littlefort, ca. 51°27′N, 120°03′W, ca. 7000 ft, *Calder, Parmelee, & Taylor 19911B* (DAO); Vancouver Is., Esquimault, *Macoun 71* (US). NORTHWEST TERRITORIES: Mackenzie Distr., N. of Brintnell L. Camp, alt. 3500 ft, *Raup & Soper 9668* (A); Mackenzie Distr., Slave R. lowlands on E side of Slave R., NE Ann's prairie, 60°46′N, 112°44′W, *Reynolds 27* (DAO). ALBERTA: Waterton Lakes Natl. Park, Mt. Crandell, elev. 7500 ft, *Breitung 17405* (US); Webster Twp., Manyberries, *Campbell 85B* (DAO); Beaverlodge, Truax Farm, E of town, *Barkworth 1460* (DAO). MANITOBA: Medora, *Dore 11067* (DAO); Brandon, *Stevenson F121* (DAO). SASKATCHEWAN: Regina, *Shevkenek 15* (DAO); Watman, *Groh s.n.* (DAO). ONTARIO: Flowerpot Is., *Barkworth 2001* (DAO). QUÉBEC: Gaspé Co., stony summit of Mt. Ste. Anne, Percé, *Pease 36592* (GH); Rimouski Co., Pointe aux Corbeaux to Cap Caribou, Bic, *Fernald & Collins 899* (GH).

United States. ALASKA: Juneau, *Hitchcock 4072* (US);* Skagway, *Hitchcock 4206* (US). WASHINGTON: Chelan Co., alpine crest of Three Brothers Peak, 7000 ft, *Thompson 12625*

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*Not a member of the *Poa secunda* complex. Eliminated from most analyses.

†*Poa curtifolia.*

(US);† Cowlitz Co., wet cliffs near Smelt Landing, *Thompson 12729* (GH); Kittitas Co., ¾ mi above Teanaway R. (N Fork) on trail to Ingalls Lake, *Kruckeberg 5037* (CAS);† Kittitas Co., Mt. Stuart region, 5000 ft, *Thompson 7813* (US),† *Thompson 7820* (US);† Kittitas Co., open talus slopes at head of Beverly Creek, 5000 ft, *Thompson 9511* (DS);† Kittitas Co., on Beverly Turnpike Trail, Wenatchee Mtns. at 5200 ft, *Kellogg 232** (field- and garden-grown specimens);† Yakima Co., Rattlesnake Mtn., *Cotton 556* (US); Pullman, *Piper 3973D* (US). OREGON: banks of Willamette R., *Howell 33* (US); Gilliam Co., W-facing slope on E side of Phillippi Canyon Rd., 3 mi S off Hwy. 80, and W of Blalock, *Kellogg 22* (field-, greenhouse-, and garden-grown specimens); Grant Co., on steep sandy cut-bank next to rd. along E side of S Fork John Day R., 11 mi S of John Day, *Kellogg 154* (field-, garden-, and greenhouse-grown specimens); Multnomah Co., on Oneonta Gorge Trail not far W of Horsetail Falls, *Kellogg 264.* CALIFORNIA: Tia Juana Valley, *Pringle s.n.,* 6 April 1882 (CAS); El Dorado Co., between Shingle Springs and El Dorado, *Heller 12297* (GH); San Bernardino Co., Mojave Desert, 15 mi NE of Barstow on Garlic Springs Rd., 8/10 mi N of 2nd summit, alt. 2800 ft, *Wolf 6516* (GH); San Bernardino Mtns., flats near Lost Creek, alt. 6800 ft, *Munz 17080* (GH); Siskiyou Co., Yreka, *Butler 1294* (GH); mtns. S Dixey Valley, *Davy s.n.,* 5 July 1894 (US). IDAHO: Clark Co., at U. S. Sheep Exp. Sta. between Spencer and Dubois, E of Rte. 15, 50 yd E of RR tracks, *Kellogg 56* (field- and garden-grown collections; 8 separate culms of field-grown clump scored as separate plants); Elmore Co., 13 mi NE of Mountain Home, on N slopes near headwaters of Rattlesnake Creek, *Christ & Christ 16655* (US); Bitterroot Natl. Forest, Salmon Mtn., *Kellogg 226* (garden- and greenhouse-grown collections); Lemhi Co., on rock outcrop at 9400 ft, 1 mi E of Doublesprings Pass and SW of Buck Creek, *Kellogg 196* (field-, garden-, and greenhouse-grown collections); Lemhi Co., just below microwave relay station near rd. running N from Bannock Pass (3 mi from pass), *Kellogg 221.* NEVADA: vic. of Reno, Hunter Creek Canyon, *Hitchcock 10554* (US); Washoe Co., Dinsmore Camp, Hunter Creek Canyon, 6000 ft, *Kennedy 1639* (CAS). UTAH: slope of Aquarius Plateau, alt. 9000 ft, *Ward 488* (US); SW side of Bald Mtn., elev. 11,500 ft, *Maguire 4004* (US); Cache Co., meadows 3 mi W of Logan, *Maguire 13874* (DAO). ARIZONA: Mojave Co., Mokiak Springs, 19 mi S of Saint George, Utah, alt. 3000 ft, *Gould 1643* (GH); Pipe Spring, alt. 5000 ft, *M. Jones 5266* (DS). MONTANA: Glacier Natl. Park, on large nearly bare rock above McDermott, *Hitchcock 11301* (US); Glacier Natl. Park, Greenwood's Camp, 4500 ft alt., *M. Jones s.n.,* 15 Aug. 1910 (US); Glacier Natl. Park, near E entrance, *Swallen 6458d* (US). WYOMING: Jacksons Hole, above Leighs Lake, alt. 9000 ft, *Merrill & Wilcox 341* (US); Yellowstone Natl. Park, S of Mt. Washburn, *Hitchcock 2036* (US). COLORADO: Gunnison Co., NW Castle Peak, Gothic Basin, ca. 12,000 ft, *Ewan 11752* (US); Rabbit Ear Pass, *Swallen 1379* (US); Moffat Co., W rim of Lodore Canyon, elev. 7500 ft, *Porter 3670* (GH). NEW MEXICO: Fitzgerald Cienaga, *Wooton s.n.* (US). NORTH DAKOTA: Billings Co., edge of Moody Plateau, *Swallen 5787* (DAO); Wells Co., Harvey, *Stevens 1208* (DAO). SOUTH DAKOTA: Black Hills, Custer, *Hitchcock 11107* (US); Pennington Co., near Wall, *Palmer 37278* (GH). NEBRASKA: Chadron, *Bates s.n.* (GH); Dawes Co., *Tolstead 7* (US). MICHIGAN: Isle Royale, Monument Rock, Tobin Harbor, *McFarlin 2175* (US). MINNESOTA: Ottertail Co., Perham, *Chandonnet 2562* (GH). MAINE: North Berwick, *Parlin 1233* (US).

APPENDIX 2. **Specimens measured for discriminant analyses and evaluations of population variation.‡**

United States. CALIFORNIA. San Diego Co.: Cleveland Natl. Forest, T15S R5E, on road from Cibbett's Flat, *Kellogg & Taylor 295* (**1**; 4 sheets); on W side of hwy. N of Mt. Laguna ca. 1 mi, *Kellogg & Taylor 298* (**2**; 4 sheets); N end of Cuyamaca Reservoir, *Kellogg & Taylor 300* (**3**; 3 sheets); on rocky outcrops at N end of Cuyamaca Reservoir, *Kellogg & Taylor 302* (**4**; 3 sheets). Riverside Co.: on N side of Hwy. 74, T7S R4E S16,

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*One specimen of each Kellogg collection is at A.

‡Numbers in boldface refer to population numbers on bar graphs.

Kellogg & Taylor 304 (**5**; 4 sheets); next to Hwy. 79 E of Rancho California (Temecula) on river banks, *Kellogg & Taylor 307* (**6**; 4 sheets). San Bernardino Co.: on Fort Irwin Rd. ca. 14 mi NE of Barstow, 0.9 mi beyond 2nd summit in side canyon 200 yd from rd., *Kellogg & Taylor 314* (**7**; 4 sheets). Kern Co.: in Red Rock Canyon, ca. 20 mi N of Mojave on steep slopes W of Hwy. 14, *Kellogg & Taylor 315* (**8**; 3 sheets). Los Angeles Co.: T7N R16W S13, in canyon ca. 100 yd below Upper Shake Campground, *Kellogg & Taylor 316* (**9**; 8 sheets); T8N R17W S29, on cut-bank above County rd. N2, *Kellogg & Taylor 321* (**10**; 4 sheets). Santa Barbara Co.: ca. ¼ mi W of LaCumbre Peak, Santa Ynez Mtns., ca. 3800 ft, *Kellogg & Taylor 322* (**11**; 3 sheets); on steep N-facing road-cut on N side of Gato Ridge on oil co. property, ca. 900 ft, *Kellogg & Taylor 323* (**12**; 4 sheets). Mono Co.: just below Carnegie Inst. Transplant Garden, Timberline Exp. Sta., *Kellogg & Kiest 370* (**16**; 5 sheets); Minarets Wilderness, on River Trail between Garnet Lake and Shadow Lake turnoffs, *Kellogg & Kiest 377* (**17**; 4 sheets). Inyo Co.: Big Pine Lakes, head of Big Pine Creek between First and Second lakes, elev. 10,000 ft, T9S R32E S33 NW¼, *Kellogg & Kiest 379* (**18**; 4 sheets). Fresno Co.: just W of Swede Lake, W of Three Sisters, Dinkey Lakes area, ca. 40 mi NE of Fresno, T9S R26E S12 SE¼, *Kellogg & Kiest 382* (**19**; 4 sheets). WASHINGTON. Ferry Co.: sandy W shore of Columbia R. at Inchelium, below 1290 ft level, *Rogers 531* (**20**; CAS, DS, GH). Grant Co.: border of alkaline pond in Grand Coulee 7 mi above Dry Falls, *Rogers 589* (**21**; CAS, DS, GH, US). Kittitas Co.: canyon of Bushy Creek, alt. 1000 ft, *Cotton 1620* (**22**; GH, US), *1621* (**22**; US), *1621½* (**22**; US); Wawawai, on banks of Snake R., *Piper 2567* (**23**; GH, US—2 sheets); Coulee City, *Piper 3912*—2 sheets, *3916, 3918, 3920*—2 sheets (**24**; GH, US). Whitman Co.: Albion, 8 mi NW of Pullman in RR right-of-way, *Keck & Hiesey 5340, 5341, 5342* (**25**; DS). Chelan Co.: alpine slopes of Chumstick Lookout, 6000 ft, *Thompson 14979* (**26**; CAS, DS, GH). Kittitas Co.: open alpine ridges at head of Beverly Creek, 5000 ft, *Thompson 9511* (**27**; CAS, DS, GH, US—2 sheets); on Teanaway Divide, Beverly Turnpike Trail, 5700 ft, *Kellogg 233* (**28**; 5 sheets).

Canada. QUÉBEC. Rimouski Co.: on shale outcrop below calcareous cliffs above St. Fabien sur Mer, *Kellogg & Kiest 351* (**13**; 8 sheets). Gaspé Co.: Grand Coupe ca. 1 mi NW of Percé, ca. 550 ft alt., *Kellogg & Kiest 358* (**14**; 7 sheets). Bonaventure Co.: on S-facing cliffs just below summit of Mt. St. Joseph, *Kellogg & Kiest 363* (**15**; 3 sheets).

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THE EOCENE NORTH ATLANTIC LAND BRIDGE: ITS IMPORTANCE IN TERTIARY AND MODERN PHYTOGEOGRAPHY OF THE NORTHERN HEMISPHERE[1]

BRUCE H. TIFFNEY

THE TRANSITION from the Cretaceous to the Tertiary marks a time of significant modernization in the history of flowering plants. During this interval, a wide range of extant families and genera first appeared, as recorded in the fossil record of pollen (Muller, 1970, 1981) and fruits and seeds (Tiffney, unpubl. data). This modernization was probably spurred by coevolution with pollinators (Crepet, in press) and dispersal agents (Tiffney, in press) and resulted in a major change in the floristic and vegetational composition of the world's plant communities.

Concomitant with this modernization, the newly evolved taxa spread rapidly over the Northern Hemisphere (Wolfe, 1975) during a period of equable climate (Kennett, 1977; Savin, 1977; Buchardt, 1978; Wolfe, 1978) to form a hemispheric flora. This flora seems unusual by modern standards since it consisted of a mixture of taxa, the modern counterparts of which are found in habitats ranging from deciduous northern hardwood forests (e.g., *Juglans* L., *Carpinus* L., *Betula* L.) to tropical and paratropical rain forests, particularly of southeastern Asia and Malaysia (e.g., *Nypa* Steck, *Mastixia* Blume, *Tetrastigma* Planchon, and members of the Icacinaceae). In recognition of its northern geography and the thermophilic affinities of many of its component taxa, Wolfe (1975, 1977) referred to this assemblage as the "boreotropical flora." The classic example of this flora is the Early Eocene London Clay assemblage of southeastern England (Reid & Chandler, 1933; Chandler, 1961, 1962, 1963, 1964, 1978). Although the boreotropical flora was apparently not a homogeneous unit, its composition was strikingly similar throughout its range. Reid and Chandler (1933) saw the modern Indomalaysian affinities of the London Clay assemblage as suggestive of a tropical flora that had moved along the coasts of the Tethys Seaway. This conclusion was subsequently supported by discovery of London Clay taxa in the Eocene of eastern Europe (Palamarev, 1973) and the Eocene (Chandler, 1954) and Oligocene (Bown *et al.*, 1982) of Egypt. The Middle Eocene Clarno Formation of Oregon represents an extension of this flora to the west (Scott, 1954; Chandler, 1964; Manchester, 1981, 1983), as do some small, unreported floras in the Rocky Mountains (pers. obs.).

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[1] This is the second of two related papers. The first, entitled "Perspectives on the Origin of the Floristic Similarity between Eastern Asia and Eastern North America," appeared in the January, 1985, issue of the *Journal of the Arnold Arboretum.*

Journal of the Arnold Arboretum **66**: 243–273. April, 1985.

Although the Clarno assemblage has not been fully investigated, it is clear that the fruit and seed portion of the flora includes several genera and perhaps some species in common with that of the London Clay. The geographic links between the Clarno and London Clay floras are conjectural; they could lie across the northern Pacific and East Asia (see data of Zaklinskaya, 1980), they could reflect the influence of the Tethys Seaway–North Atlantic route, or they could result from a combination of the two.

Once the early Tertiary boreotropical flora had spread, it was influenced and altered by subsequent geographic and climatic events, giving rise to the modern flora and vegetation of Eurasia and North America. Two geographic changes were of particular importance. In the Old World the closing of the Turgai Straits during the Oligocene (Vinogradov, 1967–1968; McKenna, 1975; see MAP 5) permitted biotic exchange between central Asia and Europe. The disappearance of this sea also introduced a more continental climate to western Siberia. This led to the evolution of increasingly drought-tolerant, continental communities of a modern aspect, which ultimately invaded Europe from the east (see Friis, 1975). The second geographic modification involved the westward movement of North America. On its trailing edge this movement was powered by expansion along the Mid-Atlantic Ridge, which caused the widening of the North Atlantic and the sundering of early Tertiary ties between Europe and North America (McKenna, 1975, 1983a; Hoch, 1983). On its leading edge the westward movement contributed to the Tertiary orogenies of western North America. This mountain building provided direct topographic barriers to plant movement and resulted in a lengthening shadow of drier climates across central North America. Consequently, a new and more drought-tolerant flora and vegetation evolved in the western mountains and eastward, while the remnants of the earlier, moisture-adapted boreotropical flora were largely confined to the western slopes or retreated southward (Leopold & MacGinitie, 1972).

The effects of these geographic alterations were further modified by climatic changes through the Tertiary (Friis, 1975; Kennett, 1977; Buchardt, 1978; Wolfe, 1978; Hickey, 1981a). The temperate global climates of the earliest Tertiary gave way to increasingly warmer climates in the Early Eocene. During the latter time, much of the Northern Hemisphere supported a warm-temperate to subtropical vegetation, and thermophilic vegetation grew at fairly high latitudes (Wolfe, 1975, 1977). A climatic deterioration involving a decrease in world temperature and an increase in seasonality occurred during the later Eocene (Collinson *et al.*, 1981; Keller, 1983) or at the Eocene-Oligocene boundary (Kennett, 1977; Buchardt, 1978; Wolfe, 1978) and extended into the Oligocene (Keller, 1983). This resulted in the contraction of the boreotropical flora and the geographic expansion of a species-poor deciduous vegetation of northern latitudes (Wolfe, 1969, 1977, 1978, 1980; Hickey, 1981a, 1981b, pers. comm.; Hickey *et al.*, 1983). In the later Oligocene and the Miocene the climate fluctuated between warm and cool, leading to selection of cool-adapted taxa from the boreotropical flora and their addition to the developing deciduous vegetation, which diversified and is now recognized as the mixed mesophytic forest (Wolfe, 1969; see also Mai, 1964, 1981). Later Miocene and Pliocene climates became increasingly cooler, leading to the extreme cold of the Pleistocene. This cooling resulted in a thermal segregation of the products of the boreotropical flora. The evergreen and cold-intolerant elements of the widespread Paleogene forests were restricted to protected southerly refugia; where these were not available, or where climatic change occurred more rapidly than dispersal and regeneration, local extinction occurred. The more recently segregated warm-temperate elements of the mixed mesophytic forests were likewise restricted to protected sites or became extinct, although the effects of glaciation were less disruptive on this group of plants than on the tropical members of the boreotropical flora. To the north a northern hardwood forest of low diversity developed, and north of it taiga and tundra communities evolved.

As a result of these geographic and climatic changes during the Tertiary, the evergreen and mixed mesophytic remnants of the boreotropical flora now occupy widely separated "Tertiary refugia." Classically, these include the Balkans, the Caucasus, Southeast Asia, Japan, western and eastern North America, and portions of the eastern highlands of Mexico (especially Veracruz) and northern Central America (see Szafer, 1964; Wood, 1972). Although these localities share common elements, they preserve different diversities and often different subsets of the boreotropical flora. Southeast Asia harbors the greatest representation of the early Tertiary flora, particularly in Japan and in the zone from the mixed mesophytic forests of China south through the tropical evergreen forests of Malaysia. The fossil record suggests that both western North America (Wolfe, 1975, 1977, 1978) and Europe (Chandler, 1964; Mai, 1964, 1970, 1981) had a rich sample of the boreotropical flora and the succeeding mixed mesophytic forest in the early and mid-Tertiary. However, the interaction of global climate and local topography caused the extinction of many of these thermophilic elements in the late Tertiary and Quaternary. This elimination was particularly pronounced in Europe, where advancing Pleistocene glaciers trapped the floras against the east–west oriented mountains, leaving only scraps of the original flora in Europe and more developed remnants in the diverse topography of the Balkans and the Caucasus. In western North America, boreotropical elements were first restricted to moister west-facing sites by the rising Rocky Mountains and were subsequently influenced by the cooling climates of the later Tertiary and Quaternary (Wolfe, 1969, 1977; Leopold & MacGinitie, 1972). Again, depauperization of the flora occurred, but with less drastic effects than in Europe.

Southeastern North America presently has a diverse representation of evergreen and deciduous woody elements of the boreotropical flora. The similarity of this flora to that of eastern Asia has been given as an example of disjunction since the time of Linnaeus (Graham, 1972) and Gray (1840, 1859; Boufford & Spongberg, 1983). However, the New World floras are generally considered to have a lower diversity of boreotropical elements than the modern floras of Japan, China, and Indomalaysia.

The contention that the modern descendant of the boreotropical flora in southeastern North America is less diverse than its counterpart in Southeast Asia is central to the discussion to follow. However, I do not believe this statement has ever been supported in a quantitative manner, and I therefore present a numerical summary (TABLE). Hu (1935) estimated that there were 969 genera of woody spermatophytes and approximately 2000 species of trees in China. The second edition of the first five volumes of the *Iconographia Cormophytorum Sinicorum* (Anonymous, 1980) suggests a woody flora of approximately 950 genera and 3400 species. The *Iconographia* is acknowledged to be incomplete and is being superseded by the *Flora Reipublicae Popularis Sinicae*. This multi-volume flora is still being published and thus cannot be used to obtain a direct count of diversity. However, comparison of reports for 19 woody families in the *Iconographia* and the *Flora* suggests increases of roughly 15 percent in generic diversity and 100 percent in specific diversity in the latter publication. If this is correct, the woody flora of China would involve about 1030 genera and 6800 species. Ohwi's (1965) *Flora of Japan* records 278 genera and 858 species of woody spermatophytes from the much smaller area of Japan.

By contrast, *Gray's Manual of Botany* (Fernald, 1950) lists 161 genera and 665 species of woody spermatophytes (including trees, shrubs, and vines) in northeastern North America. The *Manual of the Vascular Flora of the Carolinas* (Radford *et al.*, 1964) lists 211 genera and 554 species of woody spermatophytes in the flora of North and South Carolina. Small's (1933) *Manual of the Southeastern Flora* lists 412 genera and 1202 species of woody spermatophytes in the southeastern United States. Biases exist in all these tabulations, and the final figures must be taken as approximate. The *Iconographia Cormophytorum Sinicorum* embraces slightly more tropical areas than occur in the southeastern United States. The three North American sources cover separate portions of the flora of eastern North America rather than the entire flora (TABLE). Nonetheless, it is clear that the extant woody flora of eastern North America has approximately one-third to one-half the specific diversity of the woody flora of East Asia. While many of the East Asian genera are rare or monotypic, this is not the sole cause of the difference in diversity; comparison of vegetational surveys of China (Wang, 1961) and eastern North America (Braun, 1950) reveals 119 genera and 563 species of ecologically important trees in the former flora, and 46 genera and 112 species in the latter. Again, biases exist in the use of these data for the estimation of diversity, but the general picture is clear.

Herbs have not been mentioned in the above discussion inasmuch as a significant proportion of herbaceous taxa appear to have evolved locally in the middle and late Tertiary (Tiffney, 1981a, 1985) rather than spreading with the boreotropical flora. If they were included, it would only accentuate the observed pattern (see TABLE).

The cause of the lower diversity of boreotropical taxa in the modern flora of eastern North America is not immediately clear. Wolfe (1977) suggested four contributing factors: eastern North America was isolated from western North America and Europe in the Tertiary;[2] the Eocene-Oligocene climatic

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[2] Wolfe (1977, p. 49) suggested, after MacGinitie (1969), that the isolation of eastern North America is ancient, and that the original Paleogene boreotropical flora of the area was less diverse than that of Europe or western North America.

Generic and Specific Diversities of Selected Eastern Asian and Eastern North American Floras.*

LOCATION	TOTAL AREA (sq. km)	TOTAL FLORA		WOODY PLANTS		HERBACEOUS PLANTS		PERCENT OF FLORA THAT IS WOODY	
		Genera	Species	Genera	Species	Genera	Species	Genera	Species
China a.	3,556,371	2389	7702	949	3397	1440	4305	40	44
b.		2840	15,400	1030	6790	1810	8610	36	44
Japan	369,698	988	3648	278	858	710	2790	28	23.5
N.E. North America	2,515,885	815	4227	161	665	654	3562	20	16
Carolinas	216,628	826	3157	211	554	615	2603	25.5	17.5
S.E. North America	1,700,374	1510	5563	412	1202	1098	4361	27	21.5

*All figures should be regarded as approximations. Introduced cultivated plants were excluded when identifiable as such. If a genus included more than one physiognomic type (e.g., tree, vine), placement of the genus and its included species in a physiognomic class was dictated by the prevalent physiognomy. In some cases this resulted in arbitrary decisions. The total number of taxa in a given area reflects both biological reality and the systematic concepts of the reporting author(s). For example, Small (1933) is generally regarded as a "splitter," and the absolute diversity reported in his flora is presumably inflated relative to the diversity reported by others. Sources: China "a," after Anonymous (1980); China "b," estimated from Anonymous (1959–present); Japan, Ohwi (1965); northeastern United States, Fernald (1950); the Carolinas, Radford *et al.* (1964); southeastern United States, Small (1933). Data for areas taken from Bartholomew *et al.* (1980); those for China exclude the floristically poor highlands of Tibet, Mongolia, and Sinkiang.

deterioration further depauperized the flora of eastern North America; this same event separated the incipient mixed-mesophytic flora of the area from more tropical floras isolated to the south, preventing enrichment of the former by the latter in the mid-Tertiary; and the area had little topographic diversity. Although the last point may be taken as given, the first three raise three sequential questions. First, was the Eocene boreotropical flora of eastern North America significantly less diverse than that of contemporaneous Europe or western North America? This involves both a consideration of the fossil record of eastern North America and an examination of the degree of geographic isolation of this area in the early Tertiary. Second, if this flora was as rich as that of Europe and western North America, did it give rise to an equally rich mixed-mesophytic flora, or as Wolfe has suggested, was its diversity curtailed by the Eocene-Oligocene climatic deterioration? Third, if diversity was not restricted by this deterioration, at what subsequent time was it reduced?

I believe that the original Paleogene boreotropical forest of eastern North America was nearly as rich as those of western North America and Asia, and that the reduced diversity of the present southeastern North American flora is a function of the subsequent Eocene-Oligocene and/or Pleistocene climatic fluctuations. Demonstration of this supposition is circumstantial and requires evidence from the fossil record and paleogeography. First, the Tertiary fossil record of eastern North America must be shown to contain a significant number of boreotropical taxa. The stratigraphic distribution of these taxa might aid in distinguishing between an Eocene-Oligocene and a Pleistocene depauperization of the flora. Second, examination of the paleozoogeography, paleogeography, and paleoclimatology of the early Tertiary must demonstrate that eastern North America was not isolated from the rest of the Northern Hemisphere during the spread of the boreotropical flora. I will examine these two lines of evidence and suggest that the data, although equivocal, support the contention of a diverse early Tertiary flora in eastern North America that was reduced by subsequent, primarily climatic changes.

THE PALEOBOTANICAL RECORD OF EASTERN NORTH AMERICA

Our present understanding of the Tertiary paleobotanical history of eastern North America is poor. Paleogene and Neogene plant-bearing deposits are rare on the Atlantic Coastal Plain. The tectonic setting of this area in the Tertiary did not favor the formation of deep depositional basins. The few fossiliferous deposits that accumulated have been severely eroded by ice sheets in glaciated terrain and deeply weathered to the south of the limit of glaciation. The low angle of repose of the present terrain does not favor natural exposure of the coastal plain sediments, and extant vegetation hampers exploration efforts. Finally, few workers are investigating this time and area.

In spite of these difficulties, evidence for the presence of boreotropical genera may be found in both the micro- and the macrofossil records. Among microfossils, Elsik (1974) has recorded pollen of *Engelhardtia* Leschen. ex Blume, *Pterocarya* Kunth, *Platycarya* Sieb. & Zucc., *Alangium* Lam., *Ficus* L., and the Icacinaceae, and Frederiksen (1980b) reported pollen of the palm *Nypa* from Middle and Upper Eocene sediments of the Mississippi Embayment. The pollen of *Platycarya* is of particular note since it peaks both in the Early Eocene floras of the Atlantic Coastal Plain and the Mississippi Embayment (Frederiksen, 1980c) and in the Early Eocene Willwood Flora of Wyoming (Wing, 1981). Although circumstantial, this implies a degree of Early Eocene floristic exchange between the southeast and the eastern slope of the Rocky Mountains. Traverse (1955) recorded pollen of *Engelhardtia, Pterocarya, Alangium,* and *Glyptostrobus* Endl. from the Brandon Lignite of Vermont. This deposit has been dated as Oligocene (Wolfe & Barghoorn, 1960) or perhaps Early Miocene (D. Mai, pers. comm.; N. Frederiksen, pers. comm.) in age. Frederiksen (1984) has found pollen of *Sciadopitys* Sieb. & Zucc., *Pterocarya,* and the *Engelhardtia* "group" (*Engelhardtia, Alfaroa* Standley, *Oreomunnea* Oersted) in the Miocene of Massachusetts, and Rachele (1976) has recorded pollen of *Pterocarya* and *Engelhardtia* in the Miocene of New Jersey. All of these genera are members of the boreotropical flora and currently exist in the flora of East Asia. However, although present in the Tertiary pollen floras of eastern North America, these taxa formed a small percentage of the total flora; in most cases the pollen floras of this area appear to be dominated by New World taxa or by pollen taxa that lack specific biogeographic affinities.

The macrofossil record of the Gulf Coastal Plain is poor for the late Tertiary but far better for the Paleogene. Revisions of Berry's (1916, 1924, 1930) early studies on the leaves of the Mississippi Embayment deposits have only recently been initiated (Dilcher, 1971; Crepet, 1979, and references therein), and comparison of these leaf floras with others in the Northern Hemisphere is difficult. The existing data suggest some similarity between the floras of the Embayment and those of the early Tertiary of western North America (Wing, 1981). However, the degree of this similarity is not fully understood, and the timing of its onset or decline is unclear. Climatic reconstructions using leaves (Dilcher, 1973) and pollen (Frederiksen, 1980a) suggest that the warm climates of the earlier Eocene in the Northern Hemisphere were distinguished in the southeast by a pronounced dry season. If this is correct, such a seasonal drought may have promoted the evolution of a flora and vegetation distinct to some degree from that of western and northeastern North America. The one megafossil from the Mississippi Embayment with a clear boreotropical affinity is the fruit of the palm *Nypa* from the Middle Eocene of Texas (Arnold, 1952; Tralau, 1964), which is also known from pollen (Frederiksen, 1980b). *Nypa* was widely distributed in the early Tertiary of Europe (Tralau, 1964) but is presently restricted to estuarine sites in Indomalaysia and northern Australia.

Outside of the Mississippi Embayment, macrofossils have been studied less frequently than microfossils, yet they often provide more specific biogeographic information. The fossil distribution of *Nypa* is paralleled by that of two species of ?Euphorbiaceae from the Early Eocene of Maryland and Virginia, *Wetherellia* Reid & Chandler and *Palaeowetherellia* Chandler (Mazer & Tiffney, 1982). *Wetherellia* is known from Eocene sediments in England (Reid & Chandler, 1933; Chandler, 1964) and is one of the most common elements of the London Clay; *Palaeowetherellia* is known from early Tertiary deposits in northern Egypt (Chandler, 1954). Although specimens of the latter genus from Egypt and the

New World are clearly different from one another, those of *Wetherellia* from England and the Atlantic Coastal Plain are virtually indistinguishable, and their depositional context suggests that they were produced by a coastal plant. The distributions of these two taxa, and of *Nypa,* appear to reflect the westerly extension of coastal elements of the London Clay Flora along the northern shore of the Tethys.

The one exception to the dearth of macrofossil deposits in northeastern North America is the Brandon Lignite of west-central Vermont. This deposit is rich in pollen, wood, fruits, and seeds; its age is uncertain but probably falls between Oligocene (Wolfe & Barghoorn, 1960) and Miocene (Frederiksen, pers. comm.). The flora is pertinent to the present discussion because it provides an instructive comparison between the biogeographic information inherent in micro- and macrofossil floras, and because it demonstrates the presence of several boreotropical genera in the Tertiary of eastern North America that are not found in the extant flora of this area. The only boreotropical genera recorded in the microflora (Traverse, 1955) are *Alangium, Engelhardtia, Glyptostrobus,* and *Pterocarya*; the remainder of the palynoflora appears to have New World or cosmopolitan affinities. By contrast, the macroflora includes both some taxa with close relationships to modern genera restricted to East Asia, and a smaller number of taxa related to boreotropical forms found in the Tertiary floras of Europe. *Nyssa brandoniana* Eyde & Barghoorn (Eyde & Barghoorn, 1963) is very similar to *N. javanica* (Blume) Wangerin of Burma. *Phellodendron* Rupr. and *Euodia* J. R. & G. Forster (Rutaceae; Tiffney, 1980a) are presently restricted to East Asia but were common in Europe during the Tertiary. *Turpinia* Vent. (Staphyleaceae; Tiffney, 1979) is found in both the Old and New World tropics. The Brandon specimen shows closer affinity with existing New World species; a second species is found in the European Miocene (Mai, 1964). Similarly, *Cleyera* Thunb. (Theaceae; Tiffney, in manuscript) is largely a New World genus but is closely related to the Old World *Eurya* Thunb. *Cleyera/Eurya*-like fossils are common in the European Tertiary, and the two genera are probably sister groups of Tertiary origin. *Magnolia waltonii* Tiffney (Magnoliaceae; Tiffney, 1977) and *Microdiptera parva* Chandler (Lythraceae; Tiffney, 1981b) are both Brandon taxa that are closest to extinct forms of the European Tertiary. Undescribed fossils now under investigation include achenes similar to those of *Caldesia* Parl. (Alismataceae), a genus of the Old World tropics and known from the European Tertiary, and at least three species of *Symplocos* Jacq., only one of which appears to have New World affinities. In addition, endocarps of *Alangium* (Alangiaceae; Eyde *et al.,* 1969), paralleling the pollen record, are known from the deposit.

Although the fruit and seed flora of the Brandon Lignite has not been fully described, it does include several clearly boreotropical taxa and is far more closely related to the boreotropical flora than would have been judged from the associated microflora. Further, this flora is later than Eocene in age and emanates from a very small deposit (only a few cubic yards of fossiliferous sediment are available for study). These last two factors suggest that the Brandon Flora is probably a limited subset of the boreotropical flora that was originally in eastern North America.

In summary, palynological evidence suggests that a few boreotropical taxa now restricted to eastern Asia were present in the earlier Tertiary of eastern North America. However, compared to western North America (e.g., Leopold & MacGinitie, 1972), eastern North America appears to lack several common boreotropical pollen taxa in the early Tertiary. By contrast, macrofossil evidence from two isolated occurrences of fruits and seeds, and from the Oligocene or Miocene Brandon Lignite, demonstrates the presence of boreotropical elements in eastern North America. The assemblage of boreotropical taxa in the Brandon Lignite indicates that eastern North America had a greater initial diversity of boreotropical taxa—and perhaps of derived mixed mesophytic taxa—than has previously been suspected. The paleofloristic affinities of the Paleogene floras of the Mississippi Embayment are presently unclear, although limited evidence suggests some floristic interchange with western North America in the early Tertiary. The fossil record is too scanty to resolve the timing of the depauperization of the eastern North American flora.

PALEOGEOGRAPHIC EVIDENCE ON THE DEVELOPMENT OF THE EASTERN NORTH AMERICAN FLORA AND VEGETATION

If eastern North America was separated from other northern continents in the early Tertiary, this would reinforce Wolfe's (1977) suggestion that the lower current diversity of the southeastern North American flora stemmed from its early isolation from the general boreotropical flora. However, if early Tertiary connections with other portions of the Northern Hemisphere can be demonstrated, this would support the contention that the lower current diversity is a function of later Tertiary events and would parallel the fossil data enumerated above.

The connection of eastern North America to other boreal landmasses is bidirectional. The classic perception (e.g., H. L. Li, 1972), perhaps influenced by the present proximity of Siberia and Alaska, suggests a linkage through western North America. This route involves two subunits: the connection of eastern Asia to western North America across the Bering Straits, and that of western to eastern North America through the mid-continental area. The alternative route involves linkage of eastern North America to Europe across the early Tertiary North Atlantic. Although accepted by paleozoologists (e.g., Lehmann, 1973; McKenna, 1975, 1983a; Russell, 1975), the latter route is rarely considered by paleobotanists; only Tiffney (1980b) and Wolfe (manuscript submitted) have discussed its significance in early Tertiary phytogeography. This route is also bipartite, involving the linking of North America to Europe, and of Europe to East Asia. Each of these routes of connection will be considered.

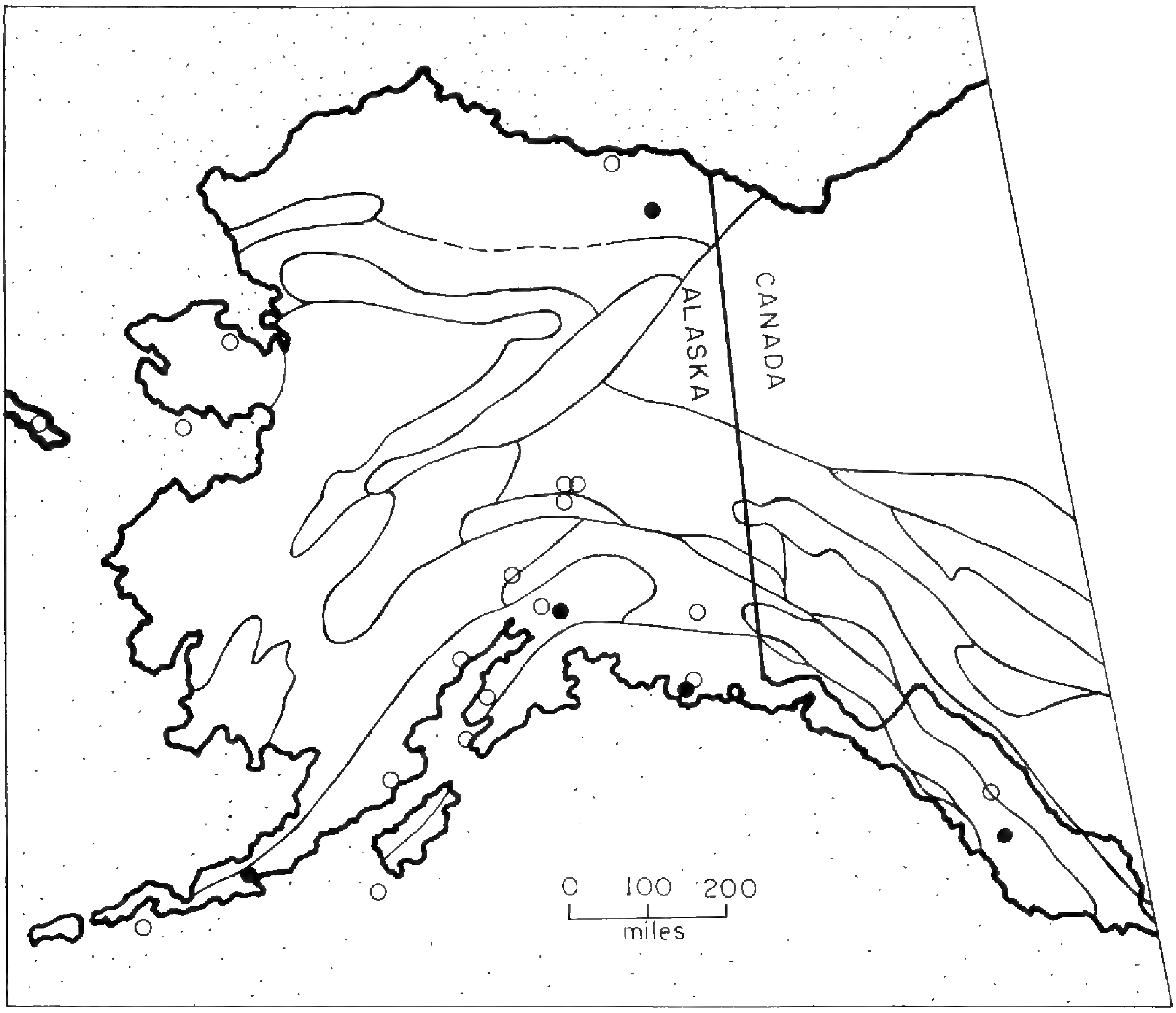
THE BERING CONNECTION

The Bering land bridge has been recognized in biogeographic discussions for nearly a century (e.g., Matthew, 1915; Hopkins, 1967). The vertebrate paleontological record of Beringia suggests a barrier to faunistic exchange in the Paleocene (Chow & Zheng, 1979), an Early Eocene period of connection between Alaska and Siberia, a Middle Eocene period of isolation, and a limited Late Eocene resumption of exchange (Kurtén, 1966; Novodvorskaja & Janovskaja, 1975). The nature of the barrier to exchange is not certain; it could involve climate and/or land position. Kurtén noted that the Early Eocene exchange between eastern Asia and western North America involved elements different than those found in Europe and North America at the same time.

During the Eocene, world climates (Kennett, 1977; Buchardt, 1978; Wolfe, 1978; Collinson *et al.*, 1981; G. Keller, 1983) were warm enough to support thermophilic vegetation and vertebrates (e.g., Estes & Hutchison, 1980; McKenna, 1980) at far northern latitudes. The primary limitation to the northerly extent of evergreen boreotropical taxa at this time was light (Allard, 1948; Hickey, pers. comm.).

In earlier papers Wolfe (1972, 1977) suggested the presence of evergreen forms in Alaska north of their modern latitudinal limit of tolerance to low light levels. On this basis he postulated (Wolfe, 1975) that the angle of inclination of the earth's axis of rotation was lower during the Eocene. This suggestion has drawn much criticism (e.g., Donn, 1982; McKenna, 1983b), and theoretical models of climate (Eric Barron, pers. comm.) suggest that such a change would actually lead to polar paleotemperatures much colder than those inferred. More recently, Wolfe (manuscript submitted) has reevaluated the distribution of floras in northwestern North America and has concluded that the Eocene Bering land bridge was primarily occupied by a broad-leaved, deciduous forest, perhaps with a thin southern fringe of evergreen, megathermal communities. As a result, Wolfe suggests that the Bering bridge is of limited importance in explaining the spread of megathermal elements of the Eocene boreotropical flora.

Estimation of the degree of floristic movement of evergreen taxa across the Bering bridge is complicated by the complex tectonic history of this area. Alaska lay somewhat north and east of its present position in the early Tertiary (Smith & Briden, 1977), but its southern margin was in flux. Much of Pacific North America is now considered to be formed of an aggregation of "microplates" that have drifted against North America. Many of Wolfe's Paleogene floras are located on these terranes (see MAP 1). The exact paths of movement and times of collision of these plates with western North America are the subject of debate and active research. The literature (e.g., Coney *et al.*, 1980; Ben-Avraham *et al.*, 1981) generally suggests that accretion was over by the early Tertiary, but recent evidence (Cowan, 1982; Bruns, 1983) demonstrates that some terranes may have moved considerable distances as recently as the mid-Tertiary. It appears that most of these plates collided with North America at about the latitude of British Columbia and then slid northwestward toward Alaska. If so, these terranes had little impact on the phytogeography of the Bering bridge. However, it is not clear at this time that this is true for all these terranes. For the present, phytogeographers should continue to consider the possibility that some of these terranes may have formed island "stepping stones" south of Alaska in the early Tertiary, perhaps connecting to Asia via islands associated with the ancestral Aleutian arc (DeLong *et al.*, 1978). However, this geographic



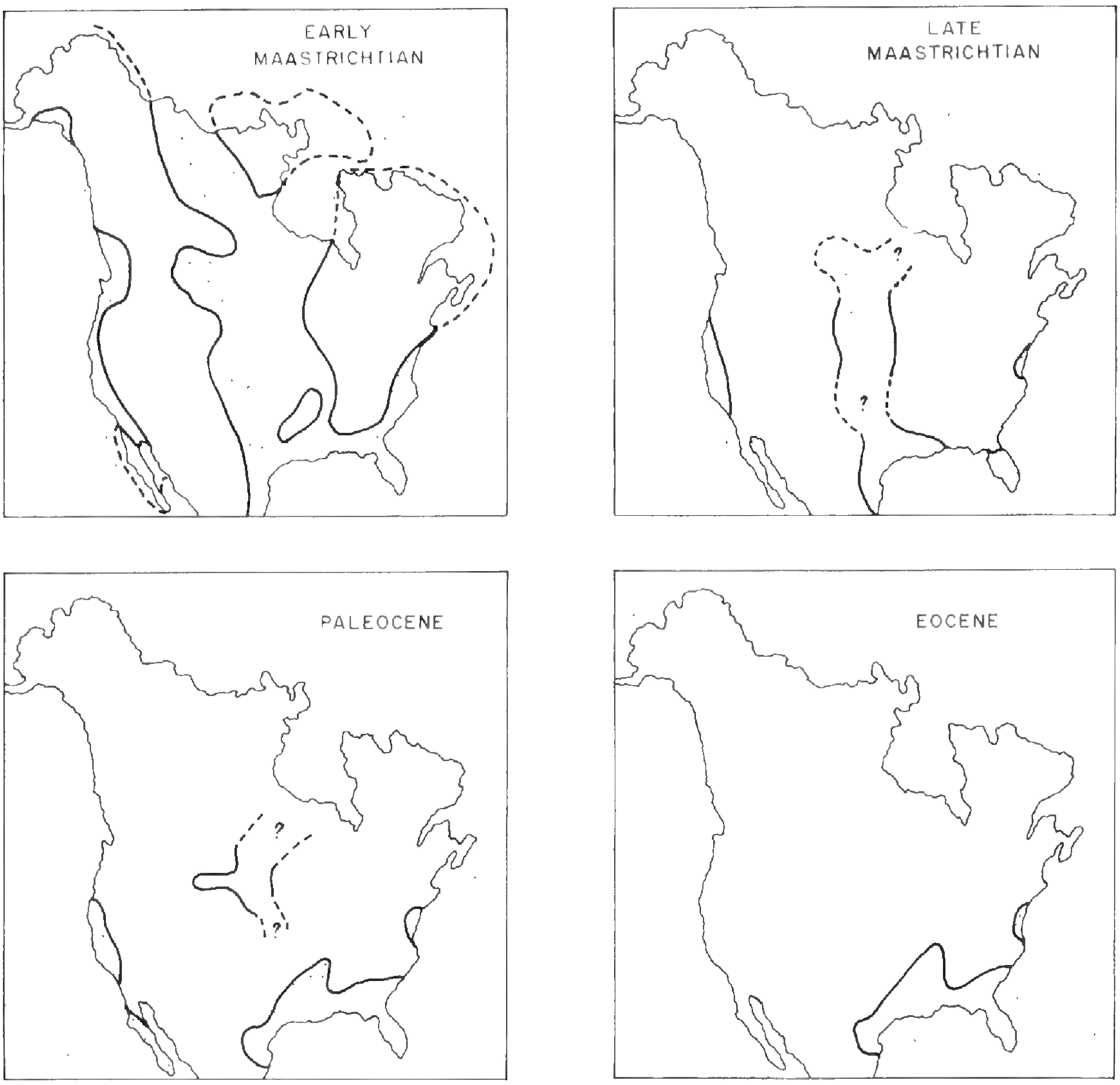
Map 1. Alaska, combining margins of presently identified allochthonous terranes (after Ben-Avraham *et al.*, 1981, *fig. 7*) with Tertiary floras reported by Wolfe (1972) from this area. Light lines = terrane margins, closed circles = Paleocene and Eocene floras, open circles = Oligocene or later floras. All Paleogene floras except Sagavanirktok on north slope lie on recently accreted terranes.

arrangement is highly tentative, and the limited available habitat of such an island chain would curtail its biogeographic significance (McKenna, 1983b).

I conclude that the Bering land bridge was a viable route for the exchange of deciduous boreotropical taxa in the early Tertiary. Evergreen elements of this flora were probably restricted in their use of the Bering bridge by day length. Alternative, more southerly routes were limited in area, if they existed. The climatic deterioration of the later Tertiary (Kennett, 1977; Buchardt, 1978; G. Keller, 1983) increasingly restricted this route to cool-temperate taxa.

The Central North American Problem

Floristic exchange between western and eastern North America involves the central portion of the continent, but evidence is inferential about the degree to which this could or did occur. The terrestrial plant record of this area is limited to a few primarily Neogene localities (e.g., MacGinitie, 1962; Segal, 1966a, 1966b; Thomasson, 1977, 1980a, 1980b), with the exception of the



MAP 2. Sequential generalized paleogeography, Late Cretaceous to early Tertiary, showing regression of North American Mid-Continental Seaway (shaded area). Data after Schuchert (1955), Reeside (1957), Gill and Cobban (1966), McDonald (1972), McGookey *et al.* (1972), and Williams and Stelck (1975).

Late Paleocene–Early Eocene Golden Valley Flora of North Dakota (Hickey, 1977).

Central North America was occupied by an epicontinental seaway in the Late Cretaceous. This formed a relatively successful phytogeographic barrier, separating the largely western North American *Aquilapollenites* floristic province from the largely eastern North American–European normapolles province (Muller, 1970). This seaway retreated to the north and south in the latest Cretaceous and Paleocene (MAP 2), eliminating its moderating climatic influence and giving way to an increasingly continental climate. This regression occurred concomitantly with the uplift of the Rocky Mountains, which as they rose, cast an increasingly long rain shadow to their east (Leopold & MacGinitie, 1972). The temporal relationship between the spread of the boreotropical flora, the retreat of the seaway, and the development of these drier climates is unclear. In particular, the exact geographic borders of the Late Cretaceous Mid-Continental Seaway and of the Paleocene Cannonball Sea have not been rigorously demonstrated in the geologic literature. Late Paleocene–Early Eocene floras from the eastern face of the present Rocky Mountains (e.g., Hickey, 1977; Wing, 1981) contain a few boreotropical elements, as well as some elements in common with the Eocene of the Mississippi Embayment (Wing, 1981). Wolfe (manuscript submitted) suggests that Wing's and Hickey's floras may have been dominated by floodplain vegetation, and that the interfluvial areas may have supported a paratropical rainforest. Leopold and MacGinitie (1972) noted that the Early Eocene floras of the Rocky Mountain region have East Asian affinities, while those of the Middle Eocene are dominated by taxa with relatives in the New World tropics. They associated this change with increasing seasonality of rainfall from the Early to Middle Eocene, presumably related to the uplift of the Rocky Mountains. This suggests that a moisture-based filter-barrier came into existence between eastern and western North America by the Middle Eocene. However, the barrier may not have been continuous; corridors of migration may have existed along rivers flowing eastward from the mountains to the plains. Perhaps the most tantalizing evidence for the later Paleogene plant communities of central North America comes from Retallack's (1983a, 1983b) investigations of fossil soils in South Dakota. These suggest that forest communities were in this area in the Late Eocene and Early Oligocene, but that they gave way first to savannas and then grasslands in the later Oligocene. This raises the possibility that a corridor of forest existed across the central-northern plains in the early Tertiary, perhaps invading drier areas along river courses. However, no evidence exists as to the composition of this forest or as to its extent beyond South Dakota. Some boreotropical elements are found in the Miocene Kilgore Flora of Nebraska (MacGinitie, 1962), but these are generally of cool-temperate affinity and have limited relations with the modern flora of East Asia. No evidence exists for the nature of Tertiary floras in the glaciated portions of Canada; it is possible that forest could have stretched across the higher latitudes of central North America in the early Tertiary.

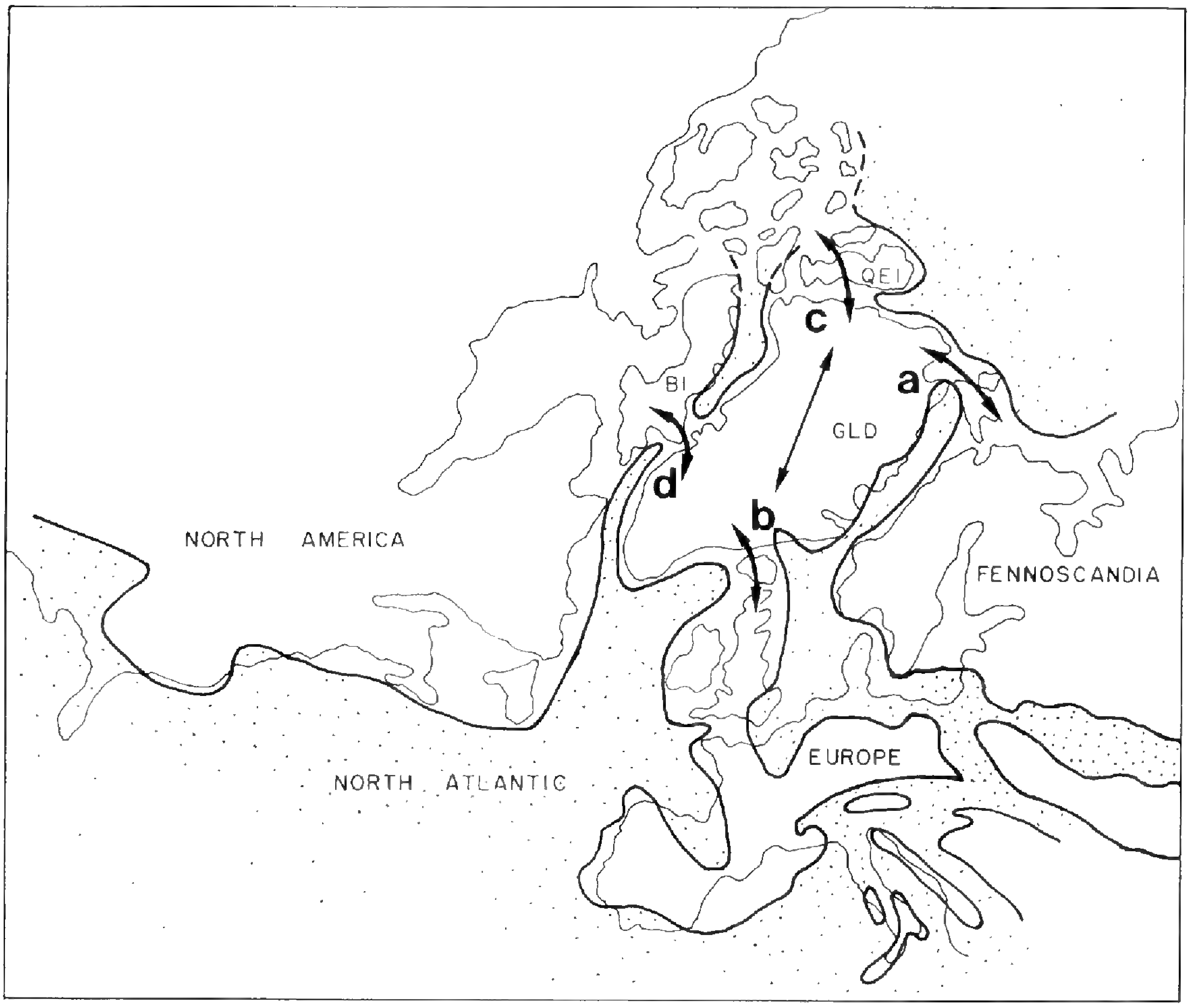
In summary, evidence for the potential and actual movement of elements of the boreotropical flora across mid-continental North America is scanty. Logic suggests that climatic changes attendant upon the retreat of first the Mid-Continental Seaway and then the Cannonball Sea, together with the rise of the Rocky Mountains, would have created a filter to the movement of moisture-loving plants. However, the timing of these events, and the nature of mid-continental climates and floras in the Paleocene and Eocene, are unknown. Further, scattered fossil evidence suggests that some elements of the boreotropical flora (e.g., *Platycarya*) did move through this area. Evidence from fossil soils suggests that closed forest may have existed in the central plains until the Early Oligocene. The Middle Eocene Clarno Flora of Oregon contains several presumably evergreen boreotropical elements (Manchester, 1981); if these did not reach the west coast of North America by way of the Bering bridge (see data of Wolfe, in press), then they must have achieved their distribution via central North America. As long as evidence for the early to middle Tertiary environments of the Great Plains is unclear, the potential importance of this area as a migration route of the boreotropical flora remains moot.

THE EUROPEAN–EASTERN NORTH AMERICAN CONNECTION

A paleofloristic link between Europe and eastern North America has been viewed as "possible" by many authors (e.g., Graham, 1964; Raven & Axelrod, 1974; Wolfe, 1975, 1977). In general, it has never been given the importance of the Beringian connection, although I suggested it earlier (Tiffney, 1980b), and Wolfe (manuscript submitted) has recently concluded that it was probably more important than the Bering bridge. A similar opinion has been held by some paleozoologists (see McKenna, 1975), who originally claimed that the Eocene faunal similarity of North America and Europe was attained by a trans-Asiatic migration route. Recent evidence, both geologic and paleontological, has suggested that this is incorrect, and McKenna (1972, 1975, 1983a) has cogently argued for the importance of North Atlantic land connections in explaining the distribution of early Tertiary vertebrates. Similarly, I believe that the North Atlantic connection has played a major part in the spread of the boreotropical flora and in the development of the similarity of the East Asian and eastern North American floras. Consideration of the North Atlantic connection will be on three levels: geologic, paleozoological, and botanical.

GEOLOGIC DATA. The potential of a North Atlantic land bridge has been recognized since Wegener's original suggestion of continental drift, but only within the last decade has definite evidence for this bridge been produced. A land link between Europe and America involves two stages: Europe to Greenland and Greenland to North America. It is appropriate to consider each separately.

The geologic evidence for a Europe-Greenland connection is excellent and has been exhaustively reviewed by McKenna (1983a), from which much of the following summary is drawn, and to which the reader is referred for references and details. McKenna recognizes two geographically and temporally separate links between Greenland and Europe: a northerly "DeGeer" route from northern Scandinavia to northern Greenland, and a southern "Thulean" route from northern Scotland through the Faeroes and Iceland to southern Greenland (MAP 3). The DeGeer route is of somewhat less interest to a discussion of the boreotropical flora for two reasons. First, it lay ten to fifteen degrees higher in latitude than the Thulean route, although it was still at a lower paleolatitude than the coeval Beringian bridge situated at almost 75°N latitude (McKenna, 1972). Second, the DeGeer route terminated in northern Scandinavia, which according to McKenna (1983a), was separated from direct contact with Europe for much of the Paleogene by the Danish-Polish trough and its southerly extension, the "Moravian portal," linking the trough to the Tethys (Pożaryska & Cuik (1976), Pożaryska (1978); see McKenna (1983a) for discussion). However, there is not agreement on the presence of this sea barrier throughout the Eocene. Plaziat (1981, *figs. 21, 22*; 1983, *fig. 5*) suggested that southwestern Europe was isolated from Fennoscandia in the Paleocene, but that the responsible seaway retreated by the Early Eocene, reconnecting the two land masses. I follow McKenna (1983a) in showing a marine barrier between southwestern Europe and Fennoscandia in MAPS 3, 4, and 6, but this is a moot point. Similarly, the Turgai Straits isolated Fennoscandia from eastern Asia for much of the Paleogene (Hoch, 1983; McKenna, 1983a). The DeGeer route was prob-



MAP 3. Generalized paleogeography of North Atlantic area in Early Eocene, showing possible routes of connection between Europe and North America. Connection "a" = McKenna's DeGeer route linking Fennoscandia and northern Greenland (GLD); "b" = McKenna's Thulean route from southwestern Europe to southern Greenland; "c" links northern Greenland to Queen Elisabeth Islands (QEI); "d" = potential link between central Greenland and Baffin Island (BI). Dispersal may have occurred in either direction over any bridge (heavy arrows); dispersal within Greenland (light arrow) may have resulted in several entry/exit route patterns. Shaded area = sea; heavy lines = paleo-coastlines; light lines = present coastlines. Assembled from, but not necessarily adhering to, McKenna (1972, 1983a, 1983b, pers. comm.), Pożaryska (1978), Heissig (1979), Buchardt (1981), Srivastava *et al.* (1981), and Pomerol (1982).

ably present as early as the Danian, although the climate of that time (Buchardt, 1978; Wolfe, 1978; Hickey, 1981a) suggests that it would be restricted to cold-tolerant organisms. This route functioned through the latest Eocene or Early Oligocene, when it was terminated by the linkage of the Greenland-Norwegian Sea and the Arctic Ocean. During the Early Eocene, warm climates may have made it passable to thermophilic biota, but the effect of winter day-length is uncertain. The Early Eocene flora from Ellesmere Island (Hickey *et al.*, 1983; Hickey, pers. comm.) appears to include only deciduous angiosperms in conjunction with a thermophilic fauna (Estes & Hutchison, 1980). This suggests that winter day-length was the limiting factor.

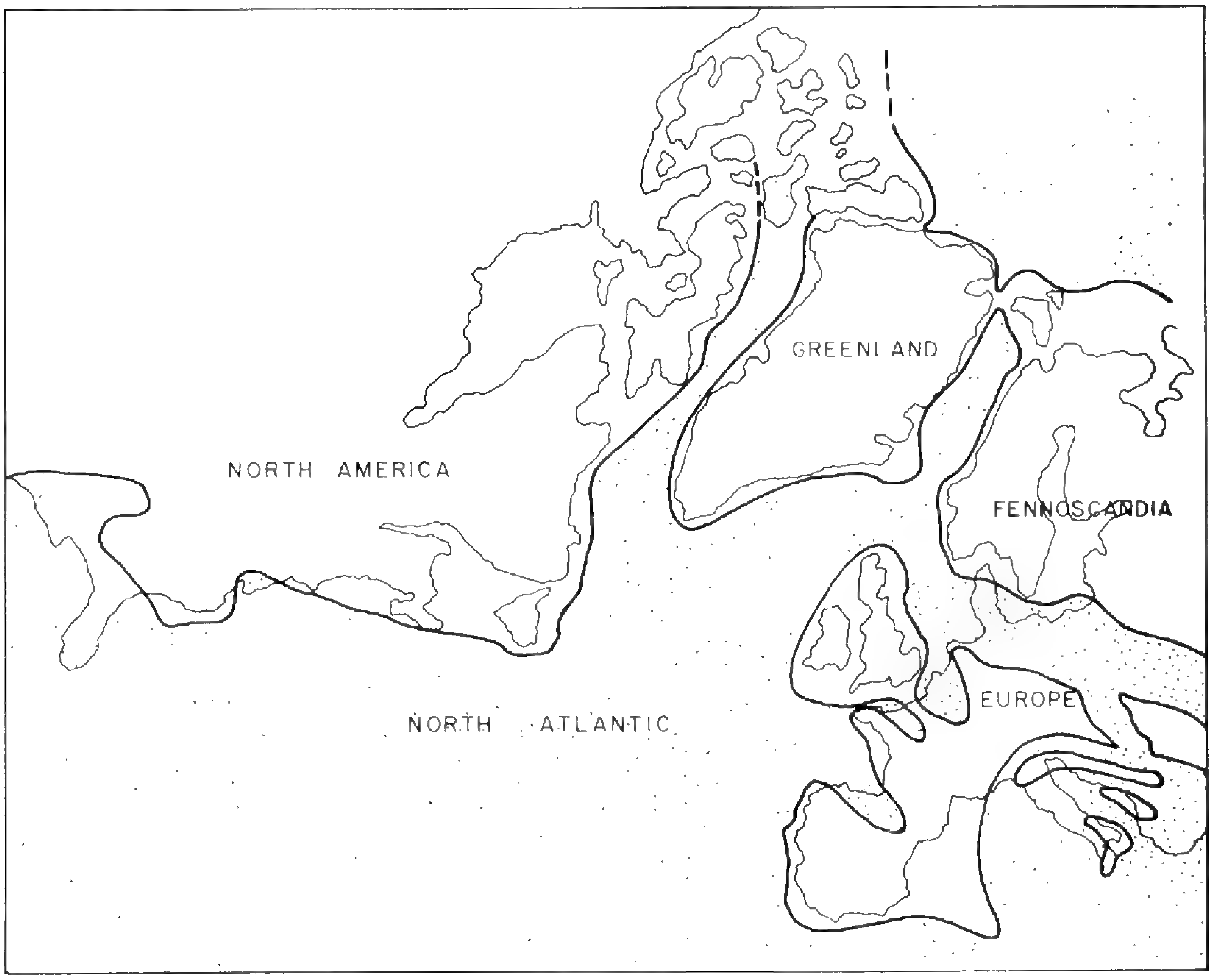
The initiation of active sea-floor spreading northwest of the British Isles in the Late Paleocene resulted in the first appearance of the Thulean bridge. Again, the cool climates of the time restricted biotic access to this route. However, the succeeding Early Eocene was a time of widespread warm climates (Wolfe, 1978; Buchardt, 1978; Collinson *et al.*, 1981), which opened the Thulean route to passage by warm-adapted organisms. Further, since this route lay between 45° and 50°N paleolatitude, winter sunlight would have been sufficient to permit the passage of evergreen taxa (MAP 3). Most evidence suggests that this connection was suddenly broken in the Early Eocene (McKenna, 1983a) or latest Paleocene (Hanisch, 1983) and was never reestablished (but see Grønlie (1979), who suggested that it may have persisted piecemeal until the mid-Miocene, and Strauch (1970, 1972), who suggested that a fairly substantial land bridge existed throughout most of the Tertiary).

The linkage between Greenland and northeastern North America across the Davis Strait is the subject of considerably more debate (e.g., Dawes & Kerr, 1982). The Davis Strait, and its extension through Baffin Bay and the Kane Basin, apparently linked the Atlantic and Arctic oceans in the latest Cretaceous and Early Paleocene. Invertebrate fossils suggest that a bridge between Greenland and the Queen Elisabeth Islands may have come into being in the Danian and have continued through much of the Eocene. Circumstantial evidence (e.g., terrestrial sediments beneath the Davis Straits (McKenna, 1983a, and pers. comm.)) exists for a land connection to the south between Greenland and Baffin Island, but the assembled data (McKenna, 1983a) are not as conclusive. The northern bridge falls at nearly the same latitude as the DeGeer route; thus, winter day-length might restrict its importance to deciduous angiosperms and conifers. The southern route is at a substantially lower latitude and would have permitted passage of evergreen taxa.

In summary, the geologic evidence suggests a clear northern connection from Scandinavia to northern Greenland and from northern Greenland to the Queen Elisabeth Islands from Late Paleocene to Late Eocene (MAP 3). A second connection from the British Isles to southern Greenland existed briefly in the Late Paleocene and Early Eocene. This probably was matched by a lower-latitude bridge from central Greenland to Baffin Island and northeastern Canada at the same time, although the geologic evidence is not clear. Certainly southwestern Europe was in connection with North America via the Thulean bridge on the east and the northern Greenland–Queen Elisabeth Islands bridge on the west during a brief portion of the Early Eocene.

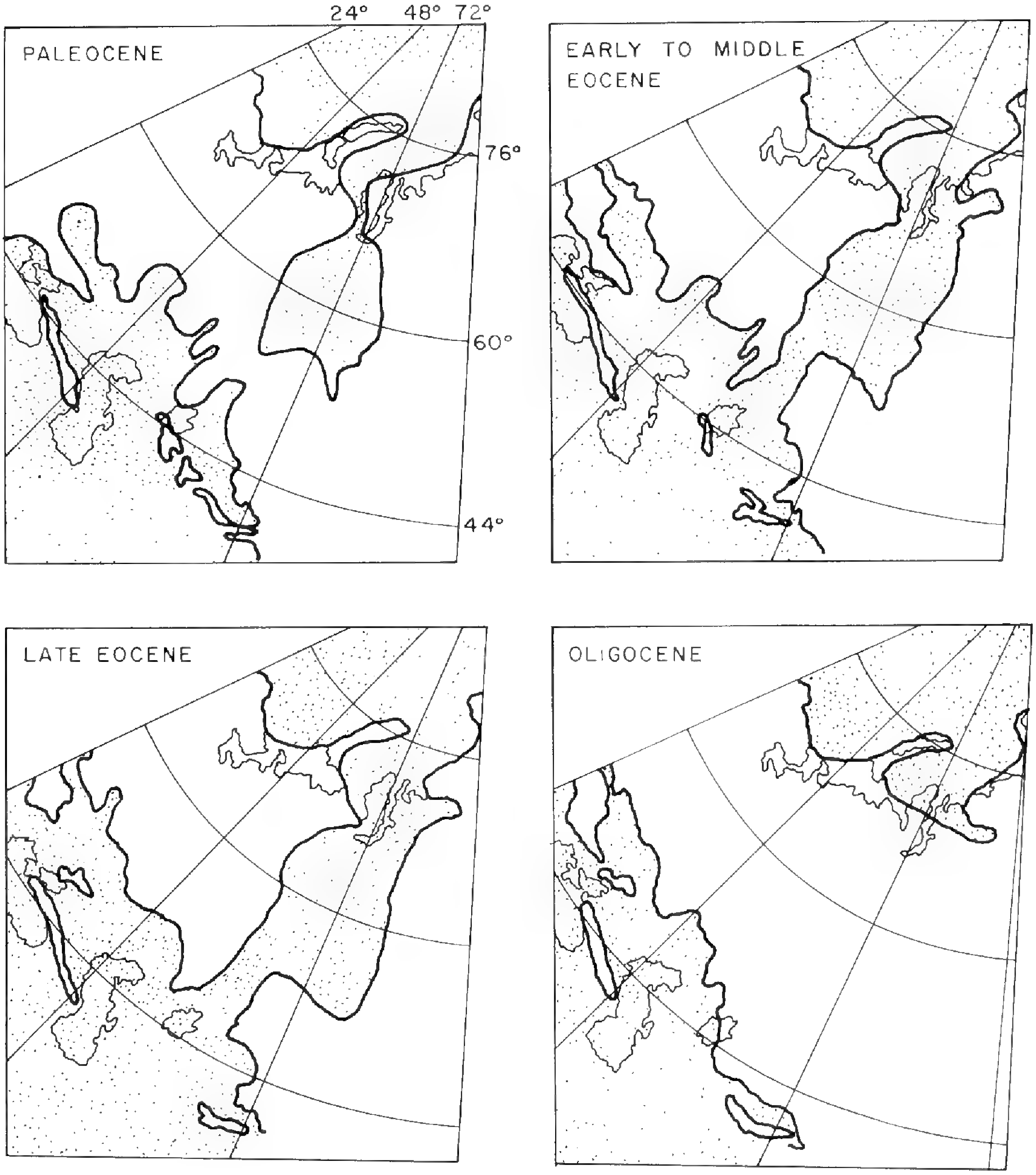
PALEOZOOLOGICAL DATA. Vertebrate paleontology supports the existence of a European–North American connection. The similarity of the Early Eocene faunas of North America and Europe was recognized by earlier workers (see McKenna, 1975, for a summary and a list of taxa in common). The degree of correspondence of the two faunas began to rise in the Late Paleocene, peaked in the Early Eocene when roughly 60 percent of the known European genera were held in common with North America (Lehmann, 1973), and then declined precipitously by the Middle Eocene. The decline in faunistic similarity probably lagged behind the actual geographic isolation, as biologic differentiation of the isolated populations took time. The rise and fall of this similarity parallels the projected appearance and demise of the Thulean route. Data concerning the early Tertiary vertebrate paleontology of Greenland are presently lacking (Hoch, 1983; McKenna, 1983a), curtailing a more exact description of the exchange.

Botanical data. Paleobotanical and botanical data regarding the Atlantic bridge are less common than paleozoological data. However, in the context of the geologic and vertebrate paleontological information given above, I believe that a convincing, if inferential, case can be made for passage of the boreotropical flora across the Atlantic bridge. Four lines of botanical data are considered. First, several fossil taxa of eastern North America are specifically similar to fossils known from the Tertiary of Europe. *Nypa* (Arnold, 1952; Tralau, 1964) and *Wetherellia* (Mazer & Tiffney, 1982) are classic European early Tertiary taxa, and the New World species are virtually identical to their Old World counterparts. Similarly, *Microdiptera parva* from Brandon (Tiffney, 1981b) has previously been described only from Europe and western Siberia. Second, several genera from the Brandon Lignite (*Phellodendron, Euodia, Turpinia, Alangium,* and *Symplocos*) are thermophilic elements that were also common in the European Paleogene. *Symplocos* provides a particular example of this pattern, because the genus is very diverse in the European Tertiary (Mai, 1970) and is disproportionately represented in the Brandon Flora by at least three species. Third, several modern taxa known as fossils in the European Tertiary presently survive only in eastern North America. Among flowering plants these include *Asimina* Adanson (Annonaceae), *Calycocarpum* Nutt. ex Torrey & Gray (Menispermaceae), *Comptonia* L'Hér. ex Aiton (Myricaceae), *Decodon* J. F. Gmelin (Lythraceae), *Dulichium* Pers. (Cyperaceae), *Fothergilla* L. (Hamamelidaceae), *Leitneria* Chapman (Leitneriaceae), *Polanisia* Raf. (Cleomaceae), *Proserpinaca* L. (Haloragidaceae), *Ptelea* L. (Rutaceae), *Robinia* L. (Leguminosae), and *Sabal* Adanson and *Serenoa* Hooker f. (Palmae). An interesting parallel is provided by the hickory aphid (*Longistigma caryae* Harris), which is presently restricted to North America but is reported from Upper Miocene–Lower Pliocene sediments in Iceland (Heie & Friedrich, 1971). An additional group of taxa is common to the extant floras of Europe and North America. Although many of these taxa attained this range in the later Tertiary or Quaternary (see Löve & Löve, 1963, for a general discussion of late and post-Tertiary links between Europe and North America), many others (e.g., *Fagus* L., *Juglans,* or the gasteromycete *Lycoperdon* Tourn.; see Demoulin, 1973) appear to represent remnants of generally dispersed boreotropical taxa. Fourth, as discussed above, several boreotropical taxa are known as fossils from eastern North America. If the Bering bridge is less important as a North American access route for evergreen boreotropical taxa (see Wolfe, manuscript submitted), then these taxa presumably came and went from North America via the North Atlantic bridge. In summary, the plant evidence is scattered and circumstantial. Taken alone, any of the above examples is weak since it is never clear where a single taxon may have occurred in the past in addition to those places from which it is presently known as a fossil. However, in its entirety, the plant evidence does not contradict the existence of a North Atlantic bridge and appears to support it.



MAP 4. Generalized paleogeography of North Atlantic area in Late Eocene, showing changes in land continuity following spreading in Greenland-Norwegian Sea and Davis Straits between Greenland and Baffin Island. Connections between Queen Elisabeth Islands and Greenland, and Greenland and northern Europe, probably existed but were likely closed to thermophilic organisms by Late Eocene climatic decline. Conventions and sources as in MAP 3.

In conclusion, geologic data indicate the presence of two Early Eocene bridges between Greenland and Europe (one to Fennoscandia and one to southwestern Europe), and two Early Eocene land bridges from Greenland to North America (one via the Queen Elisabeth Islands, and a less well defined one from Greenland to Baffin Island) (MAP 3). Evidence from vertebrate paleontology suggests that these routes were used by terrestrial and freshwater vertebrates. Flowering plants must also have passed across these same bridges, but evidence of their nature (deciduous or evergreen; cool tolerant or intolerant) is not directly available. However, it is unlikely that the vertebrates common to Europe and North America would have strayed far from familiar vegetational environments or food sources. For this reason, it can be assumed that the vertebrates migrated across the North Atlantic land bridge in conjunction with the boreotropical flora. Further, a significant proportion of this fauna was herbivorous or omnivorous (McKenna, 1975), and such animals would be expected to disperse their food plants. Thus, while the individual elements of evidence do not clearly indicate passage of the boreotropical flora across the Early Eocene North Atlantic land bridge, the sum of information argues strongly that this was the case.



Map 5. Sequential generalized paleogeography showing advance and retreat of Turgai Straits (shaded area) in central Asia from Paleocene through Oligocene time. Heavy lines = paleocoastlines, light lines = present coastlines. After Vinogradov (1967–1968).

Early Tertiary Floristic Links between Europe and Eastern Asia

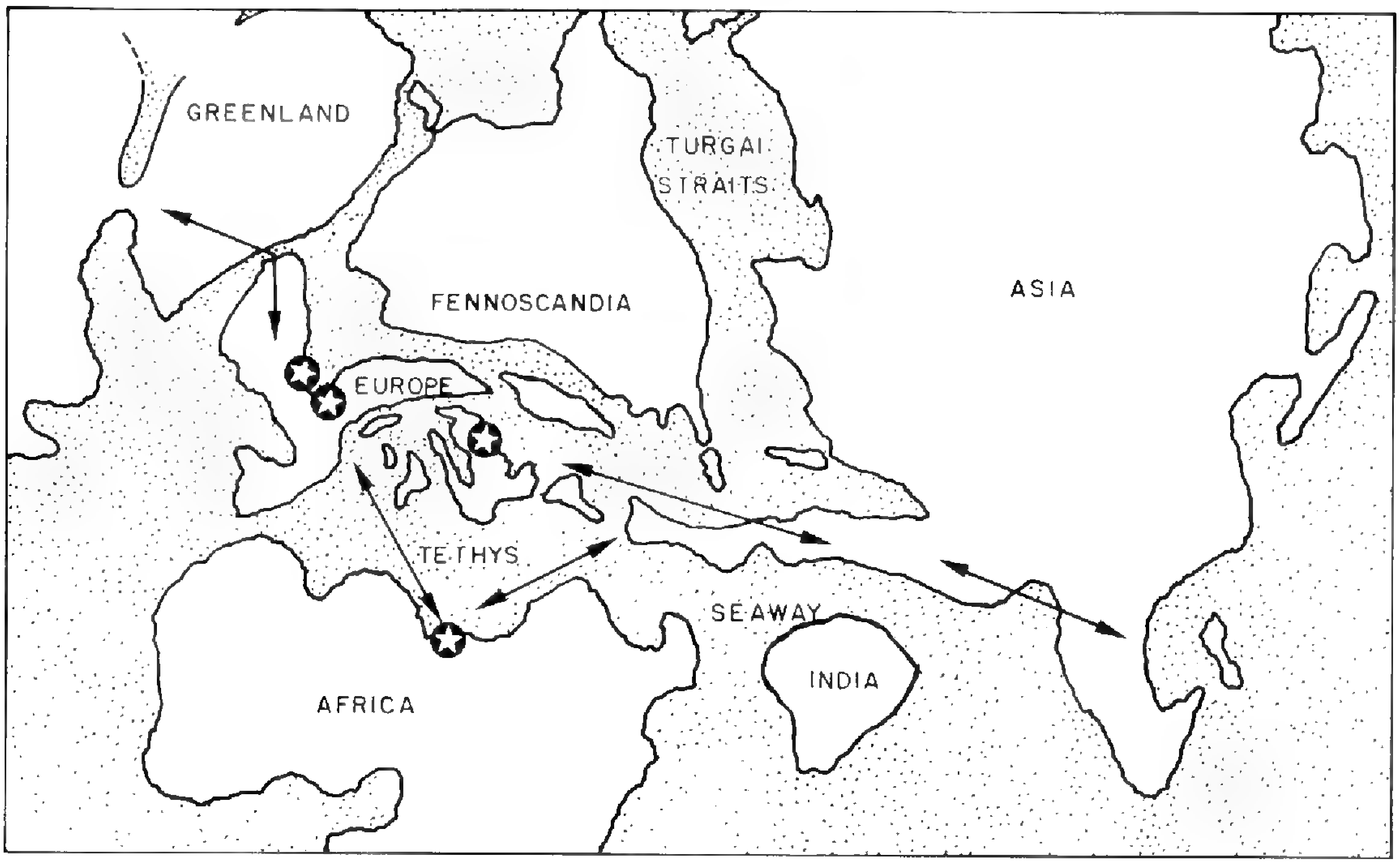
If eastern North America shared an appreciable portion of the boreotropical flora with Europe, then some degree of the present similarity between the floras of eastern Asia and eastern North America must have involved early or middle Tertiary floristic exchange between Europe and eastern Asia. The evidence for a Tertiary European-Asian link is scattered. The Turgai Straits (Map 5) separated Europe from western Siberia from the mid-Mesozoic to the end of the Eocene and are generally presumed to have formed a biogeographic barrier to animals (Kurtén, 1966; Muller, 1970; McKenna, 1975, 1983a; Russell, 1975; Hoch, 1983), although the severity of this barrier has been disputed (Savage & Russell, 1983). Its effect on plants is unclear. This seaway may have been bridged intermittently in the Eocene, linking western Siberia with Fennoscandia (Russell, 1975; Heissig, 1979; Chow & Zheng, 1980; McKenna, 1983a, 1983b). According to McKenna (1983a), Fennoscandia and southwestern Europe were not directly linked in the Paleocene and Eocene (but note the different opinion of Plaziat (1981) mentioned above). If so, biotic exchange between western Siberia and southwestern Europe in the Eocene would have involved dispersal from Fennoscandia to Greenland via the DeGeer route, and then from Greenland to southwestern Europe by the Thulean route—a roundabout track, and one crossing several climatic zones. There is no particular plant evidence applicable to this possibility. The final closure of the Turgai Straits commenced in the Early Oligocene, initiating an influx of Asiatic and southeastern European vertebrate taxa into southwestern Europe (but see Heissig, 1979, who believes that the influx is largely Balkan in origin, coming up connected islands in the Tethys from the southeast).

This resulted in what Stehlin (1909) termed the "Grande Coupure," an Early Oligocene event in which roughly 50 percent of the preceding mammal fauna went extinct and was replaced by new taxa (McKenna, 1983b). The new mammals were presumably accompanied by new plants, and indeed the Early Oligocene was a time of change and modernization of the western European flora, although the details of this transition have not been worked out.

Probably the most important avenue of dispersal of the boreotropical flora across Eurasia involved the Tethys Seaway, which has shaped the present and past distributions of a variety of organisms (e.g., corals and seagrasses (McCoy & Heck, 1976), and echinoderms (Ali, 1983)). The classic boreotropical assemblage is the London Clay Flora, located on the "midpoint" of the Eocene Tethys Seaway (MAP 6). Floras of similar composition exist in the Eocene of central Europe (Palamarev, 1973) and in the Eocene and Oligocene of Egypt (Chandler, 1954; Bown *et al.*, 1982). A single fruit of *Anonaspermum* Reid & Chandler from the Paleogene of Pakistan (Tiffney, unpubl. data) hints at the further eastward extension of elements of this flora. It is unclear how far east along the Tethys the flora ranged. McKenna (1983b) notes that the Paleocene terrestrial faunas of China (C. K. Li & Ting, in press) are quite distinct from those of the rest of the Northern Hemisphere, suggesting a distinct biotic province at the eastern end of the Tethys in the earliest Tertiary. Thus, although the Eocene flora of western Europe is similar to the modern flora of Southeast Asia, it may have been less so to the Eocene floras of Southeast Asia. The similarity between the extant floras of eastern Asia and the Tertiary floras of Europe continued through the latest Tertiary, often involving similarity on the species level in the later Miocene and Pliocene (Tralau, 1963). This suggests that some amount of European-Asian interchange occurred after the decline in importance of the North Atlantic land bridge, and even as the Tethys Seaway began to fragment.

ORIGINS AND DIRECTIONS

This discussion has often implied a place of origin and a direction of subsequent spread of the boreotropical flora. This is a complex topic and is treated



MAP 6. Generalized paleogeography of the Tethys Seaway, Early to Middle Eocene, showing possible routes of movement of boreotropical flora along seaway (arrows) and known occurrences of floras similar to that of London Clay (stars). Assembled from, but not necessarily adhering to, data from Vinogradov (1967–1968), Smith *et al.* (1973), Novodvorskaja and Janovskaja (1975), Pożaryska and Cuik (1976), Smith and Briden (1977), Pożaryska (1978), Heissig (1979), Buchardt (1981), Plaziat (1981), Srivastava *et al.* (1981), Parrish *et al.* (1982), Pomerol (1982), and McKenna (pers. comm.).

separately (see Tiffney, 1985), but certain aspects of it require consideration here.

The boreotropical flora could have evolved in tropical, temperate, or polar regions during the early Tertiary. Our present knowledge of the Tertiary paleobotanical record of the tropics is too poor to provide any but the most speculative evidence. Knowledge of temperate regions is far better, but even with the information available we lack the temporal resolution to determine place of first appearance. Knowledge of the boreal zone is limited but contributes some information. Contrary to the geofloral hypothesis (e.g., Axelrod, 1966), the Late Cretaceous–early Tertiary North Pole is not an important center of origin. Instead, it appears to have supported a species-poor flora of deciduous taxa (see Wolfe, 1977; Hickey *et al.*, 1983; Hickey, pers. comm.), several members of which intermingled with the boreotropical flora when it appeared. However, this deciduous polar forest generally appears to have remained to the north of the boreotropical forest. Thus, although these deciduous taxa played a part in the boreotropical forest, the Beringian and/or Atlantic land bridges cannot be considered the points of origin of the boreotropical flora but only as passageways in its spread.

Spread implies direction. However, I do not believe that it is presently possible to trace the direction of spread of elements of the boreotropical forest across any of the bridges or barriers discussed above. For this reason I have attempted to describe biogeographic corridors in a neutral manner; if any phraseology in the preceding seems to imply directionality, it is unintentional. It is quite likely, however, that spread will ultimately be found to involve the movement of different lineages at different times by different routes (see Tiffney, 1985). Elucidation of this assumption will only follow from careful biogeographic analysis of individual plant taxa. The use of cladistic methodology in this study (e.g., Donoghue, 1983a, 1983b, for *Viburnum*) may be very useful in demonstrating the geographic history of movement within or between taxa.

POST-EOCENE HISTORY OF THE BOREOTROPICAL FLORA IN EASTERN NORTH AMERICA

If the boreotropical flora had full access to eastern North America in the Early Eocene, the question remains as to whether its lower current diversity is a function of the Eocene-Oligocene climatic deterioration, of the Pleistocene deterioration, or of a combination of the two. Wang (1961) and Wolfe (1977) suggested that the Eocene-Oligocene climatic deterioration caused outright extinction of many boreotropical taxa, including the majority of the thermophilic elements, in eastern North America. Wolfe further suggested that the subsequent diversification of the eastern North American mixed mesophytic forest was restricted by the absence of these thermophilic evergreen taxa. This is in contrast to the situation in western North America, where a residual evergreen vegetation contributed greatly to the growth in diversity of the mixed mesophytic forest in the Miocene (Wolfe, 1969, 1977). Perhaps the only fossil evidence that bears on this supposition is that of the Brandon Lignite. The age of the deposit is presently accepted as post-Eocene (Wolfe & Barghoorn, 1960; Frederiksen, 1984 and pers. comm.), although Berry (1919) once suggested that it was Eocene. This flora includes several thermophilic boreotropical taxa (e.g., *Euodia, Alangium, Turpinia*) no longer extant in eastern North America. This implies that—at least in some portion of eastern North America—boreotropical elements survived the Late Eocene–Early Oligocene climatic deterioration but went extinct in the later Tertiary or Quaternary.

Although it is not presently possible to indicate a particular period of time for this extinction, suggestions can be made as to why extinction had a stronger effect in eastern North America than in eastern Asia. Eastern North America is geographically smaller than eastern Asia and would be expected to have a smaller flora measured on a species per area basis. The lower topography of eastern North America offers a more limited range of habitats than is encountered in eastern Asia (Wolfe, 1977). Further, the Appalachian Mountains are oriented north–south, and in conjunction with the Mississippi River valley, they provide a geographic funnel conveying cold Arctic air masses directly to the Caribbean. This contrasts with the geography of eastern Asia, where many of the mountain ranges serve as shields from cold air masses. As a result, locations in eastern North America and eastern Asia may have similar mean monthly minimum temperatures, but the absolute minima in North America are considerably lower (Wolfe, 1979). Finally, starting in the Middle Eocene, the rain shadow of the western mountains of North America created a barrier of dry environments in central North America. The southerly extent of this barrier, and its effect on floristic exchange between southeastern North America and the highlands of Mexico and Central America, is unclear. Boreotropical elements are known from the Oligocene of Puerto Rico (Graham & Jarzen, 1969). Temperate elements of the boreotropical flora were present in Mexico in the Middle Miocene and appear to have moved southward in the later Tertiary (Graham, 1973, 1976). The history of more thermophilic boreotropical taxa in this area is unknown. It is possible that the zone of central North American dry climates caused the extinction of those boreotropical taxa forced southward by winter temperature extremes. Although this situation would have been most dramatic in the Quaternary (e.g., Delcourt & Delcourt, 1981), similar events could have occurred earlier in the Tertiary, incrementally curtailing the floristic diversity of eastern North America. Like the biogeography and environments of the mid-continental area in the early and middle Tertiary, those of the southeastern United States and northern Central America offer fertile ground for synthetic inquiry.

In conclusion, the Eocene-Oligocene climatic deterioration may have influenced the diversity of the eastern North American boreotropical flora, but it did not decimate the flora. The specific pattern and timing involved in the depauperization of the eastern North American flora during the later Tertiary cannot be discerned at this time.

SUMMARY

The early Tertiary boreotropical flora of eastern North America was probably as diverse as that of any other portion of the contemporary Northern Hemisphere. This conclusion is supported by limited paleobotanical data from eastern North America and the strong paleozoological and paleogeographic evidence that eastern North America and southwestern Europe were linked by North Atlantic land bridges in the latest Paleocene or the earliest Eocene when the boreotropical flora was reaching its maximum extent.

Western North America and eastern Asia probably derived their shared component of the boreotropical flora by both the Atlantic and Bering land bridges; the relative contribution of each is unclear at this time. The potential for early Tertiary floristic exchange between eastern and western North America is an important question for which few data exist. Although dry environments may have been present in central North America by the Middle Eocene, they may have been broken by bands of forest or by riverine gallery forests.

The similarities of the modern floras of eastern Asia and eastern North America are probably due to an early Tertiary linkage between the two areas involving the North Atlantic land bridges and Europe. However, the flora of eastern North America cannot be considered as solely the product of exchange across a North Atlantic bridge; it is a composite of elements derived from Atlantic, Polar, Mexican and Central American, and western North American sources, in which the Atlantic element may dominate. This assumption can be tested by careful examination of European and eastern and western North American fossils in light of modern taxa of eastern North America, Mexico and Central America, and Asia. This implies that modern systematists studying plants with Tertiary relict distributions must consider that eastern North America may have harbored phylogenetically distinct and important taxa in the Tertiary, but that these are now extinct.

The present lower diversity of the flora of eastern North America relative to that of eastern Asia appears to be a "post-boreotropical flora" phenomenon. The geography of eastern North America is less diverse than that of eastern Asia and favors greater winter extremes. Further, a moisture barrier may occasionally or consistently have separated eastern North America from Mexico and Central America. As a result of these features, the mid- and late Tertiary derivatives of the boreotropical flora in eastern North America suffered greater extinction than did their counterparts in eastern Asia. The timing of this extinction in eastern North America (later Tertiary or Quaternary) is not clear from present evidence.

ACKNOWLEDGMENTS

I wish to thank Karl J. Niklas (Cornell University), Jack A. Wolfe (U. S. Geological Survey, Denver), Leo J. Hickey (Yale University), Alan Graham (Kent State University), and Malcolm C. McKenna (American Museum of Natural History) for criticism and suggestions; Karl M. Waage (Yale University) for assistance with the paleogeographic literature; Michael Donoghue (San Diego State University) for discussion on cladistics and geography; Zhao-bo Yu (Yale University) for assistance with Chinese; and Karen Esseichick for assistance in data collection. Research was supported in part by NSF grants DEB 79-05082 and BSR 83-06002.

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PEABODY MUSEUM OF NATURAL HISTORY AND DEPARTMENT OF BIOLOGY
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RAPHANUS BOISSIERI (CRUCIFERAE), A NEW SPECIES FROM THE MIDDLE EAST

IHSAN A. AL-SHEHBAZ

IN 1842 Edmond Boissier described *Brassica aucheri* from a specimen collected by Aucher-Éloy near Mosul in Mesopotamia (Iraq). He later (1849) transferred the species to *Raphanus* L. (*R. aucheri* (Boiss.) Boiss.) and cited two additional collections from western Persia (Iran) and Galilee (northern Israel). Finally, in 1867 he placed the species in the monotypic section *Hesperidopsis* Boiss. and cited new collections from what is now southern Lebanon. However, Boissier did not realize that he was dealing with two very distinct species, one from Iraq and Iran and another from the eastern Mediterranean area (Lebanon and Israel) (see MAP 1).

Schulz (1919) was the first to recognize two species in this complex by retaining the eastern Mediterranean plant as *Raphanus aucheri* and transferring the Iraqi-Iranian species to *Sinapis* L. (*S. aucheri* (Boiss.) O. E. Schulz). However, he did not realize that both names were based on the same type, collected by Aucher-Éloy. Many subsequent authors, particularly Hedge and Lamond (1980), Hedge and Rechinger (1968), Mouterde (1970), and Zohary (1966), have followed Boissier by considering the plants of both areas as conspecific, while Zohary and colleagues (1980) accepted two species following Schulz. Greuter and Burdet (1983) have raised sect. *Hesperidopsis* sensu Schulz to a genus (*Quidproquo* Greuter & Burdet) without presenting supporting evidence for its distinctness from *Raphanus*. In my opinion, the eastern Mediterranean plant is appropriately assigned to *Raphanus*. However, it is described below as a new species, *R. boissieri*, because the name *R. aucheri* (Boiss.) Boiss. that has been applied to this species is based on *Brassica aucheri*, the type specimen of which (*Aucher-Éloy 203*) is the nomenclatural type of *Sinapis aucheri*. *Quidproquo confusum* Greuter & Burdet cannot be used because a type specimen was not designated.

Raphanus boissieri Al-Shehbaz, sp. nov.

> *Raphanus aucheri* (Boiss.) Boiss. Diagn. Pl. Orient. Nov. **2**(8): 45. 1849, in part.
> *Quidproquo confusum* Greuter & Burdet, Willdenowia **13**: 94. 1983.

Herba annua erecta, 2–6(–8) dm alta, retrorse hispida. Folia basalia petiolata, subrosulata, lyrata vel pinnatisecta, (5.5–)8–11(–20) cm longa, 2–7 cm lata. Racemi ebracteati; pedicelli floriferi recti, ascendentes, fructiferi valde curvati, 5–10(–13) mm longi. Sepala erecta vel patentia, (3–)5–8(–11) mm longa. Petala obovata, unguiculata, flava, (8–)10–15(–20) mm longa; unguicula 4–8(–12) mm

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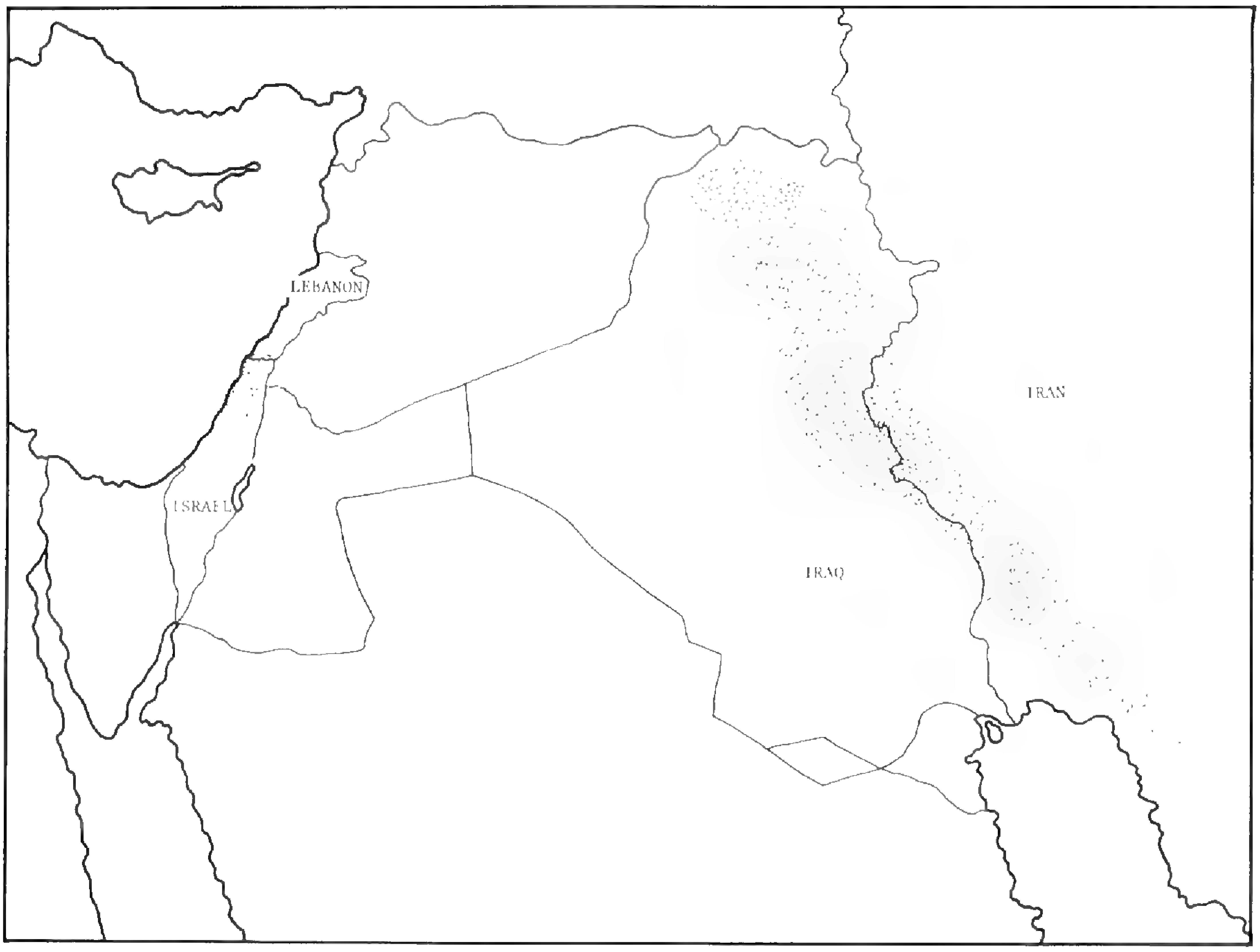

MAP 1. Distributions of *Raphanus boissieri* (left; Israel-Lebanon) and *Sinapis aucheri* (right; Iraq-Iran).

longa. Siliqua indehiscens, suberosa, cylindrica, pendula, retrorse hispida, 5–10 cm longa, 2–4.5 mm lata; segmenta inferiora asperma, obsoleta; rostrum subtorulosum, lomentaceum, 8–12 spermum. Semina oblonga, humiditate nonmucilaginosa, 2–2.5 mm longa.

Annual erect herb, retrorsely hispid throughout, rarely glabrescent above, 2–6(–8) dm high. Basal leaves nearly rosulate, petiolate, lyrate to pinnatisect, oblong to oblanceolate, (5.5–)8–11(–20) by 2–7 cm; terminal lobe broadly obovate or ovate, dentate to crenate, larger than lateral lobes. Upper cauline leaves subsessile or short petiolate, oblong to linear or lanceolate, rarely lyrate, entire or dentate. Inflorescence an ebracteate corymbose raceme, greatly elongating in fruit; flowering pedicels ascending, straight; fruiting pedicels strongly curved and usually forming loop, 5–10(–13) mm long. Sepals erect or sometimes spreading, saccate, oblong to nearly linear, obtuse, (3–)5–8(–11) mm long, glabrous or setulose; petals obovate, clawed, (8–)10–15(–20) mm long, claw 4–8(–12) mm long, yellow or rarely whitish, without or rarely with dark veins; lateral nectar glands usually flat, median ones ovoid or cylindrical; stamens tetradynamous, anthers oblong. Siliques pendulous, indehiscent, lomentaceous, subtorulose, cylindrical, straight or slightly curved, 5–10 cm by 2–4.5 mm, corky, retrorsely hispid or scabrous, smooth or slightly striate; lower segment seedless, abortive or obsolete; beak 8- to 12-seeded; style 1–2 mm long, stigma

FIGURE 1. Mature fruits of *Raphanus boissieri* (left) and *Sinapis aucheri* (right).

capitate. Seeds oblong, 2–2.5 mm long, brown, nonmucilaginous when wet; cotyledons conduplicate.

TYPE. Palestine [Israel], Galilee, April–May 1846, *E. Boissier s.n.* (holotype, GH!; isotypes, G-BOIS!).

SPECIMENS EXAMINED. **Israel:** Hunin, Galilee, *Bornmüller 114* (G-BOIS); Banias, *Boissier s.n.*, April–May 1846 (G-BOIS); Mt. Tabur, *Boissier s.n.*, May 1846 (G-BOIS). **Lebanon:** Saida, *Blanche s.n.* (G-BOIS); between Rachaya and Hasbaya, *Gaillardot s.n.* (G-BOIS).

Raphanus boissieri is endemic to southern Lebanon and northern Israel. Zohary and colleagues (1980) and Mouterde (1970) have listed it as *R. aucheri* from southern Sinai (Egypt) and Iskenderun (Turkey), respectively.

Raphanus boissieri resembles *Sinapis aucheri* in the curvature of the fruiting pedicels, the orientation and the corky texture of the fruits, and the retrorse pubescence of the fruits and stems. It is very difficult to distinguish between the two from specimens lacking fruits, and this may have been the main factor behind Boissier's failure to treat the eastern Mediterranean and the Iraqi-Iranian plants as distinct species. To my knowledge, only one specimen of *S. aucheri* with mature fruits is present in Boissier's herbarium, and this was described by Boissier (1888) as *Enarthrocarpus tragicerus* Boiss. & Hausskn. *Raphanus boissieri* is easily distinguished from *S. aucheri* by its oblong seeds and its fruits with a smooth, straight upper segment and a seedless, indehiscent, abortive or obsolete lower segment. In *S. aucheri* the seeds are globose, and the fruits usually have a falcately curved upper segment with coarse tubercles or thickenings opposite the seeds and a dehiscent, several-seeded, well-developed lower segment (see FIGURE 1).

Sinapis aucheri is anomalous in this genus because of its several-seeded, torulose, corky beaks and its haploid chromosome number of seven (Al-Shehbaz & Al-Omar, 1982; Aryavand, 1975). The other species of *Sinapis* have 1- or 2-seeded, nontorulose, noncorky beaks and a chromosome number of n = 9 or 12 (Gómez-Campo & Hinata, 1980).

ACKNOWLEDGMENTS

I wish to thank P. F. Stevens for checking the Latin, B. Nimblett for typing the manuscript, J. Lupo for photographing the fruits, C. Gómez-Campo for sending the seeds of *Sinapis aucheri,* and E. B. Schmidt and S. A. Spongberg for editorial help.

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Journal of the Arnold Arboretum *April, 1985*

CONTENTS OF VOLUME 66, NUMBER 2

Volume 66, Number 1, including pages 1–121, was issued January 22, 1985.

JOURNAL OF THE ARNOLD ARBORETUM

HARVARD UNIVERSITY VOLUME 66 NUMBER 3

ISSN 0004–2625

Journal of the Arnold Arboretum

The *Journal of the Arnold Arboretum* (ISSN 0004-2625) is published quarterly in January, April, July, and October for $50.00 per year, plus $5.00 postage for addresses outside of the United States, by the Arnold Arboretum of Harvard University. It is printed and distributed by the Allen Press, Inc., 1041 New Hampshire Street, Lawrence, Kansas 66044. Second-class postage paid at Lawrence, Kansas. POSTMASTER: send address changes to *Journal of the Arnold Arboretum,* ℅ Allen Press, Inc., P. O. Box 368, Lawrence, Kansas 66044.

Subscriptions and remittances should be sent to *Journal of the Arnold Arboretum,* 1041 New Hampshire Street, Lawrence, Kansas 66044, U. S. A. Claims will not be accepted after six months from the date of issue.

Volumes 1–51, reprinted, and some back numbers of volumes 52–56 are available from the Kraus Reprint Corporation, Route 100, Millwood, New York 10546, U. S. A.

Printed at Allen Press, Inc., Lawrence, Kansas

COVER: The stylized design appearing on the Journal and the offprints was drawn by Karen Stoutsenberger.

JOURNAL
OF THE
ARNOLD ARBORETUM

VOLUME 66 JULY 1985 NUMBER 3

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

IHSAN A. AL-SHEHBAZ

Tribe **Brassiceae** [A. P. de Candolle, Syst. Nat. **2**: 152. 1821.]

Annual, biennial, or perennial herbs [sometimes subshrubs or shrubs], unarmed [rarely spiny], glabrous or with simple trichomes only. Inflorescence usually an ebracteate corymbose raceme, often greatly elongated in fruit; flowers few to many [rarely solitary]. Sepals erect or spreading, saccate at base or not. Petals usually obovate, clawed. Stamens 6; filaments without [very rarely with] a basal appendage. Median nectar glands present or absent. Stigmas entire or 2-lobed, the lobes sometimes decurrent. Siliques usually differentiated into lower (valvular) and upper (beak) segments, sometimes transversely jointed and breaking into parts, occasionally lomentaceous [or samaroid or nutlike],

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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-8111520 (C. E. Wood, Jr., principal investigator), under which this research was done, and BSR-8303100 (N. G. Miller, principal investigator). This account, the 108th in the series, follows the format established in the first paper (Jour. Arnold Arb. **39**: 296–346. 1958) and continued to the present. The area covered by the Generic Flora includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with information about extraregional members of a family or genus in brackets [ ]. The references that I have not verified are marked with asterisks.

I am most grateful to Carroll Wood for his continuous advice and help during the preparation of this paper, and particularly for his critical review of the manuscript. I am indebted to Norton G. Miller, George K. Rogers, and César Gómez-Campo, as well as to Barbara Nimblett for the typing of the manuscript. I am grateful to Elizabeth B. Schmidt and Stephen A. Spongberg for their editorial advice.

The illustrations were made by Karen Stoutsenberger (FIGURE 1) and Rachel A. Wheeler (FIGURE 2) under earlier grants.

[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.

Journal of the Arnold Arboretum **66**: 279–351. July, 1985.

terete, angular, or flattened parallel [rarely perpendicular] to the septum, variable in length, shape, and size; lower segment dehiscent or indehiscent, 1- to many-seeded, rarely seedless and abortive or altogether lacking; upper segment indehiscent, 1- to several-seeded, rarely seedless and resembling the style or obsolete. Seeds mucilaginous or not when wet, wingless [or winged], uniseriately or biseriately arranged in each locule; cotyledons conduplicate, very rarely accumbent or incumbent, usually emarginate. Base chromosome numbers 6–13, 15, 17. (Including Cakilineae DC., Calepineae Godron, Erucarieae DC., Psychineae DC., Raphaneae DC., Velleae DC., Zilleae DC.) TYPE GENUS: *Brassica* L.

A natural tribe of 52 genera and about 230 species in six subtribes centered in the southwestern Mediterranean region, particularly Algeria, Morocco, and Spain (where some 41 genera are either endemic or exhibit maximum diversity), and extending eastward into India and Pakistan and southward into South Africa, with a poor representation in the New World. Three genera, *Conringia* Heister ex Fabr. (six species), *Enarthrocarpus* Labill. (five species), and *Erucaria* Gaertner (eight species), have diversified in the eastern Mediterranean, while *Physorrhynchus* Hooker (two species) and the monotypic *Chalcanthus* Boiss., *Douepia* Camb., *Fortuynia* Shuttlew., and *Pseudofortuynia* Hedge are endemic to parts of Iran, Afghanistan, and Pakistan. The tribe is represented in the southeastern United States by 11 genera and 21 species, of which only four of *Cakile* Miller are indigenous; the remainder are weeds most likely introduced from Europe or southwestern Asia.

The Brassiceae are the most distinctive and the most natural of all tribes of the Cruciferae. The great majority of members are characterized by having conduplicate cotyledons and/or two-segmented (occasionally called heterocarpic) siliques that contain seeds in one or both segments. These features are unknown elsewhere in the family. Segmented siliques are found in 32 genera of the tribe, and with the exception of *Ammosperma* Hooker f. (monotypic), *Pseuderucaria* (Boiss.) O. E. Schulz (three species), and *Conringia,* all of which have accumbent or incumbent cotyledons, the remaining genera with unsegmented siliques have conduplicate cotyledons. Nonconduplicate cotyledons characterize all species of *Cakile* and the closely related *Erucaria,* but these have strongly two-segmented siliques. *Calepina* Adanson (monotypic), *Orychophragmus* Bunge (monotypic; China), and *Sprygini*a Popov (six species; Central Asia) have traditionally been placed in the Brassiceae but have been excluded by Gómez-Campo (1980a) because they lack the typical features of the tribe. The removal of the last two genera is justified, but *Calepina* has somewhat conduplicate cotyledons (FIGURE 1o) and is without close relatives outside the tribe. It seems, therefore, more appropriate to retain it here.

Gómez-Campo (1980a) has proposed significant alterations to the comprehensive subtribal classification of Schulz (1919, 1923). Subtribes Zillinae (DC.) O. E. Schulz (four genera) and Vellinae Prantl (ten genera including those of the Savignyinae Hayek) are not represented in our flora. Subtribe Cakilinae (DC.) O. E. Schulz (cotyledons lanceolate or linear, accumbent or incumbent;

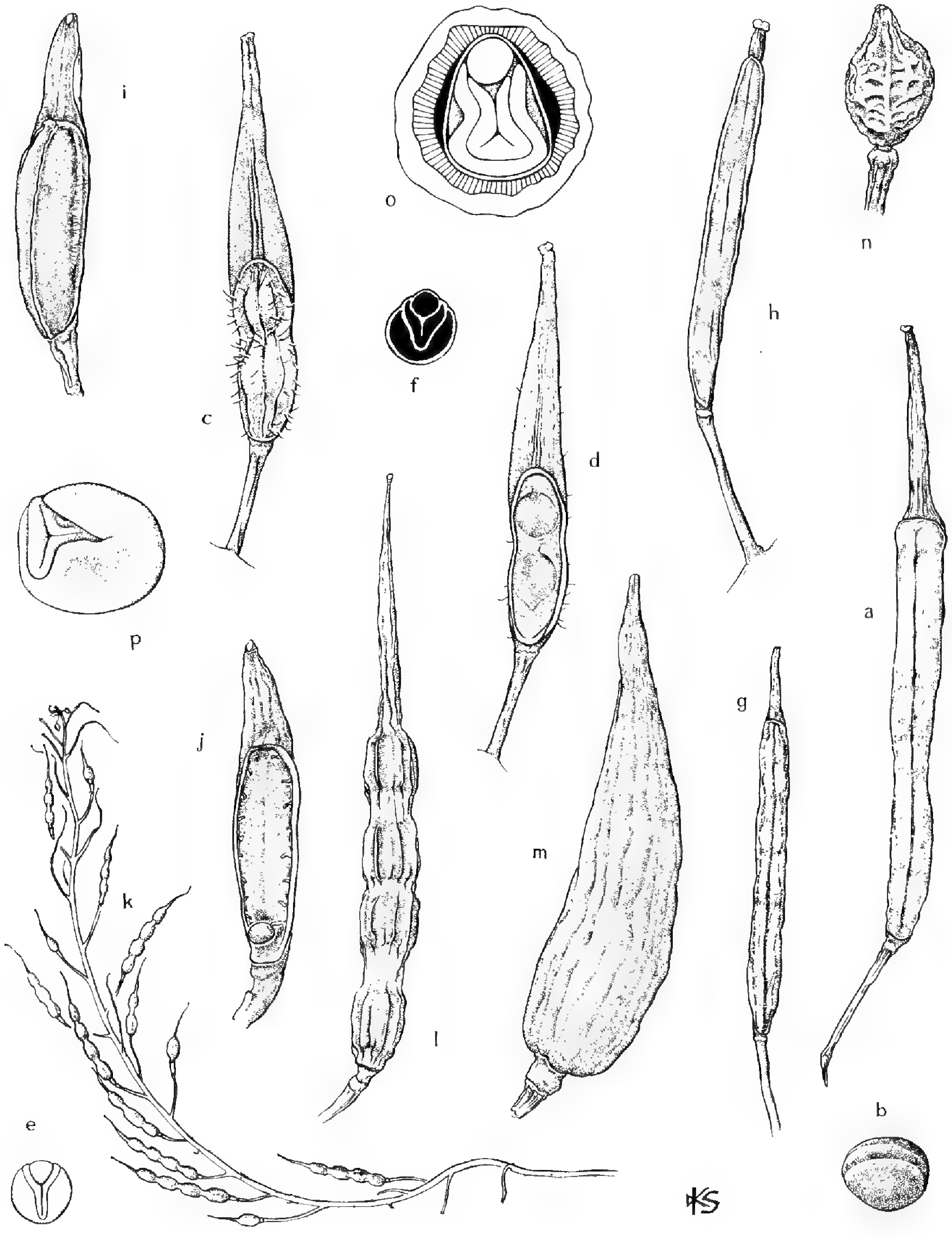

FIGURE 1. Fruits and seeds of selected Brassiceae. a, b, *Brassica campestris:* a, fruit, × 2; b, seed, × 6. c–f, *Sinapis alba:* c, fruit—note beak, × 2; d, fruit after removal of valve, × 2; e, embryo, × 6; f, diagrammatic cross section of seed showing conduplicate cotyledons, × 6. g, *S. arvensis,* fruit, × 2. h, *Diplotaxis muralis,* fruit, × 3. i, j, *Eruca vesicaria* subsp. *sativa:* i, fruit, × 2; j, fruit after fall of valve, × 2. k, l, *Raphanus Raphanistrum:* k, infructescence, × ½; l, fruit—note aborted lower segment and lomentaceous upper one, × 2. m, *R. sativus,* fruit, × 2. n–p, *Calepina irregularis:* n, fruit, × 6; o, diagrammatic cross section of fruit—note woody inner part (hatched) of fruit wall and seed with conduplicate cotyledons, × 12; p, embryo, × 12.

siliques strongly segmented, with one or few seeds in each segment) is a natural group including only *Cakile* and *Erucaria* and represented in the Southeast by five species of the former. The Moricandiinae Prantl (seven genera, including *Conringia*) are a heterogeneous assemblage of genera that have dehiscent, elongated fruits with seedless beaks and that lack median floral nectaries. Members of subtribe Brassicinae (eight genera) also have dehiscent, elongated fruits, but differ in having median nectaries and usually seeded beaks. However, the lines separating the two subtribes are undoubtedly artificial. The first six genera of the present treatment are considered typical of the Brassicinae. The Raphaninae Hayek (21 genera), probably the most heterogeneous of all six subtribes, have conduplicate cotyledons and indehiscent, usually strongly segmented fruits with seeds in both segments or in the upper one only. *Raphanus* L., *Rapistrum* Crantz, and *Calepina* represent this subtribe in the Southeast.

The Brassiceae are the best known cytologically of all tribes of the Cruciferae. Chromosome numbers have been reported for about 180 species (nearly 78 percent of the tribe) in 44 genera. The highest number (n = 75) has been found in *Crambe Gordjaginii* Sprygin & Popov (see Gómez-Campo & Hinata), while the lowest count (n = 6) was reported for *Erucaria cakiloidea* (DC.) O. E. Schulz (Al-Shehbaz, 1978). Polyploidy occurs in about 36 percent of the species and appears to be exclusive in all members of *Crambe* L., *Moricandia* DC., *Vella* L., *Boleum* Desv., *Zilla* Forsskål, and *Euzomodendron* Cosson. A continuous series from diploid to octoploid occurs in *Erucastrum* Presl. On the other hand, aneuploidy probably has played an important role in the evolution of *Diplotaxis* DC. and *Brassica*. The latter genus also exhibits the classic examples of amphiploidy that involve six cultivated species. No single base chromosome number is dominant in the Brassiceae, and the most common ones (7, 8, 9, and 15) occur in 14 to 18 percent of the species, while 10, 11, and 12 are found in 6 to 9 percent.

Natural intergeneric hybridization has been well documented between the northwestern African *Trachystoma Ballii* O. E. Schulz and *Ceratocnemum rapistroides* Cosson & Balansa, and between *Cordylocarpus muricatus* Desf. and *Rapistrum rugosum* (L.) All. Their hybrids are somewhat fertile and have been named ×*Trachycnemum mirabile* Maire & Samuels. and ×*Rapistrocarpus ramosissimus* (Pomel) Al-Shehbaz,[3] respectively. Artificial intergeneric hybrids have successfully been made on a large scale between various genera of the tribe, particularly members of subtribe Brassicinae (Harberd & McArthur, 1980). The classic intergeneric hybrid between the remotely related *Brassica* and *Raphanus*, ×*Raphanobrassica*, was produced by Karpechenko in 1924 (see *Raphanus*).

Many species of the Brassiceae, especially the economically important ones, have been surveyed extensively for glucosinolates, seed proteins, oil content, and fatty acids, and on a smaller scale for alkaloids, flavonoids, and mucilage.

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[3] ×*Rapistrocarpus* Al-Shehbaz, nothogen. nov. (*Rapistrum* Crantz × *Cordylocarpus* Desf.) — ×*Rapistrocarpus ramosissimus* (Pomel) Al-Shehbaz, comb. nov., which is based on ×*Rapistrella ramosissima* Pomel (Mat. Fl. Atlant. 11. 1860), should replace the latter because the nothogeneric name ×*Rapistrella* is not a condensed formula (see ICBN, Article H.6, p. 74. 1983).

The distribution of secondary constituents is not taxonomically useful at the subtribal level, and only in a few cases does it support the alliance of or the distinction between controversial genera. On the other hand, the distribution of glucosinolates is very useful within genera such as *Cakile* and *Brassica.*

Species of the Brassiceae occupy diverse habitats, but the majority show several adaptations to xeric environments in habit or in seed dispersal. The dustlike seeds of several species of *Diplotaxis,* the broadly winged seeds of *Savignya* DC. and *Oudneya* R. Br., and the samaras of *Fortuynia* are the most notable adaptations for dispersal by wind in desert plants. Seed mucilage is produced in at least 60 percent of the taxa with dehiscent fruits and apparently is lacking in 65 species of 18 genera with indehiscent fruits. Mucilage production may be an adaptation to anchor the seeds to the ground, as well as to enable them "to endure temporal droughts during the early stages of seed germination" (Gómez-Campo, 1980a, p. 8). Dispersal of corky fruit segments by sea water has probably evolved independently in *Crambe* (*C. maritima* L.), in *Raphanus* (two subspecies of *R. Raphanistrum* L.), and in *Cakile* (all taxa but one).

Members of 12 genera of the Brassiceae are either exclusively shrubs or herbs with a strongly woody base. In six others both herbaceous and woody taxa occur. All species of *Vella, Hemicrambe* Webb, *Boleum, Euzomodendron, Foleyola* Maire, and *Sinapidendron* Lowe, as well as the Canarian species of *Crambe,* are large shrubs or subshrubs. Carlquist, who studied the wood anatomy of the last two genera, believes that the woody condition in the family has almost always been derived from herbaceous ancestry, while Gómez-Campo (1980a) suggests that it is a primitive feature in the tribe.

The tribe includes the most economically important plants of the Cruciferae. *Brassica* and *Raphanus* provide many vegetables that are cultivated for their fleshy roots, swollen stems, leaves, buds, flowers, or young fruits. Edible and industrial oils are extracted from the seeds of *Brassica, Crambe,* and *Eruca* Miller, while condiments are obtained from seeds of *Sinapis* L. and *Brassica.* A few species are important fodder for livestock, and others of 13 genera (including the 11 treated here) are weeds naturalized throughout much of the world.

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KEY TO THE GENERA OF BRASSICEAE IN THE SOUTHEASTERN UNITED STATES

A. Fruits indehiscent, usually lomentaceous or transversely jointed, often breaking transversely at maturity into 1- or few-seeded segments; valves undifferentiated, reduced, or obsolete.
  B. Fruits transversely jointed, 2- to many-seeded, very rarely 1-seeded, more than 6 mm long; cauline leaves petiolate; petals equal.
    C. Style absent; cotyledons accumbent, rarely incumbent; glabrous and often fleshy plants of beaches or sandy shores. . . . . 12. *Cakile.*
    C. Style present; cotyledons conduplicate; usually pubescent and nonfleshy weeds of cultivated land, roadsides, or waste grounds.
      D. Fruits to 1 cm long; upper segment 1-seeded, ± equal to the 1-seeded (or rarely seedless) lower segment. . . . . 10. *Rapistrum.*
      D. Fruits more than 2 cm long; upper segment several seeded, more than 10 times longer than the lower, seedless segment. . . . . 9. *Raphanus.*
  B. Fruits not jointed, 1-seeded, 2–4 mm long; cauline leaves auriculate; petals unequal. . . . . 11. *Calepina.*
A. Fruits dehiscent, neither lomentaceous nor transversely jointed, never breaking at maturity into segments; valves well developed.
  E. Seeds biseriately arranged in each locule.

F. Beak strongly flattened, ensiform; stigma with decurrent lobes; petals with dark brown or purple veins. .... 8. *Eruca.*
F. Beak usually terete, stylelike; stigma entire or with nondecurrent lobes; petal veins not dark colored. .... 7. *Diplotaxis.*
E. Seeds uniseriately arranged in each locule.
G. Valves with 3–7 prominent nerves; beak usually ensiform.
H. Sepals erect, saccate at base; petal veins usually darker in color than the rest of blade. .... 5. *Hutera.*
H. Sepals reflexed or spreading, not saccate; petals uniform in color. .... 6. *Sinapis.*
G. Valves with 1 prominent midnerve, lateral nerves usually inconspicuous, sometimes evident and anastomosing; beak not ensiform.
I. Leaves entire, cordate-amplexicaul; fruits strongly 4-angled; cotyledons incumbent; seeds readily releasing abundant mucilage when wet. .... 13. *Conringia.*
I. Leaves (at least the lowermost ones) pinnately lobed or dentate, rarely upper ones auriculate or amplexicaul; fruits terete or flattened, sometimes slightly 4-angled; cotyledons conduplicate; seeds slightly or not at all mucilaginous when wet.
J. Inflorescence ebracteate; seeds globose; inner sepals saccate; fruits usually terete or flattened, rarely 4-angled. .... 3. *Brassica.*
J. Inflorescence (at least the lower part) bracteate; seeds oblong; inner sepals not saccate; fruits usually 4-angled. .... 4. *Erucastrum.*

3. **Brassica** Linnaeus, Sp. Pl. 2: 666. 1753; Gen. Pl. ed. 5. 299. 1754.[4]

Herbaceous annuals [or perennials with woody base], rarely biennials, glaucous or not, glabrous or with simple trichomes. Stems erect, branching above [or below], leafy [very rarely leafless]. Lower leaves petiolate, usually forming a rosette, undivided or lyrately pinnatifid [or pinnatisect]; lateral lobes few [to many or absent], smaller than the terminal one. Upper leaves short petiolate or sessile, sometimes auriculate or amplexicaul, and entire, dentate, or lobed. Inflorescence an ebracteate, few- to many-flowered raceme, much elongated in fruit. Sepals erect or ascending, rarely spreading, oblong or ovate, green or yellow-green, glabrous [or pubescent]; outer pair sometimes slightly cucullate; inner pair usually saccate at base. Petals clawed, yellow [rarely white or pink], broadly [to narrowly] obovate [or rarely oblanceolate]. Lateral nectar glands flat, reniform or prismatic; median glands oval [or filiform or oblong, very rarely absent]. Stamens tetradynamous, not appendaged; anthers oblong or ovate. Ovary sessile [or borne on a gynophore], glabrous, many ovulate; style conspicuous; stigma capitate or 2-lobed. Siliques narrowly [to broadly] linear [or occasionally oblong], dehiscent, torulose [or not], terete or sometimes compressed parallel to the septum, rarely 4-angled, erect to spreading [or reflexed]; valves convex, thin or thick [very rarely woody], obtuse or emarginate at apex, prominently [or obscurely] 1-nerved, lateral veins usually inconspicuous, sometimes finely anastomosing; beak long or short, conical or cylindrical, seedless or 1 [to 3]-seeded, usually forming a stylelike distal portion. Seeds uniseriately [or very rarely biseriately] arranged, globose [rarely oblong or slightly flattened],

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[4] Genera are numbered as in the treatment of tribes of Cruciferae in the southeastern United States (Jour. Arnold Arb. **65**: 343–373. 1984). Genera 1 and 2 appeared in *ibid.* **66**: 95–111. 1985.

wingless, slightly mucilaginous or not when wet, yellow or light to dark brown or black, finely to coarsely reticulate; cotyledons conduplicate, usually emarginate at apex. Base chromosome numbers 7–11. (Including *Brassicaria* (Godron) Pomel, *Brassicastrum* Link, *Guenthera* Andrz. ex Besser, *Melanosinapis* Schimper & Spenner, *Rapa* Miller.) LECTOTYPE SPECIES: *B. oleracea* L.; see Britton & Brown, Illus. Fl. No. U. S. ed. 2. 2: 192. 1913. (Name from classical Latin for several kinds of cabbage; a few authors believe that it is from the Greek *brazo,* I cook, in reference to the vegetables of the genus.)—MUSTARD, COLE, TURNIP.

The largest genus of the Brassiceae, with some 35 species mostly centered in the Mediterranean region, particularly in southwestern Europe and northwestern Africa, extending eastward into southwestern Asia to Afghanistan, and southward into Ethiopia and Somalia. Although the native ranges of the weedy and the cultivated species are uncertain, it is unlikely that they have originated outside the Mediterranean region and western Asia. Of the eight species introduced to the United States, at least four are naturalized in the Southeast.

The sectional classification of *Brassica* is controversial, and the three highly artificial sections recognized by Schulz (1919) have recently been divided by Salmeen into nine largely natural ones. The boundaries of sect. MICROPODIUM DC. have been arbitrarily redrawn by Salmeen to include a few unrelated species that differ in chromosome numbers and in morphology. On the other hand, sect. BRASSICARIA (Godron) Cosson (three species; southwestern Europe and northwestern Africa) is morphologically distinct from the rest of the genus, and on the basis of seed anatomy (Bengoechea & Gómez-Campo), chromosome numbers (Gómez-Campo & Hinata), juvenile characters (Gómez-Campo & Tortosa), and glucosinolates (Horn & Vaughan), the section is somewhat anomalous in *Brassica* and closely resembles the Madeiran *Sinapidendron.* However, *B. Gravinae* Ten. of sect. BRASSICARIA is intermediate between the typical members of this section and the rest of *Brassica.* Most taxa (including the type species) of sect. LIGNOSAE Widler & Bocquet are very closely related to *B. oleracea* and should be placed with it in sect. BRASSICA as defined by Stork and colleagues.

Section MELANOSINAPIS (DC.) Boiss. (sect. *Sinapioides* Peterm.) (annuals, upper leaves petiolate, sepals spreading, petals long clawed, fruiting pedicels appressed to the rachis, siliques torulose and 4-angled, valves 5–27 mm long, beaks seedless, seeds 4–10) has been reduced by Salmeen to include only *Brassica nigra* (L.) W. D. Koch (*Sinapis nigra* L.), black mustard, charlock (Small), $2n = 16$. The species may be a native of the Middle East. It is a cosmopolitan weed that grows in fields, roadsides, orchards, and waste places throughout much of the United States. It is locally common in scattered counties in Alabama, Louisiana, Mississippi, and Tennessee and may occur in the remaining states of the Southeast as well.

Section RAPA (Miller) Salmeen ex Al-Shehbaz[5] (annuals or biennials, basal

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[5] *Brassica* sect. *Rapa* (Miller) Salmeen ex Al-Shehbaz, comb. nov. Based on *Rapa* Miller (Gard. Dict. abr. ed. 4. Vol. 3 (alph. ord.). 1754). The new combination was originally proposed by the late O. J. Salmeen in her Ph.D. dissertation (see references).

leaves not forming a rosette, cauline leaves auriculate, sepals erect or ascending, valves 2.5–8 cm long, beaks seedless or 1-seeded) is represented in our area by its two species that are both crop plants and naturalized weeds. *Brassica Rapa* L., turnip, turnip rape, bird's rape, field mustard, $2n = 20$, grows in waste places, cultivated fields, orchards, disturbed sites, and gardens, and on roadsides in all of the Southeastern States. The native range of the species is obscure, but both the Mediterranean region and eastern Afghanistan–Pakistan are considered the main centers for the origin of the cultivated forms (McNaughton, 1976a). Complete interfertility, similar chromosome numbers, and lack of sufficient morphological discontinuities between this species and *B. campestris* L. justify the reduction of the latter to varietal rank (*B. Rapa* var. *campestris* (L.) W. D. Koch).[6] The fleshy roots and the biennial habit of *B. Rapa* var. *Rapa* vs. the nonfleshy roots and annual habit of var. *campestris,* which are the only characters separating the two, become unreliable differences when plants of the former escape from cultivation. *Brassica Rapa* is characterized by bright yellow flowers that overtop the floral buds, ascending ("erect-spreading" of some authors) sepals, green and usually setose-ciliate lower leaves, auriculate cauline leaves, and short (6–10 mm) petals. The closely related *B. Napus* L. (*B. Napobrassica* (L.) Miller), rape, colza, swede, rutabaga, Swedish turnip, $2n = 38$, is an amphidiploid that originated in the Mediterranean region a few hundred years ago (McNaughton, 1976b) but does not presently occur in the wild state. It differs from *B. Rapa* in having creamy or pale-yellow flowers not overtopping the floral buds, longer (10–18 mm) petals, and glaucous and glabrous or sparsely pubescent lower leaves. Although *B. Napus* has been reported as a weed from nearly all of the Southeastern States, it is very likely that most reports represent misidentifications of plants of *B. Rapa.* It is very difficult to distinguish between the two species from specimens that lack flowers and lower leaves. Several authors (e.g., Jones, Radford *et al.,* and E. B. Smith) have listed one of the two species in the synonymy of the other, but it is obvious that they are morphologically and cytologically very distinct, and that overwhelming evidence (see below) supports the amphidiploid origin of *B. Napus* from *B. Rapa* and *B. oleracea.*

Brassica juncea (L.) Czern. (*Sinapis juncea* L., *B. juncea* var. *crispifolia* Bailey, *B. integrifolia* (West) O. E. Schulz, *B. cernua* (Thunb.) Forbes & Hemsley), Chinese or Indian mustard, brown mustard, leaf mustard, mustard greens, $2n = 36$, an amphidiploid species originated from *B. nigra* and *B. Rapa* somewhere in the Middle East or Central Asia, is widely distributed in all the states of the Southeast. It is an escape from cultivation and a weed of disturbed sites, roadsides, abandoned fields, and waste grounds elsewhere in North America, the West Indies, and Central and South America. The greatest diversity of forms occurs in India and China, where the species is grown as a vegetable or as an oil-seed crop. *Brassica juncea* has short-petiolate or sessile cauline leaves;

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[6] *Brassica Rapa* and *B. campestris* were simultaneously described by Linnaeus (Sp. Pl. **1:** 666. 1753). Metzger, who was the first to unite the two species, adopted *B. Rapa* for the combined species, and consequently this name has priority (see ICBN Article 57.2. 1983).

ascending sepals; spreading, torulose siliques 3–6 cm long; and seedless, slender beaks 5–10 mm long. Small listed *B. japonica* Sieb. from our area, but it is very likely that he was dealing with plants of *B. juncea* with narrower siliques and more divided leaves. The sectional disposition of *B. juncea* has not been adequately resolved. Salmeen assigned it to sect. MICROPODIUM but placed its parental diploid species in different sections. Other authors put *B. juncea* and *B. Rapa* in the same section.

Brassica oleracea L., $2n = 18$, has been listed as a weed in a few checklists covering parts of our area (e.g., Duncan & Kartesz, Lakela *et al.*, Rich & Thomas). However, I have not seen any specimens from the Southeast, and it is doubtful that the species is a successful weed there. Wild plants of *B. oleracea* are perennials that occupy sea cliffs in Europe, as do their relatives of sect. BRASSICA (sect. *Brassicotypus* Dumort., sect. *Pseudobrassica* Presl, sect. *Lignosae* Widler & Bocquet) that have erect sepals, large (15–30 mm long) petals, auriculate, somewhat fleshy cauline leaves, conical, seedless to two-seeded beaks, and a haploid chromosome number of nine.

Brassica carinata Braun, Abyssinian mustard, Ethiopian rape, $2n = 34$, has been cultivated in Florida as an experimental plant for seed-oil production but has not become naturalized in the United States. Both *B. Tournefortii* Gouan ($2n = 20$) and *B. elongata* Ehrh. ($2n = 22$) are widespread weeds in some of the Pacific and Mountain states, but neither one has reached the Southeast.

The generic limits of *Brassica* changed a great many times in the treatments of early authors. Most North American botanists follow Bailey (1922) and Wheeler in merging *Sinapis* with *Brassica,* while those elsewhere maintain both genera. The boundaries between *Brassica* and some of its nearest relatives (*Sinapidendron, Diplotaxis,* and *Erucastrum*) are not sharply defined. Section BRASSICARIA shows close ties with *Sinapidendron,* and according to Gómez-Campo & Tortosa, the ancestors of *Brassica* may have resembled plants of this section or may have evolved along an evolutionary line phenetically represented by the sequence *Diplotaxis-Erucastrum-Brassica. Brassica* is distinguished from these in being herbs with usually saccate inner sepals, obovate petals, terete or flattened siliques, one-nerved valves, and usually uniseriately arranged globose seeds. *Sinapidendron* differs from *Brassica* in its shrubby habit, basal rosette of leaves, narrowly oblong petals, and oblong seeds, while *Erucastrum* is distinguished by its oblong seeds, usually four-angled siliques, keeled valves, nonsaccate sepals, and sometimes bracteate inflorescences. *Diplotaxis* has biseriately arranged, small (usually less than 1 mm long), oblong to elliptic or oval seeds. All species of *Sinapis, Hirschfeldia* Moench, and *Hutera* Porta have valves with three to seven prominent nerves, while *Brassica* has one prominent midnerve and occasionally inconspicuous lateral ones (FIGURE 1a, c, g).

Nomenclatural instability and lack of agreement on the number and rank of recognizable taxa among the cultivated brassicas have created persistent taxonomic problems. Bailey (1922, 1930, 1940) recognized 22 species in cultivation, while Helm (1963a) accepted more than 40 varieties and forms within *Brassica oleracea* alone. However, it is generally agreed that all the cultivated forms with $n = 10$ belong to *B. Rapa* because they are completely interfertile (P. G. Smith & Welch) and differ only in leaf characters that may be controlled by a few genes (McNaughton, 1976a). Similarly, all the cultivated forms with $n = 9$ are interfertile and clearly belong to the *B. oleracea* complex.

Species of *Brassica* are pollinated by numerous kinds of insects (Knuth), but the most constant pollinators are various species of the bee genera *Apis, Andrena,* and *Halictus* (McGregor). The flowers of *B. nigra* and *B. oleracea* have highly patterned ultraviolet reflectance (Horovitz & Cohen) and usually secrete abundant nectar daily (estimated at 0.1 ml for each of three days). The sugar concentration in nectar varies among the cultivated species but usually reaches 50 percent, except in some cultivars of *B. Rapa,* where it may approach 69 percent. Protogyny, self-incompatibility, and male sterility are well known in several species. In male-sterile plants, pollen develops normally, but the anther wall fails to dehisce because of the formation of a thick, compact layer (Chowdhury & Das).

The cytogenetic relationships of the six crop species of *Brassica* have been thoroughly investigated (see the reviews of Prakash & Hinata and Yarnell). Three basic diploid species, *B. nigra* ($n = 8$, genome B), *B. oleracea* ($n = 9$, genome C), and *B. Rapa* ($n = 10$, genome A), are the immediate progenitors of the amphidiploids *B. carinata* ($n = 17$, genome BC), *B. juncea* ($n = 18$, genome AB), and *B. Napus* ($n = 19$, genome AC). The allotetraploid origin of the last three species was elucidated first cytologically by Morinaga and U. Extensive supporting evidence obtained from the artificial synthesis and breeding (U; Frandsen, 1943, 1947; Olsson, 1960b, d; Olsson & Ellerström; Prakash, 1973b), seed morphology and anatomy (Berggren, 1962; Mulligan & Bailey), karyotype analysis (Sikka), nuclear DNA content (Verma & Rees), chloroplast DNA (Palmer *et al.*, Erickson *et al.*), glucosinolate distribution (Ettlinger & Thompson; Vaughan, Hemingway, & Schofield; Röbbelen & Thies, 1980b), phenolics (Das & Nybom), and proteins (MacKenzie & Blakely; Robbins & Vaughan; Uchimiya & Wildman; Vaughan, 1977; Vaughan & Waite, 1967b; Vaughan, Denford, & Gordon; Vaughan, Phelan, & Denford; Yadava *et al.*) undoubtedly makes the cultivated brassicas the best-documented example of evolution through allotetraploidy. Contrary to the overwhelming evidence supporting the origin of *B. carinata* from *B. nigra* and *B. oleracea,* Yadava and colleagues have suggested that it is derived from *B. nigra* and *B. Rapa.*

Except in four amphidiploid species (the three above and *Brassica balearica* Pers.) polyploidy is uncommon and probably has not played a major role in the evolution of *Brassica.* Diploid and tetraploid infraspecific taxa are known in both *B. fruticulosa* Cyr. ($x = 8$) and *B. Gravinae* ($x = 10$), while plants of *B. dimorpha* Cosson & Durieu ($n = 22$) are exclusively tetraploids. The remaining species of *Brassica* are diploids with $n = 7–11$. On the basis of the maximum number of secondarily associated chromosomes during the first metaphase, Catcheside and Alam have speculated that the original base chromosome number for *Brassica* is six. Their hypothesis is supported by many cytological observations on chromosome homology within the genome of a given species (autosyndesis) or among genomes of different species (allosyndesis) in haploid, diploid, and polyploid plants and in hybrids. According to Röbbelen (1960a), balanced secondary polyploidy derived from $x = 6$ is found in the three diploid cultivated species that have six chromosome types recognizable by certain structural features (e.g., chromosome length, symmetry of arms, and especially shapes of the heterochromatin regions). However, no extant species of *Brassica* is based on six, and all earlier counts reported as having $n = 12$ belong to species of *Sinapis* and *Hutera.*

Although a large number of artificial interspecific and intergeneric hybrids have been obtained (Harberd, 1976; Harberd & McArthur), natural interspecific hybridization is very rare in *Brassica.* Hampered by hybrid sterility (caused by endosperm deficiency and embryo abortion), hybridization among the three cultivated diploid species is very difficult, and the original natural formations of the three cultivated amphidiploid species must have been extremely rare events. All diploids with $2n = 18$ (including *B. oleracea*) are interfertile and produce hybrids with normal meiosis, viable pollen, and good seed set (Snogerup, 1980). However, the species are geographically isolated, and their ranges rarely overlap. The intergeneric hybrid ×*Raphanobrassica* is discussed under *Raphanus.*

The chemistry of the cultivated species, particularly in relation to selection of cultivars high or low in oils, erucic acids, or glucosinolates, has been adequately covered in the reviews of Appelqvist (1976), Appelqvist & Ohlson, Josefsson (1970), and Röbbelen & Thies (1980a, b). The distribution of glucosinolates appears to be most useful taxonomically at the specific level. Chemical differences between *Brassica* and *Sinapis* are found, and the latter contains 4-hydroxybenzylglucosinolate, which is generally lacking in the former. However, Horn & Vaughan have found this compound in sect. BRASSICARIA; both the compound and the section are believed to be anomalous in *Brassica.* Other chemical differences between the two genera have been reviewed by Vaughan (1977). In *B. juncea* two chemical races are recognized: an Indian race with a preponderance of 3-butenylglucosinolate and without mucilage in the seed coat, and an oriental (eastern Asiatic–European) race rich in allylglucosinolate and with a mucilaginous seed coat (Vaughan, Hemingway, & Schofield). Vaughan & Gordon suggested that either *B. juncea* has evolved independently in the two regions (thus agreeing with Olsson (1960b) on the polyphyletic origin of the species) or, more likely, the Indian race has resulted from human selection for edible oil-producing cultivars that lack the toxic allyl isothiocyanate. The seed-protein data, however, do not support such racial distinctions (Denford). The types and amounts of glucosinolates in a given plant may be directly related to its allelochemic defense against certain herbivores or fungal pathogens. The susceptibility of many cultivated brassicas to several fungal diseases, such as the downy mildew (caused by *Peronospora parasitica* (Pers. & Fries) Fries), may have resulted from man's selective breeding for more tasty cultivars with lower concentrations of glucosinolates (Greenhalgh & Mitchell).

Wild cabbage (*Brassica oleracea* subsp. *oleracea*) and all of its relatives of sect. BRASSICA have isolated and spotty distributions along sea cliffs and rocky islets of the Mediterranean, western Europe, and the Canary Islands. Baker has indicated that *B. oleracea* escaping from cultivation has reverted to occupy sea-cliff habitats on the northern side of San Francisco's Golden Gate. Long-distance dispersal of seeds of sect. BRASSICA may be accomplished by sea birds. According to Mitchell & Richards (1979), the wild cabbage may perennate for

20 years and may produce as many as 70,000–100,000 seeds annually. Although it is not known how long these seeds remain viable, those of *B. nigra* included in the classic experiments of Beal (see Darlington) survived in the soil for 50 years.

Crops of *Brassica* are the most important economic plants of the Cruciferae. Probably the earliest known utilization of mustards dates from Sanskrit records in India to 3000 B.C. (Mehra). Some authors have suggested that the ancestral cabbage was cultivated in coastal northern Europe nearly 8000 years ago. Undoubtedly several brassicas of European origin were cultivated long before the Christian Era, but at least three (Brussels sprouts, kohlrabi, and rape) originated only a few hundred years ago.

The cultivated members with $n = 9$ have traditionally been treated as varieties of *Brassica oleracea* but were listed as groups without formal rank by Bailey and colleagues. The most common types grown in our area are Brussels sprouts (var. *gemmifera* Zenk), cabbage (var. *capitata* L.), cauliflower (var. *botrytis* L.), kohlrabi (var. *gongylodes* L.), kales and collards (var. *acephala* DC.), and sprouting broccoli (var. *italica* Plenck). Several authors have stated that the diversity among these varieties could not have evolved from the limited variation presently existing in the wild cabbage and have therefore suggested a multiple origin from more than one ancestral species.

A wide range of leafy forms has been selected in China from plants originally introduced from western or central Asia for seed oils. All of the Far Eastern forms except the Chinese kale (known as *B. alboglabra* Bailey but probably a form of *B. cretica* Lam.) belong to *B. Rapa* and *B. juncea*. The classification of these oriental forms is not settled, and various specific, subspecific, and varietal ranks have been assigned to them (Kitamura; McNaughton, 1976a; Nishi; Helm, 1961, 1963b). The Chinese mustard or pak-choi (*B. Rapa* var. *chinensis* (L.) Kitam.) and the Chinese cabbage or pe-tsai (*B. Rapa* var. *amplexicaulis* Tanaka & Ono), commonly known as *B. pekinensis* Rupr., have the same chromosome number as—and produce fully fertile hybrids with—*B. Rapa*, from which they differ in leaf characters only. Hakuran, a newly developed Japanese vegetable crop, is a leafy form of *B. Napus* that produces "heads" instead of fleshy roots and has been synthesized from crossing the Chinese cabbage with our common cabbage (Nishi).

Various fresh parts of *Brassica* crops are eaten raw, stewed, cooked, fermented in brine, or pickled in vinegar. Many are important fodder for farm animals, and some colorful cabbages and kales are ornamentals. The seeds contain 30–40 percent oil, which is the principal cooking oil in India and is also used as a substitute for olive oil and in the manufacture of margarine in Europe. The seed-cake remaining after the expression of oil contains 25–35 percent protein and is used as a fertilizer. Oil of *B. napus* ranks fifth in terms of the world tonnage of vegetable oil production. It is used in the manufacture of general-purpose grease, lubricants, varnishes, lacquers, soft soap, plastics, resins, vinyl stabilizers, synthetic flavors and odors, flotation agents, insect repellents, nylons, and pharmaceuticals (Ohlson). Table mustard is manufactured from the seeds of *Sinapis alba* L. (contributing the hot principle

4-hydroxybenzyl isothiocyanate) and *B. juncea* or *B. nigra* (providing the pungent principle allyl isothiocyanate). The seeds also are used as a spice in the preparation of pickles and in the seasoning of food items.

Seeds of *Brassica nigra* and *B. juncea* have been used extensively as laxatives, vesicants, stimulants, irritants, rubefacients, emetics, tonics, and antiseptics; employed as remedies for colds, stomach disorders, abscesses, rheumatism, and lumbago; and also used in the preparation of ointments to relieve neuralgia, bronchitis, arthritis, and pneumonia (Perry). Hartwell has listed several species employed in the preparation of plasters, poultices, and juices as remedies for indurations and tumors. Preparations from the vegetative parts are used in China and India as antiscorbutics, antidysenterics, resolvents, and depuratives, and for the treatment of diabetes, chronic coughs, and bronchial asthma. Plasters are applied to swellings or blistered surfaces to promote free discharge and are used to cure warts.

In addition to being obnoxious weeds, several species of *Brassica* are harmful or poisonous to humans and livestock. Some of the weedy and cultivated members cause photosensitization, goiter, pulmonary emphysema, and several serious disorders in the digestive, nervous, and urinary systems of cattle and sheep that may eventually lead to death.

REFERENCES:

Although the references listed below may appear excessive, they represent approximately 26 percent of those consulted during the preparation of this treatment! The wealth of literature dealing with the agronomic, industrial, pathological, physiological, pesticidal, and many related agricultural aspects of the cultivated species is irrelevant to this study and has not been surveyed here. The reader is advised to consult the indexes of the *Bibliography of Agriculture* for leads.

Under family references in AL-SHEHBAZ (Jour. Arnold Arb. **65**: 343–373. 1984), see AL-SHEHBAZ (1977); APPELQVIST (1971, 1976); BAEZ MAYOR; BAILLON; BATEMAN (1955a); BENTHAM & HOOKER; BERGGREN; BOUMAN; CAIUS; COLE (1976); CRISP; HARTWELL; VON HAYEK; HEBEL; HEGNAUER; HEYWOOD; HOROVITZ & COHEN; JONES; VON KERBER & BUCHLOH; KINGSBURY; KJAER (1960); KNIGHTS & BERRIE; KNUTH; KROH; KUMAR & TSUNODA; LA PORTE; MAIRE; MARKGRAF; MEDVE; MUENSCHER; MUKHERJEE; MURLEY; PANT & KIDWAI; PERRY; PRASAD (1975, 1977); RADFORD *et al.*; ROLLINS (1981); SAMPSON; SCHULZ; SMALL; E. B. SMITH; VAUGHAN, PHELAN, & DENFORD; VAUGHAN & WHITEHOUSE; and VIEGI *et al.*

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4. **Erucastrum** K. B. Presl, Fl. Sicula 1: 92. 1826.

Annual, biennial [or perennial] herbs [rarely subshrubs], usually with simple, appressed, retrorse [or spreading] trichomes [rarely glabrous]. Basal leaves in a rosette or not, petiolate, lyrately pinnatifid [sometimes pinnatisect, runcinate, or undivided]. Cauline leaves resembling the basal ones, usually less divided [rarely pectinate or pinnatisect], short petiolate [or sessile and sometimes auriculate at base]. Inflorescence a terminal, bracteate [or ebracteate], corymbose raceme, conspicuously elongated in fruit. Sepals erect [or spreading], oblong [or linear], not saccate; outer pair sometimes cucullate, narrower than the inner one. Petals yellow or white, short [or long] clawed, obovate [rarely oblanceolate or oblong]. Nectar glands 4; lateral pair flat, prismatic or reniform; median pair usually ovoid [sometimes oblong or cylindrical]. Stamens tetradynamous; filaments not appendaged; anthers oblong or linear, obtuse at apex, sagittate at base. Ovary many ovulate; style distinct; stigma capitate, entire [rarely 2-lobed]. Fruiting pedicels slender [or stout], spreading [sometimes erect and subappressed to rachis]. Siliques linear, quadrangular, rarely subterete, torulose, glabrous [sometimes sparsely pilose or retrorsely scabrous], subsessile [or occasionally borne on short gynophores]; valves somewhat keeled, with a prominent midnerve and slender, usually anastomosing lateral veins, obtuse or emarginate at apex; beak conspicuous [rarely obsolete], usually 3-nerved, seedless [or 1- or 2- (or 3-)seeded], slender, stylelike [sometimes conical]. Seeds uniseriately arranged in each locule, oblong or oval [very rarely globose], usually reticulate, wingless, brown, slightly mucilaginous [or not] when wet; cotyledons longitudinally conduplicate, usually emarginate at apex. Base chromosome numbers 7, 8, 9. (Including *Conirostrum* Dulac.) LECTOTYPE SPECIES: *Sinapis virgata* J. S. & K. B. Presl = *E. virgatum* (J. S. & K. B. Presl) K. B. Presl; see Maire, Fl. Afr. Nord **12:** 204. 1965. (Name from *Eruca,* a genus of the Cruciferae, and *astrum,* indicating an incomplete resemblance.)

A genus of about 20 species primarily distributed in the western Mediterranean region and in most of Africa (except the Sahara and the western part of the continent), with extensions into central and eastern Europe, the Canary Islands, and the Arabian peninsula. Many taxa are endemic to the Iberian peninsula and northwestern Africa, and a few species are indigenous to the Canaries (two), tropical East Africa (two), and South Africa (two). *Erucastrum arabicum* Fischer & Meyer, probably a native of Ethiopia, is a weed widely distributed in Africa, while *E. nasturtiifolium* (Poiret) O. E. Schulz and *E. gallicum* are native in southwestern Europe and naturalized in most of that continent. The last species was introduced to the New World about the turn of the century and has since become abundant in many parts of Canada and the United States.

Erucastrum gallicum (Willd.) O. E. Schulz (*Sisymbrium gallicum* Willd., *S. Irio* L. var. *gallicum* (Willd.) DC., *S. Erucastrum* Poll., *S. hirtum* Host, *E. Pollichii* Schimper & Spenner, *E. vulgare* Endl., *E. inodorum* Reichenb., *E. ochroleucum* Calestani), dog mustard, rocket weed, $2n = 30$, has been reported from several localities in Dade and Palm Beach counties in Florida (Wunderlin) and from Caddo Parish in Louisiana (MacRoberts). The first report of *E. gallicum* in North America was based on two independent introductions in Massachusetts and Wisconsin (Robinson). The species is naturalized in all the provinces of Canada and in many parts of the United States, particularly the Midwest, where it grows in fields, waste places, gardens, and orchards, on roadsides, and along railways. From the other crucifers of our area, *E. gallicum* is easily distinguished by having deeply pinnatifid basal leaves, retrorsely appressed trichomes on the stem, pale yellow flowers, bracteate racemes, torulose linear siliques, strongly one-nerved valves, and slender, seedless beaks.

Patman listed *Erucastrum abyssinicum* (Rich) O. E. Schulz as a cultigen in Florida, but it is very likely that the record is based on a misidentification of plants of *Brassica carinata* Braun that were collected by G. Killinger and E. West and distributed under the former name. The establishment of *E. nasturtiifolium* as a successful weed in North America needs confirmation.

Although several earlier authors have reduced *Erucastrum* to a subgenus or a section of *Brassica* (De Candolle, 1821, 1824; Bentham & Hooker) or *Hirschfeldia* (Von Hayek), recent students of the Cruciferae maintain it as a genus intermediate between these two but more closely related to the former. No sections have been recognized in *Erucastrum.* The genus is distinguished by having usually quadrangular siliques; somewhat keeled, prominently one-nerved valves; oblong or oval, uniseriately arranged seeds; nonsaccate sepals; and occasionally bracteate inflorescences. *Brassica* differs in having terete or flattened siliques, convex valves, globose seeds, ebracteate inflorescences, and usually saccate inner sepals. The boundaries between the two genera are not always clearly drawn, and the distinction between them may rest on a single character. *Hirschfeldia* can easily be confused with some species of *Erucastrum* that have swollen beaks and subappressed siliques, but it is recognized by its erect sepals and three-veined siliques. The venation of valves is a difficult character to assess in mature fruits of *Hirschfeldia,* and young siliques are more useful for this purpose.

Chromosome numbers are known for at least 14 species of *Erucastrum,* and more than half of the taxa are based on eight. Diploid ($2n = 16$) and tetraploid infraspecific taxa are found in *E. rifanum* (Emberger & Maire) Gómez-Campo, *E. nasturtiifolium,* and *E. leucanthemum* Cosson & Durieu, while diploids, tetraploids, and hexaploids (based on eight) occur in *E. littoreum* (Pau & Font Quer) Maire. Octoploidy has recently been reported in *E. meruense* Jonsell ($2n = 64$), a species endemic to Tanzania. Both *E. gallicum* and *E. elatum* (Ball) O. E. Schulz have $2n = 30$ and appear to be amphidiploids. Harberd & McArthur observed eight bivalents in the triploid hybrids obtained from crossing *E. gallicum* with diploid plants of *E. nasturtiifolium* and have suggested that the former is an allotetraploid that may have originated from a parent (with $n = 8$) very closely related to the latter and from another diploid, not yet determined, having $n = 7$. No experimental evidence supports the amphidiploid origin of *E. elatum,* but according to Gómez-Campo (1983), its putative parents probably are very close to *E. littoreum* ($n = 8$) and either *E. virgatum* or *Hirschfeldia incana* (L.) Lagrèze-Fossat (both with $n = 7$). *Erucastrum abyssinicum* ($n = 16$) apparently has unselective stigmas that allow foreign pollen from unrelated genera of the Brassiceae to germinate and penetrate the style (Harberd, 1976). The triploid hybrids, obtained from crossing this species with several unrelated diploids, always have eight bivalents in meiosis—an indication of the autotetraploid origin of *E. abyssinicum.* No diploid populations, however, have been found in this species, but the closely related *E. arabicum* and *E. pachypodum* (Chiov.) Jonsell are diploids.

Seeds of a few species have been analyzed for glucosinolates and fatty acids. Large amounts of allylglucosinolate and traces of three other compounds have been identified from *Erucastrum gallicum,* while 3-methylsulfinylpropyl and 3-methylthiopropyl glucosinolates are the major components in *E. abyssinicum.* Nearly 52 percent of the fatty-acid composition of *E. cardaminoides* (Webb) O. E. Schulz is erucic acid, which makes the species a potentially useful source of industrial oils.

Except for the three weedy species mentioned above, the genus has very little economic importance. *Erucastrum arabicum* is occasionally grown in Ethiopia for seed oils, and the leaves are used as a vegetable.

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5. **Hutera** Porta, Atti Imp. Regia Accad. Rovereto, II. **9:** 109. 1891.

Annual, biennial, or perennial herbs with well-developed taproots [or much-branched rhizomes], sparsely to densely hispid [or glabrous]. Stems erect [rarely procumbent], simple or branched at base. Basal leaves in a rosette [or not], usually long petiolate, pinnatipartite or pinnatisect, with 3–10 pairs of lateral lobes [rarely undivided], entire, repand, or dentate. Cauline leaves petiolate, with fewer and narrower lobes than the basal ones [or undivided]. Inflorescence an ebracteate, corymbose raceme, greatly elongated in fruit. Sepals erect, obtuse, setulose below the apex [or glabrous]; outer pair narrowly oblong; inner one broader, saccate at base. Petals long clawed, obovate [rarely oblong or elliptic], obtuse [rarely emarginate], yellow [or white], usually with dark brown or violet veins; claws slender, usually longer than the sepals. Lateral nectar glands flat, median ones cylindrical [or absent]. Stamens tetradynamous; anthers linear [or oblong], sagittate at base, usually recurved at apex. Ovary many ovulate; style very short; stigma capitate, 2-lobed. Siliques linear, subsessile, torulose [or not], 2-segmented [very rarely transversely jointed], spreading, erect, or reflexed; lower segment dehiscent, terete [or slightly 4-angled], usually many seeded, with 3- or 5-nerved valves; upper segment (beak) indehiscent, persistent, 1–6-seeded, as wide as [or wider] and shorter [or equaling to longer] than the lower segment, linear [or oblong or ovoid], smooth [or torulose to moniliform], ensiform [very rarely inflated and corky]. Seeds uniseriately arranged in each locule, globose, dark brown to black, reticulate, wingless, slightly mucilaginous [or usually not] when wet; cotyledons longitudinally conduplicate, emarginate. Base chromosome number 12. (Including *Brassicella* Fourr. ex O. E. Schulz, *Coincya* Rouy, *Rhynchosinapis* Hayek.) TYPE SPECIES: *H. rupestris* Porta. (Name honoring Rupert Huter, 1834–1919, an Austrian clergyman, amateur taxonomist, plant collector, and distributor of exsiccatae.)

A genus of 12 species distributed in southern and southwestern Europe, particularly the Iberian peninsula, with two species endemic to western and southwestern Britain, one to northern Greece, and one to northwestern Africa. The genus is represented in North America by the naturalized weed *Hutera Cheiranthos* (Vill.) Gómez-Campo (*Brassica Cheiranthos* Vill., *Rhynchosinapis Cheiranthos* (Vill.) Dandy, *Coincya Cheiranthos* (Vill.) Greuter & Burdet), $2n$ = 24, 48, a native of western Europe. It is extremely variable, with several subspecies recognized. The species was first recorded from the New World in 1880 (Brown). It is locally common in pastures and on roadsides in Jackson and Yancey counties, North Carolina (Ahles & Radford; Rollins, 1961) but has not yet been reported from the other states of the Southeast. It is easily distinguished from other crucifers of our area in having pubescent, pinnatisect basal leaves; erect sepals; long-clawed, dark-veined yellow petals; siliques 3–8 cm long; three-veined valves; and ensiform, one- to three-seeded beaks 8–22 mm long. Radford and colleagues have listed the species as *Brassica Erucastrum* L., but according to Pugsley, this name is based on immature plants of *Raphanus Raphanistrum* L.

Both *Hutera* and *Coincya* were published in October, 1891, but the former was published five days earlier (Lacaita, González-Albo). Heywood recognized both *Hutera* and *Rhynchosinapis* and separated them by their siliques, which are transversely jointed in the former but not so in the latter. However, the extensive morphological (Gómez-Campo, 1977a; Clemente & Hernández-Bermejo, 1980a–d; Gómez-Campo & Tortosa) and cytological (Harberd, 1972;

Harberd & McArthur, 1972) data strongly support merging *Rhynchosinapis* with *Hutera.*

Although *Hutera* has been associated with *Brassica, Erucastrum, Hirschfeldia,* and *Erucaria,* its nearest relative is probably *Sinapis,* which it resembles in having three- or five-veined valves, similar chromosome numbers ($x = 12$), globose seeds, and well-developed, usually ensiform, few-seeded beaks. From *Sinapis, Hutera* is easily distinguished by its erect, saccate sepals and its dark-veined petals. The relationship between *Hutera* and *Brassica* is somewhat remote. The latter has one-nerved valves, seedless or few-seeded, nonensiform beaks, and chromosome numbers that are never based on 12.

Little is known about the floral biology of *Hutera.* Knuth suggested that the flowers of *H. Cheiranthos* (listed as *Sinapis*) form long floral tubes (ca. 1 cm) by the close coherence of the sepals and petal claws and are therefore adapted to pollination by Lepidoptera, such as members of the butterfly genus *Anthocharis.* Cross-pollination occurs as the insect probes its proboscis between the anthers of the median stamens and touches the stigma before reaching the nectar that accumulates in the pouches of the lateral sepals. According to Knuth, the large median nectaries do not secrete nectar but the small lateral ones do.

Chromosome numbers have been reported for all species of *Hutera,* and all except *H. nivalis* (Boiss. & Heldr.) Gómez-Campo are diploids or tetraploids based on 12. Although this species has $2n = 20$ (Strid & Franzén), further counts are needed to establish whether or not such a number is constant for it. Tetraploidy is known in *H. Johnstonii* (Samp.) Gómez-Campo and in some subspecies of *H. pseudoerucastrum* (Brot.) Gómez-Campo and *H. Cheiranthos.* The last species was first known as a tetraploid, and on the basis of its forming 24 bivalents at meiosis, Sikka suggested that it is an allotetraploid derived from *H. Wrightii* (O. E. Schulz) Gómez-Campo and *H. monensis* (L.) Gómez-Campo. However, the discovery of diploid populations in *H. Cheiranthos* (Favarger, 1965) and bivalent-forming autotetraploids in *Hutera* (Harberd, 1976) do not support Sikka's hypothesis.

Although natural hybridization has not yet been reported in *Hutera,* artificial crossing between *H. Cheiranthos* and *H. monensis* and between each of these and *H. hispida* (Cav.) Gómez-Campo, *H. longirostra* (Boiss.) Gómez-Campo, and *H. leptocarpa* González-Albo show an almost complete bivalency in the hybrids (Harberd & McArthur, 1972). On the other hand, artificial intergeneric hybrids between *Hutera* and *Brassica* and between *Hutera* and *Diplotaxis* gave mean numbers of bivalents of 2.2–4.7 (Harberd & McArthur, 1980).

The chemistry of *Hutera* is poorly understood. A single glucosinolate (5-methylthiopentyl) has been identified from the seedlings of *H. monensis* (Cole, 1976), and the fatty-acid composition of the seeds of *H. Cheiranthos* (listed as *Brassicella Erucastrum*), *H. leptocarpa,* and *H. longirostra* show a preponderance of linolenic and erucic acids, with substantial amounts of palmitic acid in the last species (Appelqvist, 1971; Kumar & Tsunoda, 1980).

As in several genera of the Brassiceae, *Hutera* shows reductional trends in fruit length accompanied by elaboration of the beak. The ensiform beaks probably aid in dispersal by animals. Beaks can persist for a few years in the soil, and seed germination takes place only after their walls disintegrate or break open.

Except for the weedy *Hutera Cheiranthos,* the genus has no economic importance.

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6. **Sinapis** Linnaeus, Sp. Pl. **2:** 668. 1753; Gen. Pl. ed. 5. 299. 1754.

Annual [rarely perennial] herbs, glabrous or with simple, retrorse or spreading trichomes. Stems erect, leafy, often branched above. Basal leaves petiolate, usually not in a rosette, lyrate or pinnatifid to pinnatisect, rarely undivided [or bipinnatipartite], usually coarsely dentate; terminal lobe larger than the lateral ones. Upper cauline leaves short petiolate or sessile, entire or shallowly divided. Inflorescence an ebracteate, corymbose raceme, greatly elongated in fruit. Sepals yellowish, widely spreading, rarely reflexed, not saccate at base, oblong or linear, glabrous or sparsely [to densely] hispid or villous on the dorsal side. Petals yellow, obovate; claws nearly as long as the sepals. Nectar glands 4, the lateral ones prismatic, flat [rarely lobed], the median ones oval, usually not lobed. Stamens tetradynamous; filaments linear, not appendaged; anthers oblong, obtuse. Ovary sessile, glabrous or pubescent; style long; stigma large, 2-lobed. Fruiting pedicels slender or stout, straight [rarely curved], ascending to divaricate [sometimes erect or recurved and appressed to rachis]. Siliques strongly beaked, linear or oblong, terete or somewhat flattened or angled, glabrous or hispid [or villous] with long trichomes and with or without much shorter, retrorse ones; lower (valvular) segment dehiscent, few to many seeded, usually torulose; valves convex, with 3–7 prominent veins, thin or thick [rarely hardened and inconspicuously veined]; upper segment (beak) indehiscent, 0–2[–10]-seeded, straight [or recurved], terete or strongly compressed, ensiform or conical, thick [or corky], equaling or shorter [or much longer] than the lower segment, usually smooth [rarely torulose, ribbed, or tuberculate]. Seeds uniseriately arranged in each locule, globose [very rarely slightly flattened], wingless, mucilaginous or not when wet, pendulous in the valvular part, erect in the beak, yellow or brown, sometimes black, slightly to strongly reticulate or alveolate; cotyledons longitudinally conduplicate, much wider than long, emarginate, glabrous or pubescent. Base chromosome numbers 7, 9, 12. (Including *Agrosinapis* Fourr., *Bonannia* K. B. Presl, *Leucosinapis* Spach, *Rhamphospermum* Andrz. ex Besser, *Sinapistrum* Chev.) LECTOTYPE SPECIES: *S. alba* L.; see Britton & Brown, Illus. Fl. No. U. S. ed. 2. 2: 191. 1913. (Name from Greek *sinape* or *sinapi,* mustard, in reference to the flavor of the seeds.)—CHARLOCK, MUSTARD.

A genus of seven species, all except *Sinapis Aucheri* (Boiss.) O. E. Schulz, an endemic of western Iran and eastern Iraq, native to the Mediterranean region. Two species are indigenous to Egypt, and two others are restricted to southwestern Europe and northern Africa. Both *S. alba* and *S. arvensis* L. are weeds widely naturalized throughout the world. They occur in all the Southeastern States in gardens, grainfields, cultivated land, waste places, and disturbed grounds, on roadsides, and along railroad tracks.

Four well-defined sections have been recognized by Schulz (1919). Section SINAPIS (sect. *Leucosinapis* DC.) (annuals; siliques generally with long, spreading trichomes usually mixed with more numerous short, retrorse ones, rarely glabrescent; beaks ensiform; seeds mucilaginous when wet) contains *S. flexuosa* Poiret of southern Spain and northwestern Africa and *S. alba* L. (*Brassica alba* (L.) Rabenh., *B. hirta* Moench), white mustard, yellow mustard, $2n = 24$, probably native to the Mediterranean region and Crimea. The latter is distinguished by the sectional characters above and by its dissected lower leaves and short (2–4 cm) siliques with two- to four-seeded locules.

Section CERATOSINAPIS DC. (annuals; siliques glabrous, rarely sparsely hispid; beaks conical, straight, one- or two-seeded; seeds many, not mucilaginous when wet) includes the cosmopolitan weed *Sinapis arvensis* and the Egyptian endemics *S. Allionii* Jacq. and *S. turgida* (Pers.) Delile. *Sinapis arvensis* L. (*Brassica arvensis* (L.) Rabenh., *B. sinapistrum* Boiss., *S. orientalis* L., *S. Kaber* DC., *B. Kaber* (DC.) Wheeler, *S. Kaber* var. *pinnatifida* (Stokes) Wheeler), charlock, field kale (Muenscher), wild mustard (Small), less commonly known as field mustard, crunchweed, and California rape, $2n = 18$, is one of the most widely distributed weedy crucifers in our area. It can easily be recognized by its subsessile cauline leaves, spreading sepals, strongly three-nerved valves, and conical, one- or two-seeded beaks.

The two remaining sections are monotypic, and neither is represented in our flora. Section ERIOSINAPIS Cosson contains *Sinapis pubescens* L., $2n = 18$, indigenous to northern Africa, Italy, Sicily, and Sardinia and easily recognized by its perennial habit and villous siliques with recurved beaks. *Sinapis Aucheri* of sect. CHONDROSINAPIS O. E. Schulz is anomalous in the genus because of its long, torulose, corky, six- to ten-seeded beaks and its haploid chromosome number of seven.

Sinapis can be separated from its closest allies in the Brassiceae by its combination of nonsaccate sepals; uniformly colored yellow petals; and strongly beaked fruits with one- or two- (to ten-)seeded beaks, three- to seven-veined valves, and uniseriately arranged globose seeds. It is closely related to *Hutera,* from which it is distinguished by its spreading, nonsaccate sepals and its lack of dark venation in the petals. Recent North American authors follow Bailey and Wheeler by merging *Sinapis* with *Brassica,* while botanists elsewhere maintain both genera. The latter has one-nerved valves and erect to ascending (rarely spreading) sepals, with the lateral pair usually saccate. The two genera also differ in their mustard oils and seed proteins. However, in lipid content *S. arvensis* shows more affinity to *Brassica* than does *S. alba* (Appelqvist, 1976), and some authors (e.g., Takahata & Hinata, 1980) have suggested that *S. arvensis* may be the connecting link between the two genera.

Numerous infraspecific taxa have been recognized in *Sinapis pubescens, S. arvensis,* and *S. alba,* but the majority of them are based primarily on characters such as the amount of pubescence, the orientation of the fruits, the lobing of the lower leaves, and the color of the seeds, all of which exhibit continuous variation that may be encountered within the same population. Therefore, no subordinate taxa are recognized here for plants of the last two species.

Because the sepals are spreading, the nectar in *Sinapis* may appear to be accessible to insects from the side of the flower. However, the dense grouping of the flowers makes it more convenient for sizeable insects to approach the nectar from the top of the flower, thus effecting pollination. The flowers of *S. alba* and *S. arvensis* have highly patterned ultraviolet reflectance and differ in the shape of their nectar guides (Horovitz & Cohen). More than 60 species of bees, butterflies, flies, and wasps have been recorded by Fogg and Knuth as visitors of the latter species, which is a very important source of nectar and pollen for honey bees (*Apis mellifera*) in fields that it heavily infests. The flowers of *S. alba* are odoriferous and secrete abundant nectar with a sugar concentration of 60 percent (Free). These floral adaptations (including the ultraviolet pattern) clearly contradict Hemingway's suggestion of pollination by wind in *S. alba.*

The sectional classification of the genus is supported by data on chromosome numbers. Members of sect. SINAPIS have $n = 12$, and those of sects. ERIOSINAPIS and CERATOSINAPIS have $n = 9$, while sect. CHONDROSINAPIS has $n = 7$. Easterly (1963) has reported $n = 8$ and $n = 16$ for *Sinapis arvensis,* but the counts probably are erroneous and have not been reported again. Naturally occurring polyploids have not been found in the genus. Mukherjee described the karyotype of *S. alba* (as *Brassica alba*) as consisting of one pair of long chromosomes with two constrictions and 11 pairs of short chromosomes with median or submedian constrictions.

Both *Sinapis alba* and *S. arvensis* have been thoroughly surveyed for sterols, fatty acids, tycophenols, paraffins, mustard oils, alkaloids, flavonoids, and seed proteins, but the other species of the genus have received only minimal attention in chemical studies. The two species contain 4-hydroxybenzylglucosinolate, which has not been found in the typical members of *Brassica* (see the treatment of this genus). Smaller amounts of 3-butenyl and 2-phenylethyl glucosinolates are found in *Sinapis,* but these are more abundant in *Brassica.* Other chemical differences, particularly in seed proteins, support the maintenance of *Sinapis* as a genus distinct from *Brassica.*

In seed-coat anatomy *Sinapis arvensis* resembles several species of *Brassica* and *Hutera*: all have a nonmucilaginous epidermis followed by radially elongated palisade cells. In *S. alba* two layers of subepidermal collenchyma are located between the mucilaginous epidermis and the isodiametric palisade cells (Vaughan & Whitehouse). The seed coat is coarsely reticulate in *S. alba* and minutely so in *S. arvensis* (Mulligan & Bailey, 1976), although Murley listed the former as having alveolate seeds, and Berggren indicated that both have an indistinct reticulum.

Sinapis arvensis is one of the most obnoxious weeds, and it is notoriously difficult to eradicate from crop fields. Factors contributing to its success and persistence in arable land include the immense productivity (estimated at a maximum of 25,000 seeds per plant (Markgraf)), the seed longevity (up to 75 years (Vaughan & Hemingway)—exceedingly high for a crucifer), the enforced dormancy when the seeds are buried at depths of many centimeters, the rapid germination when the seeds are exposed to favorable conditions, and the high relative growth rates of its vegetative organs (Fogg). The ability of the seeds to remain viable in the droppings of birds that feed on them probably plays an important role in the natural dispersal of *S. arvensis.* The seeds contained in the beak of the fruit may not germinate until the beak has rotted.

Sinapis alba subsp. *dissecta* (Lag.) Bonnier, a weed of flax fields in the Mediterranean region and Crimea but not yet introduced to our area, differs from subsp. *alba* in having bipinnatifid leaves, slender growth, glabrous or very sparsely pubescent siliques and stems, and flattened, reddish brown seeds. All these features have their analogues among other flax weeds and, according to Hjelmqvist, may have evolved through the selection of flax characters. It is quite difficult to remove the seeds of *S. alba* subsp. *dissecta* from those of flax (*Linum usitatissimum* L.) by winnowing because of their similarity in shape, weight, and size (Malzev).

The seeds of *Sinapis alba* are used for the manufacture of table mustard (see *Brassica*) and for the production of oils for making soap and mayonnaise, lubrication, and cooking (Vaughan & Hemingway). The seed cake contains 25–35 percent protein, and because of its high nitrogen content it is used as a fertilizer. The seeds of *S. arvensis* are used in eastern Europe for making poor-quality table mustard, while the young green parts are eaten as a salad in some parts of the Caucasus. The whole plant also is used as a green fodder.

The seeds have been used as a carminative, a diuretic, an emetic, an expectorant, a stimulant, a rubefacient, and a diaphoretic; as a remedy for bronchitis and dyspepsia; and in the preparation of an ointment to relieve neuralgia, arthritis, and rheumatism (Perry, Rosengarten). Hartwell has listed *Sinapis* *alba* as a source for preparations to cure tumors, sarcoma, carcinoma, endothelioma, and indurations of the skin.

Sinapis arvensis reduces the yield of some cereals (and probably other crops) to 53–69 percent in heavily infested fields (Mulligan & Bailey, 1975). Feeding on *S. alba* and *S. arvensis* may cause gastroenteritis, diarrhea, and irritation of the upper digestive tract and mouth of cattle and sheep, and the two species have been suspected of evoking photodermatitis (Kingsbury; Mitchell & Rook). In addition to being obnoxious weeds, these species are hosts for viruses and fungi that also attack many cruciferous vegetable crops.

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7. **Diplotaxis** A. P. de Candolle, Syst. Nat. **2:** 628. 1821.

Annual or perennial herbs, sometimes woody at base, glabrous or with spreading or retrorse trichomes [rarely scabrous], sometimes glaucous. Stems erect or ascending [rarely procumbent]. Basal leaves petiolate, forming a rosette or not, pinnatifid to pinnatisect or lyrate to sinuate-dentate, rarely entire [or bipinnatipartite]. Cauline leaves present or absent, short petiolate or sessile [occasionally auriculate]. Inflorescence an ebracteate, corymbose raceme [rarely with lowermost flowers from axils of uppermost leaves], greatly elongated in fruit. Sepals oblong or linear, erect or spreading, obtuse or acute, sometimes scarious at margin, glabrous or with a subapical tuft of hairs [or hairy on entire abaxial side]; inner pair as wide as [or much wider than] outer pair, usually not [rarely strongly] saccate at base. Petals broadly [or narrowly] obovate, attenuate to short [or long] claws, usually yellow [sometimes violet, lilac, or white]. Nectar glands 4, the lateral pair flat, usually prismatic or reniform, the median pair filiform or oval [sometimes clavate], lobed or not. Stamens tetradynamous; filaments free, linear, not appendaged; anthers oblong, cordate or sagittate at base, all fertile [or rarely the lateral pair sterile], median ones introrse or extrorse. Ovary usually with very numerous (to 260) ovules; style short [or obsolete]; stigma capitate or conical, 2-lobed [sometimes the lobes decurrent]. Fruiting pedicels somewhat stout [or slender], erect-ascending to divaricate [or reflexed]. Siliques dehiscent, linear, torulose, compressed parallel to the septum [or terete], borne on short [or long] gynophores [or subsessile]; valves 1-nerved, glabrous, somewhat thick [or membranaceous], obtuse or emarginate at apex; beaks 3-veined, seedless [or 1- or 2-seeded], narrower than [or as wide as] the valves, slightly flattened [or terete], cylindrical [or conical or obconical, rarely obsolete]. Seeds biseriately arranged in each locule, slightly compressed, usually very small (0.4–0.7(–1) mm long), ovoid, elliptic, or oblong, light brown, minutely reticulate or smooth, wingless, not [or slightly] mucilaginous when wet; cotyledons longitudinally conduplicate. Base chromosome numbers 7, 8, 9, 10, 11, 13. (Including *Pendulina* Willk.) LECTOTYPE SPECIES: *Sisymbrium tenuifolium* L. = *Diplotaxis tenuifolia* (L.) DC.; see Britton & Brown, Illus. Fl. No. U. S. ed. 2. **2**: 194. 1913. (Name from Greek, *diploös,* double, and *taxis,* row or arrangement, in reference to the two-rowed (biseriate) arrangement of seeds in each locule of the fruit.)—SAND ROCKET.

About 25 species distributed in central Europe and the Mediterranean region, particularly in northwestern Africa, and extending eastward to Pakistan and western India, with a group of five species endemic to the Cape Verde Islands (Rustan & Borgen). *Diplotaxis nepalensis* Hara (isotype at A!), recently described from the Karnali Valley in western Nepal, extends the range of the genus much farther to the east. In nearly all aspects of the plant, *D. nepalensis* can easily be treated as a minor variant of the highly polymorphic *D. Harra* (Forsskål) Boiss., a species distributed from Morocco to Pakistan. At least four species are weedy in much of Europe, western Asia, and northern Africa. Of these, three have been brought to the New World as ballast plants during the last third of the nineteenth century; two are naturalized and sporadically distributed in the southeastern United States.

The sectional classification of *Diplotaxis* has not been treated adequately. The four sections recognized by Schulz (1919) have been raised by Nègre (see Markgraf) to three subgenera, of which two are monotypic. Characters such as the number of ovules, the length of the gynophore, and the orientation of the sepals have been emphasized in recognizing infrageneric groups in *Diplotaxis,* but these may vary between the populations of a given species.

Section DIPLOTAXIS (sect. *Catocarpum* DC.) (perennials, rarely annuals; sepals spreading or ascending, not saccate at base; ovules (50–)80–150; gynophore (1–)2–8 mm long; beak obsolete, or seedless and to 2 mm long) is represented in our flora by *D. tenuifolia* (L.) DC. (*Sisymbrium tenuifolium* L., *Sinapis tenuifolia* (L.) R. Br., *Brassica tenuifolia* (L.) Fries), wall rocket, slim-leaf wall rocket, flixweed (Small), $2n = 22$, a species native to southern and central Europe but naturalized elsewhere on that continent and in North America. Although *D. tenuifolia* has been reported from ballast and waste places in Florida, Alabama, and Louisiana (Small, Mohr), it has not been included in any of the recent plant checklists covering these states. It may have been overlooked, or it may have failed to become a successful weed in the Southeast. Plants of *D. tenuifolia* can easily be recognized; they are suffruticose perennials with pinnatipartite, petiolate cauline leaves, yellow petals two to three times longer than the sepals, and ascending siliques with seedless beaks and short gynophores 1–3 mm long.

Section ANOCARPUM DC. (annuals, rarely perennials; sepals spreading or ascending, equal at base; ovules 20–60; gynophores absent or to 1 mm long; beak 1- or 2-seeded, rarely seedless, conical or cylindrical) is represented in the southeastern United States by *Diplotaxis muralis* (L.) DC. (*Sisymbrium murale* L., *Sinapis muralis* (L.) R. Br., *Brassica muralis* (L.) Boiss.), sand rocket, stinking wall rocket, cross weed (Small), $2n = 42$. A native of southern and central Europe, *D. muralis* is widely naturalized in Canada, the United States, and the West Indies, but is less so in Mexico and South America. It grows in disturbed sites, abandoned fields, waste places, and grasslands, and along beaches and roadsides. Smith has reported it from Arkansas (Howard County), but earlier records from Alabama, Florida, and Louisiana have been based on ballast plants that may have failed to persist. The record of *D. muralis* from North Carolina was based on misidentification of plants of *Hutera Cheiranthos* (under *Hutera* see Ahles & Radford). From the other crucifers of our area, *D. muralis* can be distinguished by its annual habit, its rosette-forming, lyrately lobed or sinuately dentate leaves, its leafless or few-leaved stems, its yellow flowers, and its usually sessile, erect-ascending siliques 15–45 mm long with seedless beaks.

Diplotaxis has been considered by Von Hayek and Rytz to be basal to the rest of the Brassiceae, and nearly all of the primitive characters suggested by Gómez-Campo (1980a) for the tribe are found in the genus. However, the relationships between *Diplotaxis* and its nearest relatives of subtribe Brassicinae have not been established adequately. The genus has biseriate, small (usually less than 1 mm long), oblong or oval seeds; siliques with gynophores and one-nerved flattened valves; and two-lobed stigmas. *Brassica* can be separated from *Diplotaxis* by its larger, globose, and uniseriately arranged seeds. The boundaries between the two, however, become less sharply defined if some northwestern African taxa with subbiseriate seeds are considered. *Sinapidendron* differs from *Diplotaxis* in its terete siliques, uniseriate seeds, and entire stigmas. The two species of sect. HESPERIDIUM O. E. Schulz (*D. acris* (Forsskål) Boiss., of northern Africa and Arabia, and *D. Griffithii* (Hooker & Thomas) Boiss., of the Punjab, Afghanistan, and western Pakistan) resemble *Moricandia* in nearly all aspects of the flower and in certain features of the fruit. However, *Moricandia* differs from *Diplotaxis* in lacking median nectaries and in having sessile, terete or tetragonal siliques and larger, usually margined or winged seeds.

Little is known about the breeding systems and pollination ecology of *Diplotaxis*, and the scant data indicate that a few species of flies, bees, butterflies, and beetles visit the flowers of *D. muralis* and *D. tenuifolia* (Knuth). The former is self-compatible, while the latter and *D. erucoides* (L.) DC. are usually self-incompatible. The last species was introduced to this country more than a century ago, but it appears to be restricted to a few places along the east coast north of our area. The median anthers of *D. tenuifolia* and *D. muralis* are extrorse, and in the latter they and the sepal tips reflect ultraviolet light, while the rest of the flower absorbs it (Markgraf). In *D. acris* the veins of the petals absorb UV light, but the rest of the blade reflects it (Horovitz & Cohen).

Chromosome numbers are known for at least 20 species, and with the exception of $n = 12$, which has not yet been found, a continuous series of haploid numbers from seven to 13 is present in *Diplotaxis*. Aneuploidy may have played an important role in the evolution of the genus. Species with $n = 13$

(*D. Harra,* its relatives, and the Cape Verdean species) are treated as diploids, and although Harberd (1976) agreed with that, he believed that they may have originated either by allotetraploidy between a species with $2n = 14$ and an unrecorded one with $2n = 12$, or by the aneuploid loss from tetraploids with $2n = 28$. However, there is no evidence to support either of these hypotheses. Earlier chromosome counts deviating from $2n = 42$ for *D. muralis* may have been erroneous. Harberd & McArthur (1972) have presented experimental evidence supporting the allotetraploid origin of this species from *D. tenuifolia* ($2n = 22$) and *D. viminea* (L.) DC. ($2n = 20$). Hybrids resulting from the cross *D. muralis* × *D. tenuifolia* almost always showed 11 bivalents and ten univalents at meiosis, while those obtained from *D. muralis* × *D. viminea* gave ten bivalents and 11 univalents. Furthermore, the occasional occurrence of reduced lateral stamens in *D. muralis* is most likely inherited from *D. viminea*—the only species in the genus with sterile and highly reduced lateral stamens.

Natural interspecific hybrids in *Diplotaxis* appear to be very rare. Schulz (1919) described *D.* ×*Schweinfurthii* from Egypt as a hybrid between *D. acris* and *D. Harra* and cited a few collections from Germany, Yugoslavia, and Sweden (see also Johansson) as hybrids between *D. muralis* and *D. tenuifolia.* Little experimental work has been conducted on interspecific hybridization in the genus, but extensive intergeneric crosses between *Diplotaxis* and *Brassica, Erucastrum, Hirschfeldia, Hutera, Sinapidendron,* and *Sinapis* have successfully been made by Harberd (1976) and Harberd & McArthur (1980).

Four species have been surveyed for glucosinolates. *Diplotaxis viminea* and *D. tenuifolia* have high concentrations of 4-methylthiobutylglucosinolate, but the latter also contains a few related nonvolatile compounds. Allylglucosinolate is the principal component in both *D. erucoides* and *D. muralis.* The scant chemical data show some differences between species. Analyses of the fatty-acid composition of ten species show that the pattern of *Diplotaxis* is distinct from that of the closely related *Brassica.* The latter has higher concentrations of erucic acid and usually lower amounts of linolenic and palmitic acids than does *Diplotaxis.*

Diplotaxis has the smallest and lightest seeds in the Brassiceae. They are usually less than a millimeter long and may weigh as little as 0.05 mg (*D. Harra*), which is less than one two-hundredth the seed weight of some species of *Cakile* and *Crambe* that have the heaviest (10–15 mg) seeds in the tribe. Plants of *D. acris* and *D. Harra* produce enormous numbers (more than 200 per silique) of dustlike seeds that can easily be transported by strong winds for several hundred miles. Both species are widely distributed in the Sahara and in Arabia, and the latter species has an almost continuous distribution extending more than 7400 km (4500 mi) from Morocco to western Pakistan.

No local uses have been reported for the genus, and except for the four weedy species mentioned above, *Diplotaxis* has no economic importance. Mitchell & Rook mentioned that *D. erucoides* and *D. tenuifolia* have irritant properties.

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8. **Eruca** Miller, Gard. Dict. abr. ed. 4. Vol. 1 (alph. ord.). 1754.

Annuals [or caespitose and rhizomatous perennials], hispid or pilose with simple, spreading or retrorse trichomes, sometimes glabrous. Stems leafy [or scapose]. Basal leaves petiolate, [forming or] not forming a distinct rosette, usually lyrately pinnatifid or pinnatipartite, rarely bipinnatisect or undivided. Cauline leaves (when present) sessile or short petiolate, divided or coarsely dentate to subentire. Inflorescence an ebracteate, many-flowered, corymbose raceme, greatly elongated in fruit. Sepals erect, oblong or linear, caducous [or persistent until fruit matures], green or violet, glabrous or with a subapical tuft of trichomes, sometimes pilose or setulose along abaxial side; outer [and inner] sepals cucullate, inner ones saccate at base. Petals broadly obovate [or oblanceolate], cream or yellow with dark brown or violet veins [or entire blade violet]; claws well developed, as long as or longer than the sepals. Nectar glands 4 [2], lateral pair prismatic, median pair ovoid or oblong [or absent]. Stamens tetradynamous, not appendaged; filaments linear; anthers oblong or linear, sagittate at base. Ovary many ovulate; style present; stigma 2-lobed, the lobes usually decurrent. Fruiting pedicels glabrous or pubescent, erect to ascending, subappressed to the rachis [rarely divaricate]. Siliques subsessile, dehiscent, linear or oblong to elliptic, inflated, terete or slightly tetragonal, glabrous or retrorsely hispid or scabrous; valves strongly 1-nerved, slightly keeled, convex, somewhat coriaceous; beaks seedless, prominently 1-nerved, occasionally with obscure lateral nerves, flattened [rarely tetragonal], ensiform, acute or acuminate, shorter to longer than the valves. Seeds biseriately arranged, oval, wingless, reticulate, slightly to copiously mucilaginous when wet, orange or brown; cotyledons longitudinally conduplicate, emarginate. Base chromosome number 11. (Including *Euzomum* Link, *Velleruca* Pomel.) LECTOTYPE SPECIES: *Eruca sativa* Miller (*Brassica Eruca* L.) = *E. vesicaria* (L.) Cav. subsp. *sativa* (Miller) Thell.; see Maire, Fl. Afr. Nord **12:** 303. 1965. (Name the classical Latin name for the above species, but its origin uncertain; most likely derived from *eructo* (or the Greek *ereugomai*), to belch or eruct, or from *uro,* to burn, in reference to the hot taste of the plant.)—GARDEN ROCKET, ROCKET SALAD.

Three species, of which *Eruca loncholoma* (Pomel) O. E. Schulz and *E. setulosa* Boiss. & Reuter are endemic to Algeria; the third, *E. vesicaria,* is probably a native of the Mediterranean region but is naturalized throughout Europe, in much of Asia and Africa, and sporadically in Australia and North and South America. The genus is represented in the southeastern United States by *E. vesicaria* (L.) Cav. subsp. *sativa* (Miller) Thell. (*Brassica Eruca* L., *E. sativa* Miller, *E. Eruca* (L.) Ascherson & Graebner, *Raphanus Eruca* (L.) Crantz), garden rocket, rocket salad (less commonly: rocket, edible rocket, and roquette), $2n = 22$, a weed of cultivated fields, roadsides, and waste places. Although I have not seen specimens of this taxon from the southeastern United States, there is no doubt that it occurs there. The species is found in all of the states bordering our area and is included in the treatments of Small and Rickett. *Eruca vesicaria* subsp. *sativa* is easily distinguished from the other crucifers of our flora by its yellow or cream-colored petals with dark brown or violet veins, erect sepals, appressed siliques, one-nerved valves, ensiform beaks, and biseriately arranged seeds. Subspecies *vesicaria,* which is endemic to Spain, the Balearic Islands, and northwestern Africa, differs from subsp. *sativa* in its cucullate inner sepals and its persistent calyx that remains attached until the fruits are nearly ripe.

Eruca is well defined by its erect sepals, biseriately arranged seeds, one-nerved valves, somewhat decurrent stigmas, and long, seedless, ensiform or tetragonal beaks. It is related to *Diplotaxis,* particularly to sect. HESPERIDIUM O. E. Schulz, from which it differs in the ensiform beaks of the siliques and in the larger and fewer seeds. Some authors (e.g., Von Hayek and Rytz) have suggested a direct relationship between *Eruca* and *Sinapis,* but the two should be loosely associated. The latter is readily distinguished from *Eruca* by its spreading sepals, uniseriately arranged seeds, and three- to seven-veined valves. Both *E. setulosa* and *E. loncholoma* resemble *Brassica* sect. BRASSICARIA, but the relationship between the two genera is not entirely clear.

The petals of *Eruca vesicaria* exhibit high absorbance of ultraviolet light in the blade and low reflectance in the claw (Horovitz & Cohen). More than 100 species of insects have been reported as visitors of the flowers, but the most common pollinators appear to be members of the bee genera *Apis, Andrena,* and *Halictus.* Self-incompatibility has been reported by many authors, but the expression of this character is not absolute, and selfing may lead to the formation of short siliques with few seeds. Unlike that of the rest of the Cruciferae, the incompatibility system in *E. vesicaria* is controlled by at least three pairs of complementary genes, each with several alleles (Verma *et al.,* Lewis).

Chromosome numbers are known only for *Eruca vesicaria.* Although 11 bivalents have usually been found, Wills observed quadrivalents and hexavalents, as well as frequent chromosomal bridges. Despite these meiotic irregularities, pollen stainability was nearly 99 percent. The karyotype consists of single pairs of long and short and nine pairs of medium-sized metacentric chromosomes, of which the long pair has median and subterminal constrictions and one medium-sized pair has satellites (Mukherjee).

Artificial intergeneric hybridization between certain members of the Brassiceae and *Eruca vesicaria* has been successful if the latter is used as the maternal plant and the crossing is done at the bud stage. The stigmas of *Eruca* are unselective for foreign pollen and allow germination of and style penetration by pollen tubes of members of several genera (Harberd, 1976; Sampson). On the other hand, the pollen of *Eruca* always fails to germinate on foreign stigmas.

The seeds of *Eruca vesicaria* yield 22–36 percent oil, and the plant is considered to be among the crucifers richest in erucic-acid content. The unsaponifiable matter contains sterols dominated by β-sitosterol (49 percent) and campesterol (32 percent). The seeds contain high concentrations of 4-methylthiobutylglucosinolate and an enzyme that converts the glucosinolates to thiocyanates (Schlüter & Gmelin).

The earliest cultivation of *Eruca vesicaria* dates back to the ancient Romans and Greeks. It is currently grown in Europe (and infrequently in North America) as a salad plant and is cultivated extensively in central and western Asia for seed oil. The oil is used in pickling and as an illuminant and a lubricant; in India it is used for massaging the body, applied to the hair, and employed in the treatment of vitiligo and as a vesicant. However, it is known to cause allergic dermatitis, photodermatitis, and persistent melanosis of the skin (Mitchell & Rook). The seed cake and the entire plant are used as fodder for domestic animals. In southern Europe the young leaves are used as a stimulant, an antiscorbutic, a diuretic, and a stomachic, but a strong dose may cause vomiting. In India the whole plant is considered to be an aphrodisiac (Caius), and electuary preparations have been used to cure indurations of the liver (Hartwell). Finally, the species is an obnoxious cosmopolitan weed and is a host for several fungi and viruses that also attack cruciferous crops.

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9. **Raphanus** Linnaeus, Sp. Pl. **2:** 669. 1753; Gen. Pl. ed. 5. 299. 1754.

Annual, biennial, or rarely short-lived perennial herbs, scabrous or hispid, with simple, spreading or appressed trichomes, sometimes glabrous. Roots slender or thick, slightly woody, usually fleshy and variable in size, shape, and color in the cultivated forms. Stems erect [or prostrate], simple or branched. Basal leaves petiolate, sometimes forming a rosette, lyrately lobed or pinnatifid to pinnatisect; lateral lobes in 2–20 pairs, distant or contiguous; terminal lobe broadly ovate to orbicular, much larger than the lateral ones. Upper cauline leaves short petiolate or subsessile, smaller and less lobed than the lower ones. Inflorescence an ebracteate, many-flowered, corymbose raceme, usually greatly elongated in fruit. Sepals erect, oblong or linear, glabrous or hispid; inner pair saccate at base. Petals long clawed, white, yellow, lilac, or violet, usually with dark veins, broadly obovate, obtuse or truncate at apex. Nectar glands 4, the lateral pair prismatic, the median pair filiform or cylindrical. Stamens tetradynamous; filaments slender, not appendaged; anthers oblong. Ovary sessile, 2- to many-ovulate; style slender; stigma capitate, slightly 2-lobed. Fruiting pedicels ascending to divaricate [or reflexed and subappressed to the rachis]. Siliques indehiscent, transversely jointed, 2-segmented, linear or oblong to oval, sometimes dagger-shaped, glabrous or antrorsely [or retrorsely] scabrous or hispid; lower segment seedless, very short [or obsolete], narrow and nearly as wide as the pedicel, obscurely valved; upper segment few to many seeded, terete or angled, thick, corky, torulose to strongly moniliform, sometimes not constricted between the seeds, usually lomentaceous and breaking up at maturity into 1-seeded segments, longitudinally ribbed or smooth. Seeds uniseriately arranged, pendulous, globose to slightly ovoid [or oblong], wingless, not mucilaginous when wet, brown, reticulate or nearly smooth; cotyledons longitudinally conduplicate, emarginate at apex. Base chromosome number 9. (Including *Dondisia* Scop., *Durandea* Delarbre, *Ormycarpus* Necker, *Quidproquo* Greuter & Burdet.) LECTOTYPE SPECIES: *R. sativus* L.; see Britton & Brown, Illus. Fl. No. U. S. ed. 2. **2**: 194. 1913. (From the Greek name *raphanos,* used by Dioscorides and Theophrastus for radish; derived from Greek *ra,* quickly, and *phainomai,* to appear, alluding to the rapid germination of the seeds.)—RADISH.

A genus of three species probably native to the Mediterranean region, with one species a cosmopolitan weed, and another a crop plant and an escape from cultivation. The third, *Raphanus Boissieri* Al-Shehbaz, is endemic to southern Lebanon and northern Israel and belongs to the monotypic sect. HESPERIDOPSIS Boiss., which is characterized by its short (1–1.2 cm long) petals, reflexed fruiting pedicels, retrorse pubescence on the siliques, obsolete lower fruiting segments, and oblong seeds.

Section RAPHANUS (sect. *Raphanistrum* DC.) (petals 1.7–3 cm long, fruiting pedicels ascending to divaricate, siliques glabrous or with antrorsely appressed or spreading trichomes, lower segment evident, seeds globose or nearly so) includes two weedy species that are naturalized in almost all of the Southeastern States and grow in fields, cultivated land, roadsides, waste places, orchards, and disturbed areas. *Raphanus Raphanistrum* L., wild radish, jointed charlock, jointed radish, charlock, $2n = 18$, was first reported from North America in 1814 and from Tennessee in 1901 (Gattinger) but has only recently been reported from the other states of the Southeast (Ahles *et al.,* 1958; Jones, 1961; Pullen *et al.*; Thieret; Thorne). Although the species has not yet been reported from Arkansas, it probably grows there. Individuals of *R. Raphanistrum* have corky, ribbed, torulose or moniliform, lomentaceous fruits (FIGURE 1k, l) and white or yellow petals with brown veins. The species is highly variable in flower color, fruit width, and number of seeds per fruit. The five subspecies that have been recognized on the basis of differences in these characters are completely interfertile, and natural hybridization apparently occurs in the areas where their ranges overlap.

The second species, *Raphanus sativus* L., radish, common radish, wild radish, garden radish, $2n = 18$, a vegetable grown primarily for its fleshy roots, is a naturalized weed common in many parts of our area. It differs from the preceding by having inflated, nonlomentaceous, and usually smooth, nontorulose siliques (FIGURE 1m). Thellung treated *Raphanus* as a monotypic genus and reduced the cultivated radish to a subspecies of *R. Raphanistrum,* but such a disposition has not been accepted by recent authors.

The relationships of *Raphanus* are somewhat controversial. Several authors have suggested direct associations with *Cossonia* Durieu (= *Raffenaldia* Godron) or *Hemicrambe,* but these genera appear to be only remotely related. Perhaps a more acceptable connection is with *Enarthrocarpus* or with *Trachystoma* O. E. Schulz. As pointed out by Gómez-Campo (1980a), *Raphanus* shows some affinity to subtribe Brassicinae in cotyledon morphology and in the ability to cross with several of its genera, but the genus is apparently much closer to the last two genera than to members of this subtribe. *Raphanus* is easily distinguished by its ebracteate inflorescences, erect sepals, dark-veined petals, and 2-segmented fruits with an indehiscent, inflated or lomentaceous, (2–)4–15-seeded upper segment and a seedless, aborted lower segment.

Plants of *Raphanus* with yellow or violet flowers are visited by insects more often than the white-flowered form. The low attractiveness of the white flowers may be attributed to their low reflectance. The white-flowered form apparently differs from the other color forms by a single allele (Kay). Numerous insect genera, the most common of which are *Apis, Andrena, Pieris,* and *Eristalis,* have been reported as pollinators. Self-incompatibility occurs in *R. Raphanistrum* and *R. sativus,* and male sterility has been found in the latter (Shiga).

Some cultivars of *Raphanus sativus* show karyotypic differences in number of secondary constrictions, presence or absence of satellites, arm ratios, and chromosome size. Mukherjee (1979) has postulated that karyotype evolution within *Raphanus* probably proceeded toward reduction in chromosome size. On the basis of chromosome morphology, secondary associations at meiosis, and study of haploid plants, some authors (e.g., Kaneko) have argued that the base chromosome number for the genus is six.

Natural hybridization between *Raphanus Raphanistrum* and *R. sativus* has been known since 1788, and the hybrid has been named *R.* × *micranthus* (Uechtr.) O. E. Schulz. In artificial hybrids, Harberd & McArthur (1972) have observed seven bivalents and a quadrivalent as the most frequent meiotic configuration. The reduced pollen fertility (approximately 50 percent) in the hybrids is associated with a reciprocal-translocation heterozygotic condition. The transfer of some of the weedy characters from *R. Raphanistrum* to *R. sativus* through natural hybridization may have played a major role in converting the latter from a crop plant into a very successful weed near the coastal areas of central California (Panetsos & Baker).

The classic intergeneric hybrid ×*Raphanobrassica* is an amphidiploid originally obtained by Karpechenko from *Raphanus sativus* and *Brassica oleracea* var. *capitata.* It is easily synthesized by crossing autotetraploid forms of the parental species. The cross is successful when radish is used as the maternal parent, and the failure of the reciprocal cross is caused by the inability of the pollen of *Raphanus* to penetrate the styles of *Brassica.* The fruits of ×*Raphanobrassica* are intermediate between those of the parental species in that the lower segment resembles *Brassica,* and the upper one *Raphanus.* Most of the experimental work on ×*Raphanobrassica* deals either with the transference to *Brassica* of the resistance to certain fungal diseases or with the production of forage or high oil-yielding crops. Even after successive crossings with either parent, ×*Raphanobrassica* is still impaired by meiotic irregularities and low seed set caused by endosperm deficiency. It has been suggested that the reduced fertility results from genic imbalances or perhaps from the insufficient meiotic timing between the parental genomes. The literature on ×*Raphanobrassica* and other intergeneric hybrids is extensive; the papers of Harberd & McArthur (1980), Kato & Tokumasu, McNaughton, Olsson & Ellerström, and Yarnell should be consulted for further details.

The genus has been thoroughly surveyed for glucosinolates, fatty acids, flavonoids, and sterols, and the distribution of these constituents apparently has no taxonomic value. Sinapine is the major alkaloid in *Raphanus,* and β-sitosterol and campesterol are the dominant sterols. The pungent principle in the roots of *R. sativus* is 4-methylthio-3-butenyl isothiocyanate, but several other isothiocyanates have been characterized from the other parts of the plant and from *R. Raphanistrum.* Raphanin, a seed-germination inhibitor with antibacterial properties (Ivanovics & Horvath), may well be the 4-methylsulfinyl-3-butenylglucosinolate present in the two species above.

The upper part of the root and the hypocotyl (or the latter alone) become fleshy in *Raphanus sativus.* Root succulence is markedly reduced by long days, and this may account for the failure of naturalized radishes to develop fleshy roots. The vascular cambium in young roots appears as two opposite crescent-shaped layers outside the diarch primary xylem. After forming a complete cylinder, the cambium eventually produces enormous amounts of thin-walled xylem parenchyma and much smaller amounts of vascular elements that are slightly lignified. Subsequent transformation of some of this parenchyma into secondary cambium and the extensive formation of tertiary tissues by the latter, along with the initial activities of the primary cambium, account for the fleshiness of the hypocotyl-root axis.

The corky fruit wall of *Raphanus sativus* is attributed to numerous layers of loose and thin-walled parenchyma that become lignified in the weedy forms. The inner part of the fruit wall consists of several layers of tangentially elongated storage tracheids that are lined by a layer of subepidermal fibers followed by the inner epidermis. The vascular bundles are located in the parenchymatous region and are connected with the inner part of the wall by strands of radially elongated storage tracheids. The function of these tracheids is not entirely understood, but they may transport water to maintain some moisture around the seeds (Kaniewski).

The fruits of *Raphanus Raphanistrum* break into one-seeded segments that vary in size according to the subspecies. In the inland *R. Raphanistrum* subsp. *microcarpus* (Lange) Thell. the segments are not corky and are 1.5–2 mm wide, while in the maritime subsp. *rostratus* (DC.) Thell. and subsp. *maritimus* (Sm.) Thell. they are 5–10 mm in diameter, strongly corky, and usually dispersed by sea water. None of these subspecies has been introduced in the New World, and the sole representative there is subsp. *Raphanistrum.*

The inscriptions on the inner walls of the Egyptian pyramids and the remarks of Herodotus (Banga) indicate that *Raphanus sativus* has been cultivated since at least 2780 B.C. Truly indigenous radishes have not been found, and claims of their occurrence in the original wild state in eastern Asia are based on escapes from cultivation. The direct ancestors of the radish are unknown, and certain authors believe that it may have originated as a hybrid between *R. Raphanistrum* subsp. *landra* (Moretti ex DC.) Bonnier & Layens and subsp. *mari-*

timus. However, Lewis-Jones and associates, who studied many gene loci coding for different enzymes, have suggested that the radish is much closer to the former and that subsp. *maritimus* probably is not one of its direct ancestors. Others have suggested that the eastern Asiatic, Indian, and Mediterranean radishes have evolved from different progenitors. On the basis of morphology and ecology, *R. sativus* is more closely related to *R. Raphanistrum* subsp. *Raphanistrum* than to any other subspecies (Zohary).

Selection for size of different parts in *Raphanus sativus* has led to variation unparalleled in any other cultivated herb. The diameter of the rosette ranges from less than 10 cm (4 in) to more than 2 m (7 ft), and the root may be as small as the cherry (*Prunus Avium* L.) to as large as the gigantic Japanese 'Lew-Chew' and Indian 'Jaunpuri' radishes, which are up to 1 m long and 50–60 cm wide. The 'Sakurajima' mammoth globe radishes may weigh more than 100 pounds (nearly 50 kg). All these gigantic radishes belong to var. *longipinnatus* Bailey (var. *niger* (Miller) Pers., according to Helm). The fruits of the rat-tailed radishes of India and Malaysia (previously treated as *R. caudatus* L., but more appropriately as *R. sativus* var. *Mougri* Helm) may be 1 m long; they are less than 10 cm in other radishes.

The roots, leaves, flower tops, and young fruits of the radish are eaten as a salad, and in eastern Asia the roots are preserved by canning, drying, or pickling in brine and rice hulls. The edible seed oil is used for soap making, illuminating, and crayon manufacturing. The giant radishes are cultivated in South Africa as a fodder crop. The leaves of *Raphanus Raphanistrum* are eaten as a salad by the poor in Italy, and the seeds have occasionally been used as a substitute for mustard in England.

Caius and Perry have listed some 35 medicinal properties for the radish that range from the treatment of burns, fevers, pains, and coughs to remedies for cholera, tumors, and paralysis. Contact dermatitis caused by *Raphanus sativus* has been reported by Mitchell & Jordan, and gastroenteritis, pain, and bloody diarrhea in livestock may be caused by *R. Raphanistrum*.

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10. **Rapistrum** Crantz, Classis Crucif. Emend. 105. 1769, nom. cons.

Annual [biennial or perennial] herbs, sparsely to densely hispid, occasionally glabrous or glaucous. Lower leaves petiolate, lyrately pinnatifid [or pinnatisect], rarely undivided; terminal lobe suborbicular or ovate, larger than the oblong or ovate lateral ones. Upper leaves subsessile or short petiolate, simple or sinuately lobed, subentire or dentate. Inflorescence an ebracteate, densely flowered, corymbose raceme, much elongated in fruit. Sepals ascending, glabrous or with a subapical tuft of hairs, oblong or linear, inner pair slightly saccate at base. Petals yellow, obovate, clawed. Nectar glands 4, the lateral pair small, prismatic, the median pair conical. Stamens tetradynamous; filaments linear, not appendaged; anthers oblong, median ones introrse or extrorse. Ovary cylindrical, 2–4-ovulate, glabrous or pubescent; style filiform, persistent, glabrous; stigma capitate, 2-lobed. Fruiting pedicels slender to very thick, erect to ascending, usually appressed to rachis. Siliques sessile, transversely jointed, 2-segmented, slightly to strongly constricted at the joint, erect, hirsute or hispid, sometimes glabrous; lower segment dehiscent or indehiscent, persistent, usually 1- (or 2- or 3-)seeded, occasionally seedless and nearly as wide as the pedicel, elliptic or oblong, longitudinally striate or smooth, valves rigid, septum present or absent; upper segment indehiscent, 1-seeded or very rarely seedless, spherical or oval, wider than [or nearly as wide as] the lower segment, usually rugose, with (8–)12–16 longitudinal, usually well-developed ribs, caducous at maturity, abruptly [or gradually] tapering at apex; style slender [or thick], longer [or shorter] than the upper segment. Seeds oblong or oval, slightly compressed, not mucilaginous when wet, wingless, smooth, brown, pendulous and small in the lower segment, erect and larger in the upper one; cotyledons longitudinally conduplicate. Base chromosome number 8. (Including *Schrankia* Medicus.) TYPE SPECIES: *Rapistrum hispanicum* (L.) Crantz (*Myagrum hispanicum* L.), typ. cons.; see Int. Code Bot. Nomencl. 1983, p. 350. = *R. rugosum* (L.) All. subsp. *Linnaeanum* (Cosson) Rouy & Foucaud. (Name from Latin *rapa,* turnip, and *astrum,* incomplete resemblance.)—WILD TURNIP, TURNIP WEED.

A genus of two species native to southern and central Europe and adventive elsewhere on that continent, with one species naturalized throughout much of the world. Schulz (1919) recognized three species in two sections, but it is doubtful that his sectional classification is useful or necessary. Both species have been introduced to the New World, and one has been reported from the Southeast.

Rapistrum perenne (L.) All., $2n = 16$, is known from a few localities in Canada but apparently has not yet reached the United States. The highly polymorphic *R. rugosum* (L.) All. (*Myagrum rugosum* L.), wild turnip, turnip weed, $2n = 16$, grows in waste places, along roadsides, and in fields in scattered localities in the United States, and it has only recently been recorded for the Southeast from Louisiana (MacRoberts). The species was introduced to South America long before 1830 (Cambessèdes) and was first collected from the United States as a ballast plant in 1873. *Rapistrum rugosum* is extremely variable in the shape, pubescence, rugosity, and prominence of ribs of the upper fruit segment, and in the length and thickness of the fruiting pedicels. Three poorly defined subspecies have been recognized, but complete intergradation between them has been encountered in Europe and Turkey. In *R. rugosum* subsp. *rugosum* the upper segment of the fruit is ovoid, strongly ribbed, and rugose, and the fruiting pedicel is thick and nearly as long as the lower segment; in subsp. *orientale* (L.) Arcang. the upper segments are globose, rugose, and strongly ribbed, and the fruiting pedicels are one and a half to three times longer than the lower segments. In subsp. *Linnaeanum* (Cosson) Rouy & Foucaud the upper segments are slightly rugose and weakly ribbed, and the fruiting pedicels are slender and two to five times longer than the stalklike lower segment. All three subspecies and some of their intermediates have been found in the United States.

The affinities of this well-marked genus are somewhat controversial. *Rapistrum* resembles *Ceratocnemum* Cosson & Balansa, *Octocarpus* Durieu, *Guiraoa* Cosson, and *Cordylocarpus* Desf. in chromosome number and in having jointed siliques with one-seeded upper segments. Perhaps it is closest to the last genus, with which it produces natural hybrids in Algeria and Morocco. On the basis of fruit morphology, *Rapistrum* shows some affinity to *Didesmus* Desv., but the two genera probably are not closely related. *Rapistrum* is easily distinguished from the above genera of subtribe Raphaninae by its yellow flowers and its unappendaged, terete fruits that have usually one-seeded segments with the upper one ribbed.

Little is known about the floral biology of the genus. *Rapistrum rugosum* is self-incompatible, while *R. perenne* has not been tested for this character. Petals of the former exhibit high ultraviolet absorbance at the claws and veins and high reflectance at the intercostal areas. Variation has been found among populations in the shape and size of the nectar guide, but the genetic basis for this variation is unknown (Horovitz & Cohen).

Consistent chromosome counts of $2n = 16$ have been documented for all taxa. In only one case (Murín & Váchová) has a different number ($2n = 18$) been reported.

The natural hybrid between *Rapistrum rugosum* and *Cordylocarpus muricatus*, × *Rapistrocarpus ramosissimus* (Pomel) Al-Shehbaz, resembles the former species in several aspects of the fruit but differs in having cylindrical, two- or three-seeded lower fruit segments characteristic of the latter (Maire, Solms). Madiot reported a sterile plant allegedly derived from hybridization between *Rapistrum* and *Sisymbrium* L., but the lack of experimental evidence and the extreme remoteness of the two genera cast doubts on the identity of the parents.

The major mustard-oil glucosides in the seeds of *Rapistrum perenne* and *R. rugosum* are 3-butenyl and 3-methylsulfonylpropyl glucosinolates, respectively, and traces of other compounds have also been found in the latter species. The seed-oil content in *R. rugosum* is the lowest (6 percent of dry weight) among the numerous crucifers analyzed (Kumar & Tsunoda).

The hypodermis in *Rapistrum rugosum* is much less developed in the lower segment of the fruit than in the upper. The differentiation of ribs starts with the collapse of the outer layers of hypodermis, followed by the radial elongation and strong lignification of the inner cells at certain areas that become ribs and alternate with large schizogenous intercellular spaces. These developments may have misled Saunders to suggest that the gynoecium of *Rapistrum* is composed of 40 to 50 carpels.

Dispersal in the genus is accomplished primarily by the upper segment of the fruit, which is indehiscent, one-seeded, and readily detached when mature. The lower segment is persistent in both species, but it usually dehisces in

Rapistrum rugosum. Seed size in this species is dimorphic, and it may be related to dispersal.

Although all members of *Rapistrum* are weeds, *R. rugosum* has become a very serious pest in several areas of Queensland, Australia, and it is one of the prime suspects as the cause of endemic goiter (Bachelard & Trikojus).

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11. **Calepina** Adanson, Fam. Pl. 2: 423. 1763.

Annual, or rarely biennial, glabrous herbs. Basal leaves petiolate, sometimes forming a rosette, oblanceolate or spatulate, usually lyrately pinnatifid, sometimes dentate or subentire. Cauline leaves sessile, sagittate or auriculate at base, dentate or entire. Inflorescence an ebracteate, corymbose raceme, greatly elongated in fruit. Sepals spreading, ovate or oblong, obtuse, scarious at margin, not saccate at base. Petals obovate or oblanceolate, attenuate to a clawlike base, usually unequal, with the abaxial pair larger than the adaxial one, white, very rarely rose or lavender. Nectar glands 4, the median pair subglobose, the lateral pair oblong, usually 2-lobed. Stamens slightly tetradynamous; filaments usually broadly flattened, somewhat dilated at base, white; anthers oblong or ovate, slightly sagittate at base. Ovary 1-ovulate, glabrous; stigma capitate, subsessile. Fruiting pedicels erect or ascending, slender, usually curved, sometimes subappressed to the rachis. Fruits indehiscent, nutlike, 1-seeded, oval to obpyriform, borne on slender and very short gynophores; pericarp thick, hard, usually longitudinally 4-ribbed, reticulate-rugose; septum lacking; beak conical, slightly compressed, short, blunt. Seeds pendulous, wingless, not mucilaginous when wet, subglobose to oval, brown; seed coat thin; cotyledons conduplicate at the base, involute at the distal half. Base chromosome number 7. TYPE SPECIES: *Myagrum irregulare* Asso = *Calepina irregularis* (Asso) Thell. (Name of obscure origin, considered by many to be derived from *Haleb* [or wrongly *Chaleb*], the Arabic name for the Syrian city of Aleppo, but more likely from Greek *chalepaino,* a term used by Theophrastus, probably in connection with weedy plants. Since Adanson based the genus on Bauhin's *Myagrum monospermum minus,* which was collected from the vicinity of Montpellier, France, it is highly unlikely that the generic name stems from Aleppo.)

A monotypic genus probably native to the steppes north of the Caspian Sea and widely naturalized in southern, central, and western Europe, southwestern Asia, and northern Africa for many centuries. *Calepina irregularis* (Asso) Thell. (*Myagrum irregulare* Asso, *Crambe Corvinii* All., *Calepina Corvinii* (All.) Desv., *Bunias cochlearioides* Willd., *Calepina cochlearioides* (Willd.) Dumort.), $2n$ = 14, 28, 42, is known from a few localities in North Carolina (Buncombe County), Maryland, and Virginia, where it grows primarily in fields and on farms. It occupies highly diversified habitats in Europe, however (Gómez-Campo, 1978). Fruits of *C. irregularis* were encountered some 30–40 years ago in shipments of Canary grass (*Phalaris canariensis* L.) imported to the United States from Morocco and Turkey. Most of the plants observed in Virginia (Blake) and North Carolina (Hardin) shortly after the initial introduction of the species were removed by hand, and it is uncertain whether the species still exists in our area.

Calepina has traditionally been placed in the Brassiceae, but such a disposition has recently been questioned by Gómez-Campo (1980a), who suggested its removal from the tribe due to its slightly conduplicate cotyledons with involute margins and its unsegmented fruit. However, he did not assign *Calepina* to another tribe. The genus apparently has no relatives outside the Brassiceae, and despite its deviation from the typical members of this tribe, it has been retained here. *Calepina* may be considered as a highly evolved member of the tribe with fruits lacking the septum and the valvular segment (Gómez-Campo & Tortosa, Zohary). The nutlike fruits may be interpreted as consisting of the indehiscent upper segment only, with the lower segment represented by a tiny, gynophorelike structure. However, there is no anatomical evidence that supports this interpretation.

The generic relatives of *Calepina* are obscure. Several authors have suggested direct or close ties with *Zilla* (Von Hayek), *Muricaria* Desv. (Rytz), or *Crambe* (Schulz, 1919). However, these genera are unrelated to *Calepina* and differ in fruit morphology and chromosome numbers. *Zilla* ($n = 16$) and three other genera, all shrubs, form the natural subtribe Zillinae (DC.) O. E. Schulz, while *Crambe* ($x = 15$) and *Muricaria* ($n = 12$) probably belong to two different groups within the highly heterogeneous Raphaninae. *Calepina* may also be assigned to the latter subtribe, but its nearest relatives are unknown. *Calepina irregularis* can be easily distinguished from the other crucifers of our area by its white flowers, its unequal petals, its flattened filaments, and its indehiscent, one-seeded, four-ribbed, reticulate, oval, nutlike fruits (FIGURE 1n).

Calepina irregularis consists of diploid (Manton), tetraploid (Larsen & Lagaard, Al-Shehbaz & Al-Omar), and hexaploid (Jaretzky, 1929, 1932) populations. The cytogeography of the species, however, is far from adequately known, and information about hybridization between plants with different ploidy levels is lacking.

The seed coat is composed of an epidermis (with large and hollow columns of mucilage that is not exuded when the seeds are wet), followed by a subepidermis, a palisade layer with flatly thickened inner tangential walls, and pigmented, aleurone, and hyaline layers (Vaughan & Whitehouse).

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12. **Cakile** Miller, Gard. Dict. abr. ed. 4. Vol. 1 (alph. ord.). 1754.

Annual or very rarely short-lived perennial, glabrous [or pubescent], succulent herbs. Stems usually branched at base. Lower leaves petiolate, entire or crenate, sometimes sinuate or pinnatisect and with narrow lobes. Cauline leaves gradually reduced in size and lobing. Inflorescence an ebracteate, corymbose raceme, greatly elongated in fruit; rachis straight or slightly to strongly flexuous or geniculate. Sepals erect, glabrous or sparsely pubescent at apex, usually hyaline at margin; outer pair slightly cucullate; inner pair somewhat saccate at base. Petals showy, rarely reduced to bristles or altogether lacking, white or lavender [or purple or violet], obovate or spatulate, obtuse or emarginate at apex; claws distinct, short or long. Nectar glands 4, the lateral pair 2-lobed or flat, the median pair oval or conical. Stamens tetradynamous; filaments linear, not appendaged, free; anthers oblong, acute or obtuse at apex, cordate at base. Ovary glabrous, sessile, transversely jointed, with 1 (or 2 or 3) ovules in each segment; style absent; stigma capitate, entire or sometimes slightly 2-lobed. Fruiting pedicels divaricate, rarely ascending or recurved, as wide as or narrower than the rachis. Siliques transversely jointed, 2-segmented, indehiscent, somewhat fleshy when immature, becoming dry and corky later; segments terete or angled, usually 1-seeded, occasionally 2- or 3-seeded, sometimes the lower segment seedless; septum very thin, usually appressed to the seed; articulation surface of the lower segment with 2 (rarely with more or without) conical or broad teeth that fit into the pits of the articulation surface of the upper segment; lower segment persistent, sometimes with 2 lateral horns at apex; upper segment readily separating at maturity, as long as or 2 or 3 times longer than the lower segment, obscurely to strongly 3-veined on each side, sometimes ribbed and sulcate, usually terminating in a conical or ensiform beak, obtuse to acute or retuse at apex. Seeds large, oblong or ellipsoid, slightly flattened, not mucilaginous when wet, wingless, brown, smooth or minutely punctate, large and erect in the upper segment, smaller and pendulous in the lower one; cotyledons accumbent or obliquely incumbent, lanceolate or oblanceolate. Base chromosome number 9. LECTOTYPE SPECIES: *Bunias Cakile* L. = *Cakile maritima* Scop.; see Adanson, Fam. Pl. **2:** 423. 1763; Britton & Brown, Illus. Fl. No. U. S. ed. 2. **2:** 195. 1913. (Name probably derived from Arabic *qaqoulla* (also spelled *qaqulla* or *qaqulleh*) previously used in North Africa for *C. maritima,* although a few authors believe that the name was used originally for cardamom and other aromatic plants.)—SEA ROCKET.

A genus of seven species, all except one of maritime habitats; distributed along the sandy beaches and shores of the Great Lakes of North America, the North Atlantic Ocean, the Caribbean Sea, the Gulf of Mexico, and the Baltic, North, Barents, Black, and Mediterranean seas; introduced and widely naturalized along the Pacific coast of North America, eastern, southern, and western Australia, New Zealand, New Caledonia, Japan, Uruguay, and Argentina. The single inland species, *Cakile arabica* Velen. & Bornm., is endemic to the sandy deserts of Kuwait, southern Iraq, adjacent Saudi Arabia, and southwestern Iran. The genus is the only member of the Brassiceae with indigenous species in the New World. Seven of the nine native North American taxa in four species are distributed in the southeastern United States, and an additional alien species has been reported.

Pobedimova (1953, 1964) divided *Cakile* into four sections on the bases of the dissection of leaves and the nature of the articulation surfaces of the fruit segments. However, the variation in these characters can be continuous, and it is doubtful that her sectional classification improved the taxonomy of the genus. Hadač & Chrtek raised sect. *Eremocakile* Pobed. to subgenus, but this action is not justified here either. The present treatment follows the excellent monograph of Rodman (1974), in which sections are not recognized.

Cakile edentula, the most widely distributed of our native sea rockets, is easily distinguished by its sinuate or dentate leaves, reduced (rarely lacking) petals, long (1–2 dm) infructescences, slender fruiting pedicels, and broad ((3–)5–9 mm), four-angled or eight-ribbed fruits with retuse or blunt beaks. Both of its subspecies occur in our area, and one is represented by one variety. *Cakile edentula* (Bigelow) Hooker subsp. *edentula* var. *edentula* (*Bunias edentula* Bigelow, *C. americana* Nutt., *C. californica* Heller, *C. edentula* var. *californica* (Heller) Fern.), $2n = 18$, is known from several localities along the Outer Banks of North Carolina, but its native range extends northward along the Atlantic coast to Labrador. The variety has been introduced to Japan, Australia, New Zealand, the Azores, the Great Lakes of North America, and the Pacific coast from California to Alaska. It is recognized by its fruit: the beak is shorter than the seed portion of the broad (5–9 mm), four-angled upper segment, and the articulation surface of the lower segment has two teeth. The other variety, *C. edentula* subsp. *edentula* var. *lacustris* Fern., $2n = 18$, an endemic of the shores of the Great Lakes, has narrower siliques and longer beaks.

The distribution of *Cakile edentula* subsp. *Harperi* (Small) Rodman (*C. Harperi* Small), $2n = 18$, extends from the Outer Banks of North Carolina southward to northern Florida. The northernmost limits of the subspecies is Cape Hatteras, where the warm Gulf Stream that effects its northward migration is deflected eastward by the cold Labrador Current. In that area the ranges of *C. edentula* subsp. *edentula* and *C. edentula* subsp. *Harperi* overlap, and natural hybridization occurs in the zone of sympatry (Rodman, 1980). Subspecies *Harperi,* which has been replaced by *C. constricta* Rodman in parts of northern Florida, is characterized by fruit with conical, eight-ribbed upper segments 12–20 mm long and flat and toothless articulation surfaces on both segments.

Another native species, *Cakile lanceolata,* is represented in the Southeast by three of its four subspecies. It is characterized by having white (rarely lavender) petals; four-angled or terete siliques 13–31 mm long; pinnatifid to entire, not particularly succulent leaves; and linear infructescences that usually exceed 2 dm in length. *Cakile lanceolata* (Willd.) O. E. Schulz subsp. *lanceolata* (*Raphanus lanceolatus* Willd., *C. aequalis* L'Hér. ex DC., *C. maritima* Scop. var. *aequalis* (L'Hér. ex DC.) Chapman, *C. domingensis* Tussac, *C. cubensis* Kunth, *C. americana* Nutt. var. *cubensis* DC., *C. maritima* var. *cubensis* (DC.) Chapman), $2n = 18$, is narrowly distributed in our area in Dade, Martin, and Palm Beach counties, Florida, but is common throughout the West Indies, the Caribbean coast of Central America, Colombia, Venezuela, and the Yucatan

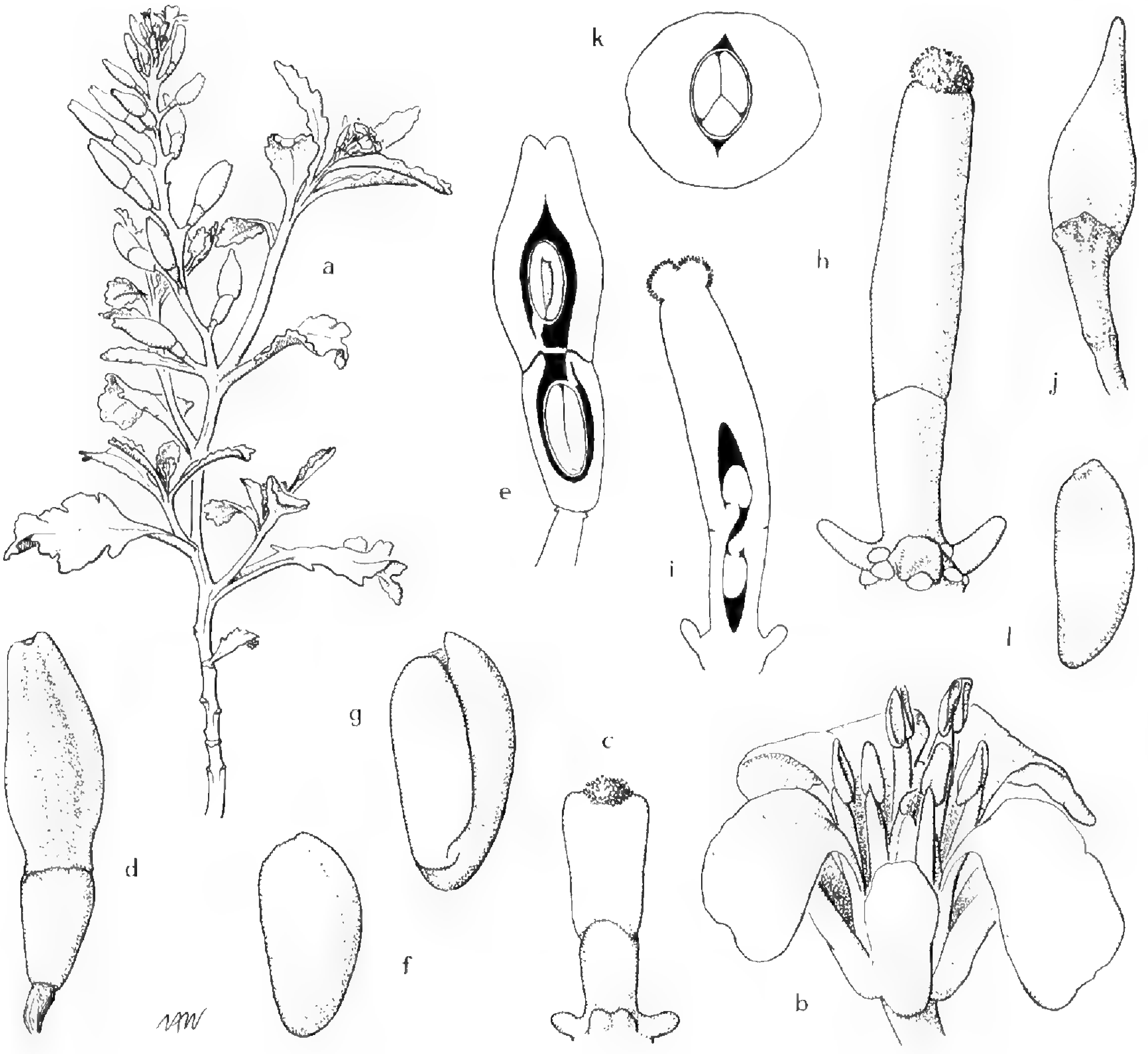

FIGURE 2. **Cakile.** a–g, *C. edentula* subsp. *Harperi:* a, portion of plant with flowers and fruits, × ½; b, flower, × 6; c, gynoecium—note transverse joint and nectar glands, × 10; d, fruit, × 1½; e, diagrammatic longitudinal section of fruit—note erect and pendulous seeds in upper and lower segments, respectively, × 1½; f, seed, × 5; g, embryo, × 6. h–l, *C. lanceolata* subsp. *fusiformis:* h, gynoecium—note cylindrical lateral nectar glands and prismatic median one, × 10; i, longitudinal section of gynoecium—note orientation of ovules, × 6; j, fruit, × 1½; k, diagrammatic cross section of upper segment of fruit—note thickness of fruit wall and accumbent cotyledons, × 4; l, seed, × 5.

peninsula of Mexico. The subspecies is easily recognized among our sea rockets by its entire or obscurely dentate leaves, narrowly lanceolate, long-beaked siliques, and short (5–10 mm) lower segments less than half the length of the upper ones.

The second subspecies, *Cakile lanceolata* subsp. *fusiformis* (Greene) Rodman (*C. fusiformis* Greene, *C. Chapmanii* Millsp.), $2n = 18$, is distributed along the coasts of the southern half of peninsular Florida and disjunctly in Honduras and the Yucatan peninsula. The frequently pinnatifid leaves and the characteristic fusiform, longitudinally four- or eight-sulcate (or -striate) siliques 16–26 mm long with lower segments 5–10 mm long easily separate this from other sea rockets. Rodman (1974) believed that the subspecies may have originated from hybridization between subsp. *lanceolata* and subsp. *alacranensis* (Millsp.) Rodman. The latter has turbinate siliques and is endemic to the Yucatan peninsula and neighboring islands.

Cakile lanceolata subsp. *pseudoconstricta* Rodman, $2n = 18$, occurs in Lee, Manatee, Sarasota, Pinellas, and Hillsborough counties on the west coast of peninsular Florida and disjunctly, possibly through recent introductions, at the southern tip of Texas and adjacent Tamaulipas, Mexico. Plants of this subspecies have finely dissected or pinnatifid leaves and narrowly lanceolate, terete or four-angled siliques with a distinct constriction at the articulation point. It resembles *C. constricta* in its fruits, but the latter has fleshy, entire to dentate (rarely sinuate) leaves and smaller flowers.

Cakile constricta Rodman, $2n = 18$, is morphologically intermediate between *C. edentula* and *C. lanceolata,* particularly in flower size, infructescence length, and leaf succulence, and according to Rodman (1974), it probably represents a link between these species. It extends along the Atlantic coast of Florida and along the beaches of the Gulf of Mexico from the Tampa Bay area northward and westward through Alabama, Mississippi, Louisiana, and southeastern Texas. It is separated from *C. edentula* by its petaliferous flowers and narrower (3–4 mm wide) siliques with acute beaks.

The most distinctive of our sea rockets is *Cakile geniculata* (Robinson) Millsp. (*C. maritima* var. *geniculata* Robinson, *C. lanceolata* var. *geniculata* (Robinson) Shinners), $2n = 18$, which extends along the Gulf of Mexico west of the Mississippi Delta in Louisiana westward along the coast of Texas and southward in Mexico to Veracruz. It is characterized by strongly geniculate infructescences, stout fruiting pedicels of the same width as the rachis, narrow (less than 2 mm wide) petals, and coarsely eight-ribbed, lanceolate siliques 20–27 mm long. Habitat instability, caused by the enormous amounts of silt and mud deposited at the Mississippi Delta as well as the repeated flooding of this area, may have been the main obstacles to the eastward migration of *C. geniculata.* Hybridization between this and *C. constricta* on the Grand Isle of Louisiana is suspected, and the heterogeneity of the populations there may have resulted from introgression (Rodman, 1974).

The alien *Cakile maritima* Scop. (*Bunias Cakile* L., *Cakile Cakile* (L.) Karsten; see Rodman (1974) for 45 additional synonyms), $2n = 18$, has been introduced in the Southeast as a ballast plant at least three different times. It has been found near Mobile, Alabama, and Wilmington, North Carolina, and in Florida (see Rodman, 1974; Small), but it has apparently failed to persist. Northward, it has only recently become naturalized in the Chesapeake Bay region of Maryland (Riefner). On the Pacific coast of North America, where it is now widespread, it was first recorded in 1936 (Rose). It has also become naturalized in Argentina, Uruguay, Australia, and New Caledonia. The native range of *C. maritima* extends along the shores of the Black and Aegean seas (subsp. *euxina* (Pobed.) E. I. Nyárády), the Baltic Sea (subsp. *baltica* (Rouy & Foucaud) P. W. Ball), and the North Sea, the European North Atlantic Ocean, and the Mediterranean Sea (subsp. *maritima*). Two characteristic lateral horns or triangular wedges on the top of the lower segment of the fruit and broad (3–6 mm wide) petals easily separate *C. maritima* from our native sea rockets.

Cakile is most closely related to *Erucaria* (Mediterranean region and southwestern Asia) and may represent an end point of an evolutionary line linked to an *Erucaria*-like ancestor by some inland species not very different from *C. arabica*. The original maritime species of *Cakile* may have inherited certain characters (e.g., annual habit, corky fruits, and succulent leaves) preadapting it to strand habitats. The range of this species probably expanded rapidly along the beaches of the Mediterranean Sea and the Atlantic coast of Europe. From the latter area, very rare successful immigrants reached North America to give rise to our present-day native sea rockets. The seed-glucosinolate evidence supports such an origin for the American *Cakile* (Rodman, 1974).

The genus is characterized by its lack of a style and by its fleshy leaves, its white to purple or violet flowers, its corky, two-segmented, jointed fruits, and its usually one-seeded upper segments. All taxa except *Cakile arabica* occupy strand habitats—an almost unique ecological specialization for the genus unknown elsewhere in the Cruciferae except for a species of *Crambe* and another of *Raphanus*. *Erucaria* differs from *Cakile* in having noncorky fruits, one- to six-seeded segments, slender styles, and nonfleshy leaves, and in occupying arid inland habitats.

The main source of taxonomic complexities in our native sea rockets is the enormous variation created by hybridization between taxa in zones of sympatry. The great dispersibility of fruits, the lack of reproductive isolation among species, and the overlap of distributional ranges are the main factors preventing the stabilization of populations in the Southeast. According to Rodman (1974, p. 115), "the southern and western Florida sea rockets present a nightmare of variation to the taxonomist."

Self-incompatibility is expressed strongly in *Cakile arabica* and weakly in the other Old World species (*C. arctica* Pobed. and *C. maritima*), while self-compatibility characterizes all the New World taxa. The shift in the breeding system toward autogamy in *C. edentula* has accompanied several changes in the flower (e.g., the total absence of petals or their reduction to bristles, the lack of scent, and the secretion of minimal nectar). The allogamous taxa exhibit variation in floral color that may be accompanied by differences in their ultraviolet absorption (Horovitz & Cohen). The apparent lack or rarity of natural hybridization between *C. edentula* and *C. maritima* in southern Australia and in California may be attributed to the breeding system. However, despite autogamy, *C. edentula* subsp. *edentula* and *C. edentula* subsp. *Harperi* produce a substantial number of hybrids (9–24 percent of the sample) in a narrow zone of sympatry on the Outer Banks of North Carolina (Rodman, 1980). The complex mixture of sea rockets along the coasts of Norway may have resulted from hybridization between *C. arctica* and two subspecies of *C. maritima* (Elven & Gjelsås). Although the potentiality for hybridization exists whenever sympatry occurs, only a few examples of natural hybridization have been carefully documented.

Uniform chromosome counts of $2n = 18$ have been reported for all taxa of *Cakile*. The single exception, which may be in error, is the tetraploid count of $2n = 36$ reported by Löve & Löve for *C. arctica*.

Cakile is the most thoroughly surveyed genus of Cruciferae for seed glucosinolates. Rodman (1974, 1976, 1980) has applied the distribution of these compounds in studies of migration, population variation, and hybridization. Sixteen glucosinolates have been identified in *Cakile,* and their overall profiles are usually taxon specific. The genus has been poorly surveyed for alkaloids, fatty acids, mucilage, and tannins. The seed-oil contents on a dry basis in *C. edentula* (49 percent) and *C. maritima* (46 percent) are the highest known for any crucifer (Kumar & Tsunoda).

The separation or articulation zone between the two segments of fruit is composed of transversely elongated small cells surrounded by larger ones that become lignified as the fruit matures. Soon after the lignification process is completed and due to a shortage of food and water, cells of the separation zone begin to degenerate, and their walls break at a stage when the mature fruit is still green. The vascular bundles in this zone consist of short tracheids instead of the vessels seen elsewhere in the fruit. These anatomical peculiarities are adaptations for the detachment of upper segments of fruit, and it is possible that they may be found in genera of the Brassiceae with articulated or lomentaceous fruits.

Cakile is remarkably adapted to long-distance dispersal by sea because of the buoyancy of the upper segment of the fruit, the inhibition of seed germination during flotation, and the maintenance of seed viability after exposure to sea water. Seed viability and fruit buoyancy decline drastically after prolonged periods of exposure to sea water. High levels of salt, particularly of sodium chloride, in the fruit wall and in the sand are the most important factors that inhibit seed germination in nature (Hocking). The naturalized range of *C. edentula* along the Pacific coast of North America has extended northward some 3200 km (2000 mi) from San Francisco Bay to Kodiak Island in a span of 50 years at the amazing migration rate of 64 km (40 mi) per year (Barbour & Rodman). Short-distance dispersal is accomplished by the tumbling of uprooted dead plants or by the rolling of upper segments of fruit along the beach during strong winds.

The green parts of *Cakile* are eaten as a salad or cooked as a potherb. In folk remedies the plants have been recommended for their antiscorbutic, purgative, and diuretic properties.

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13. **Conringia** Heister ex Fabricius, Enum. 160. 1759.

Annual or rarely perennial, glabrous and usually glaucous herbs. Stems erect, simple or branched at base. Basal leaves undivided, obovate or spatulate, subsessile, usually entire, slightly fleshy. Cauline leaves cordate-amplexicaul, rarely auriculate, oblong to elliptic or ovate [or suborbicular], entire, rarely crenulate. Inflorescence an ebracteate, corymbose raceme, usually elongated in fruit. Sepals erect or slightly ascending, obtuse; outer pair linear to narrowly oblong or lanceolate, sometimes cucullate; inner pair broader, slightly [to strongly] saccate [or not] at base. Petals yellow or white [rarely with purple veins], narrowly [to broadly] obovate, rarely oblanceolate, attenuate at base; claws usually as long as sepals. Median nectar glands usually absent, lateral ones lobed [or flat]. Stamens slightly tetradynamous; filaments not appendaged, linear, free; anthers oblong, slightly sagittate at base, equal in length [or the lateral pair 3–4 times longer than the 2 median pairs]. Ovary glabrous, many ovulate. Fruiting pedicels ascending to spreading [or erect], slender [or as thick as the fruit]. Siliques sessile, linear, dehiscent, quadrangular [or terete, 8-angled, or strongly compressed parallel to the septum], torulose [or not], beaked [or beakless], acuminate [or clavate] at apex; valves convex [or flat], somewhat keeled [or not], usually with a prominent midnerve and 2 obscure [or prominent] lateral nerves [or nerveless]; stigmas capitate, entire [or 2-lobed and the lobes sometimes decurrent]. Seeds uniseriately arranged, copiously [or not at all] mucilaginous when wet, wingless, oblong or elliptic, brown [or reddish or black], papillose [or smooth]; cotyledons incumbent [or subconduplicate]. Base chromosome numbers 7, 9. (Including *Goniolobium* Beck, *Gorinkia* J. & K. Presl.) LECTOTYPE SPECIES: *Brassica orientalis* L. = *Conringia orientalis* (L.) Dumort.; see Britton & Brown, Illus. Fl. No. U. S. ed. 2. **2**: 174. 1913. (Name honoring Hermann Conring, 1606–1681, German professor of medicine, philosophy, and jurisprudence at Helmstedt University.)—HARE'S-EAR MUSTARD.

A well-defined genus of six species centered in the eastern Mediterranean, particularly in Turkey (where all species occur), and extending eastward to Afghanistan and western Pakistan. Two species are widely distributed in southern and central Europe, and one (*Conringia grandiflora* Boiss. & Heldr.) is a narrow endemic known only from a few localities in Antalya Vilayet, a province in southwestern Turkey. The genus is represented in North America by the alien weed *C. orientalis* (L.) Dumort., hare's-ear mustard, rabbit's-ear, treacle mustard, $2n = 14$, which grows in cultivated land, disturbed sites, abandoned fields, and waste places, and along roadsides. It is most common in the plains states of the United States and in the plains and prairie provinces of Canada (Rollins). It has been recorded from all the Southeastern States except Louisiana and South Carolina, but it probably grows there as well. *Conringia orientalis*, easily distinguished from the other mustards of our area, is a glabrous annual with deeply cordate-amplexicaul cauline leaves, white or yellow flowers, tetragonal siliques 6–15 cm long, and incumbent cotyledons.

Conringia has often been associated with *Moricandia* of subtribe Moricandiinae Hayek, but Botschantzev has questioned its disposition in the Brassiceae without adequately placing it in another tribe. Features such as the conduplicate cotyledons and/or segmented siliques, typical of most members of the Brassiceae, are not found in *Conringia, Ammosperma,* and *Pseuderucaria.* The last two genera have always been associated with *Moricandia,* and there are no solid grounds for not placing *Conringia* with them. In one species, *C. planisiliqua* Fischer & Meyer, the cotyledons are nearly conduplicate, and this may support retaining the genus in the Brassiceae.

Hardly anything is known about the floral biology of *Conringia.* The diversity in flower size among species is very striking. The flowers of *C. persica* Boiss., the smallest in the genus, are only 0.5 cm long and have nonsaccate sepals, while those of *C. grandiflora* exceed 2 cm in length and have strongly saccate inner sepals with pouches usually longer than 1 mm. All anthers of *C. grandiflora* are polliniferous, but those of the lateral pair of stamens are nearly four times longer than those of the median ones. To my knowledge, such anthers have not been encountered elsewhere in the Cruciferae, except in flowers of some species of *Streptanthus* Nutt. that have aborted median ones. Unfortunately nothing is known about the pollinators of *C. grandiflora.*

Chromosome numbers are known for all species except *Conringia grandiflora.* One species, *C. austriaca* (Jacq.) Sweet, is a tetraploid based on seven. The haploid number for *C. persica* is seven, but counts of $n = 7$ and $n = 9$ have been reported for both *C. planisiliqua* and *C. clavata* Boiss. (= *C. perfoliata* (C. A. Meyer) N. Busch).

A few cardenolides (erysimosid, erycorchosid, and helveticosid) have been found in *Conringia orientalis* (Kowalewski), but it is not known whether cardiac glycosides are present throughout the genus. In *C. planisiliqua* allylglucosinolate has been identified, and in *C. orientalis* 2-hydroxy-2-methylpropyl and 2-methylpropyl glucosinolates are the dominant pungent constituents. It has been suggested that *C. orientalis* may be a potentially new oil-seed crop because of its high ratio of linoleic to linolenic acid, but the presence of cardenolides may be an obstacle to such utilization.

The seeds of *Conringia orientalis* exude abundant mucilage immediately after soaking in water. The mucilage forms series of stiff separate conical masses, each with a cap representing the outer wall of the epidermal cell that exuded it. Other species contain very little or no seed mucilage.

Except for the weedy *Conringia orientalis,* the genus has no economic importance. Young plants of this species are said to make a good salad.

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OVULES AND SEEDS OF THE POLYGALACEAE

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THE OVULES of the Polygalaceae are anatropous, bitegmic, and crassinucellate, and they frequently have a long exostome (Davis, 1966). The often-hairy seeds contain flattened or thickened cotyledons; the seed coat is endotestal, often in the form of long palisade cells, or is reduced. The larger seeds have a multiplicative testa and an extensive, postchalazal vascularization (Netolitzky, 1926; Corner, 1976). The seeds generally have a mostly white exostome aril that is highly variable in size; the raphal and chalazal regions can be swollen (Chodat, 1890–1893; Blake, 1916; Adema, 1966). The exostome and the swollen chalazal region function as an elaiosome in at least some species of *Polygala* and *Comesperma* (Sernander, 1906; Berg, 1975).

Detailed morphological studies of polygalaceous seeds are scarce (Corner, 1976, *Polygala venenosa* subsp. *pulchra* (Hassk.) Steenis; Rao, 1964, *Salomonia cantoniensis* Lour.; Wirz, 1910, *Epirixanthes*; Verkerke & Bouman, 1980, *Polygala vulgaris* L.; Verkerke, 1984, *Xanthophyllum*). Rodrigue (1893) skillfully compared different seed coats, but minor errors and incomplete material mar her conclusions, which were adapted by later investigators (see also Verkerke, 1984).

The reduction of the mesophyll in the outer integument within *Polygala* (Verkerke & Bouman, 1980) represents a neotenic trend in the development of the ovules and seeds in this genus. In the present study ovule ontogeny and seed development were examined in 14 genera. These new data permit both the elucidation of relationships between genera and a reconstruction of the evolution of polygalaceous seeds. Rodrigue (1893) emphasized the relation between fruit walls and seed coats in the Polygalaceae, and I have compiled a synopsis of fruit characters in order to further taxonomic and morphological studies of the family.

SYNOPSIS OF GENERA AND DESCRIPTION OF THE FRUITS

POLYGALEAE

ATROXIMA Stapf. Lianas or lianalike shrubs; 2 species; western and central Africa. Ovary 3-locular, with 1 epitropous, ventral ovule per locule. Fruit a subglobose, 1- to 3-locular berry, up to 5 × 5 × 4 cm, either smooth and shiny, orange, with mesocarp fleshy and endocarp thin, glossy inside, or pustulate, brown, with mesocarp crustaceous and endocarp thin, glossy inside (Breteler & Smissaert-Houwing, 1977).

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BREDEMEYERA Willd. Climbing shrubs; 50 species; South America. Ovary 2-locular, with 1 epitropous, ventral ovule per locule. Fruit an elongated, 2-locular, dehiscent capsule, up to 20 × 7 × 3 mm; pericarp fleshy (Chodat, 1896).

CARPOLOBIA G. Don. Shrubs or treelets, occasionally tall trees; 4 species; tropical Africa. Ovary 3-locular with 1 epitropous, ventral ovule per locule. Fruit a subglobose, 1- to 3-locular berry, 2 × 2.5 × 2.5 cm, smooth, yellow to orange-red at maturity; exocarp thin, mesocarp fleshy, endocarp thin (Breteler & Smissaert-Houwing, 1977; De Koning, 1983).

COMESPERMA[1] Labill. Herbs or climbing shrubs, rarely lianas; 30 species; Australia. Ovary 2-locular, with 1 epitropous, ventral ovule per locule. Fruit a flattened, often elongated (with the base attenuated), 2-locular, dehiscent capsule, up to 20 × 7 × 3 mm; pericarp membranaceous (Chodat, 1896).

EPIRIXANTHES Blume. Saprophytic annual herbs; 3 species; Indo-Malesia. Ovary 2-locular, with 1 epitropous, ventral ovule per locule. Fruit a transversely oval, 2-locular berry, not exceeding 4 × 3 × 3 mm; pericarp thin, fleshy (Backer & Bakhuizen van den Brink, 1963).

MONNINA Ruiz & Pavon. Shrubs or perennial herbs, rarely lianas; 160 species; southwestern United States to South America. Ovary mostly 1-locular, with 1 epitropous, ventral ovule. Fruit either a 1-locular samara, up to 12 × 13 × 3 mm, with a hard pericarp, or an elliptic, 1-locular drupe, up to 12 × 6 × 6 mm, smooth, green, with a fleshy mesocarp and a hard endocarp (Wendt, unpubl. ms).

MURALTIA Necker. Prickly shrubs; 115 species; South Africa. Ovary 2-locular, with 1 epitropous, ventral ovule per locule. Fruit a flattened, 2-locular, dehiscent capsule, up to 5 × 4 × 2 mm, often with 4 spines; pericarp membranaceous (Levyns, 1954).

NYLANDTIA Dumort. Spiny shrub; 1 species; South Africa (Cape). Ovary 1-locular, with 1 epitropous, ventral ovule. Fruit a subglobose, 1-locular drupe, up to 7 × 7 × 7 mm, smooth, first green, ripening red; mesocarp fleshy, endocarp hard (Chodat, 1896; Rice & Compton, 1950).

POLYGALA L. Annual herbs to small trees; over 500 species; almost cosmopolitan. Ovary 2-locular, with 1 epitropous, ventral ovule per locule. Fruit a flattened, often marginate, 2-locular, dehiscent capsule, from 4 × 2 × 2 mm up to 12 × 13 × 4 mm; pericarp usually membranaceous, sometimes fleshy (Chodat, 1890–1893, 1896).

SALOMONIA Lour. Annual herbs; 3 species; Indo-Malesia, China, and Japan. Ovary 2-locular, with 1 epitropous, ventral ovule per locule. Fruit a transversely oval to obreniform, 2-locular, dehiscent capsule, not exceeding 3 ×

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[1] Van Steenis (1968) included *Comesperma* in *Bredemeyera*, but the seeds of the two genera are described separately.

4 × 4 mm, with several long spines; pericarp membranaceous (Chodat, 1890–1893, 1896; Backer & Bakhuizen van den Brink, 1963).

SECURIDACA L. Shrubs, lianas, or small trees; 80 species; Africa, South America, and Indo-Malesia. Ovary 1-locular, with 1 epitropous, ventral ovule. Fruit a 1-locular samara with a strongly elongated unilateral wing, up to 7 × 1.5 × 2 cm, pericarp hard (Chodat, 1896).

MOUTABEAE

BARNHARTIA Gleason. Liana; 1 species; South America. Ovary 2- or 3-locular, with 1 epitropous, ventral ovule per locule. Fruit not known (Sprague & Sandwith, 1932).

DICLIDANTHERA Martius. Small trees or lianas; 8 species; South America. Ovary 3- or 5-locular, with 1 epitropous, ventral ovule per locule. Fruit a subglobose, 3- to 5-locular berry, 2.3 × 2.2 × 1.5 cm; mesocarp leathery (Gürke, 1891 (under Styracaceae); pers. obs.).

ERIANDRA Royen & Steenis. Tree to 30 m tall; 1 species; New Guinea and Solomon Islands. Ovary 7- or 8-locular, with 1 epitropous, ventral ovule per locule. Fruit a globose, 7- or 8-locular berry, up to 4 × 4 × 3.5 cm, smooth, first green, ripening orange; mesocarp leathery (Van Royen & Van Steenis, 1952; Van Steenis, 1964).

MOUTABEA Aublet. Trees to 10 m tall, shrubs, or lianas; 10 species; South America. Ovary 4- or 5-locular, with 1 pleurotropous, ventral ovule per locule. Fruit a subglobose, 4- or 5-locular berry, 4.5 × 4.5 × 4 cm, smooth, first dark green, ripening yellow to orange; mesocarp crustaceous, scented, edible (Van Roosmalen, 1985).

XANTHOPHYLLEAE

XANTHOPHYLLUM[2] Roxb. Shrubs or trees 3–50 m high; 93 species; Southeast Asia, Malesia, India, and Australia. Ovary 1-locular, with 4 to 20 epitropous, dorsal ovules. Fruit usually a globose, 1-locular berry, up to 15 × 15 × 15 cm; pericarp usually hard; rarely a subglobose, 1-locular, dehiscent, irregularly 2-valved capsule (Van der Meijden, 1982).

RELATIONSHIPS NOT CLEAR

EMBLINGIA F. Mueller. Shrub; 1 species; Australia. Ovary 3-locular. Fruit not known (Erdtman *et al.*, 1969; Cronquist, 1981).

MATERIALS AND METHODS

Specimens examined are documented in the TABLE. Fixation was with either Allen's modified Bouin's fluid (Johansen, 1940) or a mixture of formaldehyde,

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[2] Although separated by Cronquist (1981), this genus is included in the family by Van der Meijden (1982).

Specimens of Polygalaceae examined.

Species	Collector[1]	Locality	Material[2]	Herbarium[3]
Atroxima afzeliana (Oliver ex Chodat) Stapf	*Bos 6027*	Cameroon	s	WAG
A. liberica Stapf	*De Koning 2903*	Ivory Coast	s	WAG
Bredemeyera densiflora A.W. Bennett	*P.C. Heijligers 2097*	Surinam	fl	U[4]
B. floribunda Willd.	*Balansa 4714*	Paraguay	s	L
B. lucida Klotzsch	*H.L.B. 908.170-67*	Brazil	s	L
B. papuana Steenis	*Kostermans & Soegeng 30*	New Guinea	s	L
	NGF 33220	New Guinea	s	L
Carpolobia alba G. Don	*Breteler 6915*	Gabon	fl/s	WAG
C. gossweileri (Exell) Petit	*J.J. de Wilde 8697*	Cameroon	fl/s	WAG
C. lutea G. Don	*W. de Wilde 512*	Ivory Coast	fl/s	WAG
Comesperma ericinum DC.	*J. Thompson 2927*	Australia	fl	L[4]
C. calymega Labill.	*Ising s.n.* (1968)	Australia	s	L
C. confertum Labill.	*H.L.B. 908.171-761*	Australia	s	L
C. virgatum Labill.	*F. von Müller 5649*	Australia	s	WU
Diclidanthera bolivarensis Pittier	*J.J. Wurdack & J.V. Monachino 41332*	Venezuela	fl	U
	Davidse & Gonzales 1348	Venezuela	s	MO
D. elliptica Miers	*F.C. Hoehne 28421*	Brazil	s	S
Eriandra fragrans Royen & Steenis	*BSIP 1991*	Solomon Islands	s	L
	BSIP 6081	Solomon Islands	s	L
Epirixanthes cylindrica Blume	*Nooteboom & Chai 2318*	Indonesia	s	L
E. elongata Blume	*J.F. Maxwell 76-642*	Thailand	fl/s	L
Monnina ciliolata DC.	*Wendt & Lott 3454*	Mexico	fl/s	L[4]
M. wrightii A. Gray	*Wendt et al. 3457*	Mexico	fl/s	L[4]
	Krapovickas & Schinini 30760	Argentina	s	L[4]
M. xalapensis H.B.K.	*Lott & Wendt P-129*	Mexico	fl/s	L[4]
Moutabea guianensis Aublet	*P.J.M. & H. Maas 2358*	Surinam	fl/s	U
Muraltia heisteria (L.) DC.	*P.H. Roux 6754*	South Africa	s	L
Nylandtia spinosa Dumort.	*Lam & Meeuse s.n.* (1939)	South Africa	s	L
Polygala				
Sect. *Acanthoclados*				
P. klotzschii Chodat	*Hatschenbach 16952*	Brazil	s	L

Sect. *Hebecarpa*				
P. americana A.W. Bennett	*H. von Türckheim 11650*	Guatemala	is	L
P. durandii Chodat	*Antonio Molina R. 18520*	Honduras	s	U
P. jamaicensis Chodat	*K.U. Kramer 1660*	Jamaica	s	U
P. macradenia A. Gray	*C. Wright 1348*	Mexico	is	L
Sect. *Hebeclada*				
P. floribunda Bentham	*Antonio Molina R. & Albertina Molina 27713*	Guatemala	is	U
P. violacea Vahl	*Smith 1309*	Colombia	s	L
Sect. *Ligustrina*				
P. ligustroides St. Hil.	*H.L.B. 908.171-501*	Brazil	s	L
P. membranacea[5] (Miq.) Görts	*G. Stahel 383*	Surinam	s	U
Sect. *Polygala*				
P. conferta A.W. Bennett	*Wendt 3446*	Mexico	fl/s	L[4]
P. microspora Blake	*Maas & Westra 3639*	Surinam	fl/s	U
P. semialata S. Watson	*Wendt 10392*	Mexico	fl/s	L[4]
P. vergrandis W. Lewis	*Johnston, Chiang, & Wendt 12285*	Mexico	fl/s	L[4]
Salomonia oblongifolia L.	*MAK 60355*	Japan	s	MAK
Securidaca atroviolacea Elmer	*P.N.H. 12446*	Philippines	s	L
S. corymbosa Turcz.	*Cuming 1031*	Philippines	s	L
S. diversifolia (L.) Blake	*P. Teunissen s.n.* (1982)	Surinam	fl/s	L[4]
S. ecristata Kassau	*M.S. Clemens 8388*	New Guinea	s	L
S. inappendiculata Hassk.	*Blume 2226 L*	Indonesia	s	L
S. lanceolata A. St. Hil.	*H.L.B. 905.220-60*	Brazil	s	L
S. longepedunculata Fresen	*W.J. de Wilde 10740*	Ethiopia	s	WAG
S. philippinensis Chodat	*P.N.H. 2659*	Philippines	s	L
S. volubilis L.	*H.L.B. 908.171-1340*	Surinam	s	L
S. welwitschii Oliver	*Maas Geesteranus 6309*	Kenya	s	L

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1. If the collector is unknown, the specimen is identified by an institutional number.
2. Abbreviations: is = immature seeds, s = seeds, fl = flowers.
3. Herbarium abbreviations follow those recommended in Holmgren and Keuken (1974).
4. Present as alcohol-preserved material.
5. The position of this species is not clear: it is provisionally classified in *Polygala* Sect. *Ligustrina* (A. Görts-van Rijn, pers. comm.)

propionic acid, and ethyl alcohol. Alcohol-preserved flowers and immature seeds were dehydrated in an ethanol/normal butyl alcohol series, embedded in glycol methacrylate, sectioned at 5 μm with glass knives, stained with periodic acid–Schiff (PAS) reagent (Feder & O'Brien, 1968), and counter-stained with aqueous methylene blue. Ripe seeds obtained from the herbarium were soaked either for three days in a detergent mixture (Alcorn & Ark, 1953) or for two days in 10 percent aqueous ammonia. After imbibition the seeds were directly dehydrated and subsequently infiltrated with glycol methacrylate, without fixation. These seeds gave better results than freshly collected and fixed ones. Hand sections were also made.

For SEM studies alcohol-preserved material was dehydrated with dimethoxymethane (Gersterberger & Leins, 1978), critical point–dried with liquid CO_2, gold/palladium sputter-coated for 3 minutes, and studied on a Cambridge Stereoscan Mark 2A. Phloroglucinol-HCl, Sudan IV, ruthenium red, and iodine in potassium-iodide solution stains were used for specific color tests.

Placentation terminology follows Björnstad (1970) and Radford *et al.* (1974). Descriptions of embryos and endosperm are adapted from Martin (1946) and Smith (1983). In measurements of cells, the radial dimensions are given first, followed by tangential dimensions; descriptions of symmetrical plane figures are done according to Radford *et al.* (1974).

Preliminary research (Verkerke & Bouman, 1980; Verkerke, 1984) has explained the ontogeny of ovules and seeds in *Polygala* and *Xanthophyllum*. For *Comesperma* and *Monnina* ample alcohol-preserved material was available for study of ovules and seeds, and this allowed a description of the complete ontogeny. These results have allowed the ontogeny of incomplete series of other genera to be reconstructed. Many species were only represented by a few (minimum number, 5) seeds obtained from herbarium specimens (see TABLE). To avoid repetition, not all species are equally illustrated: illustrations are intended to show variations in ontogeny leading to differences in seed morphology. Depending on the quality of the material and the purpose of the illustration, a photomicrograph, a scanning electron micrograph, or a camera-lucida drawing has been included. Insofar as possible, stages were described for each specimen in the following sequence: ovule primordium, integument initiation, mature ovule, postfertilization development, and mature seed (inside to outside—embryo, endosperm, nucellar remains, inner integument, outer integument, color, shape, dimensions, indumentum, and appendages).

RESULTS

POLYGALA

SECT. HEBECARPA. In the ripe seed of *Polygala durandii* (FIGURES 1A, 2A), the spatulate embryo has flattened cotyledons measuring 220 × 1700 μm in cross section with an adaxial subepidermal parenchymatic palisade layer. The copious endosperm is up to 175 μm thick and consists of thick-walled cells. Except for the prominent cuticle, nucellar remains are only discernible on the antiraphal side and in the micropylar region. In the outer integument, cells of the inner epidermis have divided periclinally and are slightly elongated. The

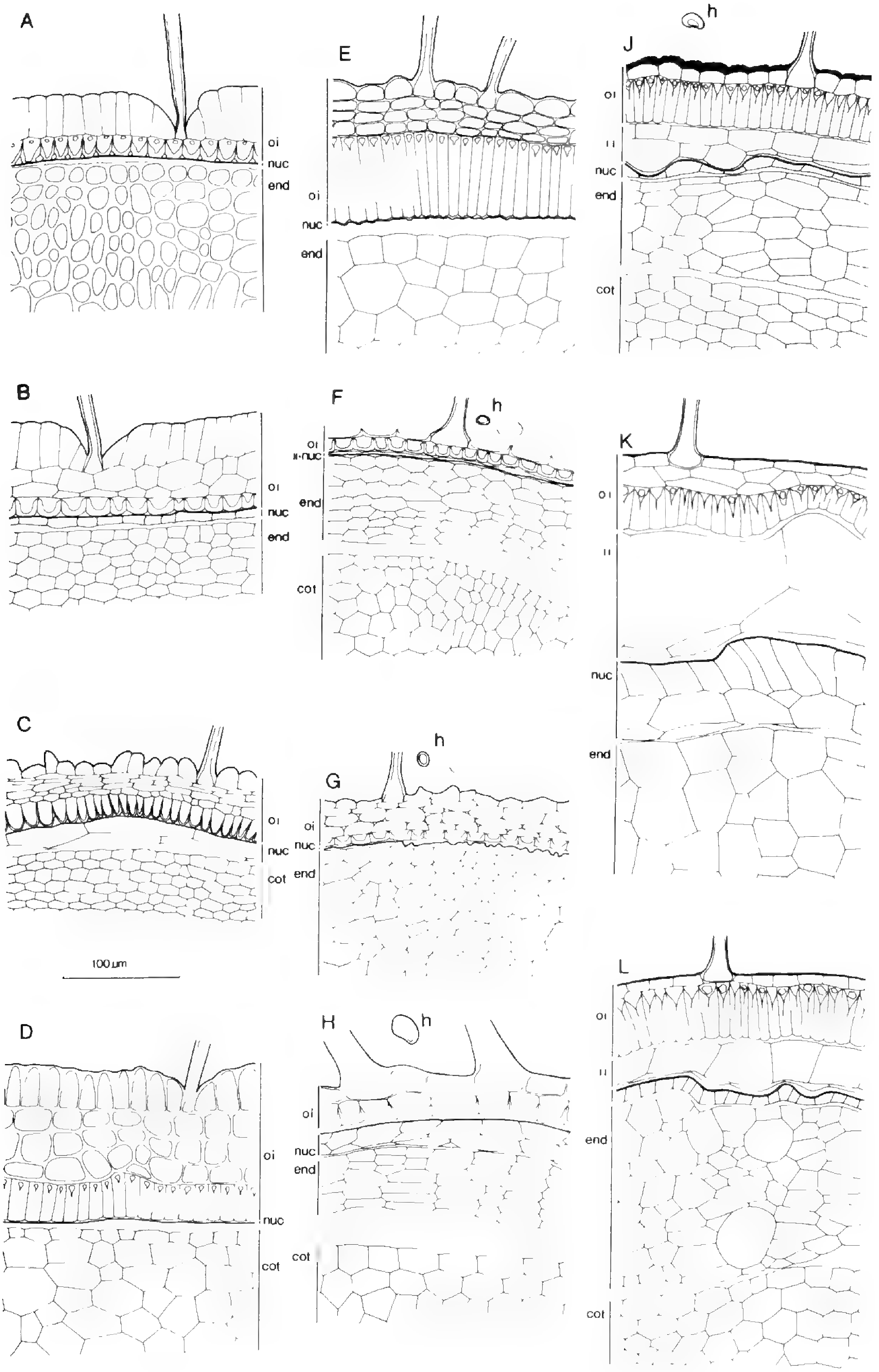

FIGURE 1. Cross sections of polygalaceous seeds: A, *Polygala durandii*; B, *P. jamaicensis*; C, *P. klotzschii*; D, *P. membranacea*; E, *P. violacea*; F, *Bredemeyera lucida*; G, *B. floribunda*; H, *B. papuana*; J, *Comesperma virgatum*; K, *Muraltia heisteria*; L, *Nylandtia spinosa*. (oi = outer integument, ii = inner integument, nuc = nucellus, end = endosperm, cot = cotyledon, h = hair.)

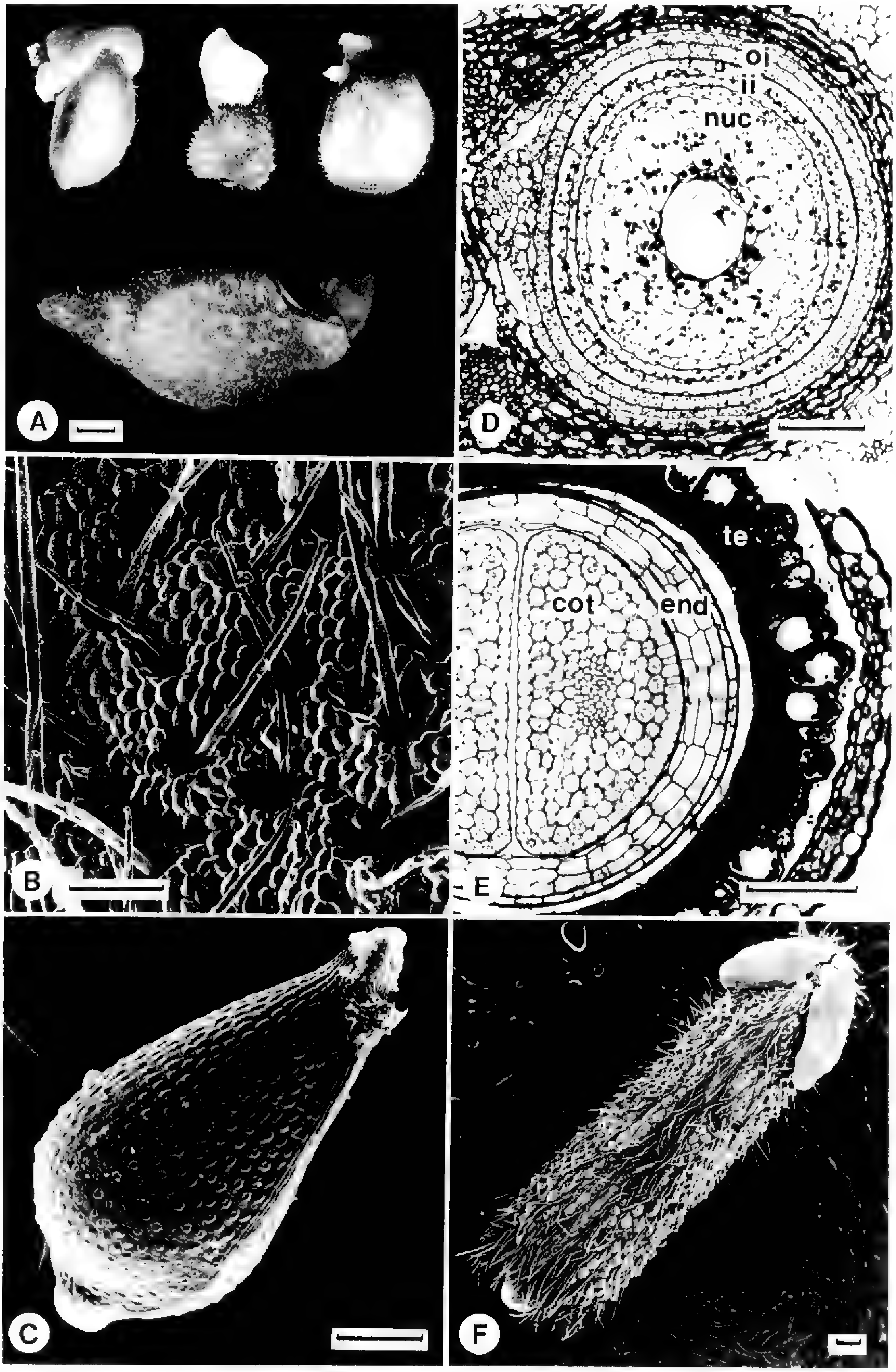

FIGURE 2. Seeds and ovules of species of *Polygala*. A, seeds: top left, *P. jamaicensis*; top center, *P. durandii*; top right, *P. klotzschii*; bottom, *P. membranacea*. B, *P. durandii*, surface of seed. C, *P. microspora*, seed. D–F, *P. vergrandis*: D, mature ovule, cross section; E, mature seed, cross section; F, seed. (Scale bars = 1 mm (A), 100 μm (B, C, E, F), 50 μm (D); symbols as in FIGURE 1.)

short endotesta cells measure 10–12 × 20–22 μm; the distal ends are split along the middle lamella but adhere to the nucellar cuticle. The cell-wall thickening is more pronounced at the distal ends, and frequently the lumina contain a rhombic calcium oxalate crystal. The subdermal mesophyll layer occurs only on the antiraphal side, where it is up to 180 μm thick and consists of globose cells with slightly thickened walls and prominent pits. Since the mesophyll layer is not present on the sides, the seed is strongly laterally flattened. The thin-walled epidermal cells are radially elongated and measure 33 × 13 μm. Some have formed an acicular hair up to 500 μm long with a striate cuticle (FIGURE 2B). The seed is black, slightly flattened, triangular in outline, 5 × 2.8 × 1.2 mm, and has a slightly protruding chalaza. A large, white, bilobed exostome aril extends 2.5 mm over the seed (FIGURE 2A).

In the ripe seed of *Polygala jamaicensis* (FIGURES 1B, 2A), the spatulate embryo has flattened cotyledons measuring 220 × 2500 μm in cross section with an adaxial, subepidermal parenchymatic palisade layer and a thick-walled epidermis. Nucellar remains adhere to the outer integument; the inner integument is crushed. In the outer integument, cells of the inner epidermis are divided anticlinally but are only very slightly radially elongated; the distal portions of the inner epidermal cell walls are thickened. The short endotesta cells measure 10–12 × 15–17 μm. The subdermal mesophyll layer consists of parenchymatic cells and is well developed on the antiraphal side, where it is up to 150 μm thick. On the sides of the seed, it is strongly reduced and only 30 μm thick. The epidermis consists of elongated cells, which have thickened distal walls with a crenulate cuticle. A few cells develop a brown, thick-walled, acicular hair up to 750 μm long. The seed is brown, elliptic in long section and transversely elliptic in cross section, 6 × 2.8 × 1.4 mm, and has a large, yellow exostome aril. The chalaza is located on the ventral side of the base of the seed.

Only immature seeds were available for *Polygala macradenia* and *P. americana*; they were similar to those of *P. durandii.*

SECT. ACANTHOCLADUS. In the ripe seed of *Polygala klotzschii* (FIGURES 1C, 2A), the investing embryo has large cotyledons. The nucellar remains adhere to the endotesta. In the outer integument the cells of the inner epidermis have divided periclinally and are radially elongated. Distally, a weakly developed cell-wall thickening is present and the lumina remain large. The slightly elongated endotesta cells measure 18 × 9 μm. The parenchymatic subdermal mesophyll layer is compressed and up to 15 μm thick. The epidermis consists of irregularly shaped, thin-walled, more or less elongated cells with a cuticle. Some cells have a curled, thick-walled, acicular hair. The seed is light brown, elliptic in long section and transversely elliptic in cross section, 6.3 × 3.3 × 1.5 mm, and has a whitish exostome aril.

SECT. LIGUSTRINA. In the ripe seed of *Polygala membranacea* (FIGURES 1D, 2A), the investing embryo has thick cotyledons measuring 1500 × 3700 μm in cross section. Of the nucellus only the epidermis and the prominent cuticle remain discernible; the inner integument is crushed. In the outer integument the inner epidermis forms an endotesta of elongated palisade cells measuring 30 × 9 μm. The subdermal mesophyll layer consists of thick-walled cells and is up to 60 μm thick. The mesophyll is not restricted to the antiraphal side but occurs throughout the outer integument, as recorded in *P. chamaebuxus* (Verkerke & Bouman, 1980). The epidermis consists of radially elongated cells measuring 30 × 15 μm with thick walls. The seed is brown, orbicular in cross section and elliptic in long section, and 7 × 3.8 × 3.8 mm. The hairy testa has faint ridges running from the apex to the base of the seed, where a firm, pointed chalazal projection 2 mm long is present.

The seed of *Polygala ligustroides* has an investing embryo with thick cotyledons measuring 2000 × 1000 μm in cross section surrounded by a thin layer of endosperm. The nucellus and inner integument are resorbed. In the outer integument, cells of the inner epidermis divide periclinally and are strongly elongated. The palisade cells measure 30 × 15 μm. The subdermal mesophyll layer is up to 50 μm thick. The epidermal cells are not radially elongated and form many unicellular hairs. The seed is black, elliptic in long section and orbicular in cross section, 3 × 2.3 × 2.3 mm. The large, white exostome aril extends over the antiraphal side.

SECT. HEBECLADA. In the ripe seed of *Polygala violacea* (FIGURE 1E), the spatulate embryo has flattened cotyledons measuring 250 × 1300 μm in cross section with a subepidermal palisade layer. The endosperm is copious. The nucellus and inner integument are resorbed, and only the nucellar cuticle remains discernible. In the outer integument, cells of the inner epidermis divide periclinally and are strongly radially elongated. The palisade cells measure 70 × 90 μm. The subdermal mesophyll layer is 40 μm thick; it consists of cells with slightly thickened walls and invests the entire seed. The epidermis consists of slightly thickened, short cells, some with a long, acicular hair. The seed is black, elliptic in long section and orbicular in cross section, 2.7 × 1.7 × 1.7 mm, and has a large trilobed exostome aril; a small chalazal appendage is also present.

In *Polygala floribunda* the immature seed has an endotesta of long palisade cells measuring 50 × 9 μm. The subdermal mesophyll layer is 30 μm thick. In all other seed characters *P. floribunda* is similar to *P. violacea.*

SECT. POLYGALA. The ripe seed of *Polygala microspora* (FIGURE 2C) has a spatulate embryo with plano-convex cotyledons measuring 30 × 80 μm in cross section. The endosperm is copious. In the outer integument an endotesta of strongly elongated palisade cells is formed; the testa does not contain a subdermal mesophyll layer. The epidermal cells are flattened and without hairs. The seed is black, obpyriform in long section and transversely elliptic in cross section, 0.5 × 0.3 × 0.26 mm, and glabrous. Next to the minute white exostome aril is a white raphe and a small chalazal appendage.

In the mature ovule of *Polygala vergrandis,* the nucellus is surrounded by a dermally initiated, 2-layered inner integument. The outer integument is also dermally initiated and completely 2-layered (FIGURE 2D). The subdermal cells on the antiraphal side, seen in *P. vulgaris* (Verkerke & Bouman, 1980), are completely lacking. In the ripe seed (FIGURE 2E) the spatulate embryo has plano-convex cotyledons measuring 150 × 300 μm in cross section. The embryo is surrounded by a thin layer of endosperm, and both are rich in fatty substances. The nucellus is resorbed, with only the epidermis remaining discernible at maturity; the inner integument is compressed. In the outer integument the inner epidermis has a well-developed endotesta of elongated palisade cells measuring 20–50 × 7–10 μm. The mesophyll layer is lacking. Cells of the outer epidermis either have formed acicular hairs up to 300 μm long or are swollen and thin walled, containing numerous PAS-positive inclusions (FIGURE 2E). The small raphe contains an amphicribral strand and is externally characterized by longitudinally enlarged cells; no stomata are present. The seed is black, narrowly elliptic in long section and orbicular in cross section, and 2 × 0.5 × 0.4 mm. It has a white chalazal swelling approximately 100 μm long and a trilobed exostome aril (FIGURE 2F).

Polygala semialata and *P. conferta* differ little from each other in the shape of the seed and aril, but in other seed characters they are similar to *P. vergrandis.*

BREDEMEYERA

In *Bredemeyera densiflora* (FIGURE 3A) the mature ovule is anatropous; the crassinucellate nucellus has a row of 5 parietal cells and a dermal cap 4 cells thick; the embryo sac fills the upper half of the nucellus. The dermally initiated inner integument is 2-layered. In the micropylar region, periclinal divisions in the outer epidermis render the endostome massive. The outer integument is also dermally initiated and 2-layered. A massive exostome develops by repeated periclinal divisions in the inner epidermis. No subdermal cells contribute to the formation of the outer integument (FIGURE 3A). The raphe is 6 or 7 cells thick and contains an amphicribral vascular strand that runs into the unswollen chalazal region, where it branches into a fan of xylem elements. The nucellus-chalaza connection is narrow.

The ripe seed of *Bredemeyera lucida* (FIGURE 1F) contains a spatulate embryo with several collateral strands. The flattened cotyledons measure 240 × 1540 μm in cross section. At the adaxial side of the cotyledon is a subepidermal layer of palisade parenchyma, but a differentiated epidermis is lacking. The embryo is surrounded by a considerable amount of endosperm; both are rich in fatty substances. The nucellar tissue is resorbed, and only the prominent cuticle remains, together with the fully crushed inner integument. In the outer integument the cells of the inner epidermis have divided anticlinally but are only slightly radially elongated; their walls are distally thickened. The lumina are frequently minute and do not contain crystals. The short endotesta cells measure 8–9 × 11–12 μm. The testa lacks a subdermal mesophyll layer. The cells of the outer epidermis are frequently crushed and have thin anticlinal walls. Some cells have long, acicular, thick-walled hairs that are circular in cross section and measure 15 × 15 × 1000–2000 μm. The seed is brown, narrowly elliptic in long section and oblate in cross section, and 7–8 × 1.7 × 1.3 mm. The chalaza, located on the ventral side near the base of the seed, contains vascular tissue and is not swollen. The small raphe is not protruding and contains an amphicribral vascular strand. The thickened, unlobed, hook-shaped, yellow exostome aril is 0.5 mm long; from its apex arises a tuft of thin-walled, white hairs up to 12 mm long and elliptic in cross section. Upon drying, the thick-walled hairs stand erect and the thin-walled ones tend to spread, thus forming an umbrellalike structure.

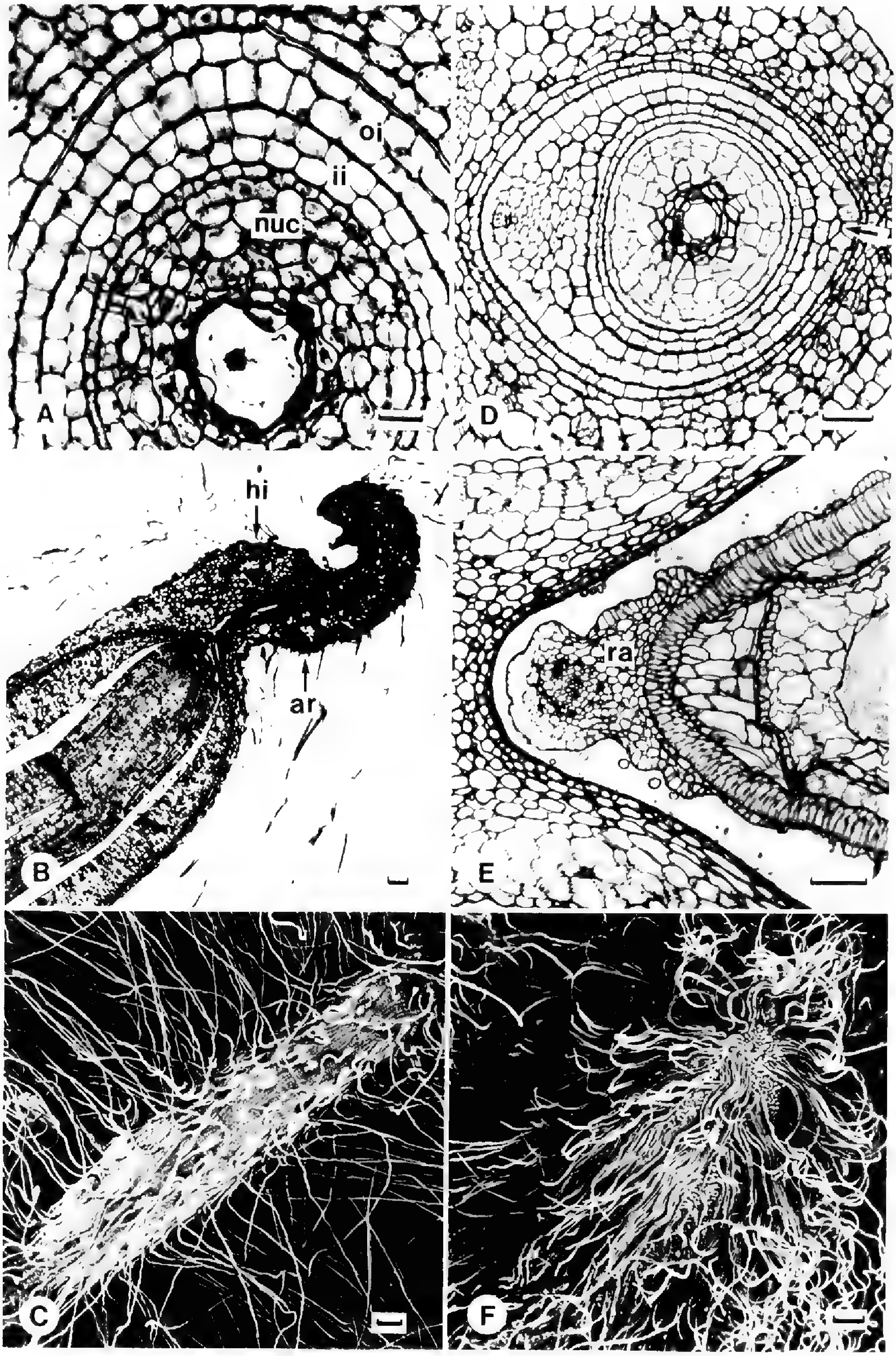

FIGURE 3. Seeds and ovules of species of *Bredemeyera* and *Comesperma*. A, *B. densiflora*, mature ovule, cross section. B, *B. floribunda*, mature seed, long section, micropylar region. C, *B. papuana*, seed. D, E, *C. ericinum*: D, mature ovule, cross section

In *Bredemeyera floribunda* the testa has a subdermal mesophyll layer 10–30 μm thick that consists of parenchymatic, loose tissue with large intercellular spaces. The epidermis consists of irregularly shaped, thin-walled cells (Figure 1G). Next to the hook-shaped exostome aril (Figure 3B) is a pronounced, vascularized, acicular chalazal appendage measuring 2200 × 500 μm with hairs up to 300 μm long. The seed is brown, narrowly elliptic in long section and orbicular in cross section, and 6.5–7 × 1.1 × 1.1 mm. These characters are in contrast to those of *B. lucida*.

In the ripe seed of *Bredemeyera papuana* (Figures 1H, 3C) the embryo is surrounded by a considerable amount of endosperm, the outermost layer of the nucellus, and the partly crushed inner integument. In the 2-layered outer integument the very slightly elongated cells of the inner epidermis measure 19–25 × 25–31 μm and have distally thickened walls. The outer epidermis consists of flattened cells, some of which have developed long hairs with uneven wall thickenings. The raphe is small, not protruding, and contains an amphicribral vascular strand that branches in the chalazal region to form a fan of xylem elements. The ripe seed is brown, narrowly elliptic in long section and transversely elliptic in cross section, and 65–70 × 12 × 10 mm. The chalaza and exostome each have a small appendage.

COMESPERMA

In *Comesperma ericinum* an anatropous ovule with a crassinucellate nucellus develops from a trizonate ovular primordium. The ovule has reduced parietal tissue and a small dermal cap. First the inner integument is initiated in the dermatogen; its primordium is ring shaped. Subsequently, the dermally initiated outer integument appears—on the antiraphal side only, due to the anatropous curvature of the ovule. As soon as the ring of the outer integument has grown to reach the level of the nucellus apically, subdermal cells start dividing and contribute to the outer integument on the antiraphal side.

In the mature ovule (Figure 3D) this small subdermal contribution to the outer integument is wedged in between the inner and outer epidermal layers. The embryo sac has extended to fill the upper half of the nucellus; a few parietal cells are still discernible. The inner integument is completely 2-layered. A thickened exostome is formed by repeated periclinal divisions in the inner epidermis of the outer integument. The chalazal region is thickened considerably by periclinal divisions in the subdermal layer, leading to the development of a swelling up to 500 μm long. The nucellus-chalaza connection is very narrow. The raphe is 10 to 12 cells thick and contains a strand of provascular tissue.

After fertilization the ovule enlarges considerably. As soon as the embryo has developed incipient cotyledons, the nuclear endosperm starts resorbing the nucellar tissue. The inner integument is not crushed, and the cells of the outer epidermis enlarge and become radially elongated. In the outer integument, cells

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(arrow indicates subdermal cells in outer integument); E, immature seed, cross section. F, *C. calymega*, seed. (Scale bars = 10 μm (A, D), 100 μm (B, C, E, F); ra = raphe, hi = hilum, ar = aril, other symbols as in Figure 1.)

of the inner epidermis divide anticlinally and elongate radially. Subdermal tissue is present as 3 or 4 isolated parenchymatic strands on the antiraphal side. The outer epidermis has divided anticlinally, and some cells have developed long unicellular hairs. The chalaza is distinctly swollen, and the raphe is pronounced (FIGURE 3E); it contains an amphicribral vascular strand that ends in the chalazal region as a fan of xylem elements.

In the ripe seed of *Comesperma virgatum* (FIGURE 1J), the spatulate embryo has plano-convex cotyledons measuring 170 × 500 μm in cross section; they contain provascular strands and lack a differentiated epidermis. The embryo is surrounded by a considerable amount of cellular endosperm; both are rich in fatty substances. Of the nucellus, only the epidermis with the prominent cuticle persists; the inner integument is not crushed. In the outer integument the elongated cells of the inner epidermis form an endotesta of long palisade cells that measure 40–45 × 6–7 μm and have strongly thickened but unlignified walls; the lumina are small, and each contains a rhombic calcium oxalate crystal. The palisade cells are arranged in a regular pattern of domelike structures. The subdermal strands in the testa become completely crushed at maturity. Cells of the outer epidermis lack thickened walls but have a very prominent, finely echinate cuticle up to 4 μm thick. Long, unicellular, white hairs elliptic in cross section and with unevenly thickened walls emerge from the entire surface of the seed. The ripe seed is black, elliptic in long section and oblate in cross section, and 1.5 × 0.9 × 0.7 mm.The seed lacks a large exostome aril but has a minute apical beak and a white chalazal appendage.

In *Comesperma confertum* the entire raphe is white and swollen due to an elongation of the epidermal cells. The seeds of *C. calymega* lack an apical beak. The hairs are straight and appressed to the seed when wet; upon drying they become helically twisted (FIGURE 3F). In all other seed characters *C. confertum* and *C. calymega* are similar to *C. virgatum*.

Previously, Rodrigue (1893) described the endotesta of *Comesperma polygaloides* F. Mueller as having short endotestal cells; no material of this species was available for the present study.

MURALTIA

In the ripe seed of *Muraltia heisteria,* the spatulate embryo has plano-convex cotyledons and is surrounded by copious endosperm. The 2 outer cell layers and the distinct cuticle of the nucellus are persistent. The inner integument persists, and cells of the outer epidermis are greatly enlarged. The inner epidermis of the outer integument constitutes a palisade layer, with cells measuring 20–35 × 15–20 μm (FIGURE 1K). The cells are arranged in a regular pattern of domelike structures, with the inner integument filling the domes. The mesophyll consists of 1 or 2 parenchymatic cell layers. The outer epidermis contains stomata, and a few cells have long, acicular hairs. The raphe contains an amphicribral vascular strand; the mesophyll lacks any post-chalazal vascularization. The seed is brown, elliptic in long section and orbicular in cross section, and 3.8 × 2.6 × 2.5 mm. In the micropylar region there is a white, faintly lobed, 500 × 700 μm exostome aril consisting of parenchymatic tissue.

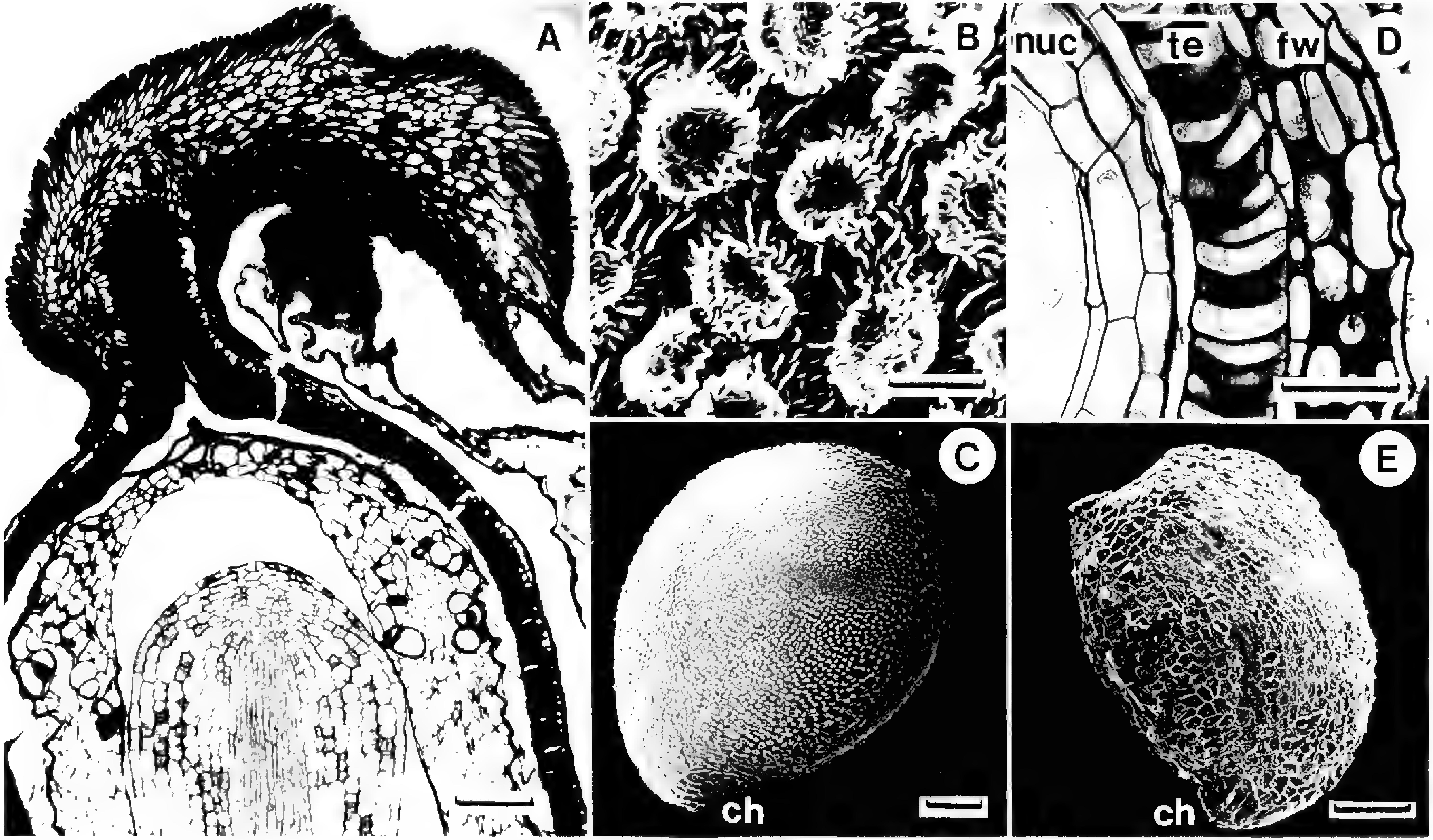

FIGURE 4. Polygalaceous seeds. A, *Nylandtia spinosa,* mature seed, long section. B, C, *Salomonia oblongifolia*: B, surface of seed; C, seed. D, E, *Epirixanthes elongata*: D, immature seed, cross section; E, seed. (Scale bars = 100 μm (A, C, E), 10 μm (B), 50 μm (D); te = testa, fw = fruit wall, ch = chalaza, nuc = nucellus.)

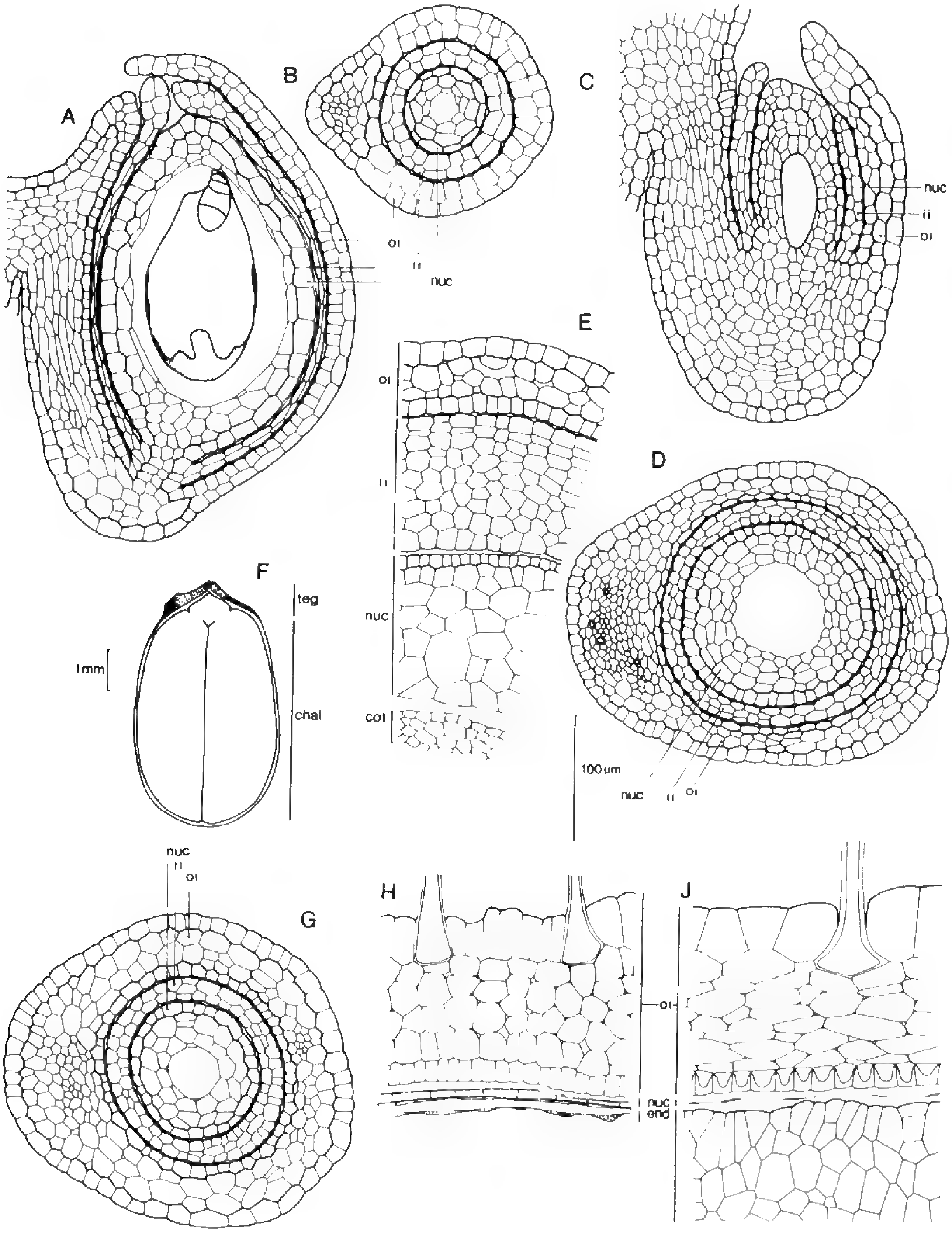

FIGURE 5. Polygalaceous seeds and ovules. A, B, *Epirixanthes elongata*: A, mature ovule after fertilization, long section; B, mature ovule, cross section. C–F, *Securidaca diversifolia*: C, young ovule, long section; D, mature ovule, cross section; E, immature seed, cross section, micropylar region; F, mature seed, long section. G, *Carpolobia gossweileri*, mature ovule, cross section. H, J, *C. lutea*: H, immature seed, cross section; J, mature seed, cross section. (teg = tegumentary part of seed coat, chal = chalazal part of seed coat, other symbols as in FIGURE 1.)

NYLANDTIA

In the ripe seed of *Nylandtia spinosa* (FIGURE 1L), the spatulate embryo has large plano-convex cotyledons 300 × 750 µm in cross section; these contain provascular strands and lack a differentiated epidermis. The copious endosperm contains a few scattered, swollen cells. The nucellus has been resorbed except for the epidermis with a prominent cuticle; the enlarged cells of the outer epidermis of the inner integument are still discernible. In the 2-layered outer integument, the elongated, thick-walled palisade cells of the inner epidermis measure 50 × 8 μm; the reduced lumina contain calcium oxalate crystals. A subdermal mesophyll layer is lacking. The cell walls of the outer epidermis are thin and are sparsely beset with acicular hairs. The seed is brown, widely elliptic in long section and orbicular in cross section, and 5 × 3 × 3 mm. A white exostome aril (FIGURE 4A) with membranaceous lobes extends up to ⅓ the length of the seed.

SALOMONIA

In the ripe seed of *Salomonia oblongifolia*, the plano-convex cotyledons measure 180 × 500 μm in cross section and completely fill the seed; no endosperm is present. The embryo is rich in fat but lacks starch. Except for some thick-walled cells in the micropylar region, the nucellus is resorbed; only the prominent cuticle is still discernible. The inner integument is crushed. The outer integument is 2-layered, and the inner epidermis has formed an endotesta of strongly elongated, thick-walled palisade cells measuring 55–65 × 7–8 μm. The outer epidermis consists of thin-walled, flattened cells that collapse at maturity (FIGURE 4B). The faintly protruding chalaza is not swollen; the raphe has longitudinally elongated cells. The black, exarillate seed is widely obovate in long section and transversely elliptic in cross section, 0.9 × 0.6 × 0.5 mm, and glabrous (FIGURE 4C).

EPIRIXANTHES

The mature ovule of *Epirixanthes elongata* (FIGURE 5A, B) is much smaller than those of the other polygalaceous genera. The crassinucellate nucellus contains reduced parietal tissue and a small dermal cap. The inner and outer integuments are dermally initiated and 2-layered throughout. The raphe is 7 to 9 cells thick and encloses a provascular strand. The small, slightly pointed chalazal region lacks provascular tissue.

After fertilization the ovule enlarges only slightly. The young embryo is initially surrounded by a thin layer of nuclear endosperm, which gradually resorbs the nucellus from the inside outward. The nucellar epidermis develops a prominent cuticle. As the seed ripens, the inner integument is gradually crushed and eventually disappears. In the outer integument, cells of the inner epidermis divide anticlinally and elongate radially (FIGURE 4D). The base of the testa thus becomes 3 cells thick while the distal portion remains 2-layered.

In each of the ripe seeds available for this study, the embryo has incipient cotyledons surrounded by a considerable amount of cellular endosperm, which is rich in fatty substances but contains no starch. Cells of the nucellus top have thickened walls and persist at maturity in the micropylar region of the seed, but the remainder of the nucellus is resorbed except for the epidermis and its prominent cuticle. The endotesta consists of radially elongated, thickened palisade cells with a hexagonal cross section measuring 45–50 × 7–12 μm; the lumina are small and generally contain a calcium oxalate crystal. Cells of the outer epidermis have slightly thickened walls; they do not develop any hairs and are strongly adherent to the endocarp. The white raphal-chalazal swelling strongly contrasts with the testa. The black, exarillate seed (FIGURE 4E) is elliptic with a flattened apex in long section and transversely elliptic in cross section, 0.8 × 0.4 × 0.3 mm, and glabrous.

In *Epirixanthes cylindrica* the outer integument is thickened in the micropylar region by periclinal divisions in the inner epidermis. Ultimately, the testa contains parenchymatic tissue located outside the palisade layer in the micropylar region. The ripe seed is obovate in long section and transversely elliptic in cross section, measuring 0.7 × 0.3 × 0.2 mm. In all other seed characters, *E. cylindrica* is similar to *E. elongata*.

MONNINA

The ovule primordium of *Monnina ciliolata* (FIGURE 6A) has a trizonate structure. The 2 tunica layers, the dermatogen (l_1) and the subdermatogen (l_2), enclose the corpus (l_3). In the subdermatogen the archespore divides into the megaspore mother cell and the parietal cells. In a young ovule (FIGURE 6B) the chalazal megaspore enlarges. The inner integument is dermally initiated, leading to a ring-shaped primordium 2 cells thick.

The outer integument is also dermally initiated and 2 cells thick, but due to the anatropous curvature of the ovule, it appears only on the antiraphal side. When the outer integument is about 10 cells long, subdermal cells start dividing on the antiraphal side (FIGURE 6C) and contribute to its growth. The nucellus has parietal cells and a small dermal cap; the embryo sac has extended, and the oblique orientation of the chalaza-nucellus connection results in the elongation of the integuments on the antiraphal side.

In a mature ovule (FIGURE 6D) the parietal tissue is not resorbed. The micropyle is formed by the inner integument; the top of the outer integument is thickened by periclinal divisions of the inner epidermis. In cross section the subdermal contribution to the outer integument appears as a crescent-shaped group of cells between the inner and outer epidermal layers (FIGURE 7A); in long section the cells are discernible as a subdermal wedge in the proximal part of the outer integument.

The prefertilization development of *Monnina xalapensis* is very similar to that of *M. ciliolata*, but in *M. wrightii* there is no subdermal contribution to the outer integument, so the outer integument is 2-layered throughout.

After fertilization in *Monnina wrightii*, the growing endosperm resorbs the nucellus and the inner integument is crushed. In the outer integument the cells of the inner epidermis elongate radially only slightly. Because anticlinal divisions cannot keep pace with the growth of the ovule, these cells become separated by extensive intercellular spaces (FIGURE 7B, C).

In the ripe seed (FIGURE 7D) the spatulate embryo has flattened cotyledons measuring 300 × 1400 μm in cross section. These lack a differentiated epidermis but have an adaxial, subepidermal layer of palisade parenchyma and

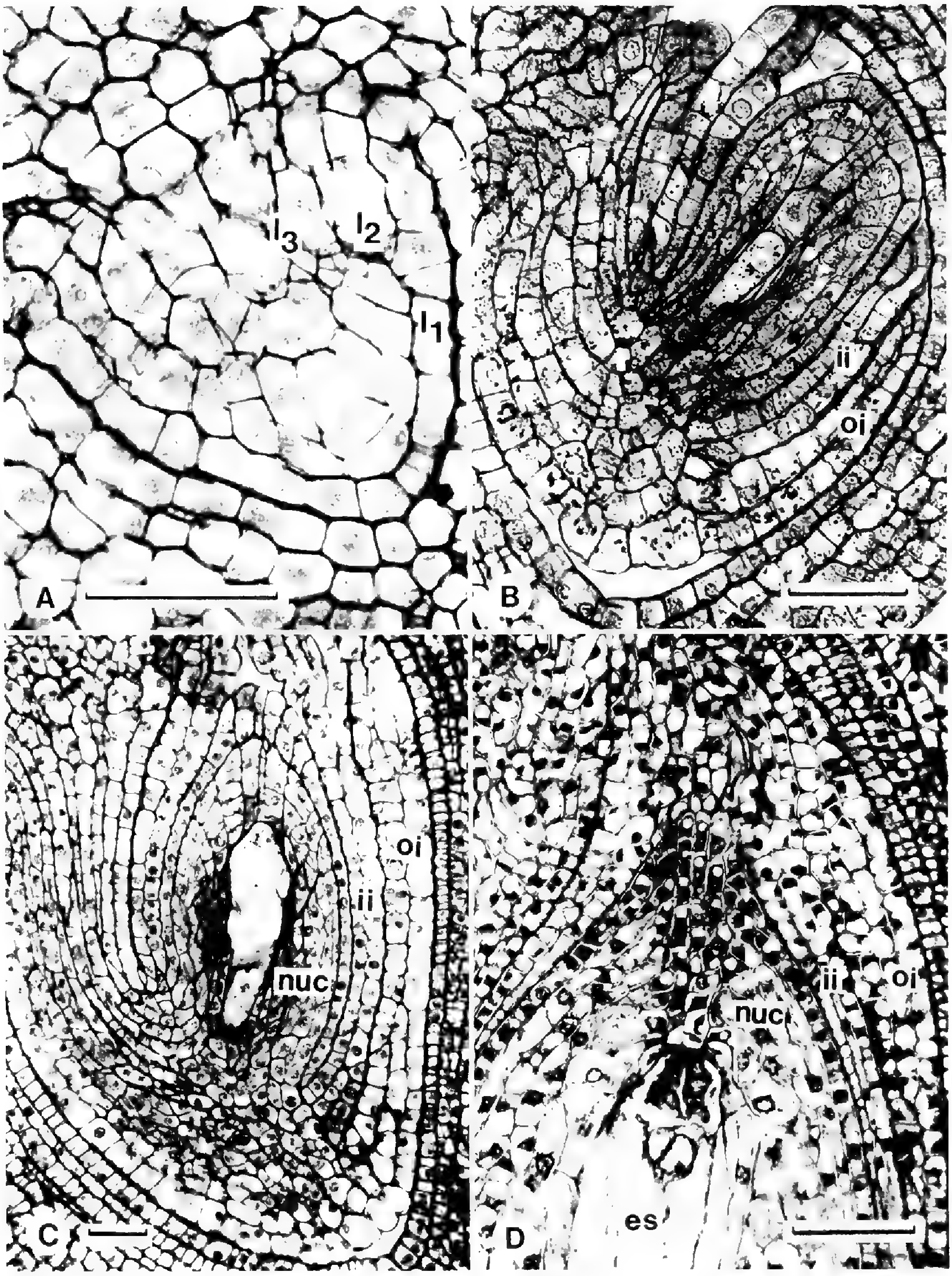

FIGURE 6. Ovules of *Monnina ciliolata*: A, ovule primordium, cross section; B, young ovule, long section; C, developing ovule, long section; D, mature ovule, long section, micropylar region. (Scale bars = 75 μm (A, B), 10 μm (C, D), 50 μm (E); es = embryo sac, l_1 = dermatogen, l_2 = subdermatogen, l_3 = corpus, other symbols as in FIGURE 1.)

well-developed collateral strands. The embryo is surrounded by 3 or 4 cells of endosperm that strongly adhere to the nucellar cuticle. Neither the endosperm nor the embryo contains any starch grains, but both are rich in fatty substances. The inner epidermis of the testa consists of distally thickened cells measuring

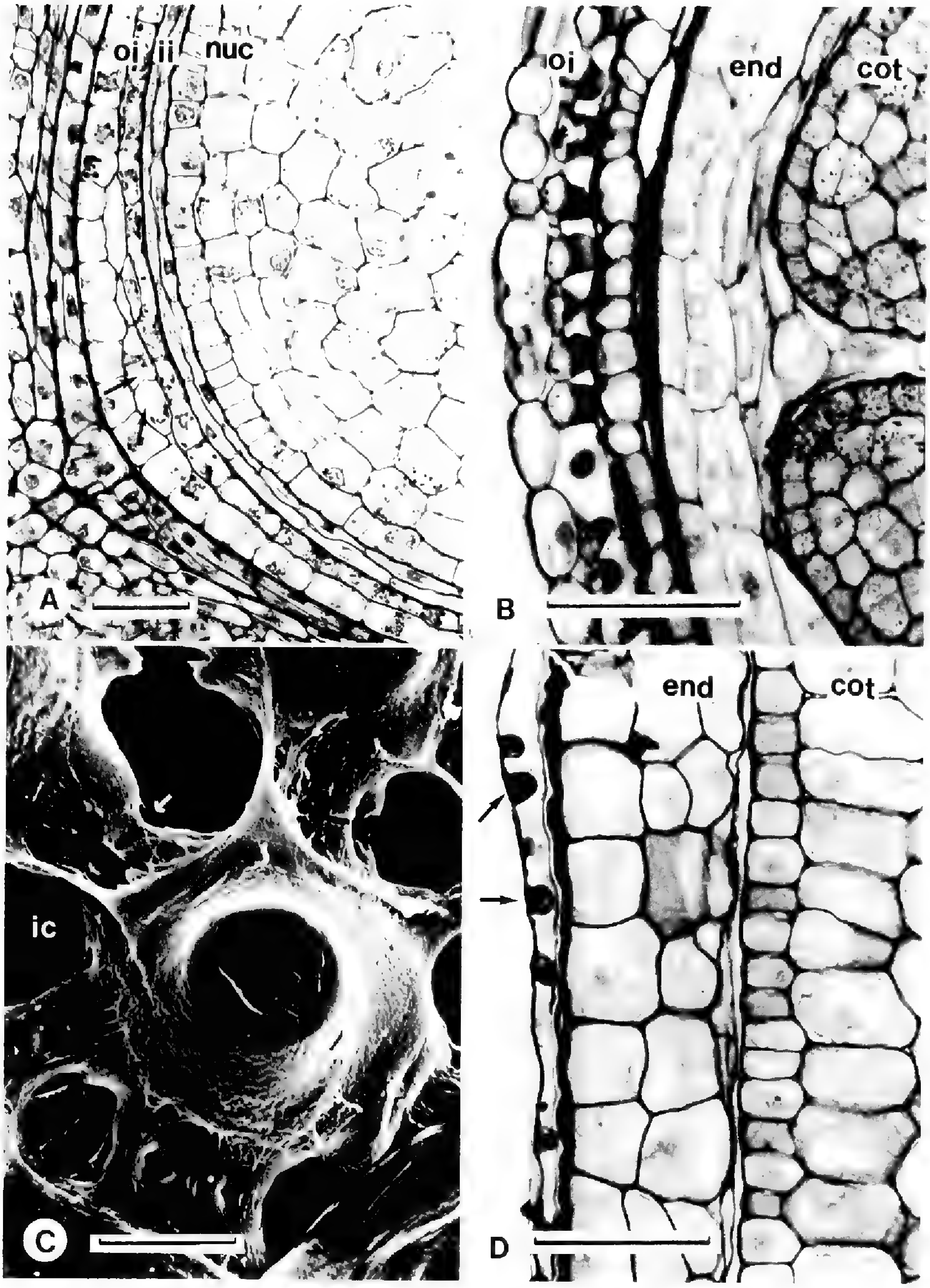

FIGURE 7. Seeds and ovule of 2 species of *Monnina*. A, *M. ciliolata*, mature ovule, cross section (arrows indicate subdermal cells in outer integument). B–D, *M. wrightii*: B, immature seed, cross section; C, reduced testa, interior view (arrow indicates connection between endotesta cells); D, ripe seed, cross section (arrows indicate isolated endotesta cells). (Scale bars = 100 μm (A), 50 μm (B, D), 5 μm (C); ic = intercellular space, other symbols as in FIGURE 1.)

10–11 × 6–7 μm. In growth this is disrupted, and the cells become separated from one another. The cells of the outer epidermis lack hairs and are crushed at maturity. The strongly tanniferous chalazal region, located near the base of the seed on the ventral side, is relatively long and narrow. The raphe contains a small amphicribral vascular strand ending in the chalazal region. The thin, translucent testa follows the form of the embryo. The seed is white, obpyriform in long section, transversely elliptic in cross section, and measures 3 × 1.2 × 0.6 mm. Externally, the isolated, thickened cells of the disrupted inner epidermis are visible as brown dots in the testa; these are more abundant in the micropylar region, where the cells are less separated.

In the ripe seeds of *Monnina ciliolata* and *M. xalapensis,* the inner testal layer is not disrupted and the slightly thickened, light-colored cells still adhere to one another. The seeds are elliptic in long section, transversely elliptic in cross section, and measure 5.5 × 2.3 × 2 mm.

SECURIDACA

Long sections of young gynoecia of *Securidaca diversifolia* show an anatropous ovule with a crassinucellate nucellus (FIGURE 5C), which contains a small embryo sac, a row of 3 parietal cells, and a dermal cap 2 cells thick. The dermally initiated inner integument is 2 or 3 cells thick. The subdermally initiated outer integument is 3 cells thick and has a small, exclusively dermal apex. Periclinal divisions enlarge the chalazal region. The chalaza-nucellus connection is 70 μm wide, and the raphe is 10 cells thick. The cross section of a mature ovule (FIGURE 5D) shows a nucellus with a large embryo sac and an undivided epidermis. The inner integument is 2 or 3 cells thick. The outer integument is 4 or 5 cells thick and consists of an inner epidermis, a mesophyll layer, and an outer epidermis. The mesophyll layer does not contain any provascular tissue. The raphe is 10 to 12 cells thick and contains an amphicribral vascular strand that runs into the thickened chalazal region, branching into a fan of xylem elements.

After fertilization the chalazal region enlarges manyfold, and a pachychalazal development gradually reduces the portion of the seed coat that is formed by the integuments. Initially, the globular embryo is surrounded by a scanty nuclear endosperm, but as the cotyledons develop the endosperm disappears. The nucellus is not yet resorbed, and the inner integument forms a massive endostome by periclinal divisions in the outer epidermis (FIGURE 5E). In the outer integument the cells of the inner epidermis divide anticlinally and elongate radially only very slightly. The mesophyll layer remains parenchymatic, and large intercellular spaces develop (FIGURES 5E, 8A).

In the ripe seed the investing embryo is rich in fatty substances and has large cotyledons 1500 × 3000 μm in cross section. The radicle is located apically, near the micropyle and hilum. The seed is pachychalazal, and the tegumentary part of the testa is restricted to the micropylar region, extending 1.5 mm apically (FIGURE 5F). The vestigial nucellar and inner tegumentary tissues are strongly compressed. In the outer integument the slightly elongated cells of the inner epidermis have faintly thickened walls and contain calcium oxalate crystals

(FIGURE 8A). The mesophyll layer consists of parenchymatic cells with large intercellular spaces; the outer epidermis is not crushed in the tegumentary portion of the testa. The chalazal part of the testa is strongly compressed (FIGURE 8B) and translucent, which makes the extensive and often branching vascularization externally discernible. The ripe seed is yellow and brown in the chalazal portion and dark brown in the tegumentary area; it is elliptic with pointed ends in long section, orbicular in cross section, and measures 6–6.5 × 3 × 2.5 mm.

The ripe seeds of *Securidaca lanceolata, S. ecristata, S. inappendiculata, S. corymbosa, S. atroviolacea, S. philippinensis,* and *S. volubilis* are very similar to those of *S. diversifolia.* The postfertilization development of *S. longepedunculata* and *S. welwitschii* is very different from that of all other species of *Securidaca.*

After fertilization in *Securidaca longepedunculata,* the chalazal region enlarges and shifts toward the dorsal side; no growth occurs in the micropylar region, and as the seed becomes more globose, the micropyle and hilum become located in the middle of the seed on the ventral side. The seed is not pachychalazal, but there is a postfertilization chalazal shift. The investing embryo has thick cotyledons 4 × 9 mm in cross section; the cotyledons contain several collateral strands not confined to the median plane, lack a palisade layer, and have the small radicle located near the micropyle. In the outer integument the elongated cells of the inner epidermis have distally thickened walls (FIGURE 8C). The elongated endotesta cells measure 22–25 × 10–12 μm and are arranged in a regular pattern of domelike structures (FIGURE 8D). The mesophyll and outer epidermis are strongly compressed. The dark brown chalazal region constitutes the dorsal side of the seed; it is elliptic in outline, 3 × 7 mm, and contains vascular tissue but is not tanniferous. The tegumentary portion of the testa is yellow, and the seed is elliptic in long section and orbicular in cross section, measuring 9 × 8 × 8 mm.

CARPOLOBIA

The ovule primordium of *Carpolobia gossweileri* is trizonate and develops into a crassinucellate nucellus with a small amount of parietal tissue. The mature ovule (FIGURES 5G, 8E) has a large nucellus and a small dermal cap; the embryo sac extends toward the chalazal region. The dermally initiated inner integument is 2- or 3-layered and forms an endostome. The subdermally initiated outer integument consists of an inner epidermis, a middle layer of 3 to 5 parenchyma cells, and an outer epidermis. At the level of the nucellus top, the inner epidermis has divided periclinally to form a massive exostome. A small dermal apex is formed on the outer integument. The chalazal region is rather large; the raphe is 11 to 15 cells thick and contains a bundle of provascular tissue that branches in the chalazal region and runs with several small provascular strands into the outer integument.

After fertilization the ovule enlarges manyfold. In *Carpolobia lutea* (FIGURE 5H, J) the nucellus is almost completely resorbed except for fragments of the epidermis and the uninterrupted cuticle; the inner integument is crushed. In

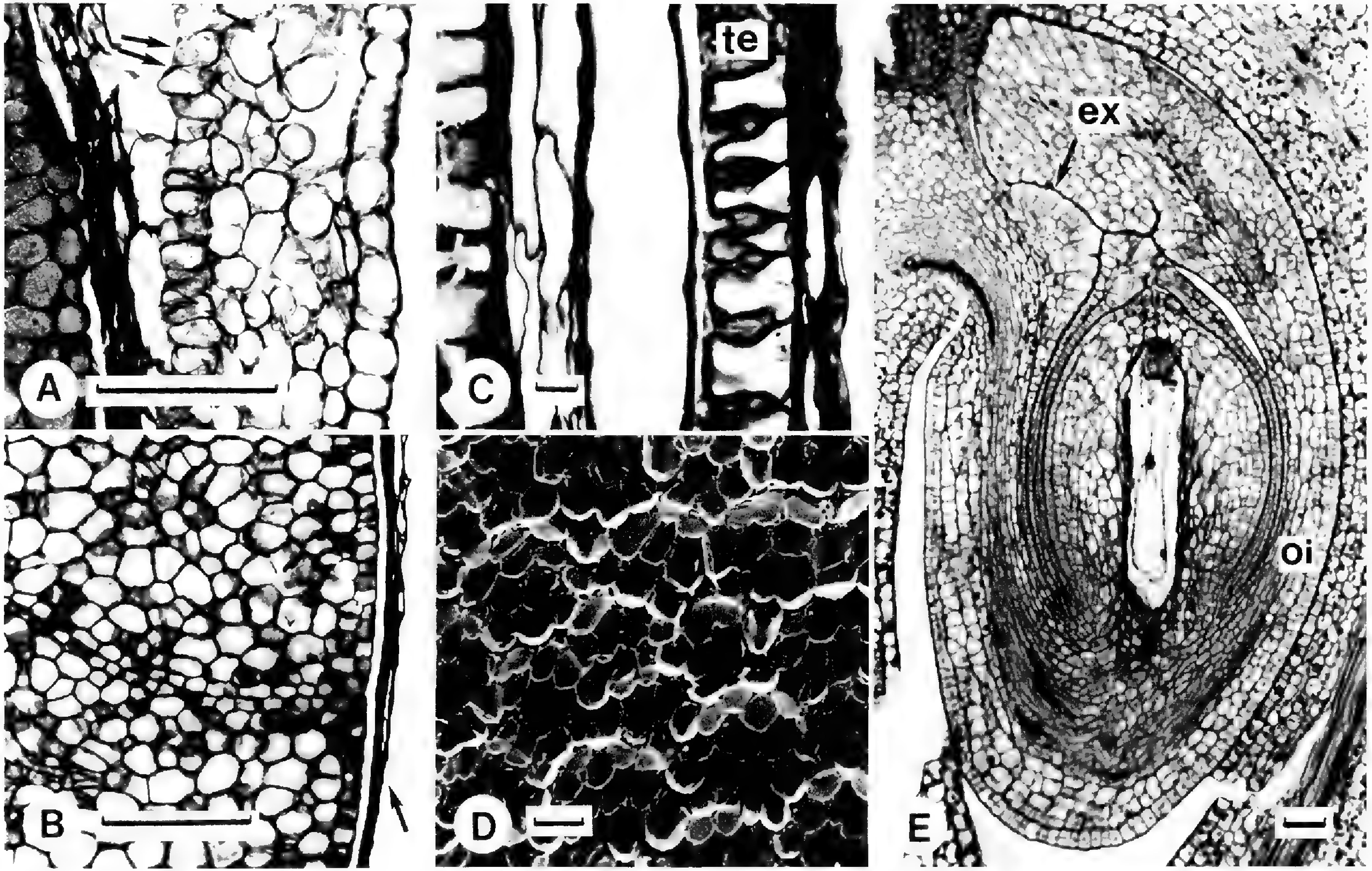

FIGURE 8. Polygalaceous seeds and ovules. A, B, *Securidaca diversifolia*: A, tegumentary part of seed coat, long section (arrows indicate weakly developed endotesta cells); B, chalazal part of seed coat (arrow), long section. C, D, *S. longepedunculata*: C, testa, cross section; D, testa, interior view. E, *Carpolobia gossweileri*, mature ovule, long section. (Scale bars = 75 μm (A, B), 10 μm (C, D), 50 μm (E); te = testa, ex = exostome, oi = outer integument.)

the outer integument, cells of the inner epidermis divide anticlinally and slightly enlarge radially, while those of the mesophyll layer enlarge tangentially and develop intercellular spaces, and those of the outer epidermis either differentiate into moderately elongated cells with thin walls or develop long unicellular hairs with thickened walls (FIGURE 5H).

In the ripe seed the spatulate embryo has a small radicle near the micropyle. The flattened cotyledons measure 130 × 4000 μm in cross section. The endosperm is copious; both embryo and endosperm are rich in fatty substances but poor in starch. Cells of the nucellus and inner integument are still discernible at the chalazal connection, but in the rest of the seed only the nucellar cuticle and compressed vestiges of the inner integument, both strongly adherent to the testa, remain. In the outer integument the cells of the inner epidermis have thickened distal walls, thin proximal walls, and large lumina without crystals; the unlignified short endotestal cells measure 11–13 × 7–8 μm. The mesophyll layer is 60–80 μm thick and consists of faintly thickened, strongly depressed cells. The outer epidermis consists mainly of moderately enlarged thin-walled cells that are rich in fatty substances and measure 50–70 × 40–45 μm; some cells form unicellular, thick-walled hairs up to 2 mm long with a prominent cuticle (FIGURE 5J). The hairs are abundant, especially on the raphe and the antiraphe. The orbicular chalazal region, 800 μm in diameter, is at the base of the seed; it contains vascular tissue but is not tanniferous. The thick amphicribral raphal strand is disrupted in the center; it branches in the chalazal region and runs into the outer integument to form many small strands and a thick antiraphal, amphicribral vascular strand. The long funicle, which shows no traces of aril formation, is near the micropyle at the apex of the seed. The seed is rust colored, elliptic in long section and transversely elliptic in cross section, and 9–11 × 8 × 4 mm.

The examined species of *Carpolobia* vary appreciably in seed-coat structure. In *C. gossweileri* (FIGURE 9A) the endotesta has slightly more elongated cells with less pronounced wall thickenings and thus larger lumina. The distal ends of the short endotesta cells are often slightly split, forming small cavities. The parenchymatic mesophyll is compressed and ca. 20–25 μm thick. As in *C. lutea,* the outer epidermis has differentiated into 2 types of cells, but the thin-walled cells form a layer up to 250 μm thick at the sides and 50 μm at the raphe and antiraphe. The seed is pubescent with many hairs up to 2 mm long; these are particularly abundant on the raphe and antiraphe but also protrude on the sides.

The ripe testa of *Carpolobia alba* (FIGURE 9B) does not form an endotesta. As the seed grows, anticlinal divisions in the inner epidermis do not keep pace with the tangential growth of the mesophyll cells. Eventually, the inner epidermis is disrupted and the compressed inner integument adheres to small, isolated cells on the inside of the testa. Only in the micropylar region is the inner epidermis undisturbed; here it consists of thin-walled, radially enlarged cells. The mesophyll is compressed as in *C. gossweileri,* but the post-chalazal vascularization is restricted to a single antiraphal strand. The outer epidermis has differentiated as in *C. lutea*; the thin-walled cells measure 50–140 × 40–50 μm. The long hairs are sometimes wavy and appressed to the testa. The seed measures 10–12 × 8 × 5 mm—somewhat larger than in the other species.

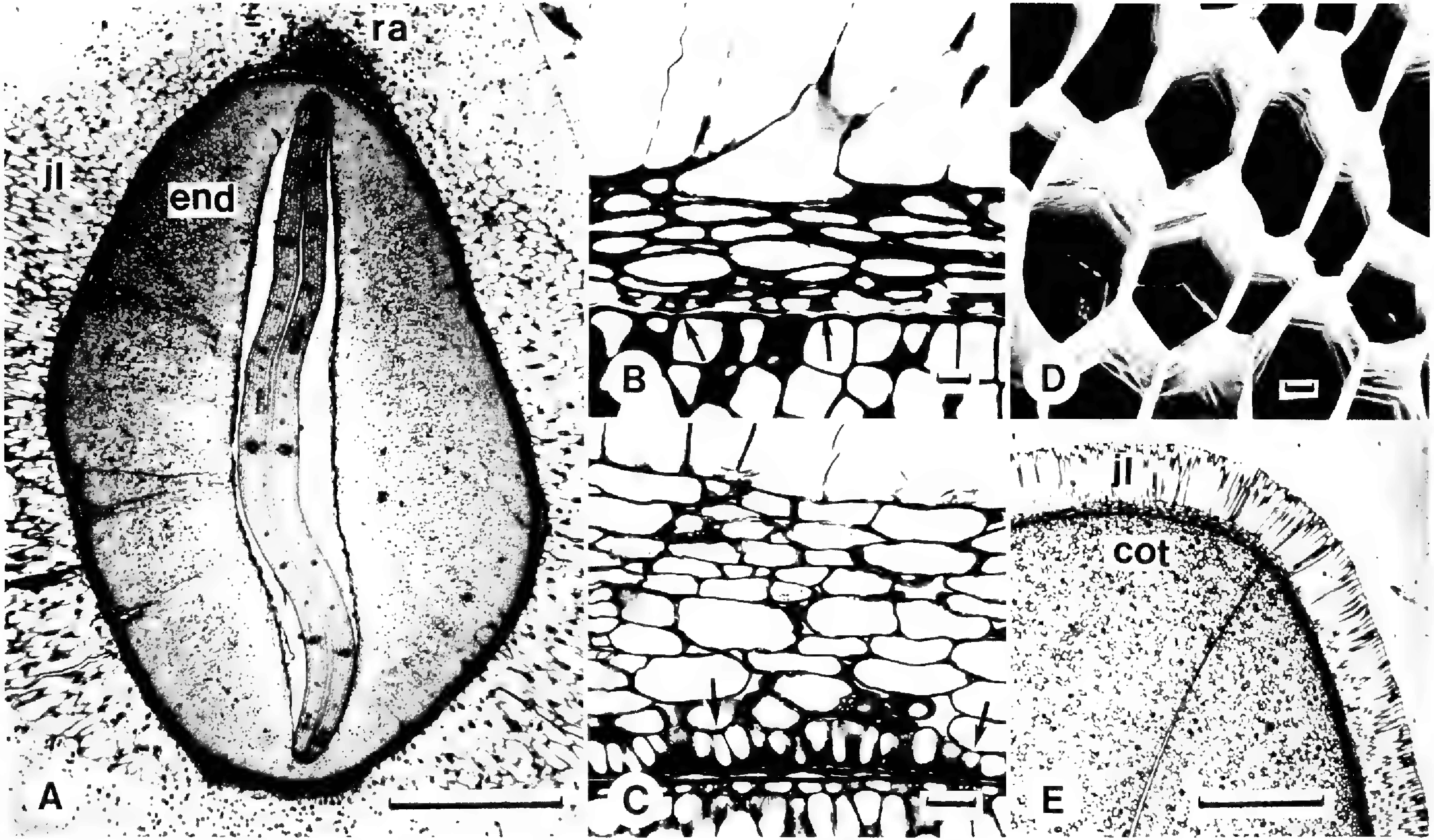

FIGURE 9. Cross sections of polygalaceous seeds. A, *Carpolobia gossweileri,* mature seed. B, *C. alba,* mature testa (arrows indicate isolated endotesta cells). C–E, *Atroxima afzeliana*: C, mature seed coat (arrows indicate endotesta); D, juicy layer; E, mature seed. (Scale bars = 1 mm (A, E), 10 μm (B–D); jl = juicy layer, other symbols as in FIGURES 1 and 3.)

ATROXIMA

In the ripe seed of *Atroxima afzeliana,* the investing embryo has thick cotyledons 7 × 11 mm in cross section. The radicle is near the micropyle and the funicle, on the ventral side near the middle of the seed. Due to a postfertilization shift, the chalazal region constitutes the dorsal side of the seed. The parenchymatic cotyledons have several collateral strands that are not confined to the median plane; the epidermis lacks a cuticle, consisting of depressed cells containing anomocytic stomata. The embryo is rich in fatty substances but poor in starch. A thin layer of endosperm, vestigial nucellar tissue, and inner integument persists in the chalazal region, but in the rest of the seed the embryo is bounded by the outer integument. In the outer integument the inner epidermis has divided anticlinally and has slightly enlarged radially. Distally, the cell walls are slightly thickened and the large lumina lack crystals. The unlignified short endotesta cells measure 12–20 × 10–20 μm (FIGURE 9C). The mesophyll layer is 50–150 μm thick and consists of depressed cells with many intercellular spaces. The outer epidermis has differentiated into a juicy layer (Breteler & Smissaert-Houwing, 1977) consisting of fat-rich, elongated cells with thin walls, measuring 40–45 × 350–550 μm (FIGURE 9D, E). Some epidermal cells, however, have developed a thick-walled, unicellular hair 15 × 15 × 350–550 μm. The chalazal region is strongly enlarged and ellipsoid, measuring 11 × 16 mm; it consists of vascular tissue but is not tanniferous. The testa contains extensive vascularization that emerges from a 3-mm-broad, depressed amphicribral raphal strand that runs into the chalazal region to branch and form many thick post-chalazal strands extending into the mesophyll; no recurrent bundles are present. The micropyle contains a vestigial endostome, and the short funicle shows no traces of aril formation. The seed is brown, reniform with rounded ends in long section and ellipsoid in cross section, measuring 19 × 15 × 9 mm.

The ripe seeds of *Atroxima liberica* differ slightly but characteristically from those of *A. afzeliana.* In the former the inner epidermis of the testa has divided anticlinally, but the cells are depressed instead of slightly elongated and measure 7–8 × 7–13 μm. The mesophyll is 200–500 μm thick, and the elongated epidermal cells are 50–60 × 900–2000 μm. The seed is reniform with tapering pointed ends in long section and almost triangular in cross section, measuring 19 × 15 × 14 mm.

ERIANDRA

The ripe seed of *Eriandra fragrans* (FIGURE 10A) contains a spatulate embryo with a small radicle situated near the funicle on the ventral side. The flattened cotyledons measure 800 × 7000 μm in cross section and contain several collateral strands. The epidermis consists of depressed parenchymatic cells and does not contain any stomata. A considerable amount of endosperm surrounds the embryo; both are rich in fatty substances but poor in starch. The cells of the nucellus are almost completely resorbed by the endosperm but persist in the bulges of the testa. The prominent nucellar cuticle stains deeply in Sudan IV and, together with the compressed remains of the inner integument, strongly

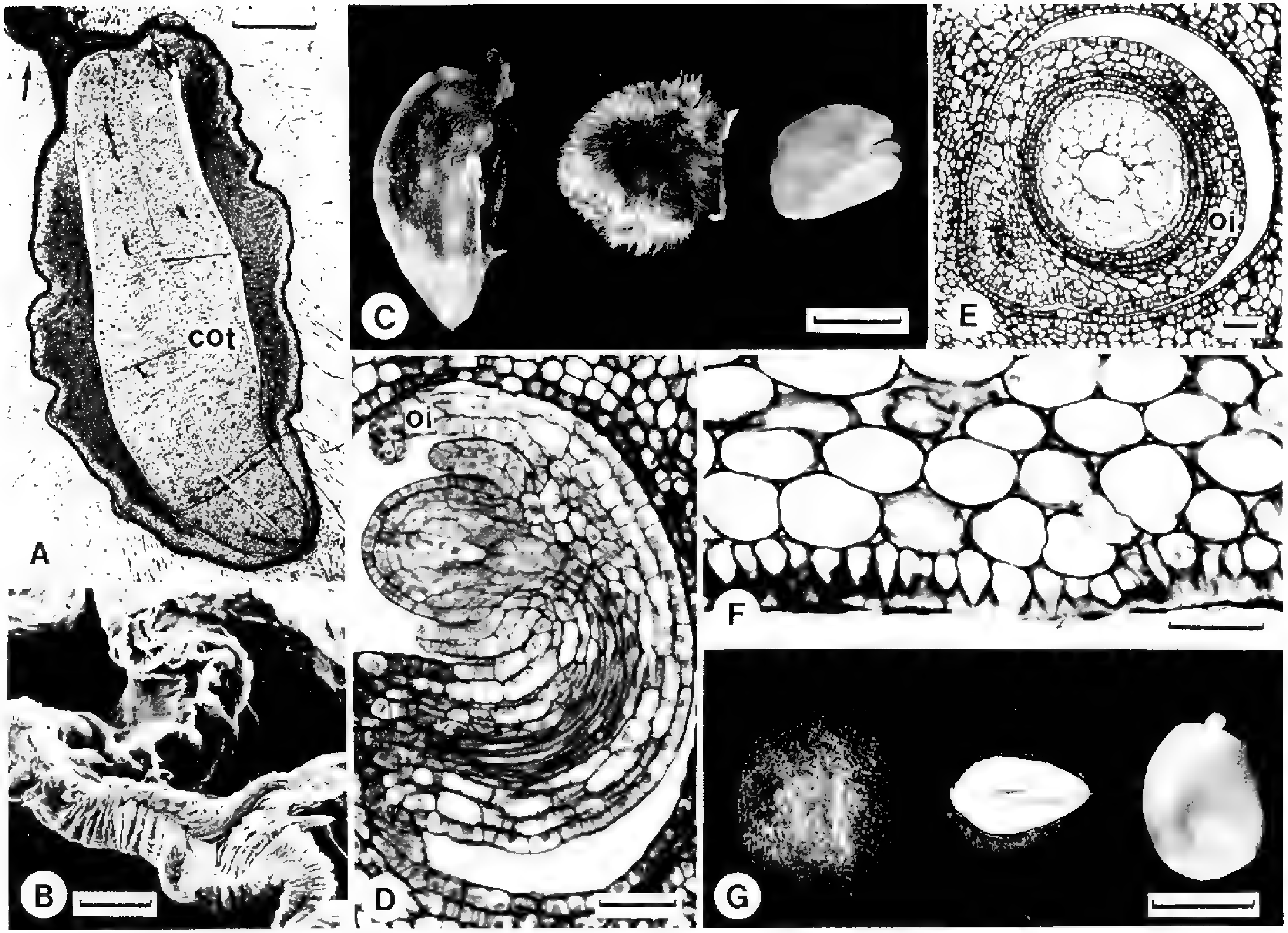

FIGURE 10. Polygalaceous seeds and ovules. A–C, *Eriandra fragrans*: A, mature seed with aril removed, cross section (arrow indicates attachment point of aril); B, scanning electron micrograph of aril, cross section; C, arillate seed (left), seed with aril removed (center), embryo (right). D–F, *Moutabea guianensis*: D, young ovule, long section; E, mature ovule, cross section; F, mature seed coat, endotesta, cross section. G, *Diclidanthera elliptica*: seed (left); seed, cross section (center); embryo (right). (Scale bars = 1 mm (A), 10 μm (B, D, E), 5 mm (C, G), 50 μm (F); symbols as in FIGURE 1.)

adheres to the inside of the testa. In the outer integument (FIGURE 11A), cells of the inner epidermis have divided anticlinally and are only slightly radially elongated; the distal walls of these cells have thickened, while the proximal ones remain thin. The lumina are wide and lack crystals. The endotesta cells measure 25–30 × 16–20 μm and are separated by cavities formed by the splitting apart of neighboring cells along the middle lamella.

The parenchymatic mesophyll layer is strongly compressed, and the relatively thin testa follows the bulges formed by the remains of the endosperm and the nucellus. The outer epidermis forms long, unicellular, rust-colored, slightly thickened hairs that are ellipsoid in cross section and measure 10 × 20 × 1000 μm; both the epidermal cells and the hairs have a prominent cuticle. The hairs are wavy and more or less appressed to the seed coat. The narrow nucellus-chalaza connection is located at the base of the seed; it contains vascular tissue but is not tanniferous. The raphe contains a thick amphicribral vascular strand that runs into the outer integument on the antiraphal side; no recurrent bundles are present. Partly due to additional mesophyll cells, the raphe and antiraphe are externally visible as a pronounced swelling on the seed. The long funicle and the micropyle are in the upper half of the seed on the ventral side. The seed has a large, yellowish, funicular aril that does not follow the bulges of the seed. Viewed in cross section, the aril is up to 400 μm thick and consists of large cells with a finely undulate middle lamella and deeply staining, bulky cytoplasm. The aril is very brittle due to plate collenchyma wall thickenings on the periclinal walls (FIGURES 10B, 11A) (sensitive to ruthenium red); it is completely devoid of fatty substances. The mature seed is brown, widely elliptic in long section and transversely elliptic in cross section (FIGURE 10C), and 8 × 7 × 3 mm.

MOUTABEA

Sections of young gynoecia of *Moutabea guianensis* show anatropous ovules, each with a crassinucellate nucellus and a linear tetrad of four megaspores (FIGURE 10D). The primary parietal cell has divided, and the nucellar epidermis is still 1 cell thick. The inner integument is dermally initiated and 2 cells thick at the apex; it can become 3 cells thick by divisions in the outer layer. The outer integument is subdermally initiated, and its growth is mainly determined by the activity of subdermal cells. Provascular tissue develops in the raphe. The pleurotropous, ventral orientation of the ovule (FIGURE 11B) influences the subsequent development of the ovule and seed.

In the growing ovule (FIGURE 11C) the embryo sac enlarges gradually and nucellar cells divide repeatedly to form a bulky nucellus; the epidermis forms a small dermal cap. The inner integument is generally 2 cells thick. In the outer integument, subdermal activity pushes the dermal portion upward, forming the mesophyll layer that extends to the top of the embryo sac. The inner layer of the dermal apex has divided repeatedly to form thick parenchymatic tissue covering the top of the ovule. The attachment zones of the integuments have shifted away from each other by intercalary growth of nucellar tissue, but the nucellus-chalaza connection is still narrow. Cross sections of a mature ovule

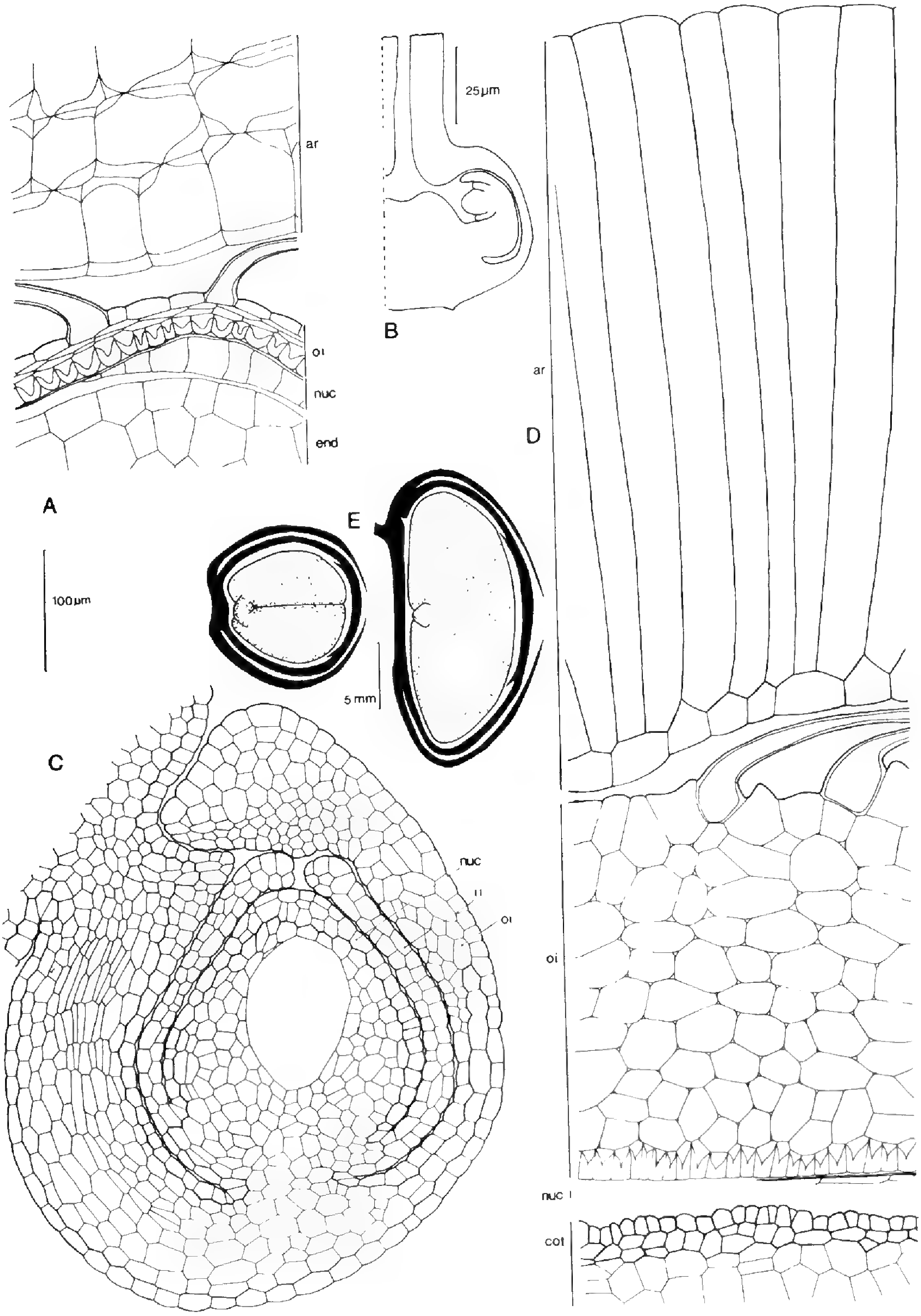

FIGURE 11. Polygalaceous seeds and ovules. A, *Eriandra fragrans,* seed coat, cross section. B–E, *Moutabea guianensis*: B, young gynoecium, long section; C, developing ovule, long section; D, mature seed, cross section; E, mature seed, cross (left) and long (right) sections. (Symbols as in FIGURES 1 and 3.)

(FIGURE 10E) show a large nucellus with an undivided epidermis surrounded by a 2-layered inner integument and a 4- or 5-layered outer integument. The raphe contains an amphicribral vascular strand that branches in the chalazal region and runs into the outer integument.

After fertilization (FIGURES 10F; 11D, E) the ovule enlarges manyfold; the characteristic shape of the seed is mainly due to expansion of the raphal and chalazal regions. The micropyle remains at the top of the seed on the ventral side. At maturity the investing embryo has a small radicle on the ventral side in the middle of the seed. The thick cotyledons measure 4 × 8 mm in cross section and are extensively vascularized by collateral strands. Most of the cotyledonary cells are parenchymatic, but the outer 3 cell layers consist of relatively small cells with thickened walls. The epidermis contains anomocytic stomata and has a cuticle. The dark red embryo is rich in fatty substances but poor in starch.

No stages of endosperm development were available, but the ripe seed does not contain any endosperm. Vestiges of the nucellus and inner integument are discernible at the chalazal connection. In the outer integument the inner epidermis divides anticlinally and the cells elongate slightly in a radial direction to form short endotesta cells measuring 27–30 × 10–12 μm. The cells have proximal walls with little or no thickening, and rather wide lumina without crystals (FIGURES 10F, 11D). The mesophyll layer is 250–300 μm thick and consists of parenchymatic cells with many intercellular spaces. The cells of the outer epidermis are slightly elongated, and some have formed long, curled, thickened, unicellular brown hairs that are ellipsoid in cross section and measure 10 × 20 × 900 μm. Both the hairs and the epidermal cells have a thin cuticle. The attachment zones of the integuments have shifted by intercalary growth, and the endotesta extends beyond the bending point, where a minor space develops; the palisade cells have formed hairs to fill this space. The elliptic chalazal region measures 7 × 12 mm, is not tanniferous, and constitutes the dorsal side of the seed. The raphe contains an amphicribral strand that branches in the chalazal region and vascularizes the rest of the testa; no recurrent bundles are present. The seed is completely surrounded by an unlobed, whitish aril that is attached in the micropylar-raphal area (FIGURE 11E). The aril is 2 or 3 cells thick; the outer cell layer is strongly elongated and 0.05–2.5 mm thick on the dorsal side of the seed, where the ends meet to form a narrow slit. The aril is rich in fatty substances and is adherent to the indumentum. The ripe seed is brown, reniform with tapering ends in long section, orbicular in cross section, and 24 × 13 × 12 mm.

DICLIDANTHERA

The mature ovule of *Diclidanthera bolivarensis* is epitropous and anatropous (FIGURE 12A). The crassinucellate nucellus has a row of 4 parietal cells and a dermal cap 4 cells thick; the embryo sac fills ¾ of the nucellus. The dermally initiated inner integument is 2- or 3-layered (FIGURE 12B). Its outer epidermis forms a massive endostome by periclinal divisions in the micropylar region. The outer integument is subdermally initiated and 5 or 6 cells thick. In the micropylar region repeated periclinal divisions in the inner epidermis of the

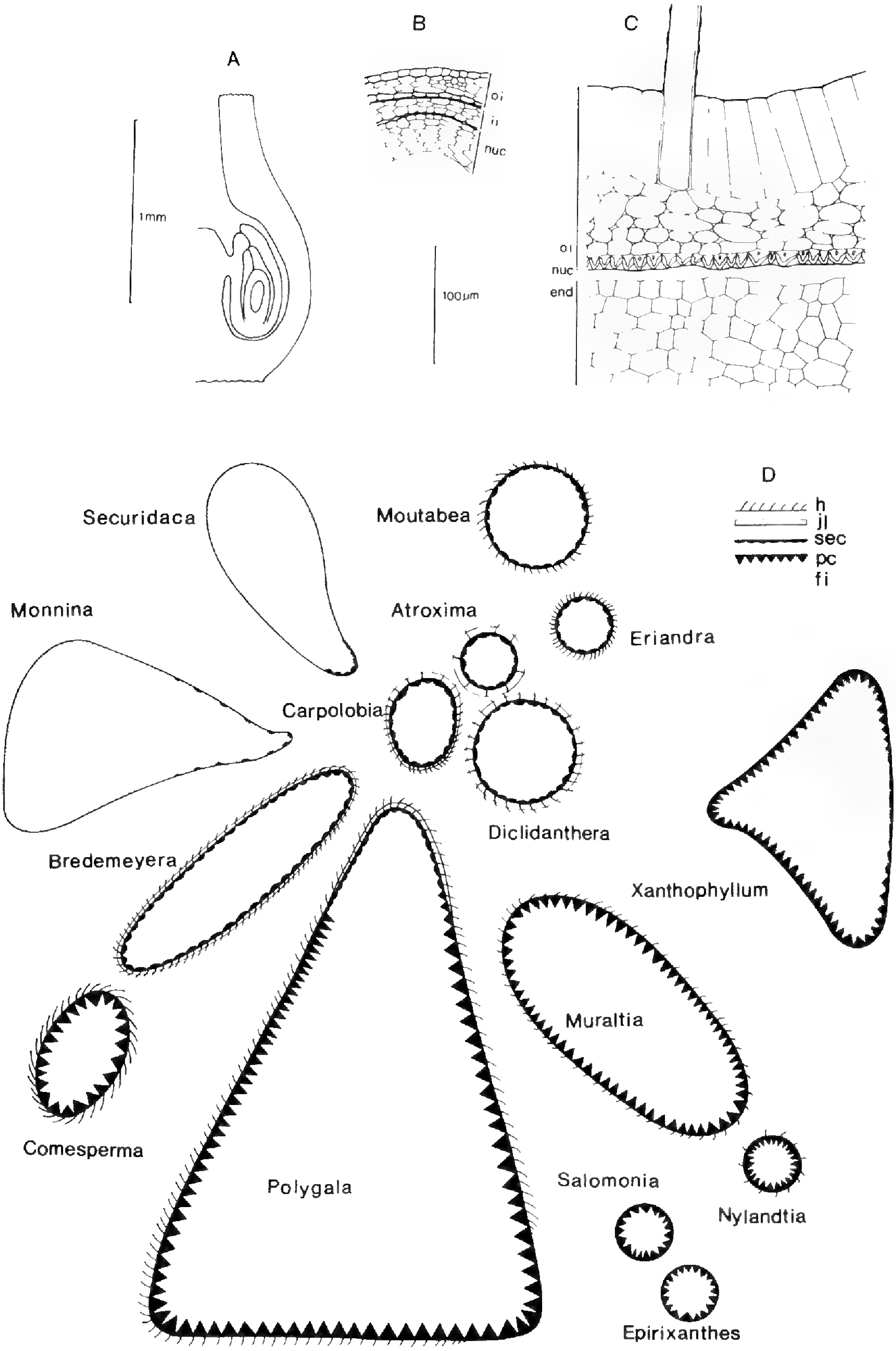

FIGURE 12. A–C, *Diclidanthera bolivarensis*: A, gynoecium, long section; B, mature ovule, cross section; C, mature seed, cross section (symbols as in FIGURE 1). D, imaginary cross section of phylogenetic tree representing taxonomic relationships of polygalaceous genera, based primarily on seed and fruit characters (h = hairy seed epidermis, jl = juicy layer, sec = short endotesta cells, pc = palisade cells, fi = fruit indehiscent).

outer integument render the exostome massive. The raphe is 8 or 9 cells thick and contains an amphicribral vascular strand that branches in the chalazal region and runs together with several small provascular strands into the outer integument.

The ripe seed contains a green, spatulate embryo with a small radicle, situated near the micropyle. The flat cotyledons measure 200 × 6000 μm in cross section. The epidermis consists of small parenchymatic cells and does not contain any stomata; it has a prominent cuticle. A considerable amount of endosperm surrounds the embryo. The cells of the nucellus are completely resorbed; only the prominent cuticle is still discernible. In the outer integument an endotesta is formed by the inner epidermis, the cells of which divide anticlinally but elongate only slightly and measure 9–10 × 10–14 μm. The distal walls are prominently thickened, but the proximal portion of these cells remains thin walled. The cells often have persistent lumina (FIGURE 12C), which frequently contain calcium oxalate crystals. Through splitting of the middle lamellae, a cavity develops between the rounded distal ends of the unlignified short endotesta cells. The mesophyll is 50–70 μm thick and consists of parenchymatic cells with many intercellular spaces. The outer epidermis either differentiates into radially enlarged, thin-walled cells measuring 40–50 × 80–100 μm or develops curled, thick-walled, unicellular hairs up to 400 μm long with a prominent, striate cuticle. The elongated thin-walled cells constitute a juicy layer. The elliptic nucellus-chalaza connection is 300 μm in diameter and is located at the base of the seed. The raphal strand branches in the chalazal region and runs into the outer integument; no recurrent bundles are present. The short funicle and micropyle are apical. The exarillate seed is black, broadly elliptic with a flat base and a more or less pointed apex in long section, transversely elliptic in cross section, and 17 × 7.5 × 5 mm.

The seed of *Diclidanthera elliptica* (FIGURE 10G) has a similar structure and measures 17 × 8 × 6 mm.

DISCUSSION

The Polygalaceae constitute a natural grouping in which small differences in ovule ontogeny are reflected in seed diversity. The ovular primordia are trizonate, and the crassinucellate nucellus has a small dermal cap. At maturity the nucellar tissue is resorbed, and only the prominent cuticle, which frequently adheres to the endotesta, remains detectable. In all genera the two- or three-layered inner integument is dermally initiated. A massive endostome is formed in *Bredemeyera, Securidaca,* and *Diclidanthera.* After fertilization the inner integument is mostly crushed, with just vestiges remaining; only in the ripe seeds of *Comesperma* and *Muraltia* does it persist. The outer integument is subdermally initiated; in the temperate herbaceous genera the subdermal mesophyll layer is gradually reduced. The Polygalaceae represent the first case in which intermediate stages of mesophyll reduction can be shown. Periclinal divisions render the dermal apex of the outer integument massive, and often an exostome aril develops in those genera with bilocular dehiscent fruits. The protective layer of the seed coat is formed by the inner epidermis of the outer integument.

As in the Cruciferae (Vaughan & Whitehouse, 1971), the seed anatomy does not support the current tribal subdivision of the family: the seeds of *Diclidanthera* have more similarities with those of *Carpolobia* than with those of *Moutabea*; seeds of *Securidaca* must be derived from a *Carpolobia*-like ancestor and are not related to *Polygala* seeds. The current tribal subdivisions in the Polygalaceae were already rendered questionable by Styer's (1977) study that indicated similarities in wood anatomy between the Moutabeae, *Bredemeyera*, and *Securidaca*.

In the present study several more or less independently acting evolutionary trends have been recognized that characterize the evolution of the seed. The most important trends are dermalization of the outer integument, decrease in seed size, development of elongated endotestal palisade cells, secondary disruption of the endotesta in some indehiscent fruits, reduction of the juicy layer, chalazal shift, and pachychalazy. Corner's (1976, p. 48) statement that "the main trend in seed-evolution has been simplification by reduction in complexity and size" certainly holds for the Polygalaceae. In her investigation of polygalaceous seed coats, Rodrigue (1893) stated that the testa is reduced when the fruit is indehiscent. The present results show that in the Polygalaceae the situation is not quite that simple: they require the designation of four groups in order to express the interwoven relations of seeds and fruits of the genera adequately (FIGURE 12D).

GROUP 1 (fruits indehiscent, endotesta cells not elongated; *Diclidanthera, Carpolobia, Atroxima, Moutabea, Eriandra*). This group of tropical genera comprises shrubs, treelets, lianas, and a large tree. The berrylike three- to seven-locular fruits contain large seeds with a well-developed seed coat.

The seeds of *Diclidanthera* and *Carpolobia* may represent a prototype from which all other seeds of this and the other three groups can be derived. Both their flattened cotyledons (Eames, 1961; Smith, 1983) and their subdermally initiated outer integuments (Bouman, 1974, 1984) are considered primitive among dicotyledons. The endotesta is not reduced but consists of isodiametric cells with a distal wall thickening. The epitropous placentation is reflected in the orientation of the ripe seed in the fruit. After the seed has ripened, the anatropous ovule simply enlarges into an ellipsoid, flattened seed with an apical micropyle and a basal chalaza; the radicle is directed upward. The epidermal cells differentiate into two types—more or less elongated, thin-walled cells, or polygalaceous hairs. In *Carpolobia* the thin-walled cells are only slightly elongated and the hairs are long and wavy. In *Diclidanthera* the thin-walled cells are relatively more elongated and constitute a juicy layer; the hairs are long and curled. The differences in seed indumentum between *Carpolobia* and *Atroxima* are gradual: in the latter the juicy layer is more strongly developed and the pubescence is sparser. The packing of the large embryo in *Atroxima* requires a specialized seed structure different from that of the preceding genera. After fertilization no growth occurs in the micropylar region, but the chalaza shifts toward the dorsal side, and at maturity the enlarged chalaza constitutes the dorsal side of the reniform seed. The micropyle and the hilum are located in the middle of the seed on the ventral side, and the radicle is oriented toward the floral axis. The chalazal shift is caused by growth more pronounced in the raphe than in the antiraphe, as in the obcampylotropous seeds of some Leguminosae (Corner, 1976). The chalazal shift allows better vascularization of large seeds and expansion of the seed above the funicular attachment. The differences in cotyledon anatomy between *Carpolobia* and *Atroxima* correspond with a different germination type: epigeal in *Carpolobia,* hypogeal in *Atroxima* (Breteler & Smissaert-Houwing, 1977). The present results confirm the conclusions of Breteler & Smissaert-Houwing (1977), who regarded the rambling *Atroxima* as derived from the closely related treelet *Carpolobia.*

The fruits of *Diclidanthera, Carpolobia,* and *Atroxima* are brightly colored, exposed, and large. The mesocarp is often fleshy (*Carpolobia*); the endocarp contains no hard structures and is sometimes glossy inside (*Atroxima*). The exarillate seeds contain a fat-rich juicy layer of elongated epidermal cells (as in *Punica granatum*) that is mixed with polygalaceous hairs. This suggests a dual function of the epidermis—both attracting and repelling animals.

These seed and fruit characteristics fit in well with Van der Pijl's (1982) syndrome of ornithochorous diaspores. Whether birds are attracted by the colored fruits and by the oily juicy layer needs investigation, but it is tempting to speculate that some frugivorous animals open the fruit, suck the seed, and throw it away because of the polygalaceous hairs. Zoochory explains why the endotesta has not been eliminated in the seeds in this group, as it has in the seeds of most of Group 4. Apparently the protective function of the testa has not been taken over by the endocarp, and the fruit and seed operate as a finely regulated dispersal unit.

The seeds of *Moutabea* are considered to be highly specialized because of the more strongly developed endotesta, the orientation of the large embryo, and the thick cotyledons with a thick-walled outer layer and stomata. At the outset the aberrant, pleurotropous ventral placentation orients the ovule so that the chalaza is dorsal (FIGURE 11B)—an evolutionary shortcut toward a chalazal shift. The aril covers the micropyle after fertilization and is attached over the entire ventral side of the seed; it consists of fat-rich parenchymatous cells and is strongly adherent to the seed hairs. The juicy layer of epidermal cells is lacking.

Field work by Van Roosmalen (1985) in Surinam indicates that fruits of *Moutabea guianensis* are distributed by monkeys of the genus *Ateles.* After the red exocarp deteriorates, it contrasts more with the yellowish, scented mesocarp and monkeys are attracted. They crack the fruits and suck the aril; the curled, firm hairs prevent them from chewing. Other monkey species are also attracted, but they chew the seeds, which subsequently fail to germinate. The seed hairs provide the main protection, but the strongly developed endotesta might also be a factor. The fruits and seeds of *Moutabea* are well adapted to monkey dispersal, which is generally considered to be derived: monkeys are relative late-comers in evolution, and they frequently open externally hard fruits with internal soft arils (*Garcinia* sp.; *Mammea* sp.) more easily than birds can (Van der Pijl, 1982).

In *Eriandra* the endotesta is similar to that of *Diclidanthera*, but the seed is not as primitive. The mesophyll layer in the seed is compressed, and the epidermis has developed wavy hairs, but the juicy layer is lacking. The embryo is intermediate between those of *Diclidanthera* and *Moutabea* with regard to size and orientation. Any animal-plant connection is less clear than in *Moutabea*; the funicular aril is devoid of fatty substances, and the peculiar wall thickenings suggest some function involved in the fruit dehiscence at germination. Monkeys are precluded because they do not occur in New Guinea or the Solomon Islands. The derived status of *Eriandra* is also indicated by Styer (1977), who showed that the wood of this large tree has many advanced characteristics of lianas.

GROUP 2 (fruits dehiscent, endotesta cells not elongated; *Polygala* sects. *Hebecarpa* and *Acanthocladus*; *Bredemeyera*). This group comprises tropical South American taxa, mainly shrubs and some lianas. Fruits and seeds are much smaller than those of the taxa in Group 1. The fruits are often fleshy, bilocular dehiscent capsules with arillate seeds. The cotyledons are flat and contain palisade parenchyma. The endotestal cells are not elongated and are frequently split along the middle lamellae, as in *Eriandra* and *Diclidanthera*. In cross section the subdermal mesophyll layer is uninterrupted in *Bredemeyera floribunda* and *Polygala* sect. *Acanthocladus*, laterally strongly reduced in *Polygala* sect. *Hebecarpa*, and not discernible in the ripe seeds of *Bredemeyera lucida*. The reduction of the mesophyll represents a dermalization of the outer integument, as recorded in *Polygala vulgaris* (Verkerke & Bouman, 1980). The epidermis in *Polygala* sect. *Hebecarpa* is very similar to that of *Diclidanthera*, involving a juicy layer mixed with hairs. The thin-walled, irregularly shaped epidermal cells occurring in *Polygala* sect. *Acanthocladus* and in *Bredemeyera floribunda* are also present in *B. collettioides* (Philippi) Chodat and *B. microphylla* Hieron. (Rodrigue, 1893) and are interpreted as remnants of the juicy layer. The seeds have an exostome aril that is yellowish in *Polygala jamaicensis* and *Bredemeyera* but white in the other species of *Polygala*; it is usually trilobed and glabrous. Only in *Bredemeyera* is it hook shaped and does it have a coma of long hairs. In Group 2 the fruits are often fleshy, and the dehiscence seems not so well organized as in the sutured, often marginate, membranaceous capsules of the species of *Polygala* in Group 3 (pers. obs.).

I have concluded that both seeds and fruits of Group 2 are intermediate between those of a *Diclidanthera*-like predecessor and those of Group 3. Obviously, the seeds of Group 2 are not primitive, and with regard to a *Diclidanthera*-like predecessor they show some clearly new acquisitions—for example, the palisade parenchyma in the cotyledon, the thick-walled endosperm in *Polygala durandii*, and the strong reduction of the mesophyll in *Polygala* sect. *Hebecarpa*. The newly developed exostome aril is correlated with fruit dehiscence.

Within *Bredemeyera* much variation in the chalazal appendages and the subdermal mesophyll layer exists, but seed anatomy indicates a close relationship between *Bredemeyera* and *Polygala* sect. *Hebecarpa*. In *Polygala* sect. *Acanthocladus* the *Diclidanthera*-like endotesta cells are slightly more elongated, the subdermal mesophyll is not reduced, and the cotyledons are thick. This suggests a divergent evolution of *Polygala* sects. *Hebecarpa* and *Acanthocladus*.

GROUP 3 (fruits dehiscent, endotesta cells much elongated; *Polygala* pro parte, *Comesperma, Muraltia, Nylandtia, Salomonia, Epirixanthes*). This group comprises shrubs and perennial and annual herbs of tropical and temperate regions. Generally the fruits are membranaceous bilocular capsules containing small, arillate seeds with a genuine palisade layer; the mesophyll layer is frequently reduced.

The endotesta consists of strongly elongated palisade cells that contain calcium oxalate crystals and are frequently arranged in a regular pattern of dome-like structures. The reduction of the subdermal tissue in the outer integument (integument dermalization), first recorded in *Polygala vulgaris* (Verkerke & Bouman, 1980), contributes to the neotenic decrease in seed size; it is widespread in the seeds of Groups 2 and 3, which are borne in a bilocular capsule. The mesophyll is well developed in *Polygala* sects. *Hebeclada, Ligustrina,* and *Chamaebuxus,* and in *Muraltia.* The lateral reduction of the mesophyll flattens the ovule (Verkerke & Bouman, 1980, *figs. 11, 12*), and a further reduction to smaller seeds leaves only a small strand of subdermal tissue wedged in between the inner and outer epidermal layers on the antiraphal side. In the herbaceous *Polygala* sect. *Polygala* one (and in *Comesperma* three or four) antiraphal mesophyll strands are present. Ultimately, fully dermal testae develop in the smallest seeds. The testae of *P. vergrandis, P. microspora, P. conferta, P. semialata, Salomonia, Epirixanthes,* and *Nylandtia* are fully dermal; in the latter genus Rodrigue (1893) apparently confused testa and endocarp.

The epidermis usually has unicellular, erect and silky (many species of *Polygala*; *Muraltia, Nylandtia*) or extremely elongated (*Comesperma*) hairs. In the smallest seeds (*P. microspora, Salomonia, Epirixanthes*) the hairs are lost altogether, and some epidermal cells form only a small papilla (FIGURE 2C). Only in *P. membranacea* do the radially elongated, thick-walled cells resemble the epidermal juicy layer in the seeds of Groups 1 and 2.

In most *Polygala* species, *Nylandtia,* and *Muraltia,* the white exostome aril is trilobed. The extreme variation of the aril in *Polygala* baffled Chodat (1890–1893), who did not then know about the myrmecochory of the seeds first reported by Sernander (1906). Myrmecochory has been established in several European and Australian *Polygala* species and in *Comesperma* species (Berg, 1975) but may have been largely overlooked in other regions (Beattie, 1983).

The raphe and chalaza can be swollen (FIGURE 2F), as well as the exostome. In *Comesperma* the exostome aril is reduced, and the white chalazal and raphal swellings have become ant attracting. The small seeds of *Polygala microspora* have only minute seed appendages. The large, thin-walled capsule is distinctly swollen, which suggests possible fruit transport through the air. In *Salomonia* the exarillate seeds are borne in a spiny capsule; this suggests epizoochory. Epizoochory was also recorded in *P. glochidiata* (Huth, 1887), but unfortunately this has never been confirmed.

In Group 3 plano-convex cotyledons are without palisade parenchyma and are surrounded by an often copious endosperm. This occurs in many *Polygala* species and in *Comesperma, Muraltia,* and *Nylandtia.* The exalbuminous seeds of *Polygala* sect. *Ligustrina* and, according to Corner (1976), also those of *P. venenosa* subsp. *pulchra* contain thick, fleshy cotyledons. The variation in cotyledon anatomy between genera and infrageneric groups presented here obviously hinders a simple characterization of the family but also reflects the divergent evolution of the taxa concerned.

Bresinsky (1963) noted that elaiosomes (as present in *Polygala*) are frequently separated from the seed by thick-walled structures that force ants to consume only the elaiosome and to reject the seed proper. Van der Pijl (1982) notes that a palisade layer renders seeds more fit for life outside the rain forest. The similarities between the seeds of Groups 1 and 2 indicate that initially fruit dehiscence did not force many internal changes in the smaller, arillate seeds of Group 2. The development of a palisade layer and a narrow nucellus-chalaza connection in Group 3 both prevented undesirable predation by the newly attracted dispersers and served as a better protection against desiccation, thereby allowing the colonization of new habitats outside the rain forest. This was accompanied by a changeover from flat cotyledons with palisade parenchyma to plano-convex ones.

In *Polygala* the tendency toward a herbaceous habit is accompanied by a decrease in seed size, but this mainly results in a flattening of the seed. Dispersal by ants is frequently coupled with a special myrmecochorous syndrome (Berg, 1975) that might also lead to anemochory of fruits. Ulbrich (1928) described the diplochorous dispersal of *Polygala vulgaris* and noted that ripe fruits, which are membranaceous, laterally flattened, and marginate, are blown off the plant by the wind. Once the fruit has fallen on the ground, a locule opens and exposes the seed (pers. obs.). Seed flattening in *Polygala* might indirectly flatten the capsule, which may have led to the diplochorous form of dispersal.

The seeds of *Polygala venenosa* subsp. *pulchra* (Corner, 1976) are not necessarily ancestral to the derived representatives of the genus. In addition to the thick cotyledons, it has some derived characters that suit the seed to the reported endozoochorous bird dispersal (Ridley, 1930). The palisade cells are extremely elongated (up to 240 μm), and a large red aril partly covers the globose, black, glabrous seed; the persistent capsule valves add further to the bird-attracting color contrast (see Van Steenis, 1972). The aril is basically of the same construction as the smaller, white, ant-attracting caruncle of the herbaceous species of *Polygala.*

The genus pairs *Muraltia-Nylandtia* and *Salomonia-Epirixanthes* show many similarities in seed structure with *Polygala. Muraltia* resembles the more primitive species of *Polygala* in having an uninterrupted mesophyll layer and an exostome aril. *Nylandtia* differs in the reduction of the mesophyll layer, but the secondary closure of the fruit wall apparently did not eliminate the exostome aril, the seed hairs, or the palisade layer.

The seeds of *Salomonia-Epirixanthes* have evolved similarly to those of the derived species of *Polygala.* The mesophyll is reduced, the palisade cells are well developed, the seeds are glabrous, and the seed appendages are very small. Wirz (1910) has already suggested that the absence of a thickened dermal apex in the outer integument of *Epirixanthes elongata* was responsible for the differences in seed form between this species and *E. cylindrica.*

Van Steenis (1968) suggested that the Australian *Comesperma* is linked with *Bredemeyera* through the New Guinean *B. papuana.* The latter lacks the coma and the exostome aril of the South American species but shares the isodiametric endotesta cells. *Bredemeyera papuana* has the same type of coma as *Comesperma* but lacks the firm cuticle and the tall palisade layer that adapt *Comesperma* seeds to life outside the rain forest. The similar tall palisade layer of *Polygala* and *Comesperma* apparently developed by convergent evolution. Although the differences in fruit morphology between *Comesperma* and *Bredemeyera* were disputed by Van Steenis, personal observation indicates that Rodrigue (1893) rightly pointed out that in both *Polygala* and *Bredemeyera-Comesperma* the development of a palisade layer is accompanied by the changeover from a fleshy fruit to a membranaceous capsule. Chalazal appendages are present in *Polygala* and *Bredemeyera* but attain their greatest development in the myrmecochorous species of *Comesperma.* Although the mode of dispersal of *Bredemeyera* has never been investigated, myrmecochory might represent a secondary development in *Comesperma,* as happened in many Australian plant groups (Berg, 1975). The present results support Van Steenis's hypothesis that the Australian *Comesperma* represents a derived branch of the South American *Bredemeyera,* which became adapted to subtropical drought conditions and assumed a virgate, microphyllous habitat.

GROUP 4 (fruits indehiscent, endotesta reduced; *Securidaca, Monnina*). This group is heterogeneous. In almost all species the protective function is completely taken over by the tough endocarp, which—unlike that occurring in the fruits of Group 1—consists of alternating layers of sclerenchymatic fibers (pers. obs.). At maturity the faintly developed endotesta reveals the polygalaceous nature of the seed coat, but in the two genera the testa reduction has followed two entirely different pathways.

In *Securidaca* ovule ontogeny is similar to that of *Carpolobia* and *Diclidanthera.* Due to different postfertilization development, major differences exist between the large seeds of the African species (*S. longepedunculata, S. welwitschii*) and the smaller seeds of the South American and Indo-Malesian representatives. The larger seeds contain an endotesta with cells slightly further differentiated than those of *Carpolobia*; the mesophyll and the glabrous epidermis are compressed. Because of an *Atroxima*-like postfertilization development, the seed contains a large, dorsal chalaza; the large investing embryo has thick cotyledons, the radicle is oriented toward the floral axis, and its almost globular shape allows expansion of the seed above the funicular attachment. In the smaller seeds of the other species, the testa is only weakly developed in the small, apical tegumentary portion of the pachychalazal seed (FIGURE 5F).

The presence of an endotesta and the *Atroxima*-like seed development in the African species suggest that these large seeds are primitive within the genus. In conjunction with the *Carpolobia*-like ovule ontogeny, this implies that *Securidaca* has evolved from a *Carpolobia*-like ancestor that became adapted to anemochory. The fruit of *Securidaca* lost its animal-attracting function and developed both a hard endocarp and an *Acer*-like samara, allowing for dynamic propulsion (Van der Pijl, 1982). The seed, in turn, lost its indumentum, and the mesophyll and the epidermis became compressed. In the smaller seeds the seed coat became further reduced by a pachychalazal development. Pachychalazy is mostly associated with large seeds, facilitating their vascularization (i.e., *Trichilia grandifolia*—Boesewinkel, 1981), and its function of eliminating the endotesta, as suggested here, has not previously been discussed.

In *Monnina* the incipient endotesta is disrupted, and only in some species do the cells thicken; then they are externally visible as brown spots dispersed over the glabrous seed. The disrupted endotesta of nonelongated cells, the dermalization of the outer integument, and the flat cotyledons with palisade parenchyma indicate a derivation from an ancestor with seeds borne in a bilocular capsule, conceivably resembling those of *Polygala* sect. *Hebecarpa* and *Bredemeyera*. This agrees with Wendt's (unpubl. ms) studies, which predict that the ancestor of *Monnina* must have had an unwinged bilocular fruit and would be classified as a *Polygala* if it had survived. With the development of the secondary closure of the capsule came an *Ulmus*-like fruit wing for gliding (Ulbrich, 1928) and a hard endocarp, which made the seed appendages and the testa redundant. Considering several floral characters and the similar fruit wing, Wendt (unpubl. ms) also suggested that *Monnina* might be related to *Polygala* sect. *Ligustrina*, but its seed anatomy is not compatible with such a derivation. Fruit wings probably developed independently in *Monnina* and in *Polygala*. Because of its giant fruit wing, *P. membranacea* has long been classified as a *Monnina*, but the seed has a well-developed testa and an aril (see Görts-van Rijn, 1974).

Hutchinson (1967) designated *Xanthophyllum* as the most primitive genus of the family, but this was criticized by Corner (1976) and Van der Meijden (1982). Although the seeds of *Xanthophyllum* were long believed to have only a reduced testa, this only holds true for the most derived infrageneric groups. The seeds of the most primitive infrageneric groups all have a subdermally initiated outer integument, thin cotyledons, a copious endosperm, a well-developed palisade layer, a thick mesophyll, radially elongated epidermal cells, and a glabrous seed with a solid hypostase (Verkerke, 1984). Compared with the seeds of Group 1 (*Carpolobia, Diclidanthera*), the most primitive *Xanthophyllum* seeds have two characters considered advanced within the family (the well-developed palisade layer and the glabrous seed), and in one species (*X. octandrum*) the orange to dark brown fruit is irregularly dehiscent. All other species have indehiscent fruits, and Van der Meijden (1982) considered the fruit dehiscence of *X. octandrum* to be a secondary development. The present results indicate that the fruit of *X. octandrum* can correctly be regarded as a locular dehiscent capsule, and that the elongated epidermal cells and the well-developed palisade layer are comparable to those of *Polygala membranacea* (FIGURE 1D). I have concluded that *Xanthophyllum* has evolved from a predecessor with dehiscent fruits, as must have happened with *Nylandtia* and *Epirixanthes*, and that the genus is not primitive within the family.

The results show that several evolutionary trends explain the great diversity in the fruits and seeds of the Polygalaceae, and that the evolution of seeds and fruits appears to be closely correlated. Complementary field observations of dispersal and germination could further enlarge our understanding of these evolutionary trends. The present results fit well with Wendt's (unpubl. ms) family cladogram but also indicate that old generic and tribal concepts may have to be changed in order to express the evolutionary relationships within the family.

ACKNOWLEDGMENTS

The author wishes to thank Dr. Tom Wendt and Dr. Ruud van der Meijden for many stimulating discussions, Dr. Ferry Bouman for valuable criticism, and Professor A. D. J. Meeuse for his critical reading of the text. Thanks are also due to Drs. F. Breteler (Landbouwhogeschool, Wageningen), P. Maas (Rijksuniversiteit, Utrecht), P. Teunissen (Surinam), M. van Roosmalen (Surinam), and J. Thompson (Sydney), who provided specimens for this study. The technical advice of Dr. F. D. Boesewinkel and Mr. H. Koerts Meijer is gratefully acknowledged.

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Journal of the Arnold Arboretum *July, 1985*

CONTENTS OF VOLUME 66, NUMBER 3

Volume 66, Number 2, including pages 123–278, was issued April 8, 1985.

JOURNAL OF THE ARNOLD ARBORETUM

HARVARD UNIVERSITY VOLUME 66 NUMBER 4

ISSN 0004–2625

Journal of the Arnold Arboretum

The *Journal of the Arnold Arboretum* (ISSN 0004-2625) is published quarterly in January, April, July, and October for $50.00 per year, plus $5.00 postage for addresses outside of the United States, by the Arnold Arboretum of Harvard University. It is printed and distributed by the Allen Press, Inc., 1041 New Hampshire Street, Lawrence, Kansas 66044. Second-class postage paid at Lawrence, Kansas. POSTMASTER: send address changes to *Journal of the Arnold Arboretum,* ℅ Allen Press, Inc., P. O. Box 368, Lawrence, Kansas 66044.

Subscriptions and remittances should be sent to *Journal of the Arnold Arboretum,* 1041 New Hampshire Street, Lawrence, Kansas 66044, U. S. A. Claims will not be accepted after six months from the date of issue.

Volumes 1–51, reprinted, and some back numbers of volumes 52–56 are available from the Kraus Reprint Corporation, Route 100, Millwood, New York 10546, U. S. A.

Printed at Allen Press, Inc., Lawrence, Kansas

COVER: The stylized design appearing on the Journal and the offprints was drawn by Karen Stoutsenberger.

JOURNAL
OF THE
ARNOLD ARBORETUM

VOLUME 66 | OCTOBER 1985 | NUMBER 4

A REVISION OF AMMANNIA (LYTHRACEAE) IN THE WESTERN HEMISPHERE

SHIRLEY A. GRAHAM

AMMANNIA L. is a genus of about 25 species of aquatic or marsh-inhabiting herbs distributed in both the Temperate and Tropical zones. It is best represented in Africa (16 species), with a maximum of seven species occurring on each of the other continents. The only monograph of the genus (Koehne, 1903) is outdated because of accumulated changes and additions to the taxonomy and nomenclature and the more extensive collections now available.

Many species of *Ammannia* are distinguished from one another by seemingly minor qualitative differences that are difficult to recognize in practice. In some cases, species limits are based more on geographic disjunctions than on morphological distinctions. Relationships of morphologically similar species occurring on different continents are unknown. The need to resolve the confusion surrounding the variability in species in the New World in order to prepare treatments for several floras now underway has stimulated this revision. The difficulty in obtaining viable seeds necessary for biosystematic investigations of the narrowly endemic African and Asian species also prompted restriction of the study to the species occurring in the Western Hemisphere.

MORPHOLOGY

The genus *Ammannia* was divided by Koehne (1880b) into two subgenera and two sections. Subgenus *Cryptotheca* (Blume) Koehne, comprising the single species *A. microcarpa* DC., is unique in the Lythraceae by virtue of its parietal placentation. The remainder of the genus comprises subgenus *Ammannia* (formerly subg. *Euammannia* Koehne), which is further divided into two sections and four series, all highly artificial in nature. Five species, representing both sections of subgenus *Ammannia,* occur in the Western Hemisphere. Section *Ammannia* (formerly sect. *Astylia* Koehne), with short or included styles, is represented by *A. latifolia* L. and the adventive *A. baccifera* L.; section *Eustylia*

Journal of the Arnold Arboretum **66**: 395–420. October, 1985.

TABLE 1. **Chromosome numbers in Ammannia.**

SPECIES	HAPLOID NO.	SOURCE
A. **auriculata** Willd.	15, 16	Graham (1979)
A. **baccifera** L.	12	Sarkar *et al.* (1982)
A. **coccinea** Rottb.	33	Graham (1979)
A. **latifolia** L.	24	Graham (1979)
A. **multiflora** Roxb.	9	Sarkar *et al.* (1980)
A. **robusta** Heer & Regel	17	Graham (1979)
A. **senegalensis** Lam.	20 ($2n = 40$)	Bir & Sidhu (1975)
A. **verticillata** (Ard.) Lam.	14 ($2n = 28$)	Krishnappa (1971, as *A. salicifolia* Monti)

Koehne, with long, exserted styles, by *A. auriculata* Willd., *A. robusta* Heer & Regel, and *A. coccinea* Rottb.[1]

All are glabrous annual herbs, mostly 10 dm or less in height, with sessile, linear-lanceolate, decussate, auriculate-based leaves. The flowers, borne in sessile or pedunculate axillary dichasia, are homostylous, 4- (or 5-)merous, 3–6 mm long, with pale pink to deep fuchsia, caducous petals. In *Ammannia latifolia* apetalous forms have been considered distinct species from petalous forms, although petals are absent or vary in number from one to four. In *A. auriculata* stamen number has provided a basis for recognition of varieties, but it too is variable (from two to eight), even in flowers from a single plant. Infraspecific taxa proposed by Koehne for several species of *Ammannia* are based on minor and/or variable morphological characteristics without geographic integrity and are hence taxonomically insupportable.

According to Koehne, the styles of all *Ammannia* species are either filiform and well exserted or short and included. He (Koehne, 1880b, p. 242) concluded that differences in style length are the key to the taxonomy of the genus, without which "species distinction in *Ammannia* becomes impossible." In his taxonomy, species that appear to differ morphologically only in style length are placed in different sections. In the long-styled, nearly cosmopolitan *A. auriculata* and the very similar but short-styled African *A. senegalensis* Lam., the species distinction, which is otherwise suspect, is supported by a difference in chromosome number (see TABLE 1).

The capsule of *Ammannia* is irregularly dehiscent with a microscopically uniform dry wall. The related genus *Rotala* L. frequently grows with *Ammannia* and can be deceivingly like it in habit but can be recognized by the microscopically dense transverse striations of its capsule wall and by its 2- to 5-valved septicidal dehiscence. The capsule characters provide the most consistent gross morphological distinction between the genera.

Anatomical features of stems and leaves have been described for eight species

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[1] The citation of *A. coccinea* as *A.* ×*coccinea* in S. Graham (1979) was meant to convey recognition of the amphidiploid origin of the species. Following Article H.3.4, note 1, of the International Code of Botanical Nomenclature (Voss, 1983), the amphidiploid is treated as a species and the hybrid sign is now better omitted.

by Panigrahi (1980), and wood anatomy of the genus, based on *Ammannia octandra* L. f., was described and compared to that of other lythraceous genera by Baas and Zweypfenning (1979). In wood anatomy the genus shares a juvenilistic character complex with the herbaceous to semiwoody genera *Nesaea* Comm. ex HBK., *Lythrum* L., *Cuphea* P. Browne, and *Crenea* Aublet.

Embryological characters for the genus are typical of the Lythraceae and generally of the order Myrtales. The ovule is crassinucellate with a two-layered inner integument, and megagametogenesis is of the *Polygonum* type (Tobe & Raven, 1983; Smith & Herr, 1971; Joshi & Venkateswarlu, 1936).

BIOLOGY

Ammannia is a predominantly autogamous genus, although outcrossing occurs, as is evidenced by the hybrid nature of *A. coccinea.* Tests for agamospermy in *A. coccinea, A. auriculata,* and *A. robusta* were negative. Flowering time is not a barrier to crossing among these species. Flowering extends from July to October in the North Temperate Zone for all species studied; in subtropical and tropical areas it is prolonged throughout the year as long as the habitat remains favorable for seed germination and new plant development. In warm areas new plants mature continuously from seeds of the prior generation.

Flowers of *Ammannia latifolia* are cleistogamous in some parts of its range. In plants grown from seeds of apetalous specimens (Puerto Rico: *Liogier 10314,* NY), the flowers never opened but a large number of viable seeds was produced. After fertilization the style may elongate to 1 mm, and this elongation together with the enlargement of the maturing capsule causes the senescent stigma to be extruded, but true anthesis does not occur. Petalous and apetalous flowers of *A. latifolia* from Manatee Co., Florida (*Graham 698,* MICH), open to varying degrees, with self-pollination occurring either prior to opening or at anthesis. Both petalous and apetalous flowers may be chasmogamous. The attractant role of the petals, when present in this species, is minimized by their small size, pale color, and brief retention time. The introrse anthers closely surround the stigma and frequently detach from the filaments to adhere to the sides of the papillate stigma at dehiscence.

In *Ammannia auriculata, A. robusta,* and *A. coccinea* self-pollination starts at anthesis, with anther dehiscence and stigma receptivity beginning simultaneously when these organs are at the level of the floral tube opening or slightly exserted. The anthers may become attached to the stigma as in *A. latifolia.* In the first three species enlargement of the capsule after fertilization causes the style to extrude prominently from the floral tube, even though the style itself does not elongate significantly. In *A. coccinea* an abscission layer forms 1 mm above the base of the style after fertilization, and the upper style withers and falls away. The remaining short style base has led to misidentification of mature long-styled *A. coccinea* specimens as the short-styled *A. latifolia.*

Plants of *Ammannia coccinea* and *A. robusta* are visited by skippers and small bees for nectar produced by the thickened glandular area surrounding the base of the ovary.

ECOLOGY AND DISTRIBUTION

Ammannia characteristically grows in wet, relatively open habitats from sea level to 1500 m. It is colonial in shallow fresh or brackish marshes, temporal pools, roadside ditches, river banks, and other intermittently wet areas. Soils in which it flourishes vary from nearly pure white sand to heavy gray clay. Appropriate water level and lack of competition appear to be the most important factors in establishment and spread of the plants. *Ammannia coccinea* and *A. robusta* develop extensive populations in fresh water to depths of 0.5 m but are most common in moist or saturated soils. In standing water extensive aerenchymatous tissue develops on the external surface of submerged stem parts. Similar aerenchyma is seen on submerged stems of *Decodon* J. Gmelin, another lythraceous genus. In India, where *A. auriculata* is one of the predominant broad-leafed weeds in rice fields of the Punjab, control is effected by maintaining an optimum (high) water level for rice in the field, since low water levels promote *Ammannia* development (Shetty *et al.*, 1975). Similar ecological requirements are shared among the *Ammannia* species in North America, as demonstrated by numerous herbarium sheets on which more than one species is mounted. Species recorded in this manner growing at the same site are *A. coccinea* with *A. latifolia, A. coccinea* with either *A. auriculata* or *A. robusta* (or rarely all three species), and *A. auriculata* with *A. robusta.*

Ammannia seeds are well adapted to dispersal in aquatic environments. They are produced in great quantity (an average of ca. 250 seeds per capsule in the species occurring in the Western Hemisphere). They are ca. 1 mm long and are buoyed by the convex-concave shape and by a large aerenchymatous float on the concave side (FIGURE 1B, C). The thin-walled cells of the float dehydrate more quickly than the seed coat proper and consequently are not always visible on older seeds (FIGURE 1D). Seeds without floats retain viability.

The epidermal cells of the seed coat enclose internal unicellular hairs that evaginate upon soaking. The hairs are tuberculate-ribbed and when fully evaginated are more or less erect and ca. 100 μm long (FIGURE 1E, F). They lack the internal spirals observed in seed-coat hairs of the lythraceous genera *Cuphea* and *Lafoensia* Vand. (Stubbs & Slabas, 1982; pers. obs.). Corner (1976) has reported seeds of *Ammannia* to be mucilaginous. The hairs may act to increase the flow of water into the seeds, thus hastening germination, and the mucilage produced may act to affix the seeds to objects during dispersal. In the American species mucilage appears on wetted seeds but is not profuse.

Observations of seed germination in the greenhouse suggest further adaptations to intermittently wet habitats. The seeds retain viability for many years, although only about 50 percent are viable after the first year. Retention of some viability for several years enables the species to persist through extensive dry periods. Even after herbarium fumigatory treatments, 5 percent of the seeds of *Ammannia coccinea* from herbarium specimens 27 years old (*Winterringer 9199,* ISM) have germinated. Germination of seeds from herbarium specimens was generally vigorous from collections up to 12 years old.

Under conditions of 100 percent humidity and high light intensity and temperature (28°C) in closed plastic bags, germination begins after six days; the

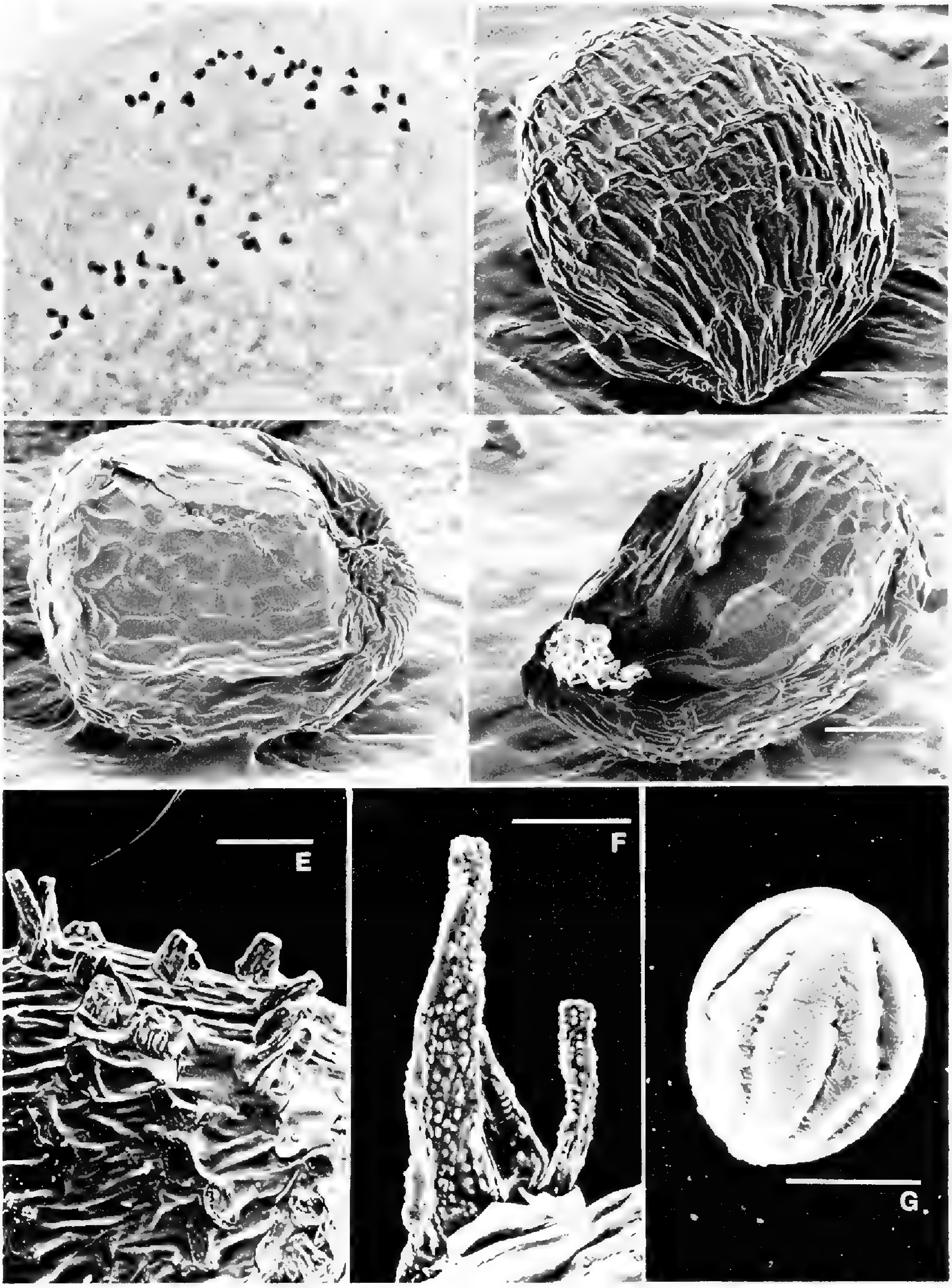


FIGURE 1. Scanning electron micrographs of *Ammannia* chromosomes, seeds, and pollen. A, *A. latifolia* (progeny of *Liogier 10314,* NY), meiotic chromosomes, metaphase II, $n = 24$ (scale = 10 μm). B–F, seeds of *A. coccinea* (*S. Graham 700,* MICH): B, convex ventral side, unsoaked (scale = 100 μm); C, concave dorsal side, aerenchymatous float occupying concavity (scale = 100 μm); D, concave dorsal side, aerenchymatous float collapsed (scale = 100 μm); E, surface of soaked seed, partially evaginated epidermal hairs visible (scale = 50 μm); F, 1 fully and 1 partially evaginated epidermal hair, tuberculae evident (scale = 25 μm). G, *A. latifolia* (progeny of *Liogier 10314,* NY), pollen, subsidiary colpi central, pore-containing colpi to left and right (scale = 10 μm).

majority of seeds germinate within fourteen days. Under natural conditions at 20°C in daylight, germination in pots begins at ten days and continues for ten weeks. Staggered germination time is not correlated with seed size. Establishment of seedlings in areas with fluctuating water levels is surely enhanced by these staggered germination rates: some seeds can be lost without completely eliminating the opportunity for species growth at those sites. The effective dispersal and germination mechanisms and long seed viability have promoted wide dispersal of the genus. This pattern is typical of aquatic plants, whose vagility and wide ranges have long been noted (Darwin, 1859; Arber, 1920).

Adventive stations for several species are known. Introduction of *Ammannia coccinea* through rice culture is recorded from Afghanistan (Shalizan, without collector or number, BM!), Italy (*fide* Abba, 1977), and Spain (*Borja s.n.,* 10 Oct. 1945, F!). It has been introduced in hay at San Blas, Panama (*Johnston 1239,* GH!), where it persists. Both *A. coccinea* and *A. robusta* are now present in the South Pacific (several collections from Guam and Saipan, US!), as well as in Hawaii and the Philippines (Koehne, 1903). The Asian *A. verticillata* has been introduced in Argentina (Molfino, 1926). Presence of *A. auriculata* in southern Patagonia and the spread of *A. robusta* along the coast of Brazil north of Rio de Janeiro are apparently the results of early introductions. Disjunct interior collections of the coastal *A. latifolia* in South America (like those of *A. robusta* in the western United States) are probably the result of accidental introductions by man.

CHEMISTRY

The leaf flavonoids of *Ammannia coccinea* have been determined (S. Graham *et al.,* 1980). Four flavonols and three flavone glycosides have been isolated: quercetin 3-D-glucoside, rutin, luteolin 7-D-glucoside, isorhamnetin 3-rutinoside, apigenin 7-D-glucoside, vitexin, and kaempferol 3-rhamnoglucoside. The predominance of flavonols is consistent with their occurrence as the major flavonoid type for Lythraceae, and for Myrtales generally.

Analysis of seed composition in *Ammannia auriculata* showed that 15.2 percent of the seed by weight was oil, 16 percent was protein. The predominant fatty acid in the seed oil (78.6% of total fatty-acid composition) was linoleic acid, typical for the family and the most commonly occurring fatty acid in angiosperms (S. Graham & R. Kleiman, unpubl. data).

PALYNOLOGY

In seven species surveyed, including all those occurring in the Western Hemisphere, the pollen has virtually the same morphology: grain prolate, 30–34 μm (P) × 24–28 μm (E), tricolporate with 6 pseudocolpi; colpi meridionally elongated, equatorially arranged, equidistant, extending to within 4–5 μm of the pole, the colpus membrane minutely granular; pseudocolpi like colpi but slightly shorter; pores circular; wall finely striate, tectate (FIGURE 1G; A. Graham *et al.,* 1985).

Pollen of *Ammannia* is most similar to that of *Nesaea,* another lythraceous genus of herbs favoring wet habitats, concentrated in Africa and resembling *Ammannia* in habit. Pollen grains of the genera share the same striate exine sculpture pattern and are distinctly 6-pseudocolpate. Pollen morphology indicates a closer relationship between the two genera than is suggested by their placement in different tribes of the family.

The inadequately known genus *Hionanthera* Fernandes & Diniz, from Mozambique, has been described as intermediate in morphology between *Ammannia* and *Rotala* (Fernandes & Diniz, 1955; Panigrahi, 1979). Cook (1974) considered the genus synonymous with *Ammannia.* On the basis of pollen features, *Hionanthera* is distinct: although its pollen is similar to that of *Ammannia* and *Nesaea,* the pseudocolpi are faint to absent. More extensive material needs to be studied to resolve the position of the genus in relation to *Ammannia.*

Ammannia and *Rotala* were considered congeneric by many botanists from Linnaeus to Bentham and Hooker, until Koehne (1880a) pointed out the subtle but consistent difference in wall structure of the capsules. An equally striking difference is found in pollen morphology. Pollen of *Rotala* has a scabrate to finely verrucate exine and no pseudocolpi. Pollen characters most closely align *Ammannia* with *Nesaea* and support the distinctiveness of *Ammannia* and *Rotala.*

CYTOLOGY

Chromosome numbers have been counted for eight species. Although nine different numbers have been reported (see TABLE 1), some have yet to be confirmed. Chromosomes are 1–2.5 μm in length. Their small size precludes karyotypic study; most appear in meiosis as spheres or short rods (FIGURE 1A). Since meiosis is often asynchronous, chromosomes are best counted in diakinesis or early metaphase I, when chromatids cannot be confused with unseparated chromosomes. Lagging and sticky chromosomes are occasionally seen, but meiosis is regular in the species growing in the Western Hemisphere. Aneuploid reduction in at least one population of *Ammannia auriculata* from Egypt probably accounts for the gametic count of $n = 15$. Four other counts from the United States and Mexico were $n = 16$. *Ammannia coccinea,* with a gametic chromosome number of $n = 33$, is believed to have originated as an amphidiploid involving *A. auriculata* ($n = 16$) × *A. robusta* ($n = 17$) (S. Graham, 1979).

HISTORIC AND TAXONOMIC CONSIDERATION

William Houston first applied the name *Ammannia* to plants now referred to *A. latifolia* in a 1736 manuscript describing his Caribbean collections. The genus was named in honor of Paul Ammann, 1634–1691, professor of botany at Leipzig (Linnaeus, 1737), and was included by Linnaeus in *Hortus Cliffortianus, Hortus Upsaliensis,* and subsequently *Species Plantarum.* In *Species*

Plantarum, Ammannia comprised three species: *A. latifolia* L., *A. ramosior* L. (now referred to *Rotala ramosior* (L.) Koehne), and *A. baccifera* L. Later, Linnaeus (1771) described *Rotala,* with one species (the East Indian *R. verticillaris* L.), but failed to recognize *A. ramosior* as a member of the genus *Rotala.* The genera were long confused until their differences were finally clarified by Koehne (1880a). The superficial similarities of *Ammannia* and *Rotala,* as well as Bentham and Hooker's (1867) rejection of *Rotala,* have necessitated the transfer of at least 45 epithets from *Ammannia* to *Rotala* (see Cook, 1979). In the Western Hemisphere most of these apply to the common *R. ramosior,* and they account for a large number of excluded specific names cited in this study (see APPENDIX).

In the following taxonomic treatment, I have included all names applied to—and misidentifications of—New World *Ammannia* listed in *Index Kewensis,* the Gray Card Index, and Koehne's monographic works (1880b, 1903). The synonymies are complete for *A. latifolia, A. coccinea,* and *A. robusta,* which are native to the New World. I have not attempted to list all later synonyms and misidentifications of *A. auriculata* and *A. baccifera* from Europe, Africa, and Asia; this would have required revision of the entire genus. The few omissions in the synonymy of *A. auriculata* are later names applied to Old World collections. *Ammannia baccifera* is a relatively recent introduction into the Caribbean, and no synonymies have been published based on New World collections. Later names based on Asian and African collections are not included in this study. A list of the exsiccatae studied can be obtained from the exsiccatae depository at A and GH, MO, or NY.

SYSTEMATIC TREATMENT

Ammannia L. Sp. Pl. **1:** 119. 1753, Gen. Pl. ed. 5. 55. 1754.

Annual or possibly short-lived perennial glabrous herbs of aquatic or marshy habitats. Leaves decussate, sessile, linear to lanceolate or oblanceolate, cordate to auriculate (rarely attenuate) at base, membranaceous. Flowers borne in sessile or pedunculate axillary cymes, (1 to) 3 to 15 per node, regular, 4- (or 5-)merous, not heteromorphic; bracteoles 2, at base of floral tube, opposite, linear. Floral tube campanulate to urceolate, becoming globose in fruit, 1.5–6 mm long, greenish to rose, 8-nerved with 4 nerves especially prominent at anthesis; calyx lobes 4 (or 5), short and broad; appendages thick, shorter than to equaling lobes, or lacking; petals lacking or 1 to 4, small, deep rose-purple to pink or white, caducous; stamens 4 (to 8), included to exserted; gynoecium without disc at base, the stigma capitate, the style thin, longer than ovary and exserted, or thick, shorter than ovary and included, the ovary incompletely 2- to 4- (or 5-)locular, upper portion of septa incomplete. Fruit a membranaceous, irregularly dehiscent capsule, the outer wall smooth, not striate. Seeds many, obovoid, concave-convex, ca. 1 mm long, golden brown.

LECTOTYPE SPECIES. *Ammannia latifolia* L.; see Britton & Brown, Illus. Fl. No. U. S. ed. 2. **2:** 577. 1913.

KEY TO AMMANNIA IN THE WESTERN HEMISPHERE

1. Style thick, ca. 0.5 mm long or less, much shorter than ovary, included within floral tube at anthesis; petals lacking or 1 to 4, pale pink to white.
    2. Floral tube 4–6 mm in diameter in fruit; calyx lobes broad with minute mucronate to cucullate apex; appendages alternating with calyx lobes short, thick; petals lacking or 1 to 4. .... 4. *A. latifolia.*
    2. Floral tube 1–2 mm in diameter in fruit; calyx lobes triangular with acute apex; appendages alternating with calyx lobes absent; petals lacking. . . 2. *A. baccifera.*
1. Style slender, usually 1 mm or more long, equal to half length of ovary or longer, well exserted at anthesis; petals 4 (or 5).
    3. Inflorescence a long-pedunculate, multiflowered simple or compound cyme; peduncle nearly filiform, 3–9 mm long; flowers 3 or more per axil; petals deep rose-purple; fruits mostly 2.5 mm or less in diameter; plant delicate, slender in aspect. .... 1. *A. auriculata.*
    3. Inflorescence a sessile or short- to long-pedunculate, 1- to many-flowered cyme; peduncle, when present, stout, to 4(–9) mm long; fruits mostly 3.5 mm or more in diameter; plant robust.
        4. Inflorescence sessile; flowers usually 1 to 3 per axil; petals pale lavender, occasionally with deeper purple vein; anthers yellow; fruits 4–6 mm in diameter. .... 5. *A. robusta.*
        4. Inflorescence a short- to long-pedunculate cyme, rarely completely sessile; flowers usually 3 or more per axil; petals deep rose-purple; anthers deep yellow; fruits 3.5–5 mm in diameter. .... 3. *A. coccinea.*

1. **Ammannia auriculata** Willd. Hort. Berol. **1:** *pl. 7.* 1803. TYPE: Egypt, near Rosette, *Willdenow Herbarium 3081* (lectotype (here designated), B-W; photo of lectotype, Berlin neg. no. 121413 at B-W!). MAP 1.

Ammannia racemosa Roth, Catal. Bot. **3:** 25. 1806. TYPE: grown from seeds sent from Royal Botanic Gardens, Copenhagen, origin unknown (existence of type specimen unknown). Description clearly of the Old World, 8-staminate form of *A. auriculata.*

Ammannia arenaria HBK. Nov. Gen. & Sp. Pl. **6:** 190. 1824. TYPE: Venezuela, Prov. Caracas, near San Fernando (holotype, P; photo of holotype, Field Museum neg. no. 38362 at F! and GH!).

Ammannia senegalensis var. *brasiliensis* A. St. Hil. Fl. Brasil. Merid. **3:** 135. *t. 187.* 1833. TYPE: Brazil, Minas Novas, S. Miguel, Jiquitinhonha River (holotype, P!).

Ronconia triflora Raf. Aut. Bot. 9. 1840, *nomen illegit. et superfl.*, based on *A. auriculata* Willd.

Ammannia pusilla Sonder, Linnaea **23:** 40. 1848. TYPE: Senegal or Nigeria, swampy places near Sandrivier, *Zeyher 541* (B, destroyed?).

Ammannia wrightii A. Gray, Pl. Wright. **2:** 55. 1853. TYPE: Mexico, Sonora, east of Santa Cruz and along the San Pedro, *Wright 1062* (holotype, GH!; isotypes, BM!, GH!, K!, P!).

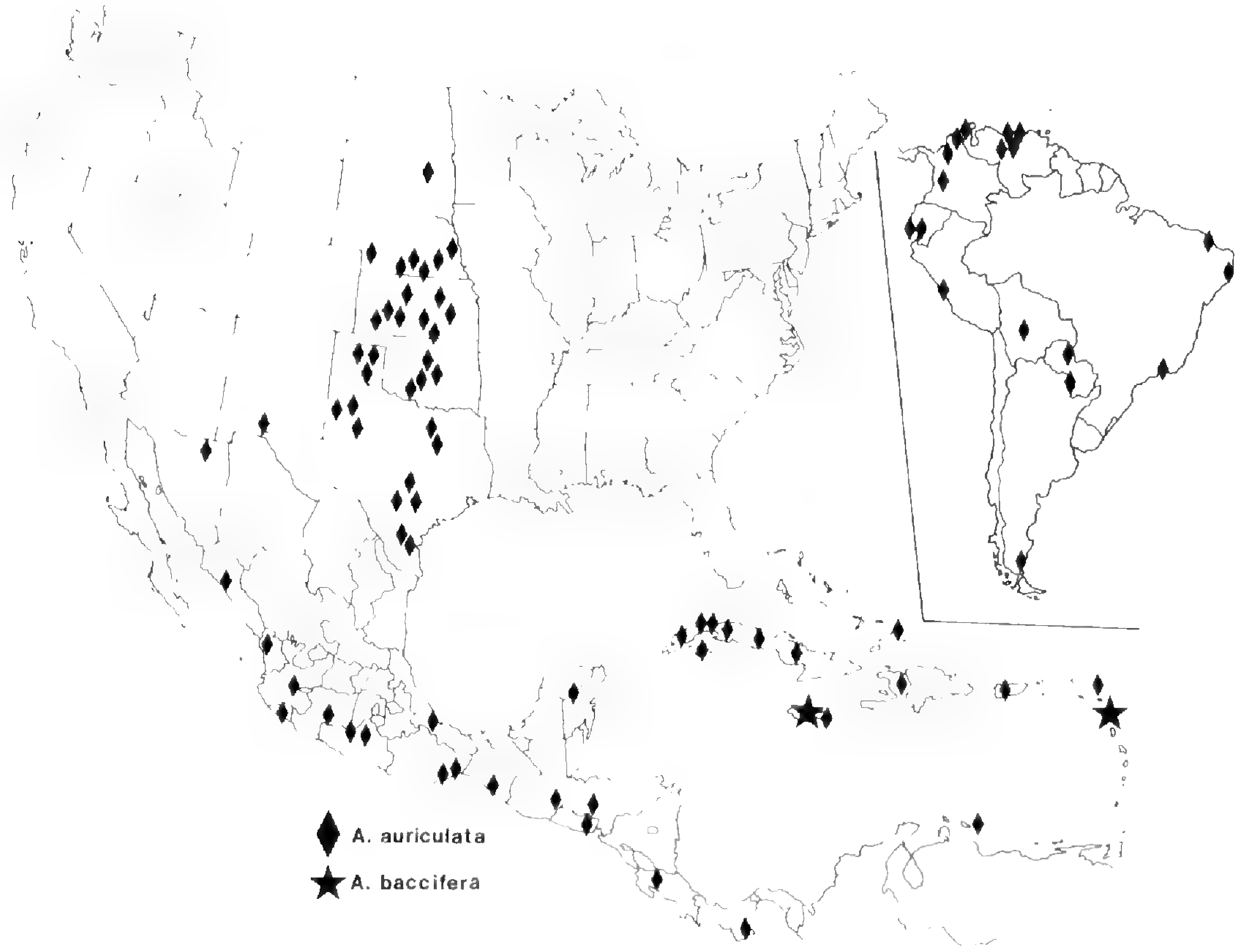
Ammannia longipes Wright *in* Sauvalle, Fl. Cubana, 53. 1868. TYPE: Cuba, near S. Gabriel, Palacios, Dec. 1865, *Wright s.n.* (holotype, GH!).

Ammannia auriculata Ledeb. ex Koehne, Bot. Jahrb. Syst. **1:** 244. 1880, *pro syn.*

Ammannia auriculata var. *arenaria* (HBK.) Koehne, *ibid.* 245.

Ammannia auriculata var. *arenaria* f. *brasiliensis* (A. St. Hil.) Koehne, *ibid.*

Annual, glabrous herbs 1–8 dm tall, unbranched to pyramidally multi-branched, the branches ascending, generally shorter than stem, progressively shorter toward top of stem. Leaves narrowly linear-lanceolate to linear-oblong,



MAP 1. Distribution of *Ammannia auriculata* and *A. baccifera* in Western Hemisphere. (Symbols on this and subsequent maps may represent more than 1 collection from area covered.)

the largest ones 17–64 by 2–10 mm, equaling or surpassing internode above, the apex acute, the base auriculate-cordate, clasping, occasionally cuneate on lowermost leaves only. Inflorescences axillary, long-pedunculate, simple or compound, multiflowered cymes; flowers pedicellate, (1 to) 3 to 12 (to 15) per cyme, commonly 7; lateral pedicels bibracteolate, 1–3(–6) mm long, emerging from bracteoles of shorter-pedicellate central flower of cyme; peduncle 3–9 mm long; pedicels and peduncle nearly filiform; bracteoles 0.5–1 mm long. Floral tube campanulate to urceolate in bud, globose in fruit, 1–3 mm long at anthesis; calyx lobes triangular, alternating with minute, thickened appendages; appendages to 1 mm long at anthesis, rarely absent; petals 4, obovate, usually ca. 1.5 by 1.5 mm, deep rose-purple; stamens 4 (to 8), well exserted; style filiform, exserted at same level as stamens, as long as to ⅓ longer than ovary, ovary incompletely 2- (to 4-)locular. Capsule at maturity equal to or mostly well exceeding calyx lobes, (1–)1.5–3(–3.5) mm in diameter; seeds numerous, ca. 1 mm long. $n = 15, 16$.

This species is distinguished by its inflorescence with slender, elongate peduncles and pedicels that bear numerous small, deep rose–petaled flowers. It is the most widely distributed species in the genus, occurring in Africa, Asia (including India and China), Australia, the Americas, and the Caribbean in the wet habitats typical of the genus. In the United States it is sympatric with *Ammannia robusta* and *A. coccinea*. Its appearance is sporadic, however, even in the Central States (where it is most frequent) and depends on the extent of suitable habitats available in any given year. It is the least collected of the species in the United States. Many collections originally determined as *A. auriculata,* including one state record (Dolbeare, 1973), are long-pedunculate plants of *A. coccinea.* In Mexico it is sympatric with *A. robusta* in the western part of its range and with *A. coccinea* to the east and south. Although geographically sympatric with *A. latifolia* in the Caribbean, it is probably ecologically isolated from that species, which occurs mainly along the coasts and prefers brackish waters to fresh. In South America *A. auriculata* is distributed along the western side south to Peru at elevations from sea level to 600 m.

Three varieties of *Ammannia auriculata* have been recognized: var. *auriculata* and var. *bojeriana* Koehne, restricted to East Africa, and var. *arenaria* (HBK.) Koehne, from Africa, Asia, and the Americas. Variety *arenaria,* in which Koehne further recognized five forms, is defined as having four to eight stamens, a glabrous calyx, and a style 1 to 1.3 times as long as the ovary. It is distinguished with difficulty from the other varieties. The five forms of var. *arenaria* are based on combinations of minor, overlapping characters among which Koehne (1903) claimed there were many intermediates. The American plants have been referred to var. *arenaria* f. *brasiliensis* (A. St. Hil.) Koehne. Forma *brasiliensis* is applied to plants from both the Americas and Africa with calyxes 1.5–2 mm long and four or five stamens. The circumscription is meaningless, given the variation now known for the species.

Koehne (1880b) considered the wide-ranging *Ammannia auriculata* to be the central species of the genus from which the other, more geographically limited species were derived. Recent studies (S. Graham, 1979) suggest the relationship between *A. auriculata* and *A. coccinea,* species frequently confused in the United States, as one of parent and hybrid derivative, with *A. robusta* as the other parent. No evidence of hybridization between *A. auriculata* and *A. latifolia* is suggested by the exsiccatae studied.

The Willdenow herbarium contains one sheet with two plants of *Ammannia auriculata* from Egypt, cultivated in the Berlin Botanical Garden (B-W no. *3081*). Neither plant exactly matches the illustration accompanying the description. Both have compound rather than simple cymes and are unbranched or have only a few short branches. Variability in inflorescence complexity and branching, however, is within the limits of the variability of the species. The Code (T.4.b) directs that a specimen be selected over a figure when a lectotype is chosen. Sheet *3081* is thus the obligate lectotype of *A. auriculata.*

2. **Ammannia baccifera** L. Sp. Pl. **1:** 120. 1753. TYPE: China, Savage H 156.4 (lectotype, LINN, IDC 177. 99: III. 4!).[2] MAP 1, FIGURE 2.

Erect annuals or possibly short-lived perennials to 1 m tall, much branched from near base to top of stem, the branches shorter than stem, ascending.

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[2] The Linnaean Herbarium today contains two sheets of *Ammannia baccifera.* One lacks any identifying marks, but the other is probably the Osbeck specimen cited by Linnaeus in the species description even though the penciled Osbeck number that assures this is lacking (Hansen & Maule, 1973). The specimen, Savage H 156.4, bears the inscription in Linnaeus's hand "baccifera 3. india." The number "3" corresponds to the position of the species in the generic treatment in *Species Plantarum.* The term "india" was applied by Linnaeus to include China (Stearn, 1957).

FIGURE 2. *Ammannia baccifera*: a, habit, × 0.16; b, axillary inflorescence, × 2.5 (from *I. Vélez 3609,* US).

Leaves lanceolate to oblanceolate, to 50(–70) by 10(–16) mm, usually equaling or surpassing internode above, becoming progressively smaller toward apex of stem, smaller on lateral branches, apex acute, base varying from cuneate to mostly truncate or slightly auriculate. Inflorescences axillary, sessile, densely flowered cymes; flowers 3 to 15 or more per cyme; peduncle to 1 mm long. Floral tube broadly campanulate, narrowly tapering at base, 1–2 mm in diameter, becoming globose in fruit, glabrous; calyx lobes sharply triangular, connivent; appendages lacking; petals lacking; stamens 4, opposite calyx lobes, included to barely exserted; style slender, 0.3 mm long, much shorter than ovary. Capsule barely included to well exserted. $n = 12$.

Ammannia baccifera is distinguished from other species of *Ammannia* in the Western Hemisphere by its numerous minute, densely clustered axillary flowers that lack petals. This widespread, variable species, native to Africa or Asia, is a relatively recent introduction in the New World. The earliest Western Hemisphere collections, from Guadeloupe, were made in the 1930's. It is now also known from Jamaica, although it is rare and local there (Adams, 1972). Koehne (1880b) recognized three subspecies, six forms, and two subforms, based primarily on differences in shape of the leaf base. The subspecies are not geographically distinct. New World collections are placed with some difficulty in subsp. *aegyptiaca* (Willd.) Koehne, the leaf base varying from the designated auriculate shape to the cuneate base of subsp. *viridis* (Hornem.) Koehne. I prefer not to recognize the subspecies as currently defined. Misidentification of *A. baccifera* is the basis for the incorrect report of the Old World species *A. verticillata* (Ard.) Lam. in the Lesser Antilles (Stehlé, Stehlé, & Quentin, 1948).

3. **Ammannia coccinea** Rottb. Pl. Horti Univ. Rar. Progr. (Hafn.), 7. 1773. TYPE: Jamaica, St. Catherine Parish, 1 mi W of Spanish Town, 15 Nov. 1958, *G. Proctor 18339* (neotype (here designated), NY!; isoneotype, A!). MAP 2, FIGURE 3.

Ammannia purpurea Lam. Encycl. Méth. Bot. **1:** 131. 1783. TYPE: Carolina, *Fraser s.n.* (neotype (here designated), P-LA!; photo of neotype, Field Museum neg. no. 38365 at F! and GH!).[3]

Ammannia sanguinolenta Sw. Nov. Gen. & Sp. Pl. Prodr. 33. 1788, Fl. Ind. Occ. **1:** 272. 1797. TYPE: Jamaica, Domingo, 1783–1786, *Swartz s.n.* (S!).

Ammannia octandra auct., *non* L. f., Cham. & Schldl. Linnaea **2:** 376. 1827. = *A. coccinea* fide Koehne, who probably saw material, no longer extant, at B.

Ammannia teres Raf. Aut. Bot. **1:** 39. 1840. TYPE: U. S., Delaware, Sussex, *Nuttall s.n.* (lectotype (here designated), P!). This specimen annotated *A. teres* by Rafinesque.

Ammannia stylosa Fischer & Meyer, Index Sem. Hortus Imp. Petrop. **7:** 41. 1841. TYPE: U. S., Louisiana, New Orleans, *Wiedemann s.n.* (LE!).

Ammannia sagittata var. *angustifolia* A. Rich. *in* Sagra, Hist. Fis. Pol. Nat. Cuba **10:**

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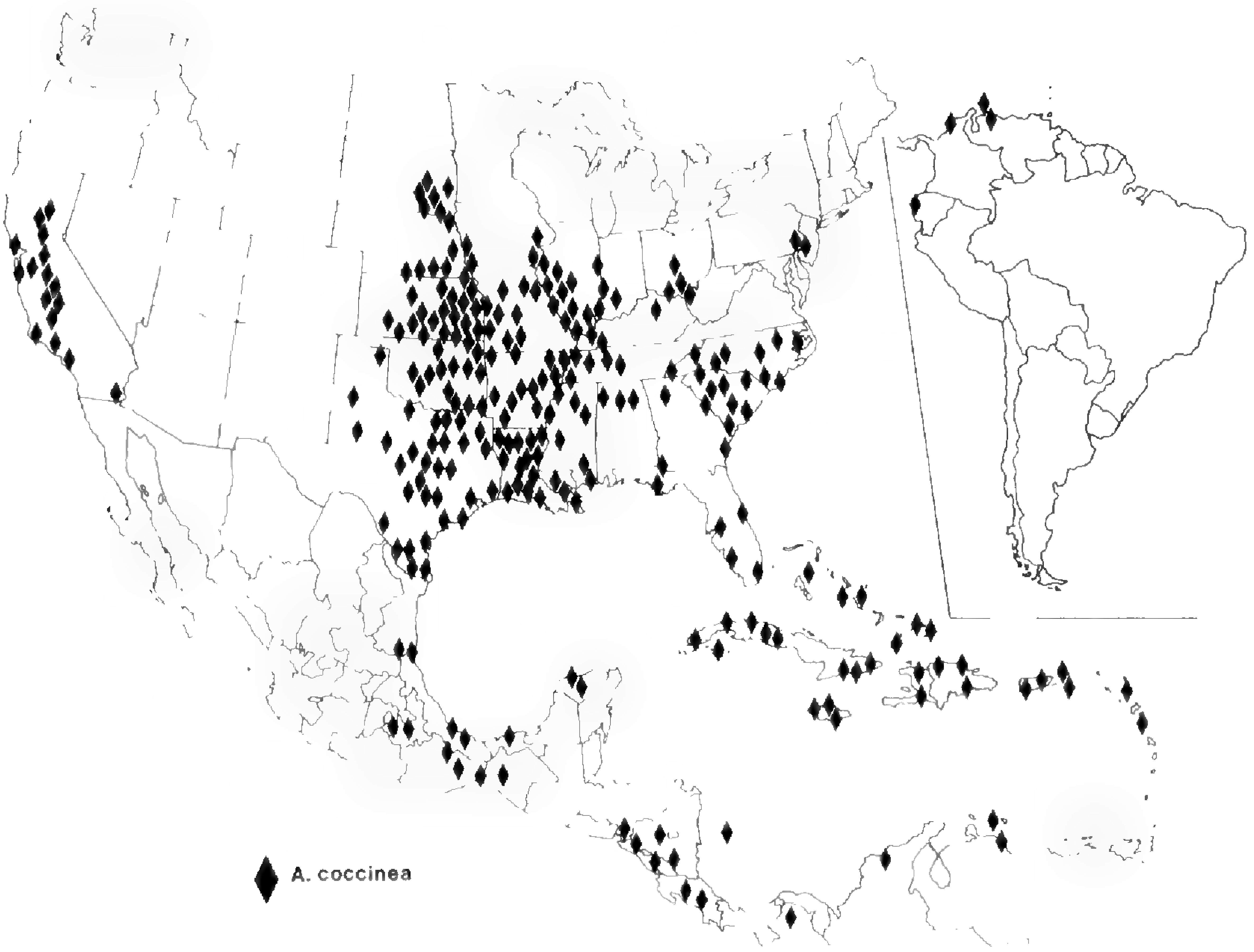
[3] Lamarck cited *Ammannia ramosior* L. (= *Rotala ramosior* (L.) Koehne) with the Linnaean phrase name and reference to the Clayton type, as if in synonymy with *A. purpurea*. However, his description is of *A. coccinea* and is based on a plant cultivated in the Jardin du Roi. A specimen in the Lamarck herbarium annotated *Ammannia purpurea* is selected as neotype.



MAP 2. Distribution of *Ammannia coccinea* in Western Hemisphere.

252. 1845, Hist. Phys. Pol. Nat. Cuba, Pl. Vasc. 542. 1846. TYPE: Cuba, near San Diego, *Sagra s.n.* (P!).

Ammannia texana Scheele, Linnaea **21**: 588. 1848. TYPE: near New Braunfels, *Lindheimer s.n.* (holotype not located). Possible type collection: "Tex.," and in A. Gray's hand "Ammannia Texana Scheele in Linnaea 21, p. 588," *Lindheimer 338* (GH!).

Ammannia latifolia var. *octandra* A. Gray, Pl. Lind. **2**: 188. 1850. TYPE: based on *A. texana* Scheele.

Ammannia sanguinolenta subsp. *purpurea* (Lam.) Koehne *in* Martius, Fl. Brasil. **13**(2): 207. 1877.

Ammannia sanguinolenta subsp. *longifolia* Koehne *in* Martius, *ibid.* 208, *pro parte.* Based in part on *A. octandra* Cham. & Schldl., *non* L. f., in part on an *A. coccinea* specimen of Gaudichaud from Hawaii, and in part on an *A. coccinea* specimen of Eschscholtz from the Philippines.

Ammannia coccinea subsp. *purpurea* (Lam.) Koehne, Bot. Jahrb. Syst. **1**: 250. 1880.

Ammannia coccinea subsp. *longifolia* (Koehne) Koehne, *ibid.*

Ammannia pedunculata Rusby, Descr. S. Amer. Pl. 68. 1920. TYPE: Colombia, near Ciénaga, 10 Sept. 1898, *H. H. Smith 548* (holotype, NY!; isotypes, CM!, F!, GH!, K!, P!).

Robust annual herbs to 1 m tall, unbranched, or branching mainly above base with branches mostly shorter than main stem, infrequently branching from base with long, semidecumbent branches. Leaves linear-lanceolate to linear-oblong, rarely elliptic to spathulate, largest ones 20–80 by 2–15 mm, apex acute, base auriculate to cordate, clasping, occasionally cuneate on lowermost leaves. Inflorescences varying from sessile (1-) to 3-flowered cymes to

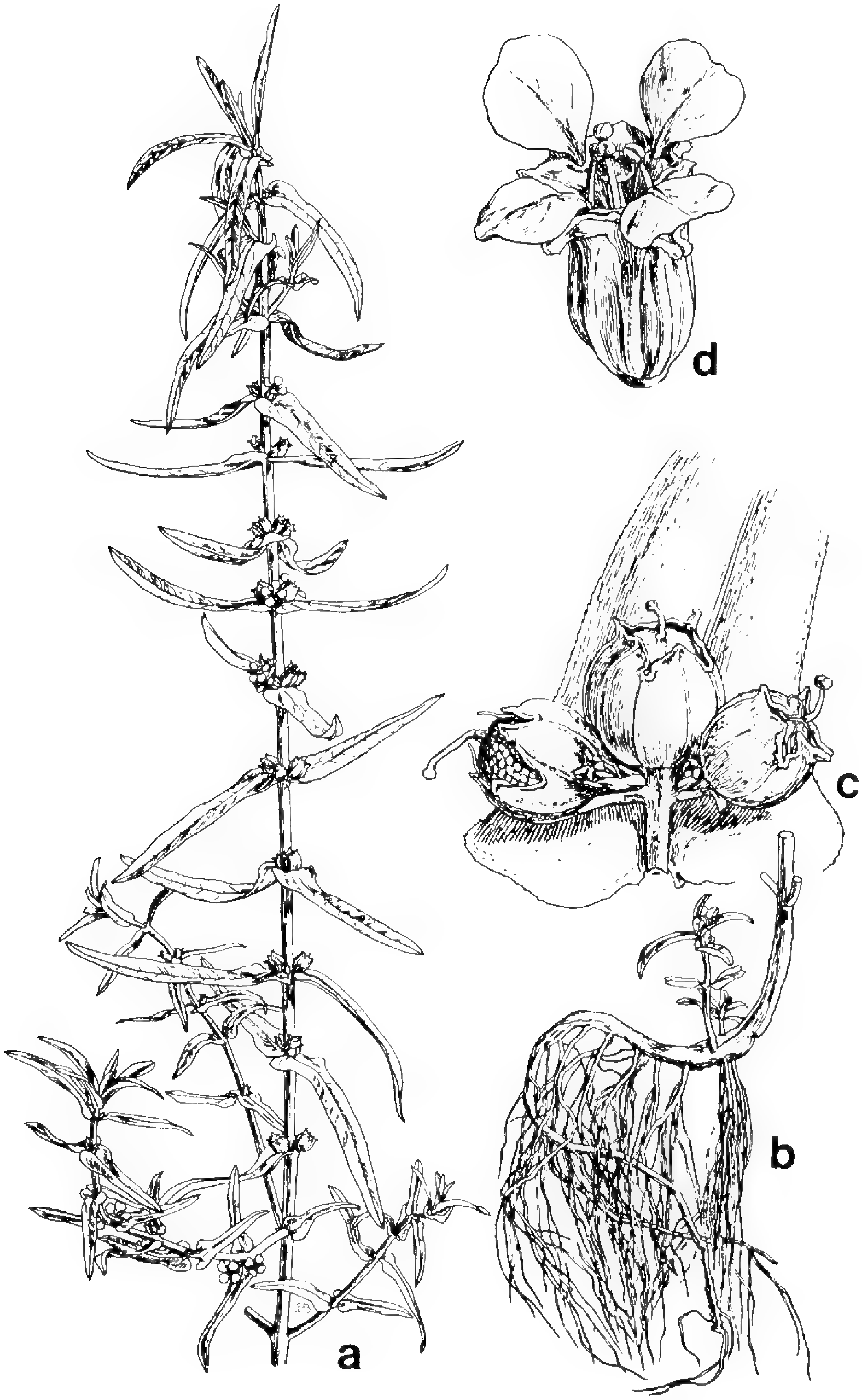


FIGURE 3. *Ammannia coccinea*: a, habit, × 0.4; b, basal part of plant with roots, × 0.4; c, pedunculate inflorescence subtended by auriculate leaf base, × 3; d, flower, × 4. (Reprinted with permission from Mason, 1957. FIGURE 4c originally published as *Ammannia auriculata*.)

TABLE 2. **Variation in floral features of Ammannia auriculata, A. coccinea, and A. robusta.***

SPECIES	n	PETAL LENGTH	PETAL WIDTH	PEDUNCLE WIDTH
A. auriculata	42	1.33 ± 0.41	1.42 ± 0.38	7.0 ± 2.70
A. coccinea	37	2.01 ± 0.30	2.03 ± 0.23	1.74 ± 2.13
A. robusta	26	2.50 ± 0.55	2.96 ± 0.40	0.11 ± 0.33
		FLOWERS PER CYME	CALYX LENGTH	CAPSULE WIDTH
A. auriculata		7.12 ± 3.90	1.95 ± 0.22	2.54 ± 0.51
A. coccinea		5.59 ± 2.29	2.86 ± 0.62	3.98 ± 0.18
A. robusta		2.36 ± 1.18	3.50 ± 0.61	4.93 ± 0.61

*Measurements in mm; first figure = mean, second figure = standard deviation.

short- to long-pedunculate 3- to 5- (to 14-)flowered cymes; peduncle, when present, to 9 mm long, sturdy, bibracteolate; pedicels mostly 2 mm or less, bibracteolate, bracteoles ⅓ or less length of floral tube. Floral tube urceolate to slightly campanulate, (2.5–)3–5 mm long, longitudinal ridges present but not conspicuously enlarged; calyx lobes triangular, alternating with thickened appendages; appendages about equal in length to lobes, mostly oriented outward from floral tube in bud; petals 4 (or 5), obovate, usually 2 by 2 mm, deep rose-purple, sometimes with deeper purple spot at base; stamens 4 (to 7), exserted, anthers deep yellow; style long, slender, equal to or longer than ovary, exserted at anthesis; ovary incompletely 2-locular. Capsule 3.5–5 mm in diameter, equal to or exceeding calyx lobes, rarely enclosed. $n = 33$.

As a successful amphidiploid derived from *Ammannia auriculata* and *A. robusta, A. coccinea* displays a range of morphological variability that, at its extremes, closely approaches the putative parent species. Since species of *Ammannia* on the whole are very similar, distinction between parent species and hybrid derivatives can be subtle. The number of characters separating *A. auriculata, A. robusta,* and *A. coccinea* are few and primarily quantitative. TABLE 2 summarizes variation in size of the floral features, and the key characters of the three species are compared in TABLE 3. Most specimens of *A. coccinea* resemble *A. robusta* more closely than they do *A. auriculata.* In the field *A. coccinea* is easily distinguished from *A. robusta* by its deep petal and anther color. On herbarium specimens the species is usually identified by the combination of stout peduncles, 3- to 5-flowered cymes, and mature capsules that are intermediate in size between those of *A. robusta* and those of *A. auriculata.* Occasional specimens that approach *A. auriculata* in peduncle length are best recognized by the usually larger flowers of *A. coccinea.*

No original material of *Ammannia coccinea* is extant (Maule, pers. comm.). Rottbøll (1773) described the species in careful detail from cultivated plants at the Copenhagen Botanical Garden. According to the protolog, these were grown from seeds brought to the Garden by a Belgian gardener, Kaesemaker. The neotype is selected from a Caribbean collection, because the original seeds were most likely collected in that region.

The name *Ammannia teres* Raf. has long been applied to the petal-bearing

TABLE 3. **Comparison of major morphological features distinguishing taxa of the Ammannia coccinea complex.***

	TAXON		
FEATURE	*A. auriculata*	*A. robusta*	*A. coccinea*
Chromosome count	15, 16	17	33
Aspect	Delicate	Robust	Robust
Leaves	Membranaceous, narrowly lanceolate	Fleshy, lanceolate, often spathulate at lower nodes	Membranaceous to fleshy, lanceolate
Peduncles	3–9 mm long, filiform	Lacking	Lacking or to 4(–9) mm long, stout
Flowers	1–3 mm long, usually 3 or more per axil	2.5–5 mm long, usually 1 to 3 per axil	2–3.5 mm long, usually 3 or more per axil
Petal color	Rose-purple	Pale lavender	Rose-purple
Anther color	Deep yellow	Yellow	Deep yellow
Capsules	Usually 2.5 mm in diameter, equal to or exceeding lobes	4–6 mm in diameter, usually enclosed to equaling lobes	3.5–5 mm in diameter, equal to or exceeding lobes

*Table modified from S. Graham (1979).

form of *A. latifolia* (Merrill, 1949). The correct application, determined by examination of the Rafinesque type located at P, is as a synonym of *A. coccinea.*

4. **Ammannia latifolia** L. Sp. Pl. **1:** 119. 1753. TYPE: Savage H 156.1 (lectotype, LINN, IDC 177. 99: II. 7!).[4] MAP 3.

Ammannia lythrifolia Salisb. Prodr. Stirp. 65. 1796, *nomen illegit. et superfl.*

Isnardia subhastata Ruiz & Pavon, Fl. Peru. & Chil. **1:** 66. *t. 86, fig. b.* 1798.

Jussiaea sagittata Poiret *in* Lam. Encycl. Méth. Bot. Suppl. **3:** 198. 1813. Type based on a plant from Santo Domingo, grown in Paris and described from Herb. Desfontaines. Description clearly *A. latifolia.*

Ludwigia hastata Sprengel, Syst. Veg. ed. 16 [17]. **1:** 446. [1824] 1825. BASIONYM: *Isnardia subhastata* Ruiz & Pavon.

Ammannia hastata DC. Prodr. Syst. Nat. Regni Veg. **3:** 78. 1828. BASIONYM: *Isnardia subhastata* Ruiz & Pavon, incorrectly cited as "*Isn. hastatum* Ruiz Pav."

Ammannia sagittata DC. *ibid.* 80. BASIONYM: *Jussiaea sagittata* Poiret.

Ammannia lingulata Griseb. Catal. Pl. Cubens. 106. 1866. TYPE: Cuba, *Wright s.n.* (probable holotype, GH!—this specimen annotated *Ammannia lingulata* Gr. in Wright's hand, with Wright's original field note attached, and labeled *Ammannia latifolia*; not at GOET or K).

Ammannia koehnei Britton, Bull. Torrey Bot. Club **18:** 271. 1891. TYPE: U. S., New Jersey, Hackensack Flats, 28 July 1868, *W. H. Leggett s.n.* (holotype, NY!; isotype, NY!).

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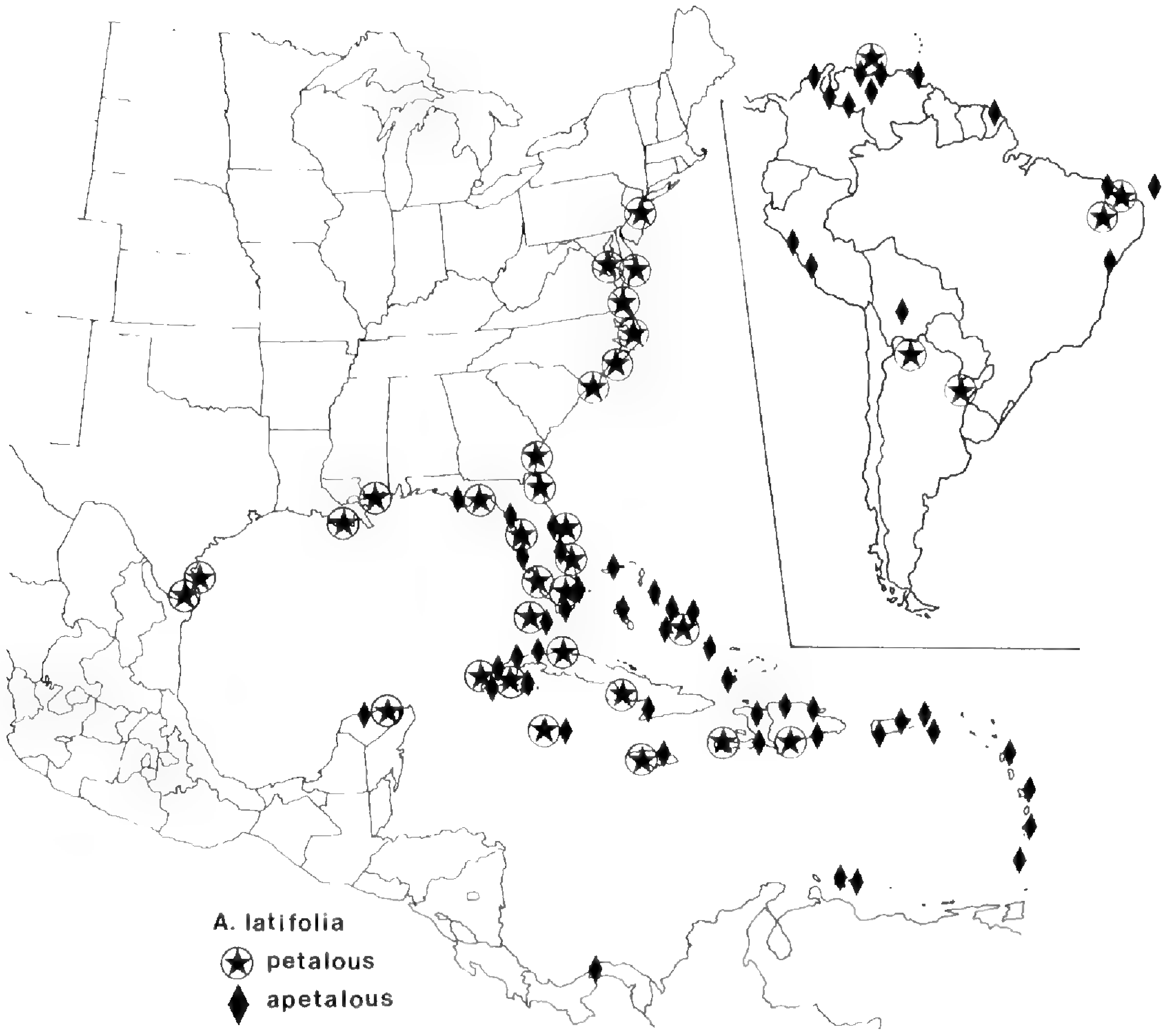
[4] This specimen bears the annotation "latifolia 1" in Linnaeus's hand. The number indicates the position of the species in *Species Plantarum,* indicating that it was seen by Linnaeus prior to publication of this work or soon after and is therefore the obligate lectotype (Stearn, 1974, and pers. comm.).



MAP 3. Distribution of *Ammannia latifolia.*

Ammannia friesii Koehne *in* Engler, Pflanzenr. IV. **216**(Heft 17): 50. 1903. TYPE: Argentina, Prov. Jujuy, Quinta, near Laguna de la Brea, *R. E. Fries 94* (holotype, B, presumably destroyed; isotype, S!).

Ammannia koehnei var. *exauriculata* Fern. Rhodora **38:** 437. *t. 449, figs. 4, 5.* 1936. TYPE: U. S., Virginia, Princess Co., *Fernald, Long, & Fogg 4954* (holotype, GH!; isotypes, MO!, NY!, US!).

Ammannia teres var. *exauriculata* (Fern.) Fern. Rhodora **46:** 50. 1944.

Robust erect annuals to 10 dm tall, unbranched or sparsely branching mainly from lower portions of stem, the branches ascending, shorter than stem. Leaves mostly linear-lanceolate to oblong, elliptic, or spathulate, 15–70(–100) by 4–15(–21) mm, usually equal to or longer than internode above, mature leaves mostly uniform in size, not significantly smaller toward apex of stem, the apex obtuse to subacute, the base strongly to moderately auriculate and rarely cuneate on middle and upper leaves, cuneate on lower ones. Inflorescences axillary, short-pedunculate or sessile, closely flowered cymes; flowers (1 to) 3 to 10 per cyme; peduncle, when present, to 3 mm long. Floral tube 4-merous, urceolate in bud, globose and 4–6 mm in diameter in fruit, subtended by linear bracteoles 1–1.5 mm long; lobes of fruiting calyx broad, apex very small or mucronate (occasionally slightly cucullate), disappearing with enlargement of capsule; appendages short, thick; petals lacking or 1 to 4 (to 6), obovate, to 1 mm long, pale pink to white; stamens 4 (to 8), included; style thick, 0.5 mm long, much shorter than ovary. Capsule incompletely 2- to 4-locular, included to barely exserted. $n = 24$.

Ammannia latifolia is a robust, erect, sparsely branched species in which the flowers are short styled, sessile, and usually three in each axil, with petals lacking or one to four. Broad calyx lobes with minute, mucronate apexes are distinctive. The species is distributed in brackish to fresh-water marshes and ditches along the Atlantic and Gulf coasts from New Jersey southward to Florida, west to Texas, throughout the Caribbean, and in widely scattered, primarily coastal localities in South America. The species is not present in California; specimens so identified are *A. coccinea.*

An initial survey of variability in *Ammannia latifolia* in the United States and the Caribbean led me to consider the eastern North American and Caribbean specimens to be a single species. A study of many more collections from throughout the entire range of the species now confirms that decision and leads me also to include *A. friesii* Koehne of northern Argentina within *A. latifolia.* The two have been distinguished weakly at best, but since the recognized species of *Ammannia* are often separated by few characters, an intensive comparison of characters was made. In Koehne's treatment (1903), *A. latifolia* is described as having calyxes 4–5 mm long, flowers apetalous, and lower leaves cordate to auriculate. *Ammannia friesii* differs from *A. latifolia* in having 4 to 6 petals 1 mm long. The eastern North American *A. koehnei* (later incorrectly referred to *A. teres* Raf.; see discussion under *A. coccinea*) is distinguished by its calyxes 5–6 mm long, 4 petals 1.5 mm long, lower leaves cuneate, lobes retuse margined, and bracteoles larger than those of *A. friesii.*

Examination of herbarium specimens indicates that the species are not consistently separable on these or any other characters. When leaves are present at the lowest nodes, they are cuneate based. Calyx length varies from 3.5 to 6 mm throughout the range, mature calyx lobes are the same shape, and bracteole length varies insignificantly.

Petalous and apetalous plants are found throughout most of the range (see MAP 3). Although all specimens collected north of approximately 28°30′N latitude in the eastern United States have petals, 24 percent of the collections studied from south of that latitude also have them, and these collections are from widely separated localities. A previous figure of 30 percent petalous plants (S. Graham, 1975) is based on fewer collections. In a Manatee Co., Florida, population surveyed (*Graham 698,* MICH) 10 percent of the plants had petals. Flowers from a single plant were either petalous or apetalous, with the single exception of a primarily apetalous plant that bore one-petaled flowers on one branch. Petalous flowers typically bear four fully developed petals, but they may also be found with one to three rudimentary ones. Presence of petals appears to be a sporadic phenomenon in all but the northernmost part of the range, and their presence there is difficult to determine unless mature buds are present. Since no other morphological character is correlated with presence or absence of petals and at least four other species of *Ammannia* have either no petals or one to four of them, maintenance of the species on this basis alone is not justified.

TABLE 4. **Geographic variation of selected characters of Ammannia latifolia.**

REGION	PERCENT PETALOUS PLANTS	MEAN CAPSULE DIAMETER (mm)	MEAN LEAF LENGTH/ WIDTH QUOTIENT
Maryland–North Carolina	100	5.5	4.05
Georgia–Texas–northern Florida	100	4.8	5.97
Florida–Florida Keys	50	4.5	5.61
Bahamas	17	4.5	7.81
Greater Antilles, Yucatan	30	4.2	7.71
Lesser Antilles	0	4.4	6.53
South America, Panama	25	4.3	7.36

Geographic variation in leaf length/width quotient, mature capsule size, and percent petalous specimens is summarized in TABLE 4. Leaves are spathulate to mainly lanceolate in the northern part of the range, and commonly linear-lanceolate from North Carolina southward, with infrequent spathulate-leaved specimens found in the Caribbean area. The spathulate leaf with a cuneate base is a juvenile leaf-form typical of the first set of leaves in the seedling. Collections of *Ammannia latifolia* from Virginia, scattered localities in the Caribbean, and Peru with only this leaf type represent cases of arrested development of the mature leaf-form. *Ammannia teres* var. *exauriculata* (Fern.) Fern. is based on plants with predominantly spathulate leaves and cuneate bases.

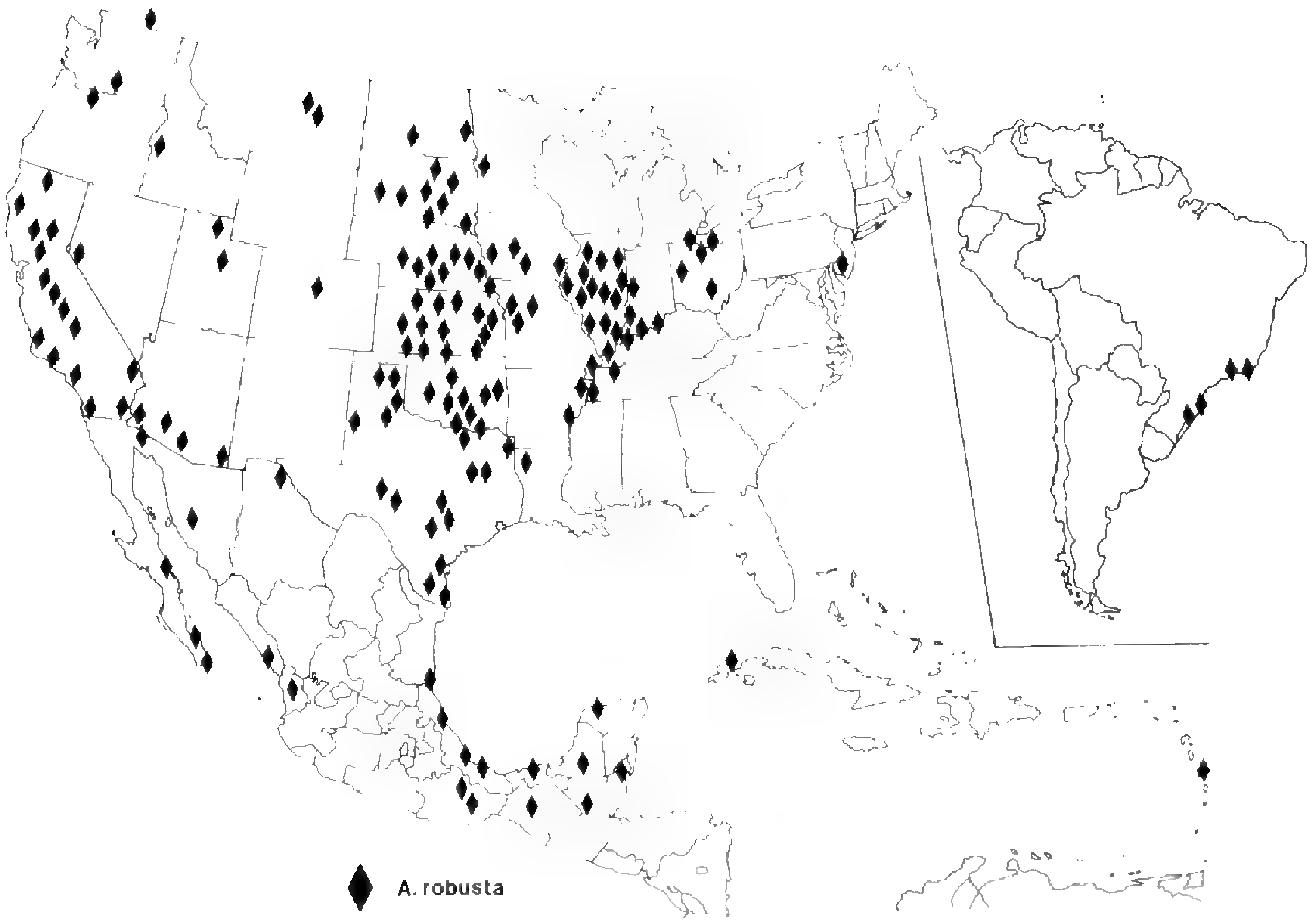
Leaf length/width quotients initially increase southward, reaching a maximum in the Bahamas and Greater Antilles, and thereafter decrease slightly, suggesting that vegetative growth for this taxon is optimum in the northern Caribbean region. Capsule size is most variable in the north, but the difference in mean size between the largest and smallest capsule on all specimens is only 1.3 mm.

There are no significant discontinuities in morphology over the approximately 7500 km north–south distribution that would justify retention of more than one species. *Ammannia latifolia* is, in fact, remarkably uniform considering its extensive range. Autogamy, particularly cleistogamy (the common mode of fertilization in the apetalous plants), is probably the major factor in maintaining this uniformity.

On the basis of Koehne's monographic descriptions, *Ammannia latifolia* is most similar to *A. urceolata* Hiern, an African endemic. Koehne's (1880b) suggestion that *A. latifolia* ($n = 24$) could have been derived from *A. coccinea* ($n = 33$) is discarded due to the difference in chromosome numbers. *Ammannia latifolia*, with $n = 24$, is more likely a hexaploid derived from an ancestral $x = 8$.

5. **Ammannia robusta** Heer & Regel, Index Sem. Horto Bot. Turic. adn. 1. 1842. TYPE: Brazil, Rio de Janeiro, Piratininga, 23 July 1875, *Glaziou 8340* (neotype (here designated), R!). MAP 4.

Ammannia sanguinolenta subsp. *robusta* (Heer & Regel) Koehne *in* Martius, Fl. Brasil. **13**(2): 208. 1877.



MAP 4. Distribution of *Ammannia robusta* in Western Hemisphere. (Collections from LAF, DUKE, and NCU not included.)

Ammannia coccinea subsp. *robusta* (Heer & Regel) Koehne, Bot. Jahrb. Syst. **1**: 250. 1880.

Ammannia alcalina Blank. Montana Coll. Agric. Sci. Stud., Bot. **1**: 1905. TYPE: U. S., Montana, Lake Bowdoin, near Malta, 25 Aug. 1903, *J. W. Blankinship s.n.* (lectotype (here designated), MONT).

Robust annual herbs to 1 m tall, unbranched or branching from base, the lowest pairs of branches decumbent, often equaling height of main stem, the upper branches fewer, shorter. Leaves linear-lanceolate, less often elliptic to spathulate, 15–80 by 4–15 mm, usually 1–3 times length of internode above, tending to be fleshy, the apex obtuse to generally acute, the base auriculate-cordate, clasping, occasionally cuneate on lowermost leaves. Inflorescences axillary, sessile, 1- to 3- (to 5-)flowered cymes. Floral tube urceolate, frequently prominently 4-ridged or subalate, averaging 3.5 by 2 mm, subtended by 2 linear bracteoles ½ height of tube; calyx lobes broadly triangular with acute apex, alternating with thickened appendages equal to lobes in length; appendages usually erect in bud; petals 4 (to 8), obovate, usually 2.5 by 3 mm, pale lavender, sometimes with deep rose spot at base of midvein or with rose-purple midvein; stamens 4 (or 5 to 12), exserted, anthers pale yellow to yellow; style long, slender, slightly exserted at anthesis; ovary incompletely 2- (to 4-)locular. Capsule 4–6 mm in diameter at maturity, enclosed in or equal to calyx lobes, rarely exceeding lobes. $n = 17$.

Ammannia robusta has been overlooked in the North American flora because of its morphological similarity to *A. coccinea* (under which most specimens have been determined). In the field it is easily distinguished from *A. coccinea* by a combination of features: pale lavender petals and light yellow anthers, one to three large, sessile flowers with four exaggerated ribs, and large, sessile capsules 4–6 mm in diameter. Mature herbarium specimens occasionally pose problems in identification due to change of petal and anther color in drying, but the presence of one to three large, sessile capsules at each axil is generally sufficient for determination. Variability in size of floral parts among *A. robusta, A. coccinea,* and *A. auriculata* is summarized in TABLE 3. Mixed collections of these species are not unusual in the herbarium since they may grow side by side at a single site and have been assumed by collectors to represent morphological variability within a single species.

Ammannia robusta is widely distributed in North America except in the southeastern United States and is most frequently collected in the Plains States. It is uncommon in the Caribbean, and it is limited to the coast north of Rio de Janeiro in South America, where it is apparently an early, but persistent, introduction.

The species was described from cultivated material of Brazilian origin. A type has not been located. Regel may have taken herbarium and library material with him to St. Petersburg on leaving Zurich (C. D. K. Cook, pers. comm.), but the type material of *Ammannia robusta* has not been located at LE. Since the description leaves no question as to the application of the name, a neotype has been selected from a Brazilian collection.

EXCLUDED NAMES[5]

Ammannia alata Steudel, Nomencl. Bot. ed. 2. **1**: 76. 1840, *nomen nudum.*

Ammannia auriculata auct., *non* Willd., Raf. Atlantic J. **1**: 146. 1832 = *A. ramosior* sensu Torrey, Ann. Lyceum Nat. Hist. New York **2**: 199. 1827 = **Rotala ramosior** (L.) Koehne.

Ammannia catholica Hooker & Arn. ex Seemann, Bot. Voy. Herald, 284. 1856, *pro syn.* = **Rotala ramosior** (L.) Koehne.

Ammannia catholica var. *brasiliensis* Cham. & Schldl. Linnaea **2**: 379. 1827 = **Rotala ramosior** (L.) Koehne; see Van Leeuwen (1974) and Cook (1979).

Ammannia coccinea auct., *non* Rottb., Pers. Synopsis Pl. **1**: 147. 1805 = **A. octandra** L.

Ammannia coccinea subsp. *pubiflora* Koehne, Bot. Jahrb. Syst. **1**: 250. 1880. TYPE: Iran, *Hohenacher 2948.* Authentic material unknown; not at BM or CAS. Description inadequate.

Ammannia dentifera A. Gray, Pl. Wright. **2**: 55. 1853 = *Rotala dentifera* (Gray) Koehne, Bot. Jahrb. Syst. **1**: 161. 1880 = **R. ramosior** var. **dentifera** (A. Gray) Lundell, Bull. Torrey Bot. Club **69**: 395. 1942.

Ammannia diffusa Raf. Aut. Bot. **1**: 39. 1840, *non* Willd., 1809, *nomen dubium.* The description is applicable to both *A. auriculata* and *A. coccinea.* Authentic material unknown.

Ammannia humilis Michaux, Fl. Bor. Amer. **1**: 99. 1803 = *Boykiana humilis* (Michaux) Raf. Neogenyton, 2. 1825 = **Rotala ramosior** (L.) Koehne.

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[5] Including misidentifications and misapplications listed by Koehne (1903) and *Index Kewensis* for the Western Hemisphere species.

Ammannia humilis auct., *non* Michaux, Chapman, Fl. So. U. S. 134. 1860, *ex descr.* = **R. ramosior,** *pro parte,* and **A. coccinea,** *pro parte.*

Ammannia hyrcanica Fischer ex Steudel, Nomencl. Bot. ed. 2. **1:** 77. 1840, *nomen nudum.*

Ammannia latifolia auct., *non* L., Wallich, Catal. no. 2096. 1829, *nomen nudum* (not validated by G. Don, Gen. Syst., 1831–1838), *nec* Walp. Rep. Bot. Syst. **2:** 102. 1843.

Ammannia linearifolia Raf. Aut. Bot. **1:** 39. 1840, *ex descr.* = **Rotala ramosior** (L.) Koehne.

Ammannia longifolia Raf. *ibid., nomen dubium* (description inadequate), synonym for either *A. coccinea* or *A. robusta.* Authentic material unknown.

Ammannia mexicana (Cham. & Schldl.) Baillon *in* Grandidier, Hist. Nat. Pl. (Madagascar Atlas) **3:** *t. 363.* 1895 = **Rotala mexicana** Cham. & Schldl.

Ammannia monoflora Blanco, Fl. Filip. ed. 1. 64. 1837, *nomen dubium* (description inadequate) = **Rotala ramosior** (L.) Koehne (Cook, 1979).

Ammannia multicaulis Raf. Aut. Bot. **1:** 39. 1840, *ex descr.* = **Rotala ramosior** (L.) Koehne.

Ammannia nuttallii A. Gray, Man. Bot. No. U. S. ed. 4. Add. 92. 1863, *ex descr.* = **Didiplis diandra** (DC.) Wood.

Ammannia occidentalis DC. Prodr. Syst. Nat. Regni Veg. **3:** 78. 1828 = **Rotala ramosior** (L.) Koehne.

Ammannia occidentalis var. *pygmaea* Chapman, Fl. So. U. S. 134. 1860. TYPE: U. S., Florida, Key West, *Dr. Blodgett s.n., ex descr.* = **Rotala ramosior** (L.) Koehne.

Ammannia pallida Lehm. Index Sem. Horto Bot. Hamburg, 3. 1823, Linnaea **3:** 9. 1828, *nomen dubium.* Authentic material unknown, not at K. Koehne followed DC. in regarding *A. pallida* as synonymous with *A. latifolia,* but description inadequate and even country of origin unknown.

Ammannia racemosa Hill, Veg. Syst. **11:** 14. 1767. An erroneous citation in *Index Kewensis* for *A. ramosior* L.

Ammannia ramosior L. Sp. Pl. **1:** 120. 1753, ed. 2. 175. 1762, *non sensu* L. Mant. Pl. Alt. 332. 1771. TYPE: U. S., Virginia, *Clayton 774* (Savage H 156.2, LINN). = **Rotala ramosior** (L.) Koehne.

Ammannia ramosior auct., *non* L., Elliott, Sketch Bot. S. Carolina & Georgia **1:** 219. 1817, *ex descr.* = **A. latifolia** L.

Ammannia sanguinolenta auct., *non* Sw., Cham. & Schldl. Linnaea **5:** 568. 1830 = **A. auriculata** *fide* Koehne, who probably saw this specimen at B.

Ammannia sanguinolenta auct., *non* Sw., Heyne ex Steudel, Nomencl. Bot. ed. 2. **1:** 77. 1840, *pro syn.*

Ammannia sanguinolenta auct., *non* Sw., Hooker & Arn. ex Seemann, Bot. Voy. Herald, 284. 1856, *pro syn.*

Ammannia wormskioldii Fischer & Meyer, Index Sem. Hortus Imp. Petrop. **7:** 42. 1841. Not from Brazil as cited by Koehne *in* Martius, Fl. Brasil. **13**(2): 205. Type (LE!) bears notation "C[ult.] e semina Congo allatis." A specimen from Koehne's herbarium (GH!) initially determined by him as *A. wormskioldii* was corrected by him to *A. latifolia* and may be the basis for the erroneous report of this species in the New World.

Ludwigia scabriuscula Kellogg, Proc. Calif. Acad. Sci. **7**: 78. 1876. Equated by Koehne with *Ammannia latifolia,* but *A. latifolia* does not occur in California, and by description, the species (with scabrulose, small-toothed leaves, clawed petals, and a 4-lobed stigma) does not belong to the genus *Ammannia.* Authentic material unknown; not at BM.

Lythrum apetalum Sprengel, Syst. Veg. ed. 16 [17]. **2**: 454. 1825. Erroneously equated with *Ammannia latifolia* in *Index Kewensis, ex descr. non Ammannia.* = **Heimia myrtifolia** *fide* Koehne, 1903.

ACKNOWLEDGMENTS

Collections of the following herbaria were studied: A, CAS, CHAPA, DS, ENCB, F, GH, ILL, IND, ISM, JEPS, KANU, MEXU, MICH, MO, NY, OKL, OSU, R, SDU, SP, TEX, UC, US, VEN, WIS; the cooperation of the curators is gratefully acknowledged. Distribution data are based on specimens from these herbaria and on collections studied earlier from LAF, LTU, MISS, NCSC, NCU, TENN, VDB (S. Graham, 1975).

I wish to thank William T. Stearn (British Museum), Werner Greuter (Botanischer Garten und Botanisches Museum, Berlin-Dahlem), and Edward Voss (University of Michigan) for nomenclatural advice and Alan Graham (Kent State University) for SEM photographs. Becky Klingenworth prepared Figure 2.

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APPENDIX. **Index of cited plant names.***

Ammannia alata Steudel = excl
A. alcalina Blank. = rob
A. arenaria HBK. = aur
A. auriculata Ledeb. ex Koehne = aur
A. auriculata Raf. = excl
A. auriculata Willd. = aur
A. auriculata var. *arenaria* (HBK.) Koehne = aur
A. auriculata var. *arenaria* f. *brasiliensis* (St. Hil.) Koehne = aur
A. baccifera L. = bac
A. catholica Cham. & Schldl. = excl
A. catholica Hooker & Arn. = excl
A. coccinea Pers. = excl
A. coccinea Rottb. = coc
A. coccinea subsp. *longifolia* (Koehne) Koehne = coc
A. coccinea subsp. *pubiflora* Koehne = excl
A. coccinea subsp. *purpurea* (Lam.) Koehne = coc
A. coccinea subsp. *robusta* (Heer & Regel) Koehne = rob
A. dentifera A. Gray = excl
A. diffusa Raf. = excl
A. friesii Koehne = lat
A. hastata DC. = lat
A. humilis Chapman = excl
A. humilis Michaux = excl
A. hyrcanica Fischer ex Steudel = excl
A. koehnei Britton = lat
A. koehnei var. *exauriculata* Fern. = lat
A. latifolia L. = lat
A. latifolia Wallich = excl
A. latifolia var. *octandra* A. Gray = coc
A. linearifolia Raf. = excl
A. lingulata Griseb. = lat
A. longifolia Raf. = excl
A. longipes Wright = aur
A. lythrifolia Salisb. = lat
A. mexicana (Cham. & Schldl.) Baillon = excl
A. monoflora Blanco = excl
A. multicaulis Raf. = excl
A. nuttallii A. Gray = excl
A. occidentalis (Sprengel) DC. = excl
A. occidentalis var. *pygmaea* Chapman = excl
A. octandra Cham. & Schldl. = coc
A. pallida Lehm. = excl
A. pedunculata Rusby = coc
A. purpurea Lam. = coc
A. pusilla Sonder = aur
A. racemosa Hill = excl
A. racemosa Roth = aur
A. ramosior Elliott = excl
A. ramosior L. = excl
A. robusta Heer & Regel = rob
A. sagittata DC. = lat
A. sagittata var. *angustifolia* A. Rich. = coc
A. sanguinolenta Cham. & Schldl. = excl
A. sanguinolenta Heyne ex Steudel = excl
A. sanguinolenta Hooker & Arn. ex Seemann = excl
A. sanguinolenta Sw. = coc
A. sanguinolenta subsp. *longifolia* Koehne = coc
A. sanguinolenta subsp. *purpurea* (Lam.) Koehne = coc
A. sanguinolenta subsp. *robusta* (Heer & Regel) Koehne = rob
A. senegalensis var. *brasiliensis* St. Hil. = aur
A. stylosa Fischer & Meyer = coc
A. teres Raf. = coc
A. teres var. *exauriculata* (Fern.) Fern. = lat
A. texana Scheele = coc
A. wormskioldii Fischer & Meyer = excl
A. wrightii A. Gray = aur
Isnardia subhastata Ruiz & Pavon = lat
Jussiaea sagittata Poiret = lat
Ludwigia hastata Sprengel = lat
L. scabriuscula Kellogg = excl
Lythrum apetalum Sprengel = excl
Ronconia triflora Raf. = aur

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*Explanation of abbreviations: aur = *Ammannia auriculata,* bacc = *A. baccifera,* cocc = *A. coccinea,* excl = excluded name, lat = *A. latifolia,* rob = *A. robusta.*

POLLEN DIVERSITY AND EXINE EVOLUTION IN VIBURNUM AND THE CAPRIFOLIACEAE SENSU LATO[1]

MICHAEL J. DONOGHUE

STUDIES OF POLLEN DEVELOPMENT and function (Heslop-Harrison, 1971), along with correlations between pollen morphology, incompatibility system, and mode of pollination (DeNettancourt, 1977; Lee, 1978; Plitmann & Levin, 1983), have prompted speculation about the adaptive significance of pollen characteristics (Heslop-Harrison, 1976, 1979; Lewis, 1977). At the same time considerable attention has been devoted to the related but logically separate task of determining the actual course of pollen evolution, with special emphasis on the exine (Erdtman, 1966; Walker & Doyle, 1975; Ferguson & Muller, 1976; Nowicke & Skvarla, 1979). A particular hypothesis about pollen evolution is usually established by considering pollen diversity in the context of presumed relationships. Pollen characters are mapped onto a classification (which is usually based on many other kinds of characters), and the most plausible sequence of evolutionary events for the pollen is established in this context. This procedure is basically sound, but clearly the results obtained can be no better than the hypothesis of relationships employed. Unfortunately, relationships have not yet been rigorously established for most plant groups, and present classifications do not always reflect these accurately or unambiguously. Thus, although considerable progress has been made in tracing the course of pollen evolution, the level of resolution has not always been very satisfactory.

Cladistic analysis can be a powerful tool for the study of character evolution. A cladogram provides a test of the congruence of characters and establishes the simplest hypothesis of the direction and sequence of character transformations. In addition, it is a rigorous means of assessing the nature and extent of homoplasy—i.e., of convergent evolution and reversal. One can also determine the relative timing of the origin of traits, information that is critical for the historical analysis of adaptation. Thus it is possible to establish the level at which a particular character transformation (e.g., from small to large pollen) occurred relative to changes in other characters of interest (e.g., style length).

Unfortunately, cladograms are now available for only a small number of plant groups, and with only a few exceptions (e.g., Kress & Stone, 1983) pollen evolution has not been studied in a cladistic context. The primary purpose of this paper is to provide a cladistic analysis of exine evolution in *Viburnum* L. This genus is especially well suited for the purpose for three reasons. First, its pollen is quite well known from previous studies, and the present survey sig-

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[1] A portion of a thesis submitted to the Department of Biology, Harvard University, in partial fulfillment of the requirements for the Ph.D. degree.

Journal of the Arnold Arboretum **66**: 421–469. October, 1985.

nificantly increases the number of species sampled and gives a clear understanding of the taxonomic distribution of pollen characters. We can now be quite confident that we know the range and pattern of pollen variation in the genus. Second, a corroborated hypothesis of the cladistic relationships of *Viburnum* to other genera is available (Donoghue, 1983b), enabling evaluation of the polarity of pollen characters using outgroup analysis (Maddison *et al.*, 1984). Finally, a preliminary cladistic analysis of the genus has been carried out (Donoghue, 1983a), making it possible to assess the congruence of pollen characters with other characters and to establish the most parsimonious hypothesis of exine evolution. An equally rigorous analysis of pollen evolution in other Caprifoliaceae is not yet possible. However, cladistic reasoning can still be applied, and it is possible to generate preliminary hypotheses that can be tested in the future.

Throughout this paper I refer to Caprifoliaceae *sensu stricto* (*s.s.*) and Caprifoliaceae *sensu lato* (*s.l.*). The family Caprifoliaceae *s.s.* is equivalent to the subfamily Caprifolioideae of Hara (1983) and contains 11 genera that he assigned to four tribes: *Leycesteria* Wallich and *Lonicera* L. of the Caprifolieae; *Diervilla* Miller and *Weigela* Thunb. of the Diervilleae; *Triosteum* L. of the Triosteae; and *Abelia* R. Br., *Dipelta* Maxim., *Heptacodium* Rehder, *Kolkwitzia* Graebner, *Linnaea* L., and *Symphoricarpos* Duhamel of the Linnaeeae. The Caprifoliaceae *s.l.* consist of the Caprifoliaceae *s.s.* plus *Viburnum, Sambucus* L., and *Adoxa* L. The last genus is frequently placed in its own family, Adoxaceae, but many characters point to a close relationship between *Adoxa* and *Sambucus,* and of these genera to *Viburnum* (Donoghue, 1983b). It is therefore essential to include *Adoxa* in evolutionary studies involving *Sambucus* and *Viburnum.*

Two new species, *Adoxa omeiensis* Hara (Wu, 1981; Hara, 1981, 1983) and *Sinadoxa corydalifolia* C. Y. Wu, Z. L. Wu, & R. F. Huang (Wu *et al.*, 1981) have recently been described in the Adoxaceae. These resemble *Adoxa moschatellina* L. and should probably also be included in the Caprifoliaceae *s.l.* They are excluded here simply because they are very poorly known and their pollen was unavailable for study. Since Wu's (1981) scanning electron micrographs show that the pollen of both new species is very similar to that of *Adoxa* and *Sambucus,* the results of the present analysis would not have been significantly altered by the inclusion of these taxa.

POLLEN DIVERSITY IN THE CAPRIFOLIACEAE S.L.

PREVIOUS STUDIES

Light microscopic (LM) studies have revealed considerable variation in pollen morphology in the Caprifoliaceae *s.l.*, and to a lesser extent within *Viburnum* (see Erdtman, 1966, and Thanikaimoni, 1972, for references to the early literature; see also Punt *et al.*, 1974; Reitsma & Reuvers, 1975). Punt and colleagues (1974) published scanning electron micrographs (SEMGs) of the pollen of three species, Rader (1976) used the SEM to study several species in *Viburnum* sect. LENTAGO, Reitsma and Reuvers (1975) published SEMGs of *Adoxa moschatellina,* and Adams and Morton (1979) presented SEMGs of

18 species in five genera. More recently, Böhnke-Gütlein and Weberling (1981) published the first part (tribes Sambuceae, Viburneae, and Diervilleae) of a careful and extensive LM and SEM survey of the pollen of the Caprifoliaceae, and Hara (1983) included SEMGs of the pollen of 30 specimens in his treatment of the Caprifoliaceae of Japan.

Unfortunately and despite considerable previous study and the evident diversity of pollen in the Caprifoliaceae *s.l.,* pollen characters have been used little—or uncritically—by phylogenists. Because most palynological work on the group has been conducted within the last decade, information pertaining to pollen morphology is entirely lacking from the most recent comprehensive revision of the tribes of the family (Fukuoka, 1972). It has been noted, however, that the pollen of *Adoxa* is very similar to that of *Sambucus* (Cronquist, 1968, 1981) and that the pollen grains of *Viburnum* and *Sambucus* are similar, but that all differ markedly from the pollen of the four tribes of Caprifoliaceae *s.s.* (Ferguson, 1966; Lewis, pers. comm. *in* Hillebrand & Fairbrothers, 1970; also cited in Bohm & Glennie, 1971). The genera of the Caprifoliaceae *s.s.* are palynologically similar (Erdtman, 1966; Lewis & Fantz, 1973), but there is significant variation in pollen size (apparently correlated with chromosome number) in *Symphoricarpos* (Bassett & Crompton, 1970), and pollen differences in *Abelia* (Ikuse & Kurosawa, 1954; Erdtman, 1966, 1969) prompted the segregation of the genus *Zabelia* Makino. Böhnke-Gütlein and Weberling (1981) discussed some taxonomic implications of pollen diversity in the family but reached few conclusions about phylogenetic relationships or the evolution of pollen morphology in the group. However, additional discussion is expected in the second portion of their survey (MS in press, *fide* Böhnke-Gütlein & Weberling, 1981).

MATERIALS AND METHODS

Pollen from mature anthers was affixed to aluminum stubs with double-stick tape. All samples are vouchered by annotated herbarium specimens (see TABLES 1, 2), most of which are deposited in the Harvard University Herbaria (A or GH). Prepared stubs were coated with approximately 200 Å of gold-palladium in two 1.5-minute steps using a Technics Hummer II sputter coater. Specimens were examined with an AMR model 1000a scanning electron microscope, in the secondary electron mode, using accelerating voltages up to 20 kv. SEMGs were recorded on Polaroid Type 55 P/N 4 × 5″ film. All photomicrographs were taken at the Museum of Comparative Zoology Scanning Electron Microscope Laboratory, Harvard University.

The method of preparation of pollen grains for the SEM can sometimes significantly affect the results obtained (Hanks & Fairbrothers, 1970). In the initial phases of this study, pollen was acetolyzed (according to Erdtman, 1960) prior to scanning. However, when it was found that unacetolyzed and acetolyzed pollen of *Viburnum* differed little (i.e., "Pollenkitt" is limited), acetolysis was discontinued. The transmission electron microscope (TEM) was not utilized in this study, but cross sections of the exine were obtained for SEM study by spreading pollen on a glass plate, cutting it with a razor blade, and transferring it with a brush to a stub.

TABLE 1. **The pollen of Viburnum.**

TAXON[1]	POLLEN DIMENSIONS[2] Polar axis (P) in μm	Equatorial axis (E) in μm	P/E[3]	POLLEN SHAPE[4]	POLLEN TYPE[5]	VOUCHER SPECIMEN[6] Locality	Collection
Odontotinus Rehder							
V. acerifolium L.	—	—	—	—	(I)a	U.S.A.: Connecticut	*Churchill s.n.*, 1952 (MSC)
V. dentatum L.	—	—	—	—	(I)a	U.S.A.: New Jersey	*Hermann 4240* (MICH)
V. dilatatum Thunb.	16.5(17.3)18.6 s = 0.576	16.5(17.7)18.6 s = 0.785	0.98	O-S	Ia	Japan: Izu Peninsula	*Ohashi, Nakaike, & Tateishi 70627* (A)
V. ellipticum Hooker	22.6(24.4)25.8 s = 0.840	19.5(22.6)24.7 s = 1.427	1.08	P-S	Ia	U.S.A.: Oregon	*Hunt 36* (A)
V. foetidum Wallich	18.6(20.7)21.6 s = 1.112	12.4(14.0)15.5 s = 0.750	1.48	EU	Ia	China: Yunnan	*Forrest 18129* (A)
V. japonicum (Thunb.) Sprengel	23.4(24.5)26.5 s = 0.879	17.3(18.6)20.4 s = 0.821	1.31	SP	Ia	Japan: Kyushu	*Ichikawa 26* (A)

V. kansuense Batalin	—	—	—	—	(I)a	China: Sichuan	Rock 16440 (US)
V. orientale Pallas	17.5(18.6)19.6 s = 0.837	16.5(18.1)19.6 s = 0.789	1.03	P-S	Ia	Turkey	Balls 1927 (A)
V. rafinesquianum Schultes	—	—	—	—	(I)a	U.S.A.: Michigan (?)	Penfield s.n., 9 June 1909 (MICH)
V. sempervirens K. Koch	24.7(26.7)28.8 s = 0.930	16.5(17.7)18.6 s = 0.718	1.51	EU	Ia	China: Guandong	Gressitt 1247 (A)
V. wrightii Miq.	22.7(25.2)26.8 s = 1.102	15.5(16.5)18.6 s = 0.775	1.53	EU	Ia	Japan: Hizen	Hatusima 4206 (A)
Oreinotinus (Oersted) Bentham & Hooker							
V. acutifolium Bentham	—	—	—	—	(I)a	Mexico: Oaxaca	Stevens, Donoghue, & Scott 2492 (MSC)
V. caudatum Greenman	—	—	—	—	(I)a	Mexico, sine loco	Gutierrez 54 (MICH)
V. ciliatum Greenman	—	—	—	—	(I)a	Mexico: Hidalgo	Maury 5786 (NY)

TABLE 1 (*continued*).

TAXON[1]	POLLEN DIMENSIONS[2]			POLLEN SHAPE[4]	POLLEN TYPE[5]	VOUCHER SPECIMEN[6]	
	Polar axis (P) in µm	Equatorial axis (E) in µm	P/E[3]			Locality	Collection
V. costaricanum (Oersted) Hemsley	—	—	—	—	(I)a	Costa Rica: San José	*Lellinger & White 1588* (F)
V. hartwegii Bentham	—	—	—	—	(I)a	Mexico: Chiapas	*Stevens, Donoghue, & Scott 2423* (MSC)
V. jucundum Morton	—	—	—	—	(I)a	Mexico: Chiapas	*Stevens, Donoghue, & Scott 2350* (MSC)
V. loeseneri Graebner	—	—	—	—	(I)a	Mexico: Michoacán	*Stevens, Donoghue, & Scott 2547* (MSC)
V. mendax Morton	—	—	—	—	(I)a	Guatemala: Huehuetenango	*Skutch 1065* (US)
V. microcarpum Schlecht. & Cham.	23.7(25.4)27.8 s = 1.337	18.5(20.1)22.7 s = 1.471	1.26	SP	Ia	Mexico: Veracruz	*Ventura A. 819* (ENCB)

V. stenocalyx (Oersted) Hemsley	—	—	—	—	(I)a	Mexico: Puebla	Purpus 163 (US)
V. sulcatum (Oersted) Hemsley	—	—	—	—	(I)a	Mexico: Oaxaca	Rzedowski 12436 (ENCB)
V. tinoides L.	—	—	—	—	(I)a	Colombia: Cundinamarca	Barclay, Juajibioy, & Gama 3146 (US)
V. triphyllum Bentham	—	—	—	—	(I)a	Ecuador: Azuay	Camp E-3900 (MICH)
V. venustum Morton	—	—	—	—	(I)a	Costa Rica: Alajuela	Jiménez 3947 (F)
Solenotinus DC.							
V. brachybotryum Hemsley	20.6(22.3)23.7 s = 0.871	19.6(20.3)21.6 s = 0.617	1.10	P-S	Ia	China: Yunnan	Henry 12790A (A)
V. erubescens Wallich ex DC.	20.6(22.4)23.7 s = 0.744	18.6(20.3)21.6 s = 0.798	1.10	P-S	Ia	Western China	Wilson 3734 (A)
V. farreri Stearn	22.6(23.9)24.7 s = 0.861	16.5(17.7)18.6 s = 0.679	1.35	EU	Ia	China: Gansu	Rock 12142 (A)
V. henryi Hemsley	26.8(28.5)30.9 s = 1.249	21.6(22.8)24.7 s = 1.115	1.25	SP	Ia	China: Hubei	Wilson 1071 (A)

TABLE 1 (*continued*).

TAXON[1]	POLLEN DIMENSIONS[2]			POLLEN SHAPE[4]	POLLEN TYPE[5]	VOUCHER SPECIMEN[6]	
	Polar axis (P) in µm	Equatorial axis (E) in µm	P/E[3]			Locality	Collection
V. odoratissimum Ker Gawler	22.7(23.9)24.7 s = 0.883	20.6(22.4)23.7 s = 0.840	1.07	P-S	Ia	Philippines: Mountain Province	Alcasid 70 (A)
V. odoratissimum Ker Gawler	—	—	—	—	(I)a	China: Sichuan	H. H. Hu 770 (A)
V. oliganthum Batalin	26.8(28.8)30.9 s = 1.172	23.7(25.0)26.8 s = 1.077	1.15	SP	Ia	China: Sichuan	H. Smith 1961 (A)
V. sieboldii Miq.	—	—	—	—	(I)a	Japan: Musashi	Maruyama 10 (MICH)
V. suspensum Lindley	22.7(23.8)25.8 s = 1.112	20.6(22.0)22.7 s = 0.770	1.08	P-S	Ia	Japan: Kyushu	Hatusima 864 (GH)
Tinus (Miller) C. B. Clarke							
V. atrocyaneum C. B. Clarke	23.7(25.2)26.8 s = 0.960	19.6(21.0)23.7 s = 1.386	1.20	SP	Ia	China: Xizang	Rock 8905 (A)
V. cinnamomifolium Rehder	21.6(24.6)26.8 s = 1.325	16.5(17.6)18.6 s = 0.929	1.40	EU	Ia	China: Sichuan	Yü 539 (A)

V. davidii Franchet	25.8(27.4)28.8 s = 0.828	22.7(24.7)25.8 s = 0.918	1.11	P-S	Ia	Western China	*Wilson 3728* (A)
V. propinquum Hemsley	17.5(19.0)20.6 s = 1.090	16.5(17.3)18.6 s = 0.901	1.10	P-S	Ia	China: Hubei	*Henry 3415* (A)
V. tinus L.	36.1(38.8)42.3 s = 1.700	22.7(23.5)24.7 s = 0.861	1.65	EU	Ia	Italy: Istria	*Marchesetti 2752* (GH)
Tomentosa Nakai							
V. hanceanum Maxim.	22.7(24.7)26.8 s = 1.036	14.4(15.8)16.5 s = 0.729	1.56	EU	Ia	Hong Kong	*Chun 5314* (A)
V. plicatum Thunb.	——	——	——	——	(I)a	Japan: Sagami	*Ohwi & Okamoto 502* (MICH)
Opulus DC.							
V. edule (Michaux) Raf.	18.6(20.9)22.7 s = 1.253	15.5(16.5)17.5 s = 0.755	1.27	SP	Ia	U.S.A.: Washington	*Suksdorf 2063* (A)
V. sargentii Koehne	21.6(22.9)24.7 s = 0.797	19.6(20.7)21.6 s = 0.915	1.11	P-S	Ia	Japan: Shinano	*Furuse s.n.*, 20 June 1961 (A)
V. sargentii Koehne	——	——	——	——	(I)?[7]	Japan: Iwashiro	*Furuse s.n.*, 9 June 1958 (A)

TABLE 1 (*continued*).

TAXON[1]	POLLEN DIMENSIONS[2]			POLLEN SHAPE[4]	POLLEN TYPE[5]	VOUCHER SPECIMEN[6]	
	Polar axis (P) in µm	Equatorial axis (E) in µm	P/E[3]			Locality	Collection
Pseudotinus C. B. Clarke							
V. cordifolium Wallich ex DC.	26.8(28.9)30.9 s = 1.427	18.6(20.9)22.7 s = 1.045	1.38	EU	Ic	China: Yunnan	*Forrest 11892* (A)
V. furcatum Blume	17.5(19.5)21.6 s = 1.256	17.5(18.2)18.6 s = 0.557	1.07	P-S	Ia	Japan: Niigata	*Togashi 7145* (A)
V. lantanoides Michaux	17.5(18.4)19.6 s = 0.718	17.5(19.3)20.6 s = 0.831	0.95	O-S	Ia	U.S.A.: Massachusetts	*Andrews s.n.*, 1897 (GH)
Megalotinus (Maxim.) Rehder							
V. cylindricum Ham. ex D. Don	24.7(26.3)30.9 s = 2.199	19.5(20.7)21.6 s = 0.516	1.27	SP	Ia	China: Yunnan	*Forrest 11513* (A)
V. cylindricum Ham. ex D. Don	—	—	—	—	(I)a	Thailand: Chiang Mai	*Iwatsuki, Koyama, Fukuoka, & Nalampoon 9424* (A)

V. punctatum Ham. ex D. Don	20.6(21.2)23.7 s = 1.088	19.5(21.3)22.7 s = 0.854	0.99	O-S	Ib	China: Sichuan	*Schneider 691* (A)
V. ternatum Rehder	24.7(26.4)29.9 s = 1.645	21.6(22.9)26.8 s = 1.381	1.15	SP	Ia	China: Guizhou	*Teng 90584* (A)
Viburnum							
V. burejaeticum Regel & Herder	20.6(22.1)22.7 s = 0.687	23.7(25.3)26.8 s = 0.960	0.87	SO	Ic	N. Korea: N. Hamkyong	*Ishidoya s.n.*, 1918 (A)
V. carlesii Hemsley	17.5(19.8)21.6 s = 1.220	18.6(20.3)21.6 s = 0.978	0.98	O-S	Ib	Japan: Honshu	*Togashi 7761* (A)
V. lantana L.	——	——	——	——	(I)c	England, *sine loco*	*Fisher s.n.*, 1883 (MICH)
V. macrocephalum Fortune	23.7(24.5)25.8 s = 0.808	24.7(25.9)27.8 s = 0.892	0.95	O-S	Ib	China: Zhejiang	*Chiao 7962* (A)
V. macrocephalum Fortune	——	——	——	——	(I)b	China: Hubei	*Wilson 1835* (A)
V. mongolicum (Pallas) Rehder	29.9(32.2)35.1 s = 1.437	20.6(23.2)24.7 s = 1.008	1.39	EU	Ic	China: Gansu	*Rock 12480* (A)
V. rhytidophyllum Hemsley	——	——	——	——	(I)c	China: Hubei	*Wilson 654* (US)
V. shensianum Maxim.	24.7(25.3)26.8 s = 0.835	21.6(23.7)24.7 s = 1.033	1.07	P-S	Ib	China: Shanxi	*Tang 776* (A)

TABLE 1 (*continued*).

TAXON[1]	POLLEN DIMENSIONS[2]			POLLEN SHAPE[4]	POLLEN TYPE[5]	VOUCHER SPECIMEN[6]	
	Polar axis (P) in μm	Equatorial axis (E) in μm	P/E[3]			Locality	Collection
V. urceolatum Sieb. & Zucc.	20.6(21.8)23.7 s = 1.060	19.6(20.6)21.6 s = 0.539	1.06	P-S	Ia	Japan: Kyushu	Tashiro s.n., 1917 (A)
V. utile Hemsley	20.6(22.7)23.7 s = 0.879	22.7(24.5)25.8 s = 0.989	0.93	O-S	Ib	China: Hubei	H. C. Chow 145 (A)
V. veitchii C. H. Wright	17.5(18.6)19.6 s = 0.561	19.6(20.5)21.6 s = 0.639	0.91	O-S	Ic	China: Zhejiang	Lingnan Univ. Herb. 78294 (A)
Lentago DC.							
V. elatum Bentham	25.8(27.1)28.8 s = 1.032	19.6(21.3)22.7 s = 1.015	1.27	SP	Ic	Mexico: Chiapas	Alexander 1049 (NY)
V. nudum L.	—	—	—	—	(I)b	U.S.A.: Florida	Churchill s.n., 1956 (MSC)
V. nudum var. cassinoides (L.) Torrey & Gray	28.8(33.8)36.1 s = 1.906	19.6(22.3)24.7 s = 1.438	1.52	EU	Ic	U.S.A.: New Hampshire	Russell s.n., 1924 (GH)

V. prunifolium L.	34.0(35.5)38.1 s = 1.214	19.6(21.0)22.7 s = 1.222	1.69	EU	Ic	U.S.A.: West Virginia	Bartholomew 1518 (GH)
V. prunifolium L.	___	___	___	___	(I)c	U.S.A.: Missouri	Bush 7939 (GH)
V. rufidulum Raf.	___	___	___	___	(I)c	U.S.A.: Florida	Godfrey 61912 (MSC)

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[1] Species arranged alphabetically within sections *sensu* Hara (1983); sections arranged according to pollen type as in Plates I-XI.

[2] Measurements made from scanning electron micrographs as described under materials and methods above. First figure = smallest grain; second figure = mean; third figure = largest grain; s = standard deviation; sample size = 15 grains; dash = measurement not obtained.

[3] Mean polar length (P) divided by mean equatorial length (E).

[4] Shapes classified according to Walker and Doyle (1975): EU = euprolate; O-S = oblate-spheroidal; P-S = prolate-spheroidal; SO = suboblate; SP = subprolate.

[5] Size-shape class (I) and exine structure-sculpture class (a, b, c) define pollen type (see text). Size-shape class in parentheses if grain size determined solely by comparison with grains of known size.

[6] Locality data consist of country and state or province provided on herbarium label. Chinese provinces spelled according to the Pinyin system. Herbaria: Arnold Arboretum (A), Escuela Nacional de Ciencias Biologías (ENCB), Field Museum of Natural History (F), Gray Herbarium (GH), University of Michigan Herbarium (MICH), Beal-Darlington Herbarium, Michigan State University (MSC), New York Botanic Garden (NY), and U. S. National Herbarium (US).

[7] This grain from unopened (not fully mature?) anther not assigned to an exine structure-sculpture class.

TABLE 2. **The pollen of the Caprifoliaceae s.l. (except Viburnum).**[1]

	POLLEN DIMENSIONS[3]					VOUCHER SPECIMEN[7]	
TAXON[2]	Polar axis (P) in µm	Equatorial axis (E) in µm	P/E[4]	POLLEN SHAPE[5]	POLLEN TYPE[6]	Locality	Collection
Adoxaceae Trautv.							
Adoxa moschatellina L.	32.0(33.9)37.1 s = 1.577	15.5(18.2)19.6 s = 1.096	1.86	EU	Ia	Japan: Shinano	*Furuse s.n.*, 15 May 1961 (A)
Caprifoliaceae A. L. Juss.							
Sambucoideae (Endl.) Luerssen							
Sambucus pubens Michaux	22.7(24.2)25.8 s = 0.847	12.4(13.5)14.4 s = 0.516	1.79	EU	Ia	U.S.A.: Massachusetts	*Forbes 3433* (GH)
Caprifolioideae							
Caprifolieae							
Leycesteria formosa Wallich	43.6(46.4)48.7 s = 1.783	48.7(51.6)56.4 s = 2.535	0.90	O-S	IId	China: Sichuan	*Schneider 1394* (A)
L. gracilis (Kurz) Airy Shaw	—	—	—	—	(II)d	China: Yunnan	*Forrest 9377* (A)

Lonicera chrysantha Turcz.	—	—	—	—	(II)d	China: Weichang	*Purdum 6b* (A)
L. semper-virens L.	—	—	—	—	(II)d	U.S.A.: Virginia	*Fernald & Long 7973* (GH)
L. tatarica L.	—	—	—	—	(II)d	Canada: Québec	*Bro. Victorin 181* (A)
Diervilleae C. Meyer							
Diervilla lonicera Miller	30.9(34.4)37.1 s = 2.202	36.1(39.0)41.2 s = 1.652	0.88	O-S	II(f)[8]	Canada: Newfound-land	*Jamison*(?) *s.n.*, 1930 (GH)
Weigela florida (Bunge) DC.	41.0(42.2)43.6 s = 1.370	43.6(46.8)51.3 s = 2.122	0.90	O-S	IIf	S. Korea: Anyang	*Moran 4257* (GH)
Triosteae Hutch.							
Triosteum aurantiacum Bickn.	51.3(53.8)56.4 s = 2.208	56.4(60.2)64.1 s = 2.335	0.89	O-S	IIe	U.S.A.: Pennsyl-vania	*Pennell s.n.*, 1924 (GH)
T. perfoliatum L.	—	—	—	—	(II)e	U.S.A.: Kansas	*McGregor 14287* (GH)

TABLE 2 (*continued*).

TAXON[2]	POLLEN DIMENSIONS[3]			POLLEN SHAPE[5]	POLLEN TYPE[6]	VOUCHER SPECIMEN[7]	
	Polar axis (P) in μm	Equatorial axis (E) in μm	P/E[4]			Locality	Collection
Linnaeeae Dumort.							
Abelia spathulata Sieb. & Zucc.	45.0(47.0)50.0 s = 2.297	50.0(55.8)60.0 s = 3.493	0.84	SO	IId	Japan: Kai	*Furuse s.n.*, *7 May 1957* (A)
Dipelta yunnanensis Franchet	43.6(49.1)53.8 s = 2.728	43.6(49.2)56.4 s = 2.582	0.99	O-S	IId	China: Sichuan	*Rock 16150* (A)
Heptacodium jasminoides Airy Shaw	47.5(50.0)52.5 s = 1.636	50.0(51.5)55.0 s = 2.275	0.97	O-S	IId	China: Zhejiang	*Keng 1068* (A)
Kolkwitzia amabilis Graebner	—	—	—	—	(II)d	U.S.A.: Massachusetts (native to China)	*Rehder*, *Arnold Arb. 6475* (GH)
Linnaea borealis L.	33.0(35.4)37.1 s = 1.423	35.1(36.8)38.1 s = 1.182	0.96	O-S	IId	Canada: Labrador	*Woodworth 388* (GH)
Symphoricarpos albus (L.) Blake	26.8(27.5)28.8 s = 1.154	30.9(32.5)34.0 s = 1.180	0.85	SO	IIe	Canada: Ontario	*Pease & Bean 26146* (GH)

Valerianaceae Batsch							
Nardostachys jatamansii (D. Don) DC.	46.2(49.9)56.4 s = 3.158	51.3(54.0)56.4 s = 1.939	0.92	O-S	IId	China: Xizang	*Rock 14168* (GH)

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[1] Caprifoliaceae *s.l.* includes Adoxaceae (Donoghue, 1983b); one species of Valerianaceae included for comparison.

[2] Species arranged alphabetically within families, subfamilies, and tribes *sensu* Hara (1983).

[3] Measurements made from scanning electron micrographs as described under materials and methods above. First figure = smallest grain; second figure = mean; third figure = largest grain; s = standard deviation; sample size = 15 grains; dash = measurement not obtained.

[4] Mean polar length (P) divided by mean equatorial length (E).

[5] Shapes classified according to Walker and Doyle (1975): EU = euprolate; O-S = oblate-spheroidal; SO = suboblate.

[6] Size-shape class (I, II) and exine structure-sculpture class (a, d, e, f) define pollen type (see text). Size-shape class in parentheses if grain size determined solely by comparison with grains of known size.

[7] Locality data consist of country and state or province provided on herbarium label. Chinese provinces spelled according to the Pinyin system. Herbaria: Arnold Arboretum (A) and Gray Herbarium (GH).

[8] Cross section of exine not seen.

Pollen of 63 *Viburnum* species and 18 species of 14 other genera was examined. In preliminary investigations a number of specimens were studied from different parts of the geographic range of several species (e.g., *Viburnum acutifolium, V. hartwegii, V. prunifolium, V. elatum, Sambucus pubens,* and *Diervilla lonicera*). There was little variation in the size, shape, structure, and sculpturing of the grains within or between individuals of a species (with the exception of one specimen of *V. sargentii*—see footnote 7, TABLE 1, and PLATE VB). Therefore, for the majority of species, pollen from only one specimen was photographed and measured.

All size measurements were obtained from SEMGs of air-dried, unacetolyzed pollen. Low-magnification (×200 or ×500) SEMGs were taken to include at least 15 grains. By means of the bar scale, micrometers were converted to millimeters, and polar and equatorial measurements were obtained directly from the photographs. The bar scale is presumed to be accurate to within 5–10 percent. Sample sizes were small; however, standard deviations were uniformly low. Grain sizes of different individuals of the same species were not compared, so statistical significance was not calculated. The measurements presented in TABLES 1 and 2 can therefore serve only as rough indicators of grain size. Measurements made by this method were compared in several instances to those of acetolyzed grains mounted in glycerin jelly, as well as to published LM measurements. In all cases there was good correspondence between SEM and LM measurements.

The terminology used throughout this paper is taken from Walker and Doyle's (1975) modification and consolidation of the terminologies developed by Erdtman (1969) and Faegri and Iversen (1975). Precise definitions of some terms, especially those relating to exine sculpturing, are given by Reitsma (1970).

POLLEN MORPHOLOGY

SIZE-SHAPE CLASSES. The range of pollen sizes, the mean size, and the standard deviation are recorded in TABLES 1 and 2 for 52 of the 81 species examined. Quotients of polar/equatorial (P/E) axis-length were obtained from the mean sizes, and these were converted into shape classes using Walker and Doyle's (1975) classification.

In FIGURE 1 mean polar length is plotted against mean equatorial length for each species measured. There is a wide range of pollen sizes, but within this range there are correlated differences in grain length and width, with the wider grains tending to be longer. In addition, shape and size differences are clearly correlated. Perfectly spherical grains would lie along the 45° line in FIGURE 1, with oblate grains above this line and prolate ones below it. Note that the larger grains are oblate, while the smaller ones are generally prolate. There are several exceptions to this correlation in *Viburnum,* especially within sect. VIBURNUM, and the possible significance of these is discussed below.

On the basis of the correlation between size and shape, two size-shape classes are recognized. Pollen in class I ranges from 16.5 (*Viburnum dilatatum*) to 42.3 μm long (*V. tinus*), and from 12.4 (*V. foetidum* and *Sambucus pubens*) to 26.8 μm wide (*V. oliganthum, V. ternatum,* and *V. burejaeticum*). The mean length

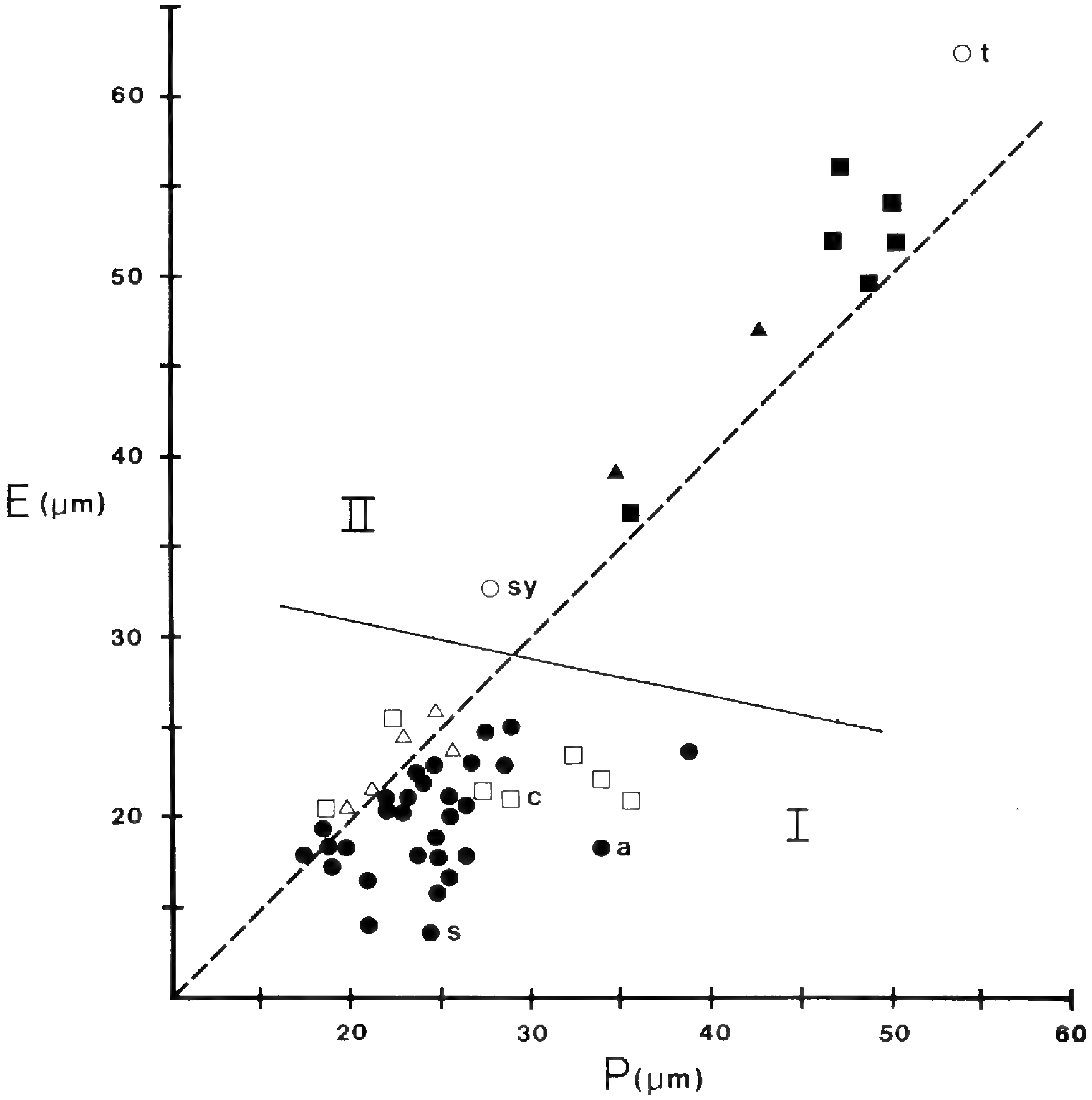

FIGURE 1. Pollen size-shape and structure-sculpture classes in Caprifoliaceae *s.l.* P = length of polar axis, E = length of equatorial axis, 45° dashed line = spherical grains, I and II = size-shape classes. Symbols for structure-sculpture classes: closed circles = class a, open triangles = class b, open squares = class c, closed squares = class d, open circles = class e, closed triangles = class f. a = *Adoxa moschatellina,* s = *Sambucus pubens,* c = *Viburnum cordifolium,* sy = *Symphoricarpos albus,* t = *Triosteum aurantiacum.*

(P) of pollen in this class is 24.4 µm (s = 4.719), the mean width (E) is 20.4 µm (s = 2.995), and the mean P/E quotient is 1.23 (subprolate).

Pollen in size-shape class II ranges from 26.8 (*Symphoricarpos albus*) to 56.4 µm long (*Triosteum aurantiacum*), and from 30.9 (*S. albus*) to 64.1 µm wide (*T. aurantiacum*). The mean length (P) of pollen in this class is 43.6 µm (s = 8.481), the mean width (E) is 47.4 µm (s = 8.942), and the mean P/E quotient is 0.91 (oblate spheroidal).

Those species for which size data were not obtained have been tentatively assigned to one of the two size-shape classes based on visual comparisons with pollen of known size. There is little chance of misclassification because the two classes are nonoverlapping and readily contrasted.

EXINE STRUCTURE-SCULPTURE CLASSES. There is great diversity in exine structure and sculpture within the Caprifoliaceae *s.l.*, and to a lesser extent within *Viburnum*. The pollen of each species was assigned to one of six exine structure-sculpture classes described below. Within some of the classes there is considerable variation, and they may be subdivided as SEM studies are extended and augmented by LM and TEM investigations.

Class a. Exine semitectate, ± regularly reticulate; reticulum elevated on columellae (height variable both within and between grains); muri psilate, variable in width; lumen dimensions variable; free-standing bacula and/or pila present, generally visible in lumina, variable in size and number (e.g., PLATE I).

Class b. Exine semitectate, ± regularly reticulate; reticulum ± elevated on columellae (these sometimes laterally continuous); muri regularly scabrate; lumen dimensions variable; bacula present and visible in lumina, variable in size and number but often smaller and less abundant than in class a (e.g., PLATE VI).

Class c. Exine intectate or with some fusion of heads of adjacent pila, ± regularly retipilate (Erdtman, 1966) to pilate; pila short stalked or nearly sessile (gemmae), scabrate (except in *Viburnum cordifolium*; see PLATE VE, F, and discussion); distinct lumina absent; surfaces between pila verrucate to irregularly baculate (e.g., PLATE VII).

Class d. Exine tectate, imperforate, bearing spinelike processes (echinae ≥ 1 μm, microechinae < 1 μm) of variable size and abundance; surfaces between spines psilate to verrucate; tectum supported by columellae of variable height and width (e.g., PLATES XD–F, XIA–D).

Class e. Similar to class d, except lacking spinelike processes on tectum (e.g., PLATE XA–C).

Class f. Exine lacking columellae; tectum bearing large, often irregularly shaped spinelike processes; surface between spines ± verrucate (e.g., PLATE IXC–F).

These exine structure-sculpture classes fall into two categories. The first includes classes a–c, in which the exine is semitectate and reticulate to intectate. The second comprises classes d–f, which are characterized by a complete tectum, either raised on columellae (d and e) or not (f).

POLLEN TYPES. Together, size-shape class and structure-sculpture class define a pollen type. Structure-sculpture classes a–c occur only in pollen grains in size-shape class I, while the structure-sculpture classes d–f are found only in grains of size-shape class II (FIGURE 1). Hence, there are two very different kinds of pollen grains in the Caprifoliaceae *s.l.*: those that are smaller, prolate, and lacking a complete tectum; and those that are larger, oblate to spheroidal, and completely tectate.

APERTURE MORPHOLOGY AND POLLEN TYPES. Since variation in aperture morphology was not analyzed in detail in this study and has not received sufficient attention previously, aperture differences were not included in the descriptions of pollen types given above. Only the SEM was employed in this survey; careful studies with the LM and TEM are necessary to understand the nature and extent of variation in aperture structure. However, some general observations about aperture morphology in the Caprifoliaceae *s.l.* can be made, and it is possible to relate what little is known about aperture variation to variation in the characters discussed above. These comments are based in part on the LM studies of Bassett and Crompton (1970), Richard (1970), Punt and colleagues (1974), and Böhnke-Gütlein and Weberling (1981).

Pollen of all members of the Caprifoliaceae *s.l.* is normally triaperturate, with an occasional two- to four-apertured grain (e.g., in some specimens of *Abelia spathulata,* PLATE XIC). The apertures are distinctly colporate in *Viburnum, Sambucus,* and *Adoxa,* and brevicolporate to porate in the Caprifoliaceae *s.s.* Thus, the taxonomic distribution of aperture shapes seems to correlate perfectly with the distributions of the size, shape, and exine characters just described (see below).

Minor variations in aperture structure have been reported in *Viburnum,* and some of these may prove taxonomically useful. Presently, however, the nature of this variation is very poorly known. For example, Bassett and Crompton (1970) noted variation in the extent to which the furrows appeared open. Unfortunately, this trait appears to vary within some species and may be affected by the method of preparation. A somewhat more promising character is the presence or absence of a bridge over the colpus, a feature recorded both by Punt and colleagues (1974) and by Böhnke-Gütlein and Weberling (1981). In their combined sample of 31 species, a bridge was present in 15, including all 6 species examined with an exine of type b or c. Variation in this trait is apparently common within several sections (e.g., ODONTOTINUS) and in some cases might be useful in distinguishing between closely related species. However, this character should be treated very cautiously until it is studied in more detail because there are several conflicting observations. In *V. tinus,* for example, Böhnke-Gütlein and Weberling (1981) reported the presence of a bridge, while Punt and co-workers (1974) recorded its absence. The latter observation is supported in the present study (PLATE IIIC). Other similar conflicts, and the observation of apparently intermediate conditions in some grains, suggest that there can be considerable variation within species and/or that this trait can be affected by sample preparation.

Within the Caprifoliaceae *s.s.* there appear to be slight but consistent differences in aperture shape between the genera. In *Heptacodium* (PLATE VIIIF), *Diervilla* (PLATE IXC), *Weigela* (PLATE IXE), and *Triosteum* (PLATE XA, B) the apertures are porate or only slightly elongate, while in the remaining genera they are usually brevicolporate. However, in *Symphoricarpos* the apertures reportedly vary (Bassett & Crompton, 1970), and they may be intermediate in length (PLATE XC). Obviously, many more species will have to be examined before this character can be used with any confidence.

POLLEN TYPES AND PHYLOGENETIC RELATIONSHIPS IN THE CAPRIFOLIACEAE S.L.

The taxonomic distribution of pollen types within the Caprifoliaceae *s.l.* is quite clear cut. Type Ia grains characterize *Sambucus, Adoxa,* and most species of *Viburnum*; types Ib and Ic are also found in *Viburnum.* Type IId is most common in the Caprifoliaceae *s.s.*, but IIe and IIf are also present. Thus, pollen types are congruent with many other characters that suggest the presence of two distinct lineages within the Caprifoliaceae *s.l.* (Donoghue, 1983b). It is noteworthy that pollen size appears to be positively correlated with style length. This supports the conclusions of Plitmann and Levin (1983), who studied pollen-pistil relationships in Polemoniaceae. Style length is in turn correlated with other floral characters (e.g., length of corolla tube) that relate to mode of pollination.

A cladistic analysis aimed at determining the phylogenetic relationships of *Viburnum* (Donoghue, 1983b) demonstrated that there are shared derived character states (synapomorphies) uniting *Viburnum* with *Sambucus* and *Adoxa* almost regardless of what outgroup arrangement is used in assessing character polarities. The ten genera of Caprifoliaceae *s.s.* may form a monophyletic group, but they are probably paraphyletic (i.e., would not include all of the descendants of their common ancestor) if the Valerianaceae and Dipsacaceae are treated as separate families. There is no evidence that the Caprifoliaceae *s.l.* are a monophyletic group (I have been unable to find a synapomorphy linking *Viburnum, Sambucus,* and *Adoxa* with the Caprifoliaceae *s.s.*).

Since there is no reason to think that the Caprifoliaceae *s.l.* form a monophyletic group, it is inappropriate to consider the evolution of pollen morphology in the group as a whole, as has been done in previous studies (e.g., Böhnke-Gütlein & Weberling, 1981). Therefore, I will consider pollen evolution only within the two distinct groups of Caprifoliaceae *s.l.*, especially within the *Viburnum-Sambucus-Adoxa* clade, for which there exists a corroborated hypothesis of phylogenetic relationship. Thus I will consider transformations between pollen types Ia, Ib, and Ic, and between types IId, IIe, and IIf, but I will not treat relationships between the two main pollen types because a direct transformation between them may never have occurred.

EVOLUTION OF THE EXINE

EXINE EVOLUTION IN VIBURNUM

TAXONOMIC DISTRIBUTION OF EXINE CHARACTERS. Only type Ia pollen is known in *Sambucus* and *Adoxa,* and this type predominates in *Viburnum.* There do appear to be slight variations in pollen type Ia between the genera. On average, the lumina in *Sambucus* and *Adoxa* are smaller than those in *Viburnum,* and therefore the reticulum appears to be tighter (Plate VIIIA–D). Pollen of *Sambucus* and *Adoxa* is also somewhat smaller on average than that of most species of *Viburnum.* More free columellae are visible within the lumina of *Viburnum* and *Sambucus* than in those of *Adoxa.* Each of these differences is slight, and there is considerable overlap. Thus, without additional study of a larger sample, they cannot be considered statistically or taxonomically significant.

Type Ia pollen not only is the most common one in *Viburnum* but is also taxonomically widespread. Rehder (1908, 1940) recognized nine sections in the genus. These are widely accepted but have been subdivided in a few cases (e.g., Kern, 1951). Hara (1983) provided an overview of the subgeneric classification and modified Rehder's classification, recognizing 10 sections; he placed the Latin American species (Killip & Smith, 1931; Morton, 1933) in sect. OREINOTINUS. In TABLE 1 the species of *Viburnum* examined in this study are arranged according to Hara's sections. The table shows that type Ia pollen is present in all examined members of sects. ODONTOTINUS (PLATE IA–D), OREINOTINUS (PLATE IE, F), SOLENOTINUS (PLATES IIA–F; IIIA, B), TINUS (PLATE IIIC–F), TOMENTOSA (PLATE IVE, F), and OPULUS (PLATE VA, B), as well as in *V. cylindricum* of sect. MEGALOTINUS (PLATE IVA, B), *V. urceolatum* of sect. VIBURNUM (PLATE IVC, D), and *V. furcatum* (PLATE VC, D) and *V. lantanoides* of sect. PSEUDOTINUS. Type Ia pollen is not known in sect. LENTAGO.

There is some variation in pollen type Ia within *Viburnum*; upon additional study of a larger sample, this is likely to be of some taxonomic significance within sections and species complexes. Variation in the size of the lumina and in the abundance and visibility of bacula is especially pronounced in sect. SOLENOTINUS (formerly *Thyrsosma* (Raf.) Rehder), which contains 15 to 20 species native to Asia. In *V. farreri* (subsect. LONICEROIDES (Oersted) Hara; PLATE IIA) the lumina are narrow and the bacula are hardly visible. In contrast, in *V. erubescens, V. oliganthum,* and *V. suspensum* (all subsect. SOLENOTINUS), and in *V. odoratissimum* (subsect. MICROTINUS (Oersted) Hara; PLATE IIE, F), the reticulum is loose and conspicuously raised. In *V. brachybotryum* (subsect. MICROTINUS; PLATE IIIA, B) the lumina are especially wide and numerous bacula are visible.

Section SOLENOTINUS is generally believed to include the most primitive species in *Viburnum* (Wilkinson, 1948; DeVos, 1951; Egolf, 1962; Hara, 1983), and it may be paraphyletic (Donoghue, 1983a). Since there is extreme diversity within the section in leaf venation, margin, size, and shape, and in flowering time, fruit morphology, and growth pattern (Donoghue, 1982, 1983a; Hara, 1983), the range of variation in pollen morphology is not altogether surprising. It is noteworthy that the minor variations in pollen noted above do seem to distinguish some of Hara's subsections, suggesting that these may be natural groups.

Some of the range of variation in sect. SOLENOTINUS is paralleled in sect. TINUS, a monophyletic group of approximately eight species. The pollen of *Viburnum atrocyaneum* (PLATE IIIF) is similar to that of *V. odoratissimum* (PLATE IIE, F), and *V. tinus* pollen (PLATE IIIC, D) is like that of *V. brachybotryum* (PLATE IIIA, B). Pollen of *V. cinnamomifolium, V. davidii* (PLATE IIIE), and *V. propinquum,* all of which have trinerved leaves (i.e., acrodromous venation), does not appear to differ significantly from that of the remaining species of sect. TINUS, which have pinnate (eucamptodromous) venation.

Compared to pollen type Ia, types Ib and Ic are much less common and more limited in taxonomic distribution. Type Ib characterizes *Viburnum punctatum* of sect. MEGALOTINUS subsect. PUNCTATA Kern (PLATE VIE, F) and four of the ten species examined from sect. VIBURNUM. Section VIBURNUM, with 15 to 20 species, is divided by Hara (1983) into three subsections: subsect. VIBURNUM has pollen types Ib and Ic; *V. carlesii,* the only species of subsect. SOLENOLANTANA (Nakai) Hara, has type Ib; and *V. urceolatum* of the monotypic subsect. URCEOLATA Nakai has type Ia. The last species may not be closely related to the others (see below and Donoghue, 1983a). Species of sect. VIBURNUM with types Ib and Ic pollen have never been placed in separate groups. Type Ib pollen is also known from sect. LENTAGO but is extremely rare in this group; it was found in only one out of the four individuals of *V. nudum* var. *cassinoides* examined.

Pollen type Ic characterizes the majority of the examined species of sects. VIBURNUM (PLATE VIID–F) and LENTAGO. *Viburnum cordifolium* (PLATE VE, F) of sect. PSEUDOTINUS was also initially scored as having type Ic pollen, but as noted above, the pila in this species appear to lack scabrae. The analysis below indicates that this kind of pollen is best considered a distinct type.

There are some differences in grain shape in groups with pollen types Ib and Ic, and these may prove taxonomically useful when examined in more detail. Most *Viburnum* species have prolate or subprolate grains, but there is a trend toward spheroidal or oblate ones, especially in sect. VIBURNUM (PLATES VIC, D; VIID, E). The bearing of this observation on the interpretation of exine evolution is considered below.

POLARITY AND TRANSFORMATION SERIES. Only shared derived character states (synapomorphies) may be considered evidence of common ancestry; within a particular group shared ancestral states (symplesiomorphies) are uninformative about cladistic relationship (Hennig, 1966). Hence, before the *Viburnum* pollen data assembled here can be used to assess phylogenetic relationships, the polarity of the exine characters must be determined. Numerous criteria have been used to assess polarity, but outgroup comparison is now widely acknowledged to be the only generally valid one (Stevens, 1980, 1981; Watrous & Wheeler, 1981; Wheeler, 1981; Farris, 1982; Maddison *et al.,* 1984).

Elsewhere (Donoghue, 1983b), I have defended the hypothesis that *Sambucus* and *Adoxa* together are the sister group of *Viburnum. Sambucus* and *Adoxa* can therefore be used as an outgroup to assess the polarity of characters that vary in *Viburnum.* If *Sambucus* and *Adoxa* share a state that occurs in some members of *Viburnum,* then it is most parsimonious to consider that state to be ancestral within *Viburnum,* and the alternate state(s) to be derived (Maddison *et al.,* 1984). Thus pollen type Ia can be considered the ancestral state in *Viburnum,* and types Ib and Ic derived.

It would be desirable to include outgroups in addition to *Sambucus* and *Adoxa* in the analysis of polarity (Maddison *et al.,* 1984), but the sister group of the *Viburnum-Sambucus-Adoxa* clade is equivocal. In cases such as this, plausible sister groups can usually be substituted to see what effect they might have on polarity assessment (Donoghue & Cantino, 1984), but in this instance all plausible sister groups are highly variable in pollen morphology and/or homologies are difficult to establish. The Cornaceae, for example, are a likely secondary outgroup but are quite variable, and intrafamilial relationships are so poorly understood that the family cannot be employed in outgroup comparison. Chao (1954) noted that pollen of the Cornaceae resembles that of *Viburnum, Sambucus,* and *Adoxa* in size, shape, and aperture number and morphology. Ferguson (1977) revealed a wide variety of pollen types in the

Cornaceae, none of which is identical to pollen of *Viburnum, Sambucus,* or *Adoxa.* It is noteworthy, however, that species of *Melanophylla* Baker have pollen similar to type Ia; *Kaliphora madagascarensis* Hooker f. pollen resembles type Ib; and *Aucuba japonica* Thunb. pollen is similar to type Ic. Derivation of the *Viburnum-Sambucus-Adoxa* clade from ancestors similar to extant Cornaceae would not have required major changes in pollen morphology but would necessitate a transformation to the trinucleate condition from the binucleate state characteristic of the Cornales (Brewbaker, 1967).

By outgroup comparison it is possible to establish the most parsimonious hypothesis of ancestral state in the ingroup. For two-state (binary) characters, the derived state and its relation to the ancestral state are automatically determined. When there are three or more states, a transformation series must be established, specifying the relation among the states. There have been attempts to develop rigorous methods to establish transformation series (Mickevich, 1982), but this requires that other characters be examined simultaneously and that an initial hypothesis of cladistic relationships be formulated. In the absence of such information, transformation series have been constructed on the basis of the "logical" relations among the states and/or by reference to general trends in similar organisms (Stevens, 1980). Fortunately, in the case of the exine characters considered here, it is possible to use parsimony as a criterion to choose among the possible transformation series because the exine structure-sculpture classes involve two independently varying characters (scabrae present or absent; regular reticulum present or absent). Furthermore, these characters are nested such that retipilate or pilate grains are scabrate (except in *Viburnum cordifolium*), but some grains with scabrae are reticulate. For these reasons it is most parsimonious to posit that Ia → Ib → Ic (FIGURE 2A). This transformation series requires two state changes: from smooth to scabrate, and from reticulate to retipilate/pilate. Any other arrangement of pollen types (Ia → Ic → Ib, or Ib ← Ia → Ic) requires a minimum of three steps. The most parsimonious transformation series is consistent with a supposedly common trend from semitectate and reticulate to intectate pollen (Walker & Doyle, 1975; Walker, 1976).

In contrast, Böhnke-Gütlein and Weberling (1981) concluded that Ic → Ib → Ia, based on unsubstantiated preconceptions about phylogenetic relationships and the relative advancement of species within *Viburnum,* and on a presumed trend (Erdtman, 1966) from pilate to reticulate grains. This conclusion is rejected here based on outgroup comparison. A phylogenetic analysis of relationships within *Viburnum* (see below and Donoghue, 1983a) also shows that it is most parsimonious to hypothesize that Ia is ancestral in *Viburnum.*

CLADISTIC RELATIONSHIPS AND EXINE EVOLUTION. If pollen type Ia is ancestral within *Viburnum,* possession of this trait does not provide evidence of cladistic relationship within the genus. Types Ib and Ic are derived and provide *prima facie* evidence of monophyly. The simplest hypothesis, based on the transformation series established above, is that type Ib evolved once and characterizes a monophyletic group, and that type Ic likewise evolved from Ib only once (FIGURE 2B). To test this hypothesis and establish the level at which these

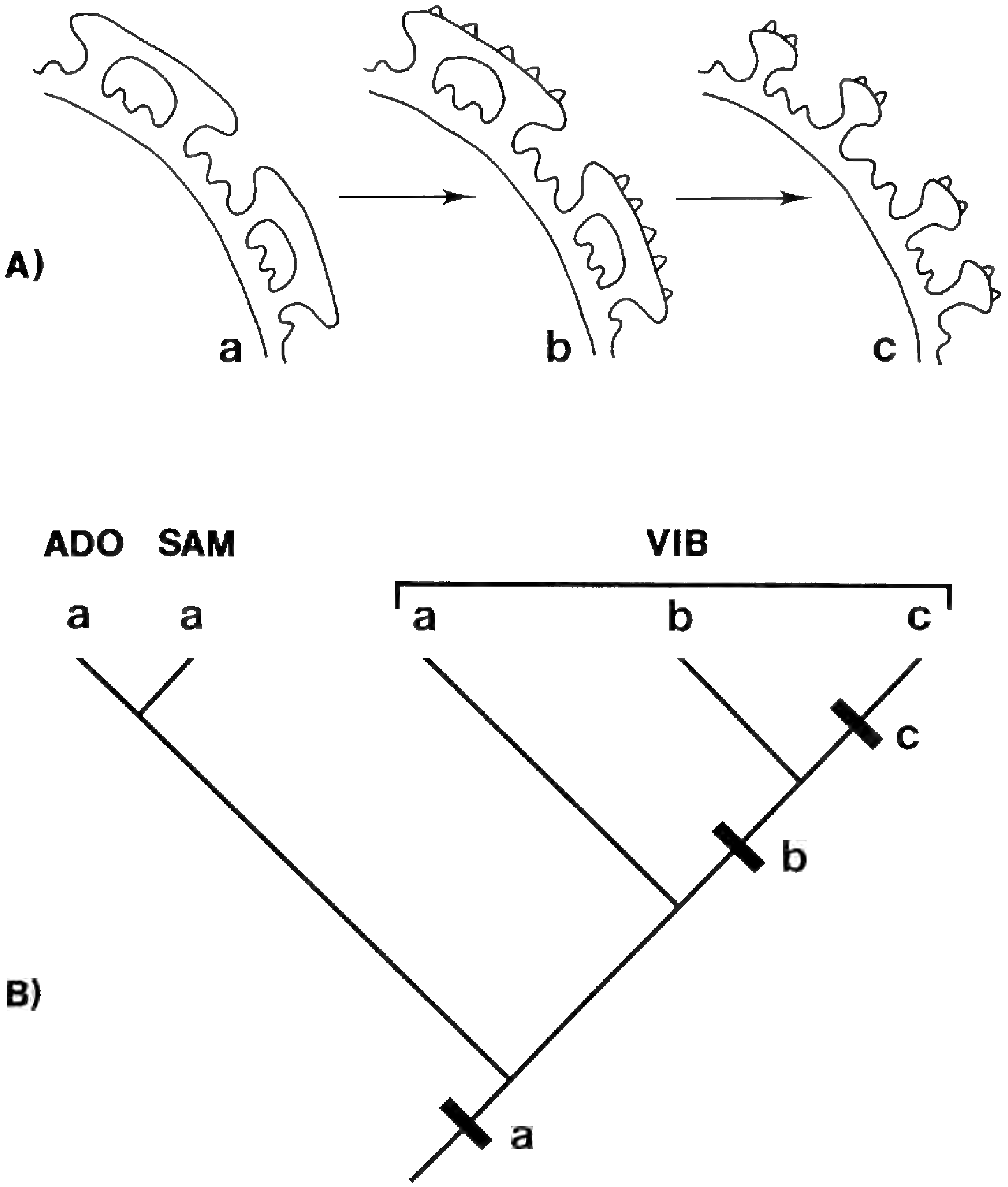

FIGURE 2. A, hypothesized transformation of pollen structure-sculpture classes a, b, and c within *Viburnum* (all size-shape class I). B, simplest *a priori* phylogenetic hypothesis for evolution of pollen in *Viburnum* (VIB), with *Sambucus* (SAM) and *Adoxa* (ADO) as first outgroup.

states characterize monophyletic groups, it is necessary to consider the congruence of the pollen characters with other characters. Such congruence will test whether plants with type Ic pollen, for example, form a monophyletic group, and hence whether Ic is truly a homology (Patterson, 1982). In practice the congruence test of homology is performed by using a variety of characters to construct the most parsimonious cladogram.

In a preliminary cladistic analysis of *Viburnum*, I used a data set of 23 species

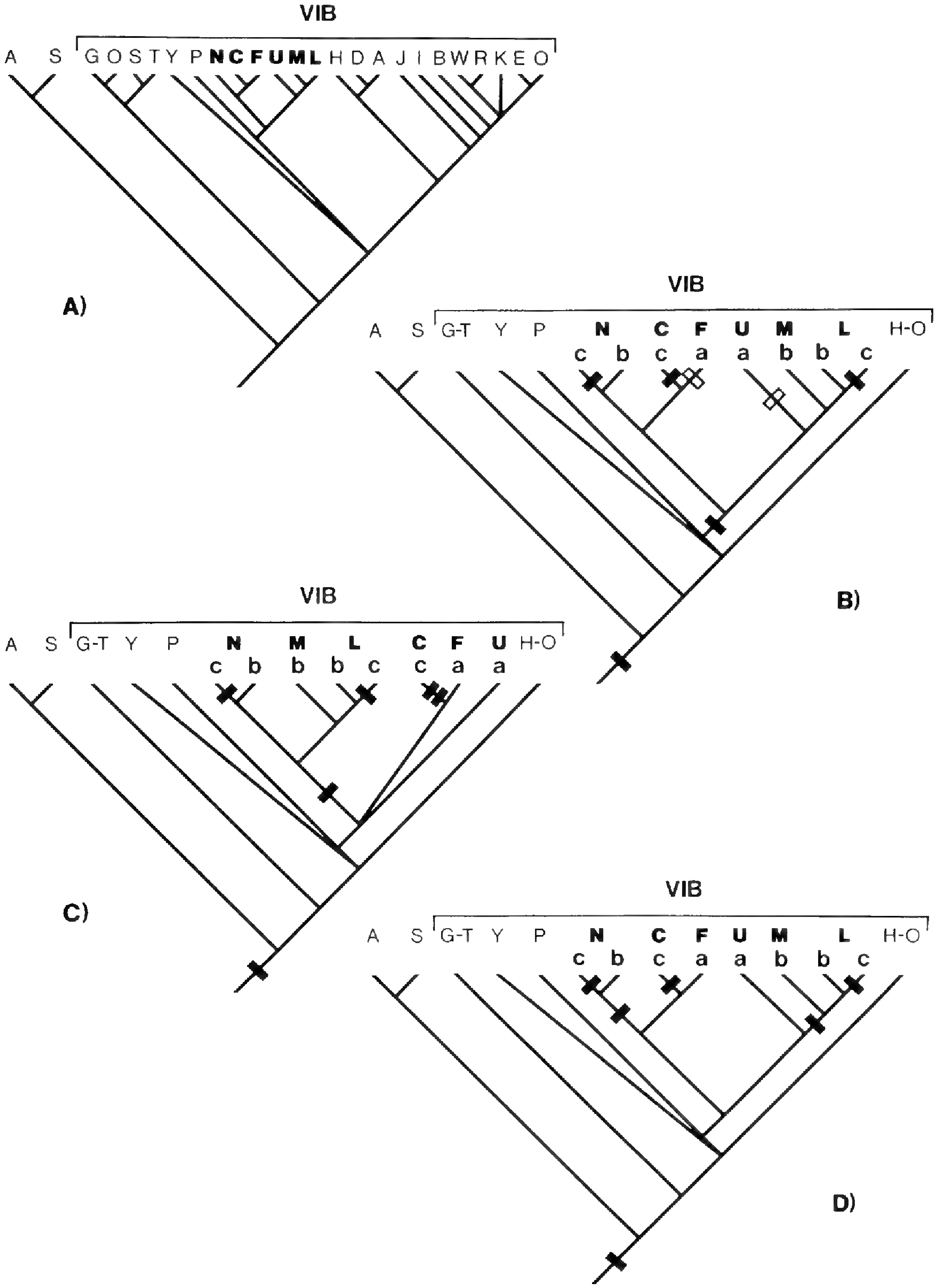

FIGURE 3. A, cladogram of *Viburnum* (VIB) used in evaluating pollen evolution; *Sambucus* (S) and *Adoxa* (A) as first outgroup. Clade N, C, F, U, M, L (boldface) expanded in B–D. B, most parsimonious interpretation of pollen evolution using transformation series in FIGURE 2A (black bar = forward transformation; open bar = reversal; a, b, c = structure-sculpture classes of size-shape class I). C, rearrangement of cladogram A, eliminating reversals in the pollen character but entailing extra steps in other characters. D, most parsimonious arrangement of character-state transformations on cladogram A after reinterpretation of homologies.

complexes scored for 34 characters involving buds, leaves, branching patterns, trichomes, inflorescences, flowers, and fruits (Coombs *et al.*, 1981; Donoghue, 1983a). Exine morphology was one character in the analysis: the states were pollen types Ia, Ib, and Ic; polarity and transformation series were assessed as discussed above. Cladograms were constructed using the WAGNER '78 computer program, which searches for the arrangement of taxa that minimizes the total number of character state changes, allowing both forward and reverse transitions (Farris, 1970). Several cladograms were generated because some characters exhibiting the most homoplasy, and about which there was the most uncertainty, were removed. The cladogram obtained using 28 characters (see FIGURE 3A) will serve as the basis for discussing exine evolution. The general conclusions below would not change substantially if any of the other cladograms shown in Donoghue (1983a) were used, because most of the changes in the exine occur within "stable clades" that remained unchanged on all cladograms or, more often, within the terminal taxa used in the analysis.

Detailed information about the cladistic analysis of *Viburnum* is given in Donoghue (1983a). It is important to note that each letter in FIGURE 3 symbolizes a species or a species complex, each of which is thought to be monophyletic. Of particular importance for this discussion, sect. MEGALOTINUS was split into *V. cylindricum* (Y) and subsect. PUNCTATA (M); *V. urceolatum* (U) was removed from sect. VIBURNUM (N); and *V. cordifolium* (C) was treated as distinct from *V. lantanoides* and *V. furcatum* of sect. PSEUDOTINUS (F). Section LENTAGO is symbolized by L.

On the cladogram in FIGURE 3A, pollen character-state changes occur only within the clade comprising taxa N through L; therefore, in FIGURE 3B–D this clade is enlarged while others are represented by single lines. On this cladogram it is most parsimonious to hypothesize that Ib pollen arose once in the common ancestor of *Viburnum urceolatum, V. cordifolium,* and sects. VIBURNUM, LENTAGO, PSEUDOTINUS, and MEGALOTINUS subsect. PUNCTATA (FIGURE 3B). However, the arrangement of these taxa in the cladogram requires reversals to type Ia pollen in *V. urceolatum* (U) and in sect. PSEUDOTINUS (F). In addition, according to this hypothesis, pollen type Ic must have been derived independently from type Ib in *V. cordifolium* (C) and within sects. VIBURNUM (N) and LENTAGO (L).

If this cladogram of *Viburnum* is substantially correct, there must have been reversals and parallelisms in the pollen character. However, the relatively small change in the cladogram of FIGURE 3A shown in FIGURE 3C makes it possible to do away with reversals from Ib to Ia that palynologists may consider to be unlikely. In this cladogram sect. VIBURNUM (N) is linked with sects. LENTAGO (L) and MEGALOTINUS subsect. PUNCTATA (M), and taxa C, F, and U are excluded. Such a change would, of course, entail some additional steps overall. However, many more steps would be necessary to eliminate the need to postulate the independent origin of Ic pollen; in particular, one would have to assume that C, L, and N were a clade within which sects. LENTAGO and VIBURNUM were not monophyletic. This is very unparsimonious because there is strong support from other characters for the linkage of C with F and of L with M, and for the monophyly of the terminal taxa, especially L (Donoghue, 1983a).

From the foregoing it seems that pollen type Ib may be a homology but that type Ic is very probably not, having arisen three separate times. The hypothesis that type Ic is not a homology leads to the question of whether the exact same morphology evolved three times, or whether there are morphological differences that corroborate the hypothesis of convergence. Comparison of type Ic pollen in sect. LENTAGO with that in sect. VIBURNUM reveals a rather consistent difference in shape (see FIGURE 1): grains in sect. LENTAGO are subprolate or more often euprolate, while both Ib and Ic pollen in sect. VIBURNUM (excepting *V. mongolicum*) is spheroidal or oblate (e.g., compare PLATE VIIA to VIID, E). This difference in shape between the groups lends support to the hypothesis of convergence suggested by the cladogram.

On reexamination *Viburnum cordifolium* pollen was found to lack scabrae on the pila, unlike type Ic pollen in sects. LENTAGO and VIBURNUM. This distinction, also noted by Böhnke-Gütlein and Weberling (1981), supports the hypothesis that the pilate exine of *V. cordifolium* was achieved independently. Because *V. lantanoides* and *V. furcatum* (both with type Ia pollen) are the sister group of *V. cordifolium* in FIGURE 3A, it may be that *V. cordifolium* pollen evolved directly from type Ia. This interpretation is more parsimonious than one that postulates a derivation through type Ib, which would require both the gain and loss of scabrae.

These observations suggest the alternative explanation of pollen character-state transformations, shown in FIGURE 3D. According to this interpretation, relationships remain the same as in the original cladogram (FIGURE 3A, B), but there are two origins of type Ib—one in the ancestor of N (oblate grains) and the other in the ancestor of M plus L (prolate grains). Type Ic has then evolved independently within each of these groups. *Viburnum cordifolium* pollen is considered to have evolved directly from type Ia. This hypothesis entails no reversals and requires a total of five state changes—one less than in FIGURE 3B.

In future cladistic analyses of *Viburnum,* pollen characters should be recoded to reflect the understanding of homologies obtained from the first cladograms. Indeed, it is now evident that pollen variation involves at least three characters that can vary independently: presence or absence of a reticulum, presence or absence of scabrae, and shape of the grain.

EXINE EVOLUTION IN CAPRIFOLIACEAE S.S.

TAXONOMIC DISTRIBUTION OF EXINE CHARACTERS. All species of the Caprifoliaceae *s.s.* examined have pollen in size-shape class II, but there is considerable variation in grain size (see FIGURE 1). With further study of a larger sample, this variation may prove taxonomically significant. However, size differences do not appear to be correlated with differences in exine structure and sculpture, nor do they correspond to the standard tribal classification of the group. Bassett and Crompton (1970) noted that variation in grain size within *Symphoricarpos* was correlated with chromosome number. The size reported here for *S. albus* is close to that reported for tetraploid individuals; octaploids are said to have larger grains.

The most significant pollen difference within the Caprifoliaceae *s.s.* is in exine structure. In tribes Caprifolieae, Triosteae, and Linnaeeae the complete tectum is raised on columellae of various sizes (pollen types IId and IIe, PLATES IXA, B; XB, D; XID). In contrast, in *Diervilla* and *Weigela* (tribe Diervilleae) columellae appear to be lacking (pollen type IIf, PLATE IXF).

The sculpturing of the exine also varies. In all species of tribes Caprifolieae and Diervilleae and most species of tribe Linnaeeae examined, spines are present. These processes vary somewhat in shape, size, and abundance. The two species of *Triosteum* (Triosteae) and the single species of *Symphoricarpos* (Linnaeeae) examined differ in lacking supratectal spines; instead the tectum is psilate or fossulate (pollen type IIe, PLATE XA–C).

POLARITY AND TRANSFORMATION SERIES. Since there is no well-corroborated hypothesis of the broader cladistic relationships of the Caprifoliaceae *s.s.*, it is difficult to employ outgroup comparison to assess polarity. Indeed, as noted above, it is not clear that the Caprifoliaceae *s.s.* constitute a monophyletic group. If both the Dipsacales (excluding *Viburnum, Sambucus,* and *Adoxa*) and the Caprifoliaceae *s.s.* were assumed to be monophyletic, then the Valerianaceae and the Dipsacaceae could be used as outgroups to assess polarities in the Caprifoliaceae *s.s.* The pollen of the Valerianaceae (e.g., PLATE XIE, F) and the Dipsacaceae is most like type IId (Clarke & Jones, 1977; Patel & Skvarla, 1979), which could therefore be considered ancestral in the Caprifoliaceae *s.s.* There are, however, some noteworthy differences between the pollen of these families. In particular, spines of various kinds are associated with the apertures in the Valerianaceae (Patel & Skvarla, 1979; PLATE XIE) and the Dipsacaceae.

Since many botanists (e.g., Wilkinson, 1949) believe that the Valerianaceae and the Dipsacaceae are derived from tribe Linnaeeae of the Caprifoliaceae *s.s.* through an ancestor similar to the extant genus *Nardostachys* DC. of the Valerianaceae, these two families may not be an appropriate outgroup. Even if the Caprifoliaceae *s.s.* were paraphyletic, pollen type IId might still be the ancestral condition in the Dipsacales, retained and modified in the evolution of the Valerianaceae and the Dipsacaceae.

The Rubiaceae are often considered to be closely related or even ancestral to the Caprifoliaceae (e.g., Cronquist, 1968, 1981). Pollen morphology is extremely variable within Rubiaceae (Erdtman, 1966), and without a better understanding of phylogenetic relationships within this family one cannot use it as an outgroup for the Caprifoliaceae *s.s.*

Lacking an outgroup, it would be possible to assess polarity tentatively if cladistic relationships were known within the Caprifoliaceae *s.s.* Although a cladistic analysis has not been performed, it is widely believed that tribe Caprifolieae (especially *Leycesteria*) is the most primitive group, from which the other three tribes have been derived (e.g., Wilkinson, 1949). Since all Caprifolieae have type IId pollen, this might provisionally be considered the ancestral state, with types IIe and IIf derived.

If type IId is considered ancestral based on the circumstantial reasoning above, how are the derived types IIe and IIf related to it—i.e., what is the transformation series? Two binary characters are involved in defining these exine types: presence or absence of columellae, and presence or absence of

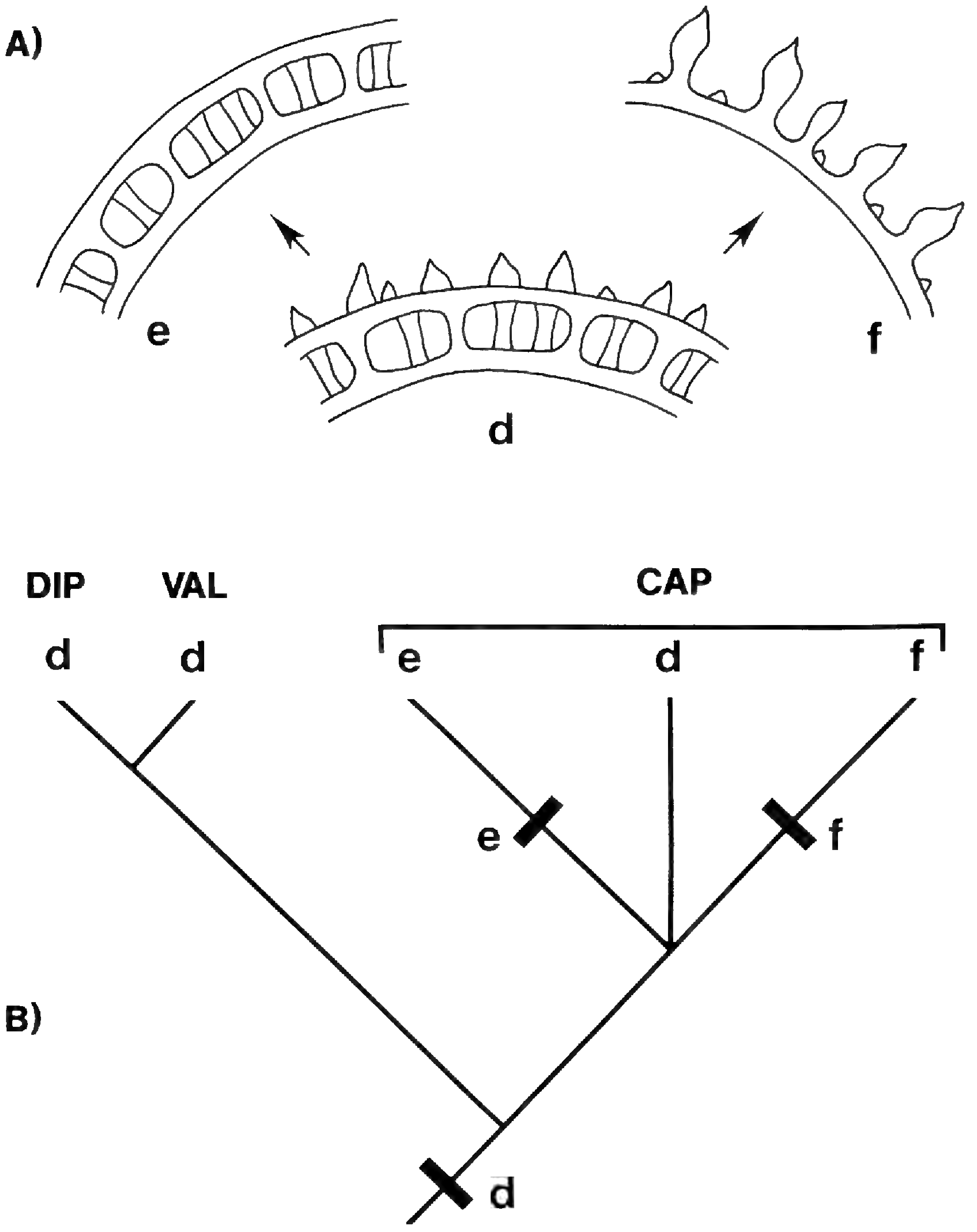

FIGURE 4. A, hypothesized transformation of pollen structure-sculpture classes d, e, and f within Caprifoliaceae *s.s.* (all size-shape class II). B, simplest *a priori* phylogenetic hypothesis for evolution of pollen in Caprifoliaceae *s.s.* (CAP), with Valerianaceae (VAL) and Dipsacaceae (DIP) as first outgroup.

supratectal spines. As in the case of *Viburnum, Sambucus,* and *Adoxa* discussed above, it is possible to choose from among possible transformation series based on parsimony. In this instance it is most parsimonious to assume that IIe and IIf are independently derived from IId (FIGURE 4A). Any other arrangement requires at least one additional step.

The derivation of type IIe from IId simply entails the loss of spines on the tectum. The most parsimonious explanation for the derivation of type IIf is that the columellae were lost, with the tectum therefore resting on the foot layer. An alternative explanation requires the loss of both the tectum surrounding the spines and the columellae not directly subtending spines. If this were the case, the spines in tribe Diervilleae would be derived in part from columellae and in part from tectum and supratectal spines. There is currently no evidence to support this more complicated explanation, but TEM studies might be useful.

CLADISTIC RELATIONSHIPS AND EXINE EVOLUTION. If pollen type IId is considered ancestral, then only possession of types IIe or IIf can provide evidence of monophyly. The simplest hypothesis would be that both IIe and IIf evolved only once (FIGURE 4B). If this is so, then type IIf indicates that tribe Diervilleae is monophyletic, which is corroborated by several other unique features (notably the elongate bilocular ovary that develops into a many-seeded capsule).

Pollen type IIe suggests that *Triosteum* and *Symphoricarpos* form a monophyletic group. *Triosteum* has previously been allied with *Viburnum* (Fritsch, 1891; Wagenitz, 1964) or has been placed in its own tribe, but Lewis and Fantz (1973) concluded that it is most similar to *Lonicera. Symphoricarpos* is generally considered the basal member of tribe Linnaeeae (Wilkinson, 1949). A phenetic analysis (Hsu, 1983) showed that *Triosteum* and *Symphoricarpos* have much in common, but to my knowledge, a direct phylogenetic relationship between them has never been defended. It is noteworthy that both genera have dry or mealy drupes with several one-seeded endocarps, and that the seedlings and sucker shoots of *Symphoricarpos* often have lobed leaves similar to those of *Triosteum.* On the other hand, the possibility that pollen type IIe arose independently in the two genera is suggested by a marked difference in pollen size. *Triosteum* has the largest and *Symphoricarpos* the smallest grains of any members of the Caprifoliaceae *s.s.* examined (TABLE 2, FIGURE 1). Determining whether IIe is a homology or if there has been convergence will require a detailed phylogenetic analysis of the Caprifoliaceae *s.s.*

SUMMARY

Although the pollen of the Caprifoliaceae *s.l.* is now very well known, the evolution of pollen diversity has not been considered in detail and the phylogenetic significance of pollen characters is not widely appreciated. This study confirms that there are major differences in pollen size and shape, as well as significant variation in exine structure and sculpturing, in the Caprifoliaceae *s.l.* These variables define two very different kinds of pollen: the large, oblate, tectate grains of the Caprifoliaceae *s.s.*, and the small, usually prolate, semitectate ones of *Viburnum, Sambucus,* and *Adoxa.* This distribution of pollen types is consistent with the idea that the Caprifoliaceae *s.l.* are divisible into two distinct lineages and do not constitute a monophyletic group. It may therefore be inappropriate to consider the evolution of pollen morphology in the Caprifoliaceae *s.l.* as a whole because there may never have been a direct evolutionary transition between the two main pollen types within the group. However, it is appropriate to consider pollen evolution within each of the two component lineages, especially within the clade comprising *Viburnum, Sambucus,* and *Adoxa.*

Previous discussions of pollen evolution in the Caprifoliaceae *s.l.* (and in most other groups) have been based upon generally accepted but mostly untested ideas about which groups are relatively primitive and which ones advanced, and upon presumably general trends. In the present analysis pollen evolution is considered in the context of explicitly cladistic hypotheses for the groups involved. Polarity of pollen characters is assessed by outgroup comparison, and the most parsimonious transformation series is established. In *Viburnum* semitectate, reticulate grains with smooth muri appear to represent the ancestral condition; the addition of scabrae and the breakdown of the reticulum are derived. When exine characters are used along with others, a cladogram is obtained that may require reversals but quite certainly necessitates the independent evolution of retipilate or pilate grains in three separate groups. Upon reexamination of the pollen in these three groups, slight but consistent differences are found that corroborate the hypothesis of convergence and suggest a more parsimonious interpretation of pollen evolution. The retipilate/pilate condition should not be considered a homology, and pollen characters should be recoded in subsequent phylogenetic analyses of *Viburnum.*

A detailed analysis of pollen evolution in the Caprifoliaceae *s.s.* is not possible at this time because this group may not be monophyletic, its outgroups are equivocal, and a hypothesis of cladistic relationships within the group is not yet available. Circumstantial evidence suggests, however, that grains with the tectum raised on columellae and with supratectal spines are probably ancestral. Spines are lacking in *Symphoricarpos* and *Triosteum,* which may indicate a sister-group relationship between these genera. The absence of columellae in the Diervilleae corroborates the monophyly of this tribe.

ACKNOWLEDGMENTS

I first studied pollen diversity in *Viburnum* at Michigan State University, where I was assisted by B. Scoviac. The SEMGs presented here were executed by E. Seling, of the Museum of Comparative Zoology SEM Laboratory, Harvard University. Funding for microscopy was provided by the Arnold Arboretum of Harvard University and by an NIH Genetics Training Grant awarded to the Department of Biology, Harvard University. I thank the directors of ENCB, MICH, MSC, NY, US, and especially A and GH, for allowing me to remove pollen from specimens in their collections. N. Miller, P. Stevens, A. Tryon, and C. Wood gave encouragement and advice, and J. Doyle provided a very helpful review of the manuscript. M. Carter aided in preparing samples, S. Fansler drew the figures, and K. Horton typed the text and tables.

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EXPLANATION OF PLATES

PLATE I

Pollen of *Viburnum* sects. Odontotinus (A–D) and Oreinotinus (E, F): A, *V. foetidum* (*Forrest 18129,* A); B, *V. dilatatum* (*Ohashi, Nakaike, & Tateishi 70627,* A); C, *V. japonicum* (*Ichikawa 26,* A); D, *V. wrightii* (*Hatusima 4206,* A); E, F, *V. microcarpum* (*Ventura A. 819,* ENCB); all type Ia. Scale bars = 10 μm (A–C, E) or 1 μm (D, F).

PLATE II

Pollen of *Viburnum* sect. Solenotinus: A, *V. farreri* (*Rock 12142,* A); B, *V. suspensum* (*Hatusima 864,* GH); C, *V. oliganthum* (*H. Smith 1961,* A); E, *V. odoratissimum* (*Alcasid 70,* A); F, *V. odoratissimum* (*H. H. Hu 770,* A); all type Ia. Scale bars = 10 μm (A–E) or 1 μm (F).

PLATE III

Pollen of *Viburnum* sects. Solenotinus (A, B) and Tinus (C–F): A, B, *V. brachybotryum 12790A,* A); C, D, *V. tinus* (*Marchesetti 2752,* GH); E, *V. davidii* (*Wilson 3728,* A); F, *V. atrocyaneum* (*Rock 8905,* A); all type Ia. Scale bars = 10 μm (A, C, E, F) or 1 μm (B, D).

PLATE IV

Pollen of *Viburnum* sects. Megalotinus (A, B), Viburnum (C, D), and Tomentosa (E, F): A, B, *V. cylindricum* (*Iwatsuki, Koyama, Fukuoka, & Nalampoon 9424,* A); C, D, *V. urceolatum* (*Tashiro s.n.,* 1917, A); E, F, *V. hanceanum* (*Chun 5314,* A); all type Ia. Scale bars = 10 μm (A, C, E) or 1 μm (B, D, F).

PLATE V

Pollen of *Viburnum* sects. Opulus (A, B) and Pseudotinus (C–F): A, *V. sargentii* (*Furuse s.n.,* 20 June 1961, A); B, *V. sargentii* (*Furuse s.n.,* 9 June 1958, A); C, D, *V. furcatum* (*Togashi 7145,* A); E, F, *V. cordifolium* (*Forrest 11892,* A). A–D, type Ia; E, F, type Ic. Scale bars = 10 μm (A–C, E) or 1 μm (D, F).

PLATE VI

Pollen of *Viburnum* sects. Viburnum (A–D) and Megalotinus (E, F): A, B, *V. macrocephalum* (*Wilson 1835,* A); C, D, *V. utile* (*H. C. Chow 145,* A); E, F, *V. punctatum* (*Schneider 691,* A); all type Ib. Scale bars = 10 μm (A, C, E) or 1 μm (B, D, F).

PLATE VII

Pollen of *Viburnum* sects. Lentago (A–C) and Viburnum (D–F): A, B, *V. prunifolium* (*Bartholomew 1518,* GH); C, *V. prunifolium* (*Bush 7939,* GH); D, *V. burejaeticum* (*Ishidoya s.n.,* 1918, A); E, *V. veitchii* (*Lingnan Univ. Herb. 78294,* A); F, *V. mongolicum* (*Rock 12480,* A); all type Ic. Scale bars = 10 μm (A, D, E) or 1 μm (B, C, F).

PLATE VIII

Pollen of *Sambucus* (A, B), *Adoxa* (C, D), and Caprifolioideae tribes Caprifolieae (E) and Linnaeeae (F): A, B, *Sambucus pubens* (*Forbes 3433,* GH); C, D, *Adoxa moschatellina* (*Furuse s.n.,* 15 May 1961, A); E, *Lonicera chrysantha* (*Purdom 6b,* A); F, *Heptacodium jasminoides* (*Keng 1068,* A). A–D, type Ia; E, F, type IId. Scale bars = 10 μm (A, C, E, F) or 1 μm (B, D).

PLATE IX

Pollen of Caprifolioideae tribes Caprifolieae (A, B) and Diervilleae (C–F): A, *Leycesteria formosa* (*Schneider 1394*, A); B, *L. gracilis* (*Forrest 9377*, A); C, D, *Diervilla lonicera* (*Jamison*(?) *s.n.*, 1930, GH); E, F, *Weigela florida* (*Moran 4257*, GH). A, B, type IId; C–F, type IIf. Scale bars = 10 μm (A, C, E) or 1 μm (B, D, F).

PLATE X

Pollen of Caprifolioideae tribes Triosteae (A, B) and Linnaeeae (C–F): A, *Triosteum aurantiacum* (*Pennell s.n.*, 1924, GH); B, *T. perfoliatum* (*McGregor 14287*, GH); C, *Symphoricarpos albus* (*Pease & Bean 26146*, GH); D, *Kolkwitzia amabilis* (*Rehder, Arnold Arb. 6475*, GH); E, F, *Linnaea borealis* (*Woodworth 388*, GH). A–C, type IIe; D–F, type IId. Scale bars = 10 μm (A, C, E) or 1 μm (B, D, F).

PLATE XI

Pollen of Caprifolioideae tribe Linnaeeae (A–D) and Valerianaceae (E, F): A–C, *Abelia spathulata* (*Furuse s.n.*, 7 May 1957, A); D, *Dipelta yunnanensis* (*Rock 16150*, A); E, F, *Nardostachys jatamansii* (*Rock 14168*, GH); all type IId. Scale bars = 10 μm (A, C, E) or 1 μm (B, D, F).

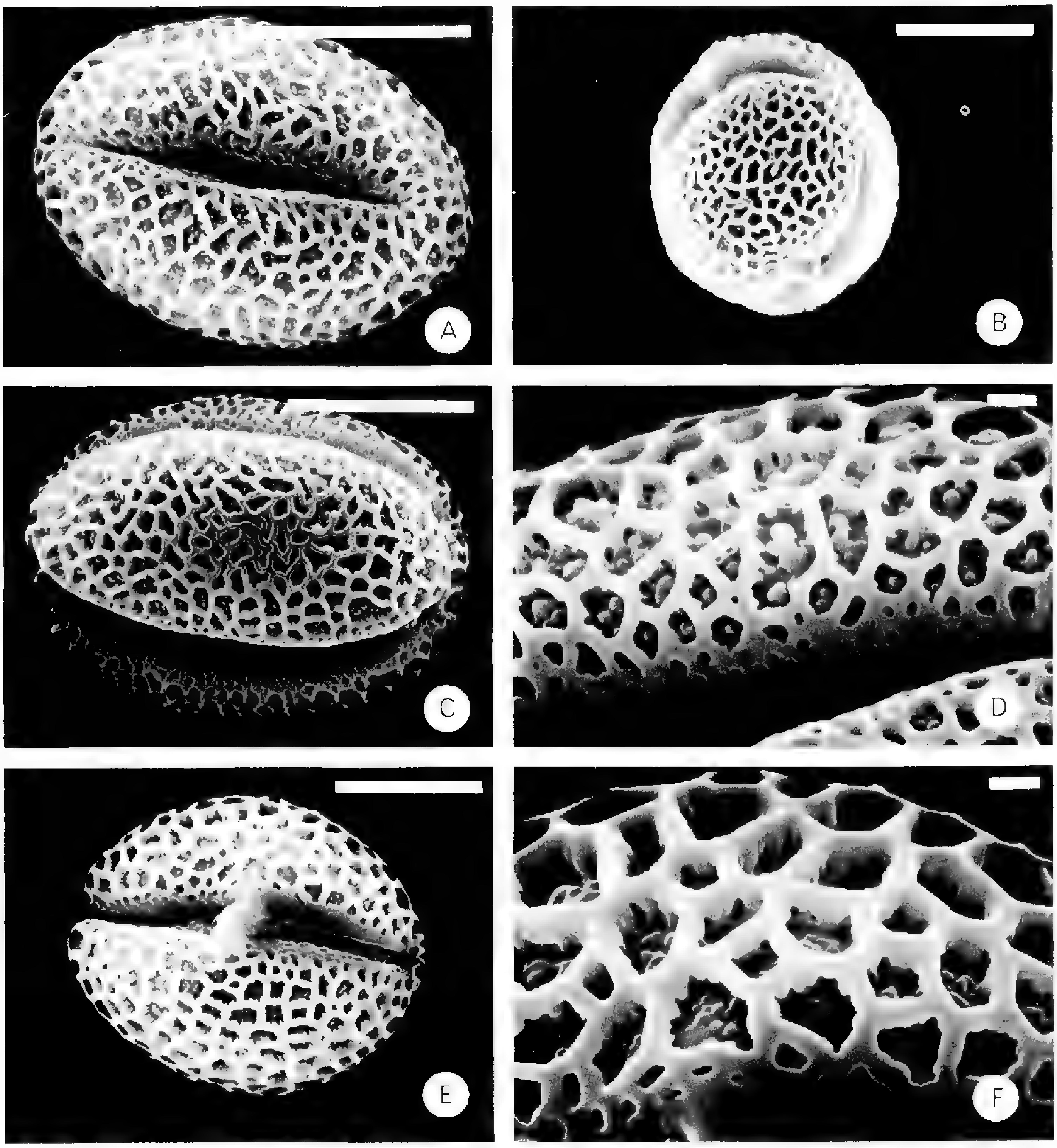
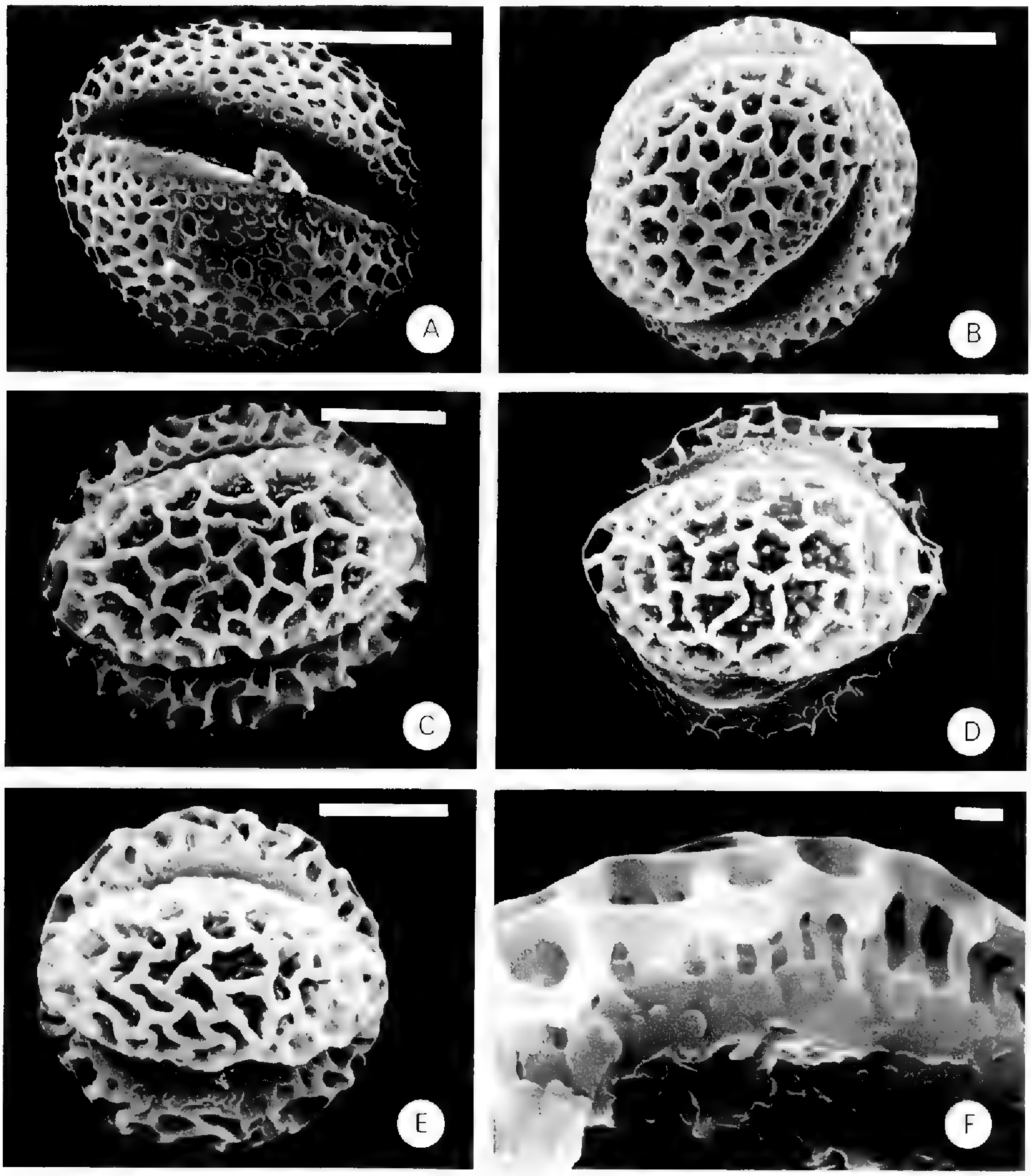


PLATE I



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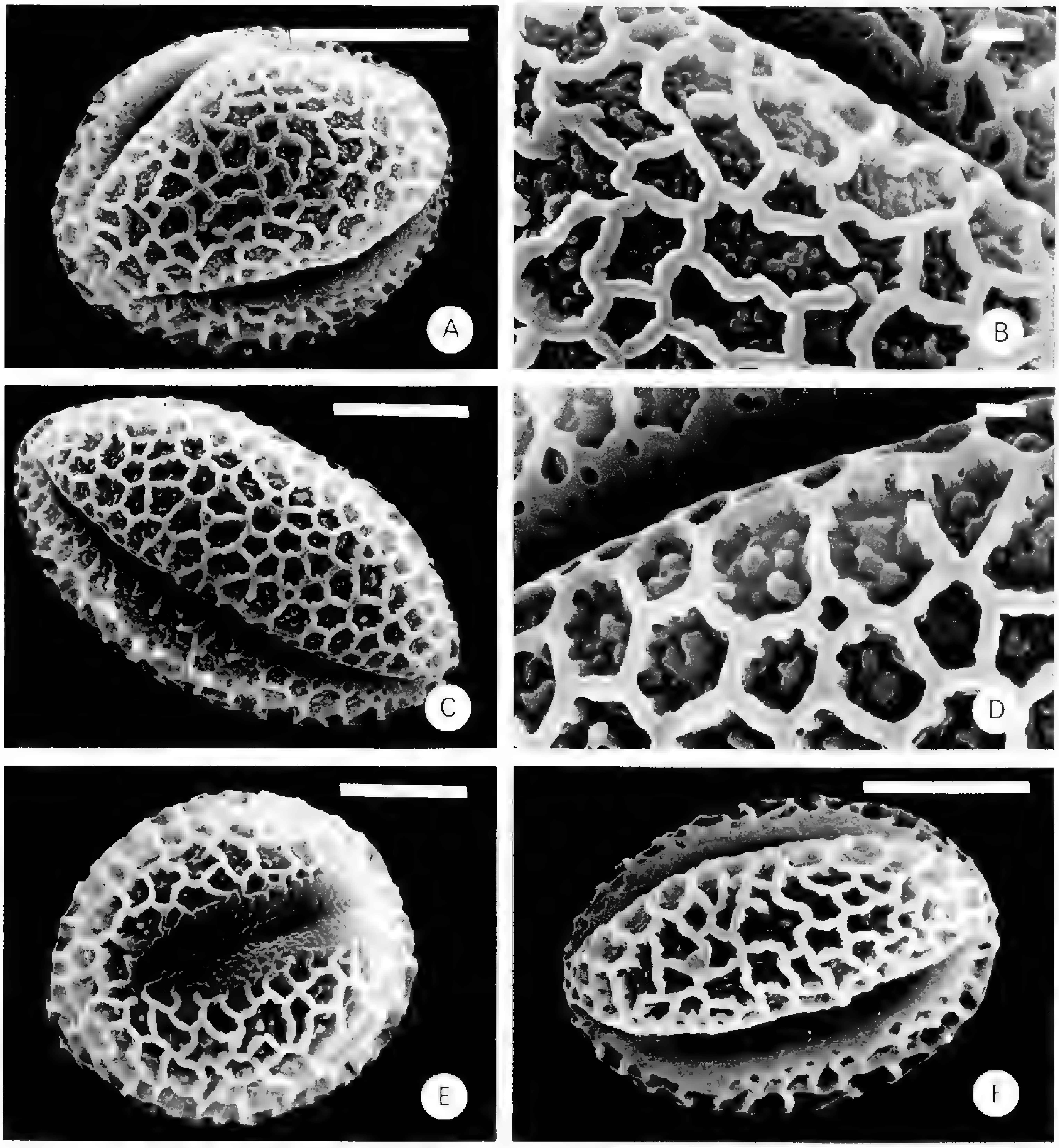

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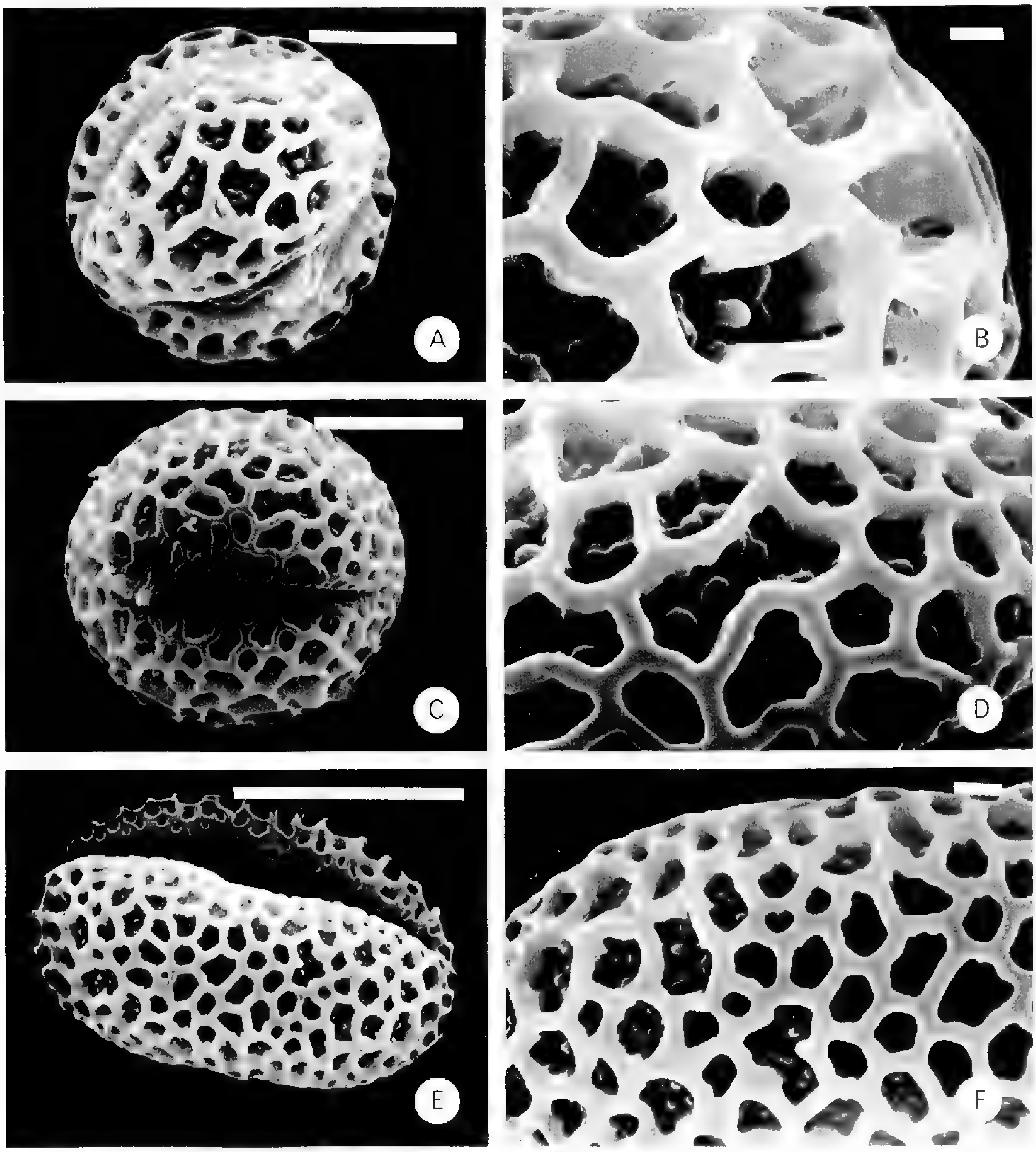

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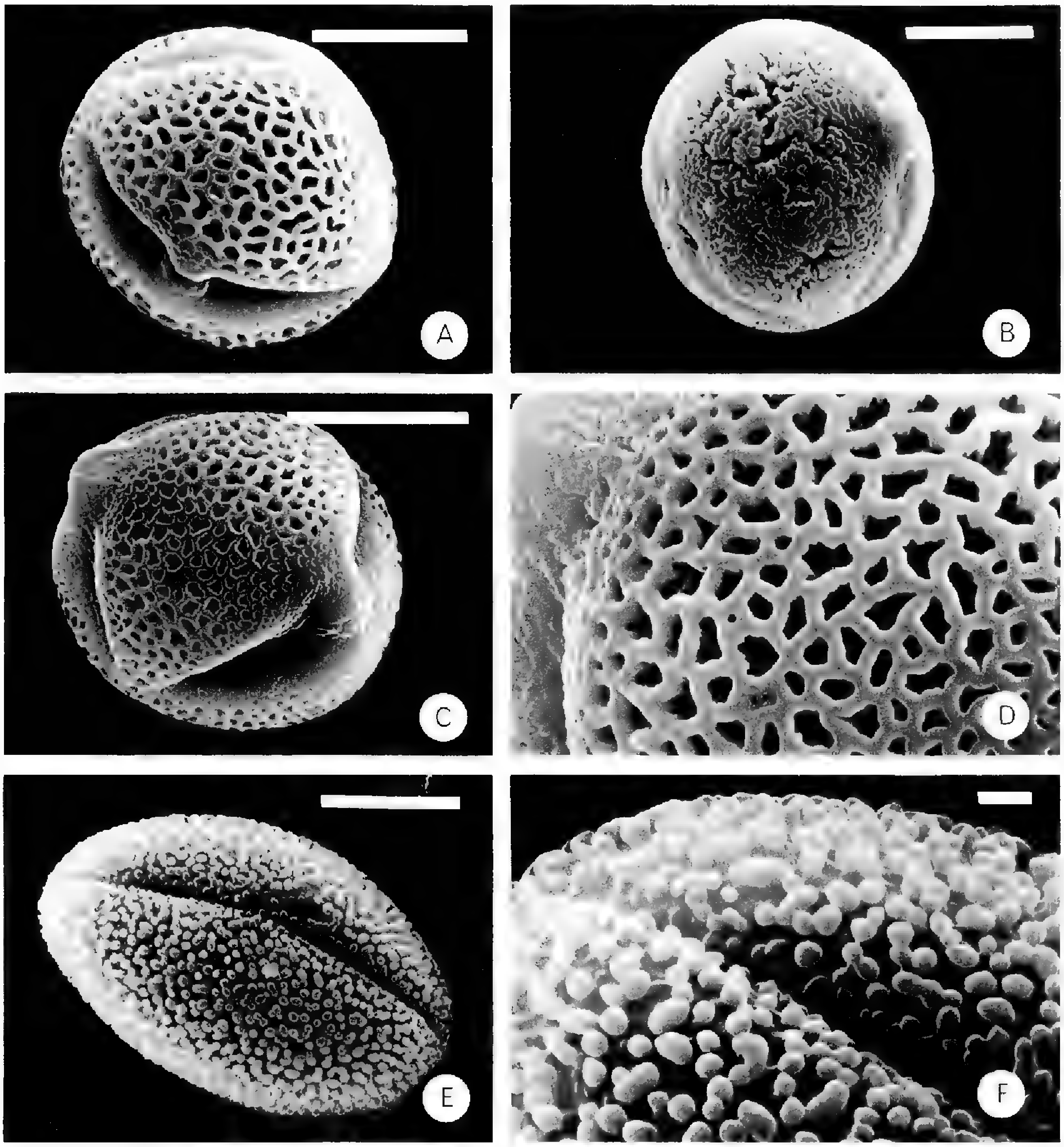

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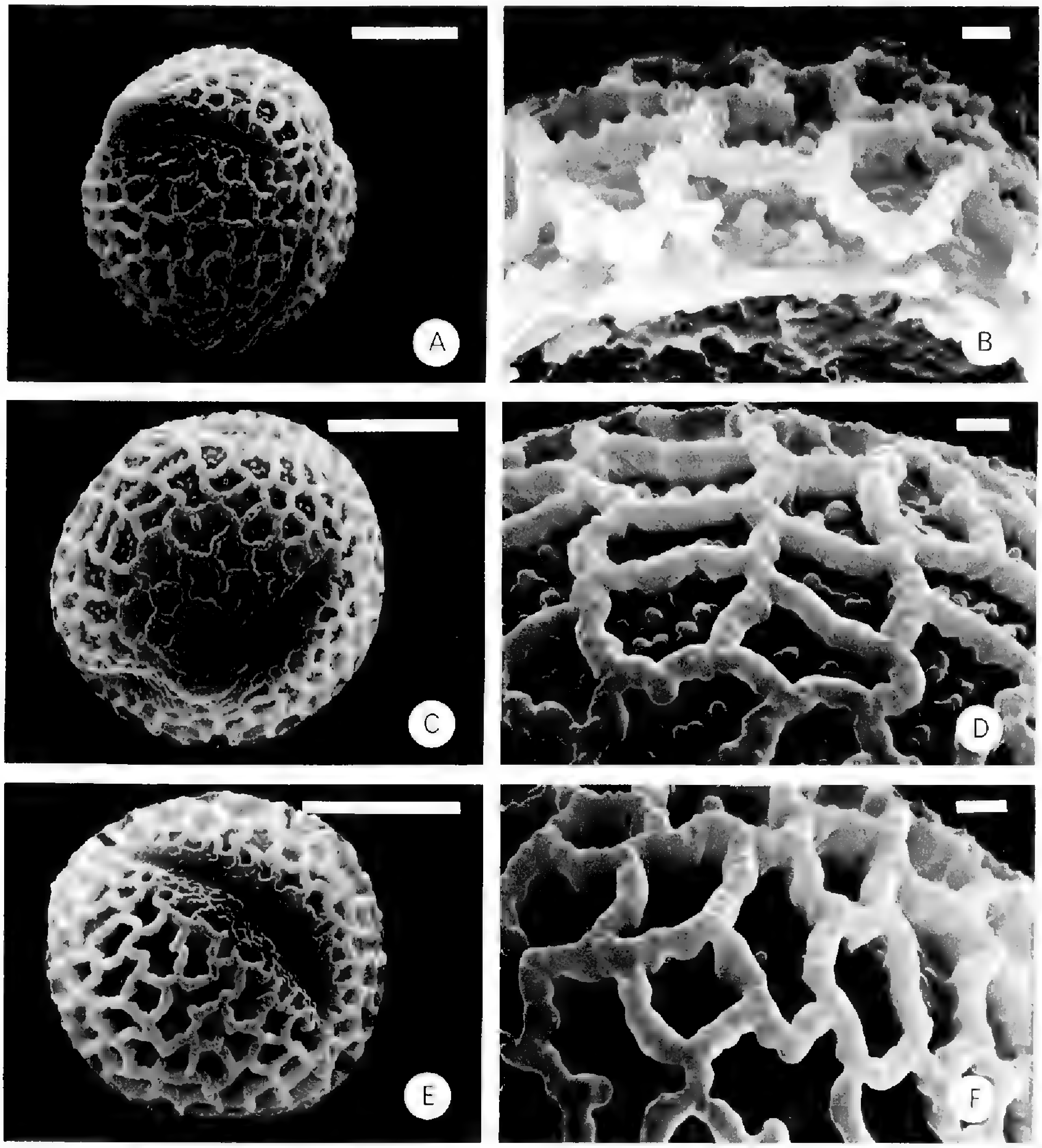

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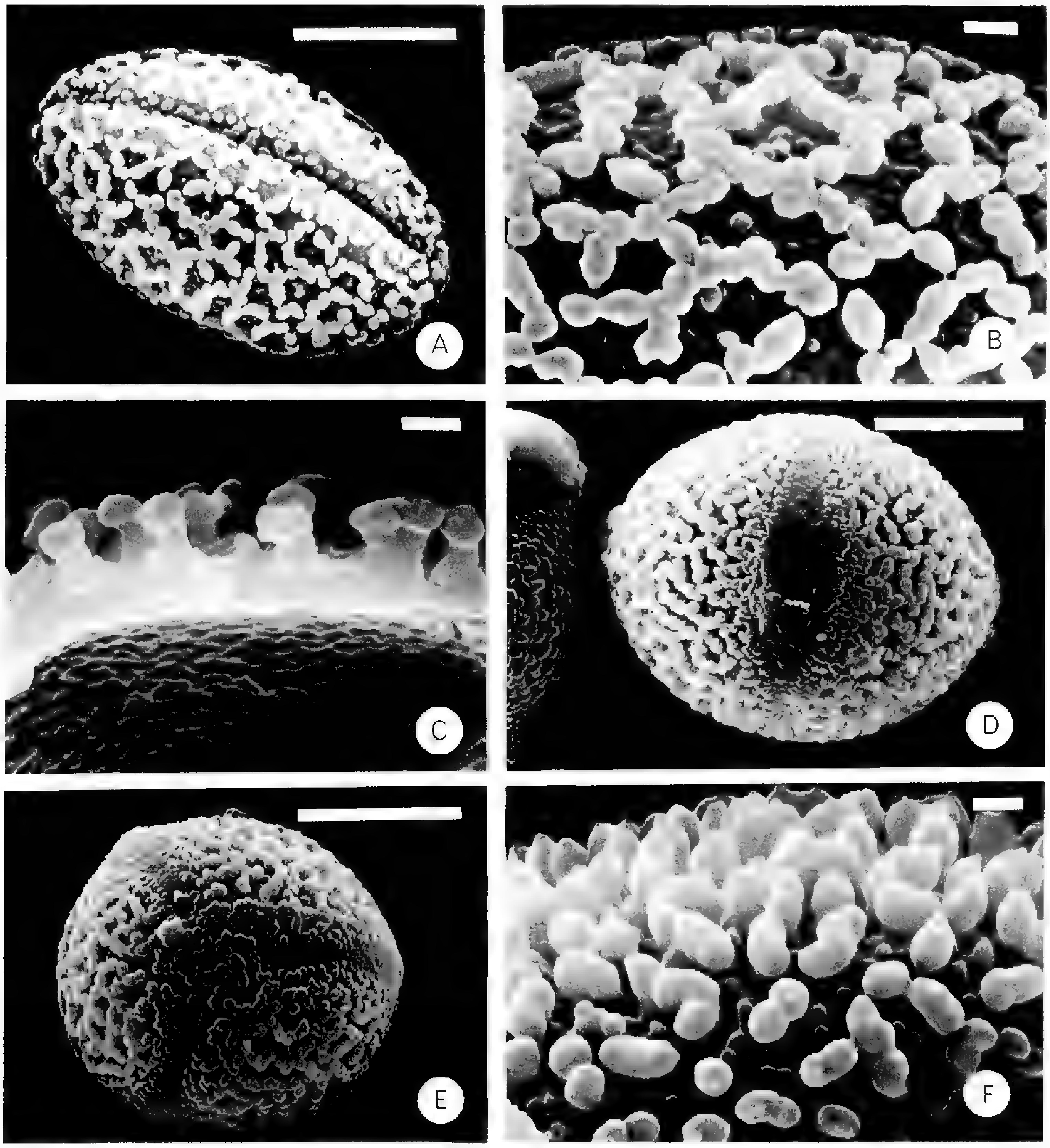

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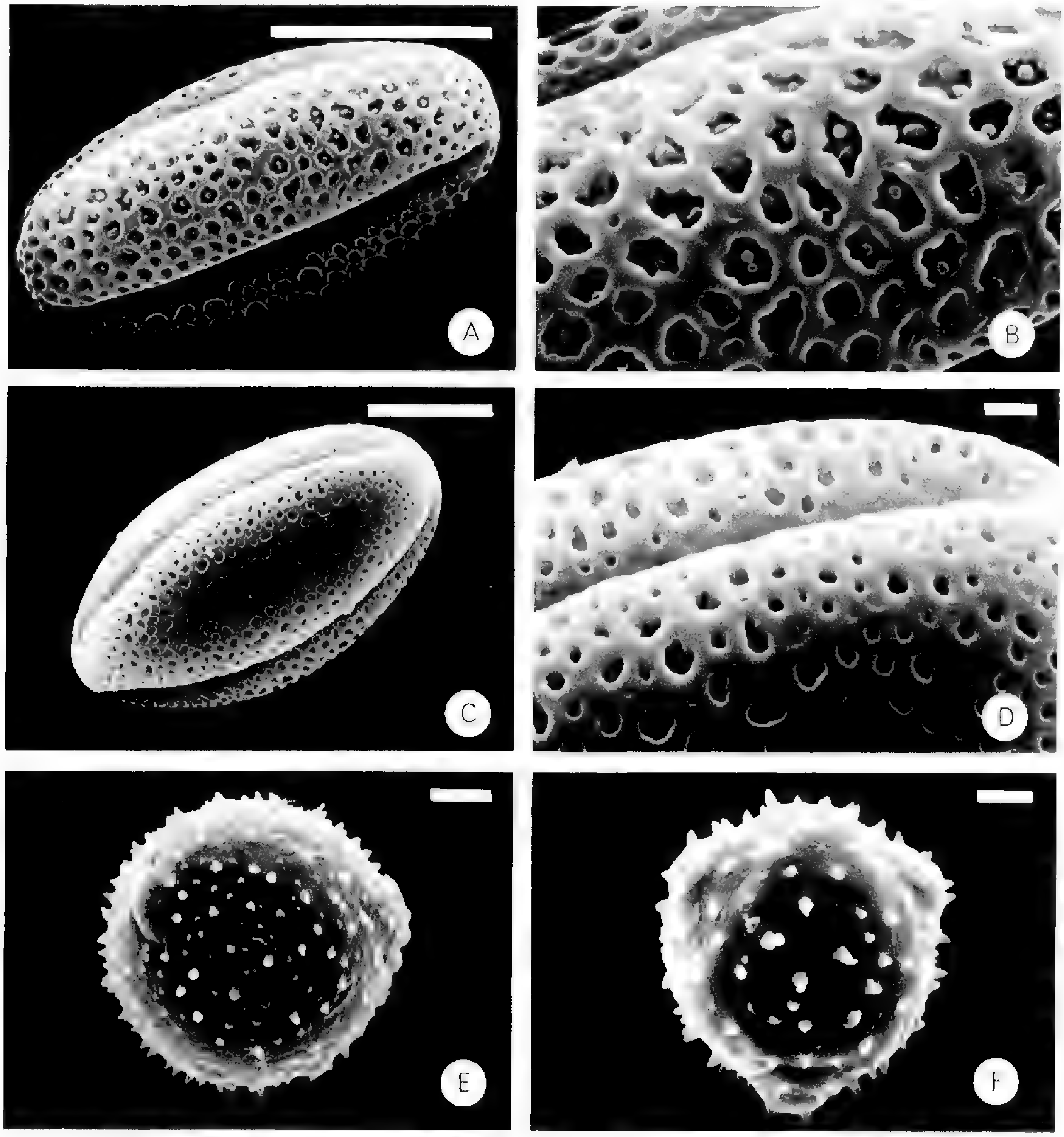

PLATE VIII

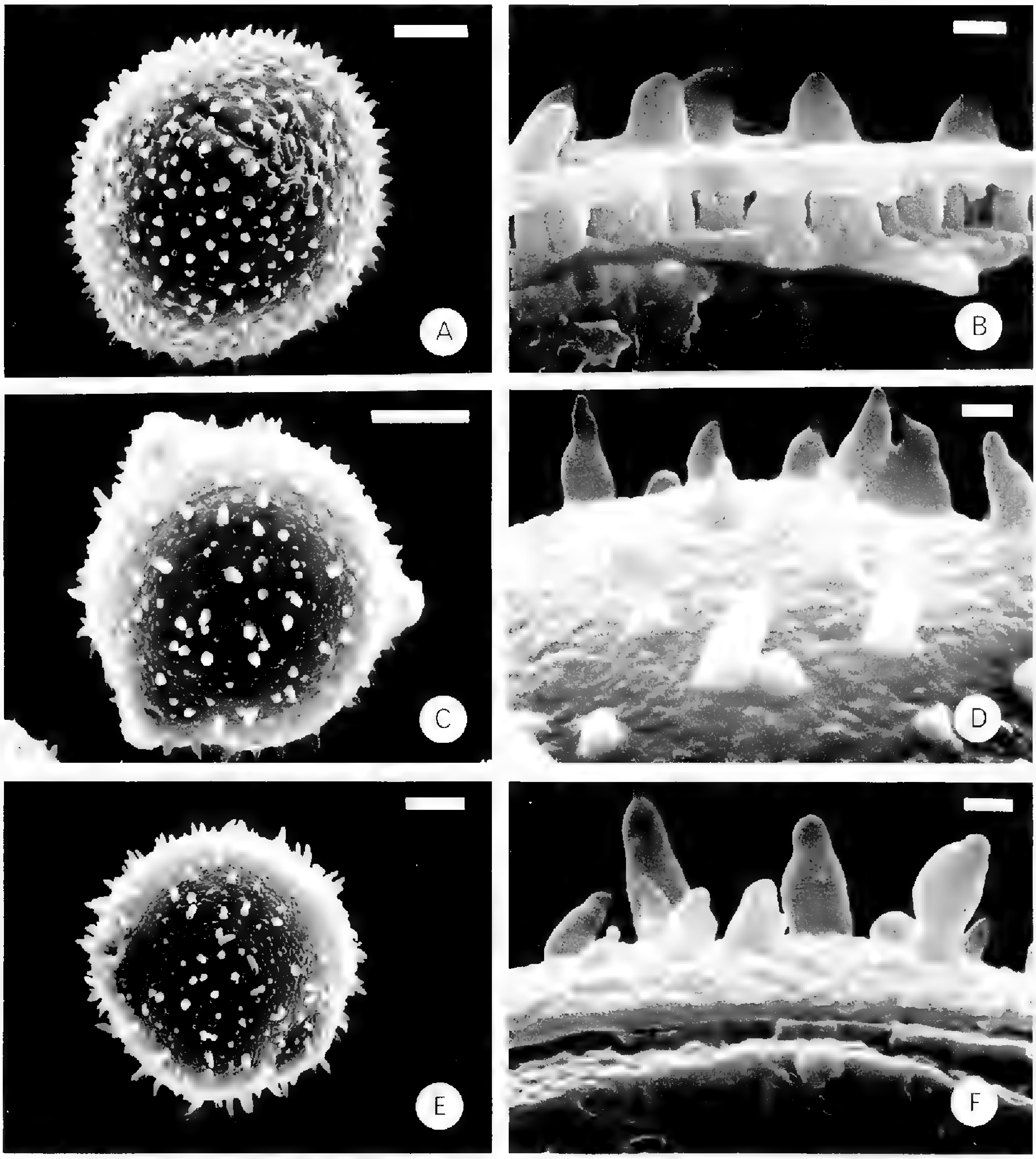

PLATE IX

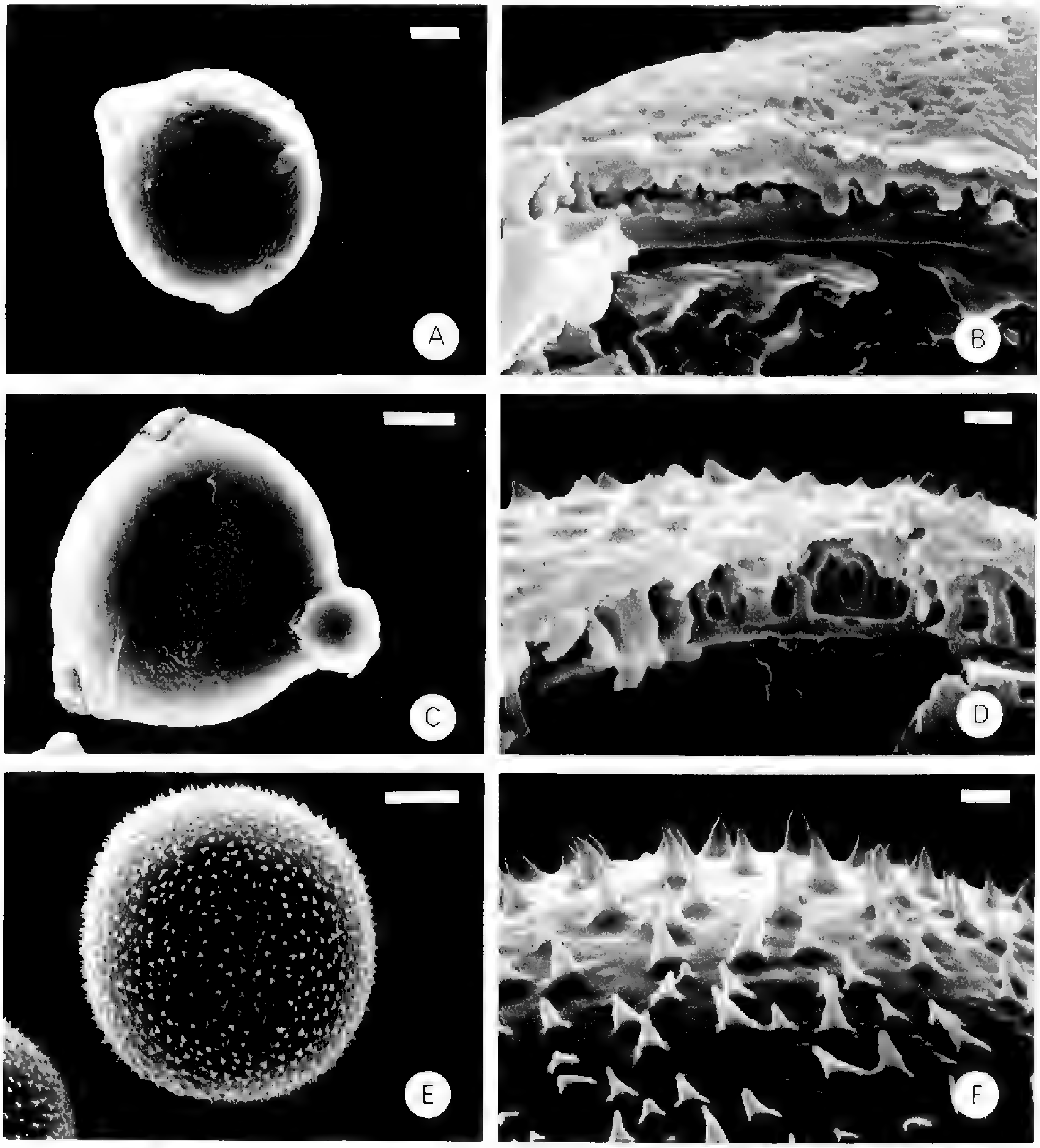

PLATE X

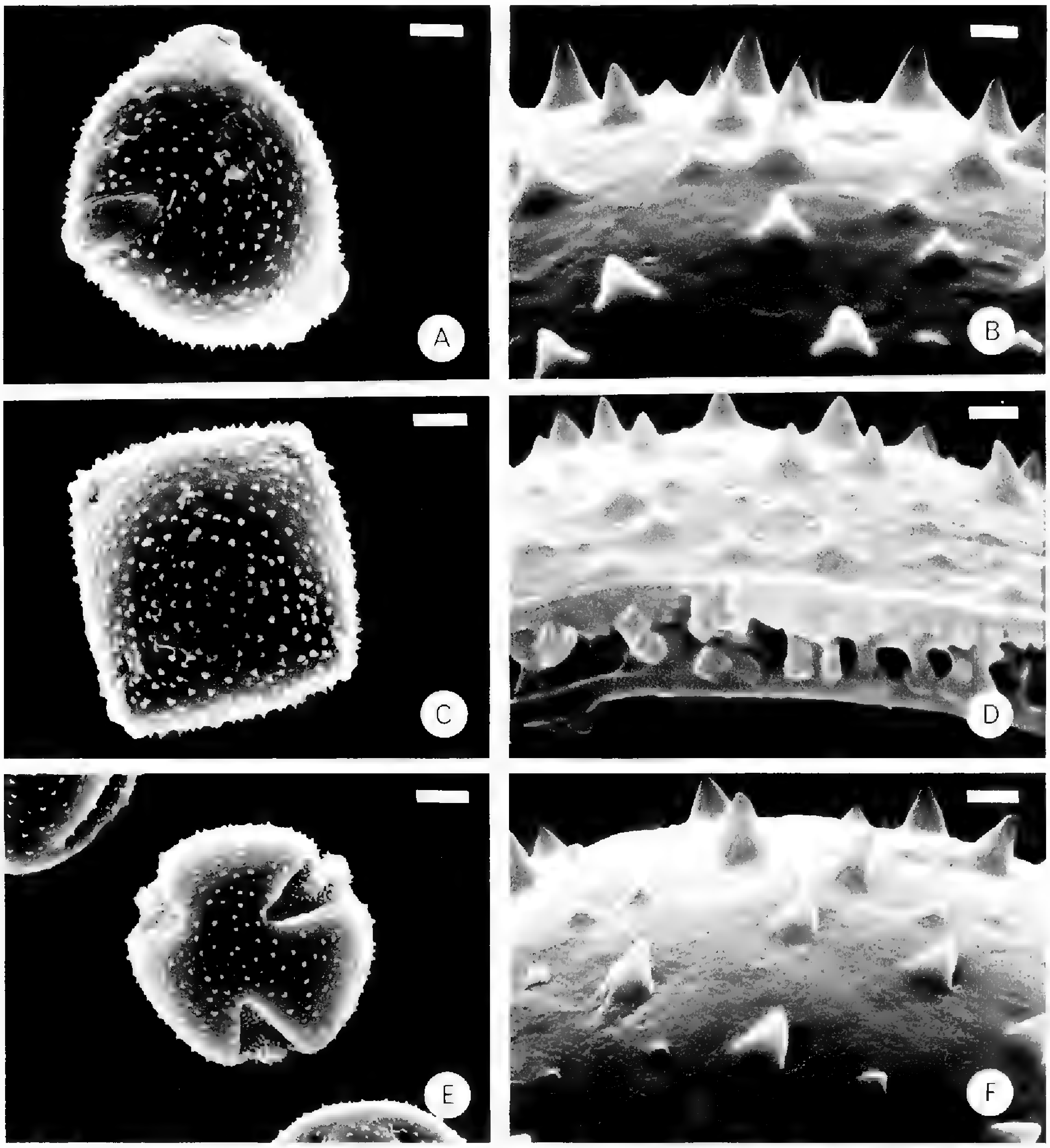

PLATE XI

NOTES ON VACCINIUM AND AGAPETES (ERICACEAE) IN SOUTHEAST ASIA

P. F. Stevens

Agapetes D. Don ex G. Don subg. *Agapetes* and a number of sections of *Vaccinium* L. from mainland Southeast Asia, especially sects. *Galeopetalum* J. J. Smith, *Aëthopus* Airy Shaw, *Epigynium* (Klotzsch) Hooker f., and *Conchophyllum* Sleumer, are clearly closely related in a number of morphological and anatomical features. *Agapetes* and *Vaccinium* can be distinguished, albeit very unsatisfactorily, mainly by inflorescence and flower size (Stevens, 1972; *Agapetes* subg. *Paphia* (Seemann) P. F. Stevens is not immediately related). *Agapetes* subg. *Agapetes* usually has inflorescences with fewer than 15 flowers; the flowers sometimes have wings on the calyx and corolla, or sometimes on only one of these; and the corolla is usually tubular, more than 1 cm long, and with thick walls. *Vaccinium* species of the Southeast Asian mainland ordinarily have inflorescences with more than ten flowers; the flowers are generally unwinged; and the corolla is usually urceolate, less than 1 cm long, and with thinner walls.

During identification of material of the two genera, a number of previously undescribed or imperfectly known taxa of *Vaccinium* and *Agapetes* from the northwestern India–Burma–Vietnam–southern China area were found; these are described below. Huang (1983) has recently treated the genus *Agapetes* in Yunnan in considerable detail, and Fang and Pan (1981) described a number of new taxa of *Vaccinium* from China. Their findings are integrated with those presented here. Additional notes, mostly range extensions, are also given for a few species.

Since the distinction between *Vaccinium* sect. *Epigynium* and *Agapetes* subg. *Agapetes* ser. Robustae Airy Shaw subser. Chartacea Airy Shaw is rather slight and new taxa are described in both groups, a combined key to all the taxa recognized in these two groups is also presented.

The various taxa discussed are dealt with alphabetically by genus, section or series and subseries, and species. Full literature citations to species previously described are not given, but reference is made to the basionym and to a work where pertinent literature is traceable; overlooked or subsequent literature is also cited where necessary. In the descriptions "filament length" is the length by which the filament exceeds the anther. In all taxa described the receptacle-pedicel junction is articulated, and the fruit has a five-locular ovary with five inpushings of the ovary wall alternating with the five septae. All taxa also have a phellogen that is superficial in origin (i.e., arising just below the epidermis), and leaves that lack a hypodermis.

Journal of the Arnold Arboretum **66**: 471–490. October, 1985.

Four of the taxa discussed here, *Agapetes rubropedicellata, Vaccinium praeces, V. lamellatum,* and *V. brevipedicellatum* C. Y. Wu, combine the characteristics of the two genera in various ways. Two previously overlooked characters, unicellular hairs borne on epidermal papillae and mucilaginous seed coats, also occur in some of these taxa, as well as in some, but not all, species of both *Agapetes* subg. *Agapetes* and the related sections of *Vaccinium*; they are of limited distribution elsewhere in the Vaccinieae (both occur in South American taxa, which are not immediately related). Although it is becoming increasingly apparent that *Agapetes* subg. *Agapetes* is polyphyletic (as is discussed further), I have described species under that taxon below. Generic limits in tropical Vaccinieae as a whole are in considerable disarray, but we still need to know a great deal more about the basic variation in the tribe before radically rearranging these limits, as is needed.

PREVIOUSLY OVERLOOKED CHARACTERS USED IN CLASSIFICATION

INDUMENTUM

Many Vaccinieae have unicellular hairs and also multicellular, often glandular hairs with short to long stalks. Unicellular hairs are nearly always scattered evenly on a smooth epidermis, although in a few taxa (e.g., *Vaccinium didymanthum* Dunal, from South America, and *V. acuminatissimum* Miq., from Malesia) they may be aggregated around the bases of (or even borne on!) the multicellular glandular hairs. Some of the taxa described below have a minutely papillate epidermis, with the unicellular hairs borne singly or in small groups on the papillae.

The occurrence of hairs on the papillae can be considered a derived condition; they are known from only a few small-leaved species of *Agapetes* (e.g., *A. mannii* Hemsley, *A. forrestii* W. E. Evans) and many species of *Vaccinium* sect. *Conchophyllum*[1] in the Old World Vaccinieae. In the latter taxon these hairs occur in *V. manipurense* (Watt ex Brandis) Sleumer, which has the same flower type as *V. conchophyllum,* a species that lacks hairs on papillae. *Vaccinium triflorum* Rehder, a member of the section with the broader flowers, also has hairs borne in groups on papillae!

SEED TYPE

Variation in the structure of the seed has been almost completely neglected in tropical Vaccinieae. However, this has considerable systematic and ecological significance, as a survey in progress is showing.

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[1] As was shown earlier (Stevens, 1972), the species of *Vaccinium* sect. *Vitis-Idaea* (Moench) Koch endemic to Southeast Asia are dissimilar in details of anatomy and morphology from *V. vitis-idaea* L., the type species of the section. However, they agree in all these details with *V. conchophyllum* Rehder, the type of *Vaccinium* sect. *Conchophyllum,* and thus belong there. *Vaccinium* sect. *Conchophyllum* as so defined is rather heterogeneous, since the type species and the species transferred from sect. *Vitis-Idaea* have inflorescences borne near the ends of the twigs and have urceolate flowers, while the other members of the section (as delimited by Sleumer, 1941) have inflorescences often borne along the twigs and broader, urceolate-campanulate flowers.

The species described below as having a testa with thin-walled cells that become mucilaginous on wetting also have an embryo that dries a dark color; the embryo was probably green when living (Airy Shaw, 1968; Stevens, 1972). Although the walls of testa cells are thin (often ca. 3 μm thick or less), they have distinctive anastomosing bands of thickening running more or less down the long axes of the cells or sometimes slightly oblique to them. Between these thickened bands are elongated unthickened areas.

The more common testa type in the Vaccinieae also occurs in some of the species described here. The inner periclinal and anticlinal cell walls are much thickened; the thickenings sometimes almost obscure the cell lumen, being up to 30 μm wide on anticlinal walls. Unthickened areas are minute (less than 3 μm wide) and circular in surface view; they usually do not show any obvious patterning, although in a few taxa (but not in the ones discussed below) they may be in lines. The embryo is commonly, but not always, white. In both testa types the outer periclinal walls of the testa cells are very thin.

The mucilaginous seed is also probably a derived condition, although it has a rather wide distribution within the Vaccinieae. In Indo-Malesian Vaccinieae it is known only in several species of *Agapetes* and *Vaccinium* sects. *Aëthopus, Epigynium,* and *Rigiolepis* (Hooker f.) Sleumer (perhaps a modified type), and in some, but by no means all, species of sect. *Galeopetalum,* as well as in *V. piliferum* (Hooker f. ex C. B. Clarke) Sleumer, a species of uncertain affinity. It is also known in a number of Vaccinieae from South America, although the crustaceous testa frequently occurs there also; variation in South America may also be at the infrageneric level, despite the narrower generic limits adopted there.

SIGNIFICANCE OF CHARACTER-STATE VARIATION

The described pattern of variation in seed and epidermis is not congruent with the limits of *Vaccinium* and *Agapetes* as delimited here: some taxa of both genera have the derived character states. Other distinctive characters show the same pattern of distribution. Thus, pseudoverticillate leaves in the Vaccinieae occur in a number of the larger-leaved species of *Agapetes* and also in *Vaccinium* sect. *Epigynium*: expanded leaves separated by short internodes alternate with leaves reduced to scales and separated by long internodes. Such pseudoverticillate leaves can be considered a derived condition (cf. Sleumer, 1941); they are extremely uncommon elsewhere in the Vaccinieae. Characters such as the early development of lenticels and the presence of setular hairs or coarsely serrate leaf margins show a similar pattern of occurrence.

Many of these characters vary independently, and none occurs only in the group of species that has been called *Agapetes* subg. *Agapetes,* let alone in *Agapetes* sensu lato (including subg. *Paphia*—Stevens, 1972). *Agapetes* subg. *Agapetes* is still definable as only those Vaccinieae on mainland Southeast Asia that have large, thick-walled, often tubular corollas and few-flowered inflorescences. These characters are loosely functionally correlated: when flowers are large, one expects fewer of them in an inflorescence. In addition, distinguishing between *Agapetes* and *Vaccinium*—even using flower size—is becoming less easy, as is clear from the descriptions of the new taxa below.

Since many taxa with the distinctive character states discussed above are placed in different genera because of differences in flower size but are similar in other characteristics (see also Airy Shaw, 1935), the evidence very strongly suggests that large flowers are of polyphyletic origin in Southeast Asian Vaccinieae, and that *Agapetes* subg. *Agapetes* is a group that represents a grade or level of organization. As might be expected of such a group, its limits coincide only with the character used to circumscribe it, and it has little predictive value. This idea is more likely than the suggestion that characters of indumentum, seed, and leaf are all of polyphyletic origin within both *Agapetes* and *Vaccinium* and agrees with the notion that ornithophily is a factor of major significance in the evolution of montane tropical Ericaceae (Stevens, 1976, 1982).

KEY TO VACCINIUM SECT. EPIGYNIUM AND AGAPETES SUBG. AGAPETES SER. ROBUSTAE SUBSER. CHARTACEA[2]

1. Leaves pseudoverticillate, all fully developed leaves of an innovation separated by less than 1.5 cm.
   2. Lamina entire. . . . . *V. ardisioides* Hooker f.
   2. Lamina serrate or serrulate.
      3. Inflorescences corymbose/subumbellate; bracts at base of inflorescence inconspicuous, deciduous or not.
         4. Inflorescence axis, pedicels, and flowers pubescent. . . . . . 10. *V. praeces.*
         4. Inflorescence axis, pedicels, and flowers glabrous.
            5. Lamina (10–)13–18 cm long; inflorescence axis 4–10 cm long, if less, with flowers along its length.
               6. Inflorescence axis 8–10 cm long; corolla urceolate, 6–7 mm long. . . . . *A. dispar* Airy Shaw.
               6. Inflorescence axis less than 5.5 cm long; corolla cylindrical, at least 1 cm long.
                  7. Upper surface of lamina with raised venation; inflorescence axis 4–5.5 cm long; corolla ca. 1.2 cm long. . . 4. *A. rubropedicellata.*
                  7. Upper surface of lamina with venation not raised; inflorescence axis less than 2.5 cm long; corolla ca. 2 cm long. . . . . *A. miniata* (Griffith) Hooker f.
            5. Lamina 4–10 cm long; inflorescence axis less than 2 cm long, with flowers congregated at end.
               8. Lamina coriaceous, with prominent continuous submarginal vein; ovary smooth. . . . . *V. bulleyanum* (Diels) Sleumer.
               8. Lamina chartaceous, continuous submarginal vein absent; ovary with 10 fleshy, longitudinal lamellae ("wings"). . . . . 8. *V. lamellatum.*
      3. Inflorescences long-racemose; bracts at base of inflorescence sometimes conspicuous and persistent.
         9. Lamina (7.5–)11–19 cm long; inflorescences prominently bracteate at base. . . . . *V. nuttallii* Sleumer.
         9. Lamina 3–10.5 cm long, if as large as in *V. nuttallii,* then inflorescences not prominently bracteate at base.
            10. Lamina 3–6 cm long, upper surface drying brownish green. . . . . 9. *V. leucobotrys.*
            10. Lamina 4–10.5 cm long, upper surface drying dark- or blackish-green.
                11. Lamina subcoriaceous, with lateral veins and midrib on upper surface impressed. . . . . *V. venosum* Wight.

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[2] Only the taxa with numbers are treated in this account.

11. Lamina chartaceous, with lateral veins and midrib on upper surface slightly raised.
    12. Lamina 3–4 cm wide, with lateral veins spreading at ca. 80° from midrib; pedicels ca. 2 mm long. .... *V. kingdon-wardii* Sleumer.
    12. Lamina 1–2.5 cm wide, with lateral veins spreading at ca. 60–70(–80)° from midrib; pedicels (3.5–)5–12 mm long.
        13. Corolla pubescent inside; petiole (1–)2–3(–4) mm long. .... 12a. *V. vacciniaceum* subsp. *vacciniaceum*.
        13. Corolla glabrous inside; petiole 1–2 mm long. .... 12b. *V. vacciniaceum* subsp. *glabritubum*.

1. Leaves clearly separated by internodes, although often restricted to upper half of innovation.
    14. Petiole ca. 2 mm long; lamina to 8(–15) cm long.
        15. Lamina less than 5 cm long, base more or less cuneate; bracts at base of inflorescence inconspicuous. .... *V. scopulorum* W. W. Smith.
        15. Lamina 4–8(–15) cm long, base rounded; bracts at base of inflorescence conspicuous, persistent. .... 11. *V. subdissitifolium*.
    14. Petiole (4–)8–13 mm long; lamina usually over 8 cm long.
        16. Stem pale and smooth, not obviously lenticellate; petiole 4–6 mm long; lamina coriaceous. .... *V. kachinense* Brandis.[3]
        16. Stem dark, becoming clearly lenticellate; petiole at least 8 mm long; lamina chartaceous.
            17. Corolla cylindrical, at least 12 mm long.
                18. Corolla ca. 1.2 cm × ca. 1.5 mm; anthers shorter than filaments, with long hairs. .... *A. leptantha* Airy Shaw.
                18. Corolla 1.4–2.5 cm × at least 3 mm; anthers much longer than filaments, glabrous. .... 3. *A. angulata*.
            17. Corolla urceolate, up to 12 mm long.
                19. Corolla 9–12 mm long; inflorescences from foliate axils. .... 7. *V. jacobeanum*.
                19. Corolla 3–4 mm long; inflorescences from defoliate axils. .... *V. acuminatum* D. Don ex G. Don.

RANGE EXTENSIONS AND PREVIOUSLY UNDESCRIBED TAXA[4]

AGAPETES SER. LONGIFILES AIRY SHAW

1. **Agapetes inopinata** Airy Shaw, Kew Bull. **14:** 229. 1960.

Vaccinium glandulosissimum C. Y. Wu ex W. P. Fang & Z. H. Pan, Acta Phytotax. Sin. **19:** 109. 1981; *Agapetes glandulosissimum* (C. Y. Wu ex W. P. Fang & Z. H. Pan) S. H. Huang, Acta Bot. Yunn. **5:** 148. *fig. 1.* 1983. TYPE: China, Yunnan, Tsang-yuan [Cangyuan], 1600 m, *C. W. Wang 73251* (holotype, PE; isotype, A!).

DISTRIBUTION. Burma and China (Yunnan).

Wang 73251 is the only collection of *Agapetes inopinata* known to me from China; the species was previously known only from Burma. *Wang 73251* agrees with the isotype specimen of *Agapetes inopinata* (*Kingdon-Ward 8788,* A!) very

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[3] Despite its urceolate corollas and the facies of species in sect. *Epigynium, Vaccinium kachinense* is a member of sect. *Galeopetalum*; its relationships are unclear.

[4] Herbarium abbreviations follow those given in Holmgren, Keuken, and Schofield (1981).

well, although it has a slightly longer (to 1.3 cm, vs. ca. 9 mm in the type) corolla. In both specimens the glandular indumentum on the flowers and inflorescence is so dense (and presumably sticky) that the flowers tend to stick together.

2. **Agapetes pensilis** Airy Shaw, Bull. Misc. Inform. **1935:** 52. 1935; Hooker's Ic. Pl. **33:** *t. 3256.* 1935; S. H. Huang, Acta Bot. Yunn. **5:** 150. 1983. TYPE: Burma, Valley of the Seinghku, 2400–2700 m, 25.ix.1926, *Kingdon-Ward 7458* (holotype, K; isotypes, A!, K).

Agapetes dulongensis S. H. Huang, Acta Bot. Yunn. **5:** 150. 1983. TYPE: China, Yunnan, Taron-Taru Divide [Du-long-jiang], Lungnan [Gongshan], 2300 m, 28.viii.1938, *T. T. Yü 20038* (holotype, KUN; isotypes, A!, E!).

DISTRIBUTION. Burma and China (Yunnan).

Agapetes dulongensis is distinguished from *A. pensilis* by its smaller, ovate to suborbicular leaves that are described as being puberulent above and glandular-hirsute below. The leaf surface is bullate-rugulose, and the lateral nerves are obscure. In *A. pensilis* the leaves are described as being 1–1.6 × 0.5–1.1 cm, ovate to elliptic-oblong, the surface rugulose above and flat below, both surfaces with a few short hairs but more or less pubescent when young. The illustration of *A. pensilis* in Hooker's *Icones Plantarum* shows the lower surface, at least, to be rather densely covered with fine hairs.

When the descriptions of the two species are compared with fragments of the type specimen of *Agapetes pensilis,* the specimen of the paratype of *A. pensilis,* and the isotype of *A. dulongensis* (all at A), numerous discrepancies become evident. It can be seen from the TABLE that the differences in vegetative characters used to separate the species break down. The type specimen of *A. pensilis* differs from the other two specimens in lacking glandular-setular hairs on the lower surface of the leaves. It is, however, covered with long, unicellular hairs similar to those found on the upper surface of all specimens. Such unicellular hairs are found, albeit sparsely, on the under-surfaces of the leaves of both *Handel-Mazzetti 9352* (a paratype of *A. pensilis*) and *T. T. Yü 20038.* There are no obvious differences in anatomy in the leaves of the three specimens examined, although *Handel-Mazzetti 9352* and *T. T. Yü 20038* both have a zone around the edge of the leaf that is only three cells thick but up to 0.15 mm wide; this zone is present but much less evident in *Kingdon-Ward 7458.* The floral characters of the two type specimens are very similar.

The only variation of any possible importance is in the indumentum on the underside of the leaf. I do not think it wise to recognize taxa, even at the varietal level, on this character until its occurrence is better understood. Therefore, *A. dulongensis* is reduced to synonymy under *A. pensilis.*

AGAPETES SER. ROBUSTAE AIRY SHAW SUBSER. CHARTACEA AIRY SHAW

3. **Agapetes angulata** (Griffith) Hooker f. *in* Bentham & Hooker f. Gen. Pl. **2:** 571. 1876; *Ceratostemma angulatum* Griffith, Ic. Pl. Asiat. *pl. 503.*

Leaf characters used to distinguish Agapetes dulongensis from A. pensilis.

	Agapetes dulongensis		*Agapetes pensilis*	
CHARACTER	HOLOTYPE*	ISOTYPE (A)	PARATYPE (A)	HOLOTYPE†
Length (mm)	5–7	6.5–10	(8.5–)9–11.5	7.5–14
Indumentum				
Pubescence on upper surface	Present	Present	Present	Present
Glandular-setular hairs on lower surface	Present	Present	Present	Absent
Wrinkles on surface	Distant	Dense	Dense	Subdistant
Lateral veins	Not evident	Not evident	Obscure	Evident to obscure

*Details taken from the protolog.

†Details taken from five leaves of the type; leaf length given as 10–15 mm in protolog.

1854. See Merrill, Brittonia **4:** 157. 1941, and Airy Shaw, Kew Bull. **13:** 481. 1958, for additional references and typification.

DISTRIBUTION. India (Assam) and Upper Burma.

DESCRIPTION OF INFLORESCENCES AND FLOWERS. Inflorescences corymbose to subumbellate, the axis 0.4–1.5 cm long, 5- to 15-flowered, glabrous; bracts ovate, 0.7–1.5 mm long (also inconspicuous bracts at base of inflorescence); pedicels 0.9–2.2 cm long, slender, slightly expanded at apex, glabrous, the bracteoles inserted near base of pedicel, 1–1.5 mm long. Receptacle obpyramidal, 1.5–1.7 mm long, slightly 5-angled, glabrous; calyx limb 1.6–2.5 mm long, divided almost to base or to ¾ of its length into 5 triangular lobes, glabrous; corolla 1.5–2.7 cm long, rather thinly fleshy, red to reddish yellow, with deeper-colored horizontal bands, glabrous, with 5 triangular lobes 3.5–5 mm long; stamens 10, the filaments 0.5–1 mm long, with sparse unicellular hairs, the anthers weakly connate by their tubules, the thecae 3.5–4 mm long, rounded to acute and somewhat downward-pointing at base, granulate, the tubules 1.3–1.7 cm long, opening by introrse slits 5–6 mm long, the spurs small (ca. 0.05 mm long) or absent; disc glabrous; style 1.5–2.1 cm long.

SPECIMENS SEEN. **Burma:** Nam Tesang, 762 m, *Toppin 6356* (K); Kachin State, Sumprabum Subdiv., surrounds of Hpuginhku Village, ca. 1525 m, *Keenan et al. 3789* (A, E, K), *3797* (E); banks of Hpuginhku R., at least 1220 m, *Keenan et al. 3921* (A, E, K); between Ning W'Krok and Kanang, 1219–1525 m, *Keenan et al. 3341* (E), ca. 1525 m, *Keenan et al. 3939* (A, E, K), at least 1525 m, *Keenan et al. 3950* (A, E, K); E aspect of Gwe-Kya-Kat-Bum, 1220–1525 m, *Keenan et al. 3366* (A, K); North Triangle, Arahku, 1219 m, *Kingdon-Ward 20606* (E). **India.** ASSAM: Lohit Valley, *Kingdon-Ward 19143* (BM); Mishmi Hills, Glo Lake, Kamlang Valley, 1067 m, *Kingdon-Ward 18461* (A).

Agapetes angulata is a rather variable species, especially in floral characters, hence the description of the inflorescence and flowers. It is less variable vegetatively, although the twigs vary from strongly ridged and angled to subterete. It is not possible to recognize infraspecific taxa.

4. **Agapetes rubropedicellata** P. F. Stevens, sp. nov.

A Agapetes leptantha, qua floribus similibus habet, in foliis grandioribus pseudoverticillatis et corollis antherisque glabris, et a A. acuminata in foliis subsessilibus pseudoverticillatis et corollis maioribus cylindricis, non urceolatis, et a A. dispar in foliis leviter parvioribus, calycibus parvioribus et corollis maioribus cylindricis, non urceolatis, differt.

Shrub ca. 1.8 m tall or small tree to 3.6 m tall. Twigs terete, 2–2.5 mm wide, with small, subadpressed, multicellular hairs, lenticellate when older; buds with narrowly subulate perulae ca. 2 mm long. Leaves pseudoverticillate, verticils 6–12 cm apart and with 5 to 7 leaves, leaves in intervening region reduced to scales to 6 mm long; petiole very short; lamina subovate to elliptic, (7–)8.5–13.5 × (1.7–)2.6–4.6 cm, acute at apex, narrowed toward rounded base, serrulate, chartaceous, glabrous, drying dark brown above and brown below, with 11 to 16 pairs of broadly ascending lateral veins, midrib and venation raised and prominent above and slightly less so below. Inflorescences from foliate axils, corymbose-umbellate, with 7 to 16 flowers, the axis 4–5.5 cm long, with flowers restricted to distal 1–1.5 cm, glabrous; bracts narrowly subulate, to 2 mm long, with subsessile glandular marginal hairs (bracts at base and along axis inconspicuous); pedicels 1–2.2 cm long, glabrous (in fruit rather abruptly expanded and ca. 2 mm thick at apex), the bracteoles basal, ca. 1.5 mm long. Receptacle ca. 1.3 × 1.3 mm, glabrous; calyx limb 1.3–1.5 mm long, divided to base into 5 triangular lobes, glabrous; corolla (old) cylindrical, ca. 1.2 cm × 2.2 mm, glabrous, lobes ca. 1.3 mm long; stamens 10, the filaments 4.3–4.4 mm long, with unicellular hairs, the anthers ca. 8 mm long, the thecae 2.3–2.4 mm long, rounded at base, granulate, the tubules ca. 5.8 mm long, opening by introrse slits ca. ½ their length, the spurs absent; disc glabrous; style ca. 1.35 cm long. Fruits (submature) ca. 4 × 4 mm, red; seeds ca. 1.4 mm long, the testa with thin-walled cells, becoming mucilaginous on wetting, the embryo blackish.

TYPE. Burma, Kachin State, Sumprabum Subdivision (lat. ca. 26°40′N, long. ca. 97°20′E), between Hpuginhku and N'Dum Zup, 5000–6000 ft [1524–1829 m], 15 Jan. 1962, *Keenan et al. 3253* (holotype, E!; isotypes, A!, K!).

DISTRIBUTION. Known only from Burma.

ADDITIONAL SPECIMENS SEEN. **Burma:** Kachin State, Sumprabum Subdiv., near Hpuginhku village, ca. 1525 m, *Keenan et al. 3830* (A, E, K).

Agapetes rubropedicellata is related to a group of species in *Agapetes* subser. Chartacea that all have rather similar leaf texture and margin. These species differ from each other mainly in whether or not the leaves are pseudoverticillate and sessile, and in the shape and size of the corolla. *Agapetes leptantha* has petiolate leaves much smaller (only 5–8 × 1–2 cm) than those of *A. rubropedicellata* and scattered along the stem, there are remarkable long hairs on the anthers, and the inside of the corolla tube is hairy. The leaves of *A. acuminata* are scattered and petiolate, and the flowers are very small (only 3–4 mm long) and urceolate. *Agapetes dispar* has leaves similar in shape and arrangement to those of *A. rubropedicellata,* but the lamina is somewhat larger (13–18 × 6–9.5 cm), the calyx is longer (ca. 3 mm), and the urceolate corolla is only 6–7 mm long.

Agapetes rubropedicellata was collected in "subtropical hill jungle" (*Keenan et al. 3830*) at 1525–1830 m altitude; it was recorded as being locally plentiful. The Maru vernacular name was recorded (*Keenan et al. 3253*) as "Burn-Baing."

AGAPETES SER. ROBUSTAE AIRY SHAW SUBSER. CORIACEA AIRY SHAW

5. **Agapetes brandisiana** W. E. Evans, Notes Roy. Bot. Gard. Edinburgh **15:** 201. 1927. See Airy Shaw, Kew Bull. **13:** 479. 1958, and S. H. Huang, Acta Bot. Yunn. **5:** 145. 1983, for additional references and typification.

DISTRIBUTION. Burma, China (Yunnan).

CHINESE SPECIMENS SEEN. YUNNAN: Tsang-Yuan, 1550 m, *C. W. Wang 73261* (A); Keng-Ma, 1670 m, *C. W. Wang 72913* (A); Lu-Se, 1750 m, *H. T. Tsai 56821* (A).

These specimens are the only ones recorded from China, *Agapetes brandisiana* previously having been known only from the Bhamo district of Burma. The specimens cited agree fairly well with the type (in fruit: *Cubitt 351* (holotype, E!)) and with the description of the flowers given by Airy Shaw (1935). The following additional details should be noted (where they differ from those in the earlier descriptions, these latter are included in parentheses):

Leaves scattered, or loosely aggregated into pseudoverticels; lamina more or less entire, with 2 or 3 pairs of glandular punctations near base that sometimes project notably (margin then serrulate), the fine venation between submarginal and marginal veins prominent. Inflorescences usually from defoliate axils, sometimes (*Wang 73261*) from foliate ones. Calyx lobes to 3.5 mm long, with middle nerve prominent; corolla 2.2 cm long (2.4–2.6 cm), lobes to 3 mm long (5–6 mm); stamens with filaments 1.7–2.2 mm long, with ± dense hairs at top [as Airy Shaw noted, filaments are strongly curved and adnate to base of corolla tube], thecae 4–4.5 mm long (5–6 mm), tubules ca. 1.7 cm long (1.8–2 cm).

VACCINIUM L. SECT. CONCHOPHYLLUM REHDER

6. **Vaccinium papillatum** P. F. Stevens, nom. nov.

Agapetes poilanei Dop *in* Lecomte, Fl. Gén. Indo-Chine **3**: 702. 1930; non *Vaccinium poilanei* Dop, 1930. TYPE: Viet Nam, col de Lô Gui Hbô, km 9, près de Chapa, 1000 m, 28 août 1926, *Poilane 12603* (holotype, P!; isotype, A!).

Shrub 0.9–1.8 m tall. Twigs subterete or obscurely angled, 1.3–1.7 mm wide, with unicellular hairs arising from epidermal papillae; buds with ovate perulae 0.8–1.3 mm long. Leaves scattered; petiole 1.2–2 mm long, sparsely pubescent; lamina elliptic, 1–2.8 × 0.5–1.2 cm, rounded and retuse at apex, ± cuneate at base, entire, coriaceous, with 2 glandular punctations and 1 or 2 pairs of steeply ascending lateral nerves arising near base, midrib raised on both surfaces, the upper surface glabrous, drying brown-green, veins ± impressed, the lower surface with multicellular hairs throughout and unicellular hairs on and near midrib, drying brown, veins ± raised. Inflorescences from foliate or rarely defoliate axils along twigs, corymbo-racemose, with 2 to 5 flowers, the axis slender, 0.6–1.8 cm long, sparsely pubescent; bracts ovate, 1–1.5 mm long; pedicels 4.5–6 mm long (in fruit 0.6–1 cm long, ca. 1.5 mm wide at apex), sparsely pubescent, the bracteoles subbasal, ca. 1.3 mm long. Receptacle 1.1–1.2 × 1.1–1.2 mm, pubescent; calyx limb 1.5–2.1 mm long, divided almost to base into 5 triangular lobes, pubescent; corolla ± campanulate, 4.5–5.5 mm long, ca. 4.5 mm wide when flattened, glabrous, with 5 triangular lobes ca. 1.5 mm long; stamens 10; the filaments ca. 0.5 mm long, flattened, fringed with hairs, the anthers ca. 4 mm long, rounded at base, minutely granulate, the connective with hairs, the tubules ca. 2.4 mm long, opening by introrse slits ca. 0.5 mm long, the spurs at anther-filament junction alternately suberect, ca. 0.7 mm long, and subspreading, ca. 0.9 mm long; disc glabrous; style ca. 5 mm long. Fruits ca. 4 × 4 mm, greenish yellow or whitish pink; seeds ovoid, 1.3–1.5 × 0.5–0.7 mm, the testa cells slightly elongated, with strongly thickened anticlinal walls and slightly thickened inner periclinal walls, the embryo 0.7–0.8 mm long, pellucid.

DISTRIBUTION. Vietnam and southwestern China.

ADDITIONAL SPECIMENS SEEN. **China.** YUNNAN: Si-chour-hsein, Ma-chia, 1300–1500 m, *K. M. Feng 12451* (A); Faa-doou, 1500 m, *K. M. Feng 12028* (A); Mar-li-po, Pan-chia-chu, 1700 m, *K. M. Feng 12622* (A); Tung-ting, 1500–2000 m, *K. M. Feng 13586* (A). **Vietnam:** Chapa, 1400–1500 m, *Chevalier 29469* (P), ca. 1500 m, *Pételot 3755* (P), *4999* (P); massif [de] Sa Fan tri Pan, ca. 1300 m, *Pételot s.n.*, ii.1931 (A, P).

Agapetes poilanei Dop was originally described from material in fruit, but the unicellular hairs borne on epidermal papillae and the short, broadly campanulate corolla of the species show its affinity to species in *Vaccinium* sect. *Conchophyllum. Vaccinium tonkinense* Dop and *V. emarginatum* Hayata of this section both have similar flowers and elongated inflorescence axes, but in neither are the unicellular hairs borne on epidermal papillae. Flowering specimens of *V. papillatum* are known only from Vietnam, but there is no doubt that this material is conspecific with the specimens cited from China. Since the epithet *poilanei* is occupied in *Vaccinium* (*V. poilanei* Merr.), a new epithet is required. The species was previously only imperfectly known, having been dealt with neither by Sleumer (1941) nor by Airy Shaw in his various papers on *Agapetes,* so a full description has been given above.

Three of the Chinese specimens (*Feng 12028, 12451,* and *13586*), and *Chevalier 29469,* from Vietnam, have shoots with very characteristic subterminal, rosettelike structures. These are made up of numerous ovate perulae ca. 3.5 × 2 mm that are fringed with unicellular hairs. The rosettes probably represent teratological buds that produce nothing but enlarged perulae, instead of the few small perulae followed by fully developed leaves produced by normal buds.

The type specimen of *Vaccinium papillatum* has swellings along the roots; the young plant is reported to have a tubercle.

VACCINIUM L. SECT. EPIGYNIUM (KLOTZSCH) HOOKER F.

7. **Vaccinium jacobeanum** P. F. Stevens, sp. nov.

A Vaccinio vacciniaceo in foliis subdissitis petiolatis laminis basibus decurrentibus subverticillatis (non subsessilibus, lamina basi cuneata vel rotundata) et corollis grandioribus 9–10(–13) mm longis (non 5–7(–8.5) mm longis), differt.

Epiphytic or terrestrial shrub 0.9–1.2 m tall. Twigs subterete, 1.3–3 mm wide, with multicellular setular hairs especially at base of innovations, becoming lenticellate. Leaves ± scattered in upper half of innovation, in lower half reduced to narrowly triangular perulae to 1 cm long; petiole (0.7–)1–1.5 cm long, glabrous; lamina narrowly elliptic, (4–)7–16 × (1.3–)1.9–3.2 cm, acuminate or narrowly acute at apex, decurrent at base, serrate, chartaceous, glabrous, drying blackish green above and dark green below, with 9 to 14 pairs of ascending lateral veins, midrib and venation raised above and slightly less so below. Inflorescences from upper foliate or perulate axils, racemose, with (7 to) 15 to numerous flowers, the axis (1.5–)3–8 cm long, glabrous; bracts narrowly ovate, to 4.5 mm long (bracts at base inconspicuous, ca. 2 mm long); pedicels 0.5–1 cm long, glabrous, not incrassate in fruit, the bracteoles subbasal, ovate, ca. 0.5 mm long. Receptacle ca. 1 × 1 mm, glabrous; calyx limb 1–1.3 mm long, divided to base into 5 triangular lobes, glabrous; corolla tubular-urceolate, 9–10 mm long, yellow to green, glabrous, with triangular lobes ca. 1 mm long; stamens 10, the filaments ca. 3 mm long, with unicellular hairs, the anthers 5 mm long, the thecae ca. 2 mm long, ± rounded at base, granulate, the tubules 2.8–3 mm long, opening by introrse slits ca. ½ their length, the spurs minute, arising at junction of thecae and tubules, or absent; disc glabrous; style ca. 9.5(–12.5) mm long. Ripe fruits not known.

TYPE. Burma, Kachin State, Sumprabum Subdivision, ca. 26°40′N, 97°20′E, surrounds of Hpuginhku village, ± 5000 ft [1524 m], March 1962, *Keenan et al. 3774* (holotype, A!; isotypes, E!, K!).

DISTRIBUTION. Known only from Burma.

ADDITIONAL SPECIMENS SEEN. **Burma.** KACHIN STATE: Sumprabum Subdiv., summit of Kanat Bum, 2438 m, *Keenan et al. 3449* (A, E, K); surrounds of Hpuginhku village, ca. 1524 m, *Keenan et al. 3775a* (E); between Ning W'Krok and Kanang, 1524 m, *Keenan et al. 3954* (A, E, K), at least 1524 m, *Keenan et al. 3951* (A, E, K); Sumprabum, 914 m, *Kingdon-Ward 20471* (BM).

Although clearly allied to *Vaccinium vacciniaceum* (Roxb.) Sleumer, *V. jacobeanum* differs in the characters noted in the diagnosis. Note that the petiole proper may measure only 2–3 mm in length, with the prominent teeth on the upper part of what is apparently the petiole representing the extremely attenuate basal part of the lamina. *Vaccinium jacobeanum* is also close to *Agapetes leptantha* Airy Shaw, from which it can be distinguished by its slightly shorter corolla that has thicker walls and is twice as wide, and by its glabrous anthers that are less than half the total length of the stamens.

The specimen collected by Kingdon-Ward cited above has rather small leaves.

Vaccinium jacobeanum grows in subtropical hill jungle and open mixed deciduous and evergreen forest at altitudes of 914–2438 m. Flowering specimens have been collected in February, March, and July. The Jingpaw name for this plant is "Pin-lawng-Lap" (*Keenan et al. 3449*).

The specific epithet commemorates the collector, James Keenan.

8. **Vaccinium lamellatum** P. F. Stevens, sp. nov.

A Vaccinio bulleyano in foliis minoribus coriaceis nervis submarginalibus destitutis, receptaculis lamellis 10 longitudinalibus ornatis, et antheris valde granulatis, differt.

Epiphytic shrub. Twigs terete, 1.2–2.2 mm wide, glabrous or sparsely pubescent when young, becoming lenticellate; buds with ovate perulae ca. 3 mm long. Leaves pseudoverticillate, 2 to 6 per verticil, intervening region (1–)4–9 cm long with leaves reduced to lingulate scales up to 6 mm long; petiole 1–2 mm long; lamina elliptic to subovate, 3–9.7 × 1.3–3.8 cm, acute at apex, rounded at base, serrulate, subchartaceous, glabrous, drying gray-brown above and brown below, with 7 to 10 pairs of ascending lateral veins, the midrib raised above and strongly raised below, notably more prominent toward margin. Inflorescences from axils of reduced leaves, corymbose-umbellate, with 5 to 12 flowers, the axis 0.7–1.4 cm long, with flowers restricted to distal part, (?)glabrous or with glandular multicellular hairs to 1 mm long; bracts subpersistent, ovate, to 3 mm long, with marginal glands (bracts at base and along axis inconspicuous); pedicels 1.3–1.9 cm long (in fruit to 2.5 cm long, ca. 2 mm across at abruptly widened apex), glabrous, the bracteoles subbasal, ca. 2 mm long. Receptacle 1.5–2 × 1.5–2 mm, with 10 irregular, fleshy, longitudinal lamellae, glabrous; calyx limb 2.3–2.6 mm long, divided almost to base into 5 triangular lobes, glabrous, corolla urceolate, ca. 5.5 × 2.5 mm (ca. 1.3 mm wide at mouth), white, the lobes triangular, ca. 0.6 mm long, green; stamens 10, the filaments ca. 0.5 mm long, glabrous, the anthers 4.5–4.7 mm long, the thecae ca. 2.5 mm long, rounded at base, strongly granulate, the tubules ca. 2.3 mm long, opening by introrse slits ca. 1 mm long, the spurs absent; disc glabrous; style ca. 5 mm long. Fruits ca. 4.5 × 4.5 mm; seeds obovoid, ca. 2 × 1.2 mm, the testa with thin-walled cells that become mucilaginous on wetting, the embryo ca. 1 mm long, drying blackish.

TYPE. India, Manipur, Sirhoi, 6500–7000 ft [1980–2135 m], 10 April 1948, *Kingdon-Ward 17246* (holotype, A!; isotypes, BM!, NY!).

DISTRIBUTION. Known only from Manipur, India.

ADDITIONAL SPECIMENS SEEN. **India.** MANIPUR: Sirhoi, 2286 m, *Kingdon-Ward 17688* (BM, NY); Khaiyang, 2135–2438 m, *Kingdon-Ward 17393* (A, BM).

Vaccinium lamellatum is superficially similar to *V. bulleyanum* (Diels) Sleumer (*Agapetes bulleyana* Diels) but can easily be recognized by the characters mentioned in the diagnosis. *Vaccinium lamellatum* has a less coriaceous leaf blade that lacks the prominent intramarginal vein of *V. bulleyanum* but nevertheless has a very distinctive margin, since the fine venation at the very edge of the lamina is prominently raised on both surfaces. I do not know of any other species of *Vaccinium* with the ten irregular, fleshy lamellae on the receptacle that are found in *V. lamellatum.* The stamens of *V. lamellatum* differ considerably from those of *V. bulleyanum,* having prominently papillate thecae that are more or less rounded at the base (at least alternate stamens of *V. bulleyanum* are pointed at the base, with prominent papillae restricted to the base) and anthers that are abruptly incurved at the theca-filament junction.

The lamellate receptacle of *Vaccinium lamellatum* approaches that of *Agapetes miniata,* which has ten raised longitudinal lines; the latter species also has a subumbellate inflorescence. However, *A. miniata* has a leaf blade that is at least 10 cm long and a cylindrical corolla over 2 cm long; the latter character is responsible for the placement of *A. miniata* in *Agapetes.*

The field notes on the type specimen of *Vaccinium lamellatum* ("an epiphyte with water-storing tissue") suggest that it has a swollen stem base. The fruit color of *V. lamellatum* is not known.

9. **Vaccinium leucobotrys** (Nutt.) Nicholson, Ill. Dict. Garden. **4:** 130. 1886; *Epigynium leucobotrys* Nutt. Bot. Mag. III. **15:** *t. 5103.* 1859. See Sleumer, Bot. Jahrb. Syst. **71:** 478. 1941, for additional references and synonymy.

DISTRIBUTION. India (Assam), Burma, China (Tibet, Yunnan).

SELECTED SPECIMENS SEEN. **Burma:** above Zuklang, ca. 2438 m, *Kingdon-Ward 418* (A, NY); Adung Valley, 1829–2134 m, *Kingdon-Ward 9219* (A); North Triangle, Tagulam Bum, 2286 m, *Kingdon-Ward 21604* (A); Kachin State, Sumprabum Subdiv., Janrawng Bum, 2134–2743 m, *Keenan et al. 3179* (A, E).

The first two specimens cited above have been included in *Vaccinium vacciniaceum* (Roxb.) Sleumer var. *hispidum* (C. B. Clarke) Sleumer (Sleumer, 1941; Merrill, 1941). However, they both agree with *V. leucobotrys* in having prominently and subpersistently bracteate inflorescences and ovate, usually green-drying leaves that are usually broadly rounded at the base; these characters readily separate *V. leucobotrys* from *V. vacciniaceum.*

The specimens cited above are the first record of the species from Burma. Although they were collected at somewhat lower altitudes (in Assam, Tibet, and Yunnan *Vaccinium leucobotrys* grows at altitudes of 2100–3300 m), they agree well with other specimens of the species.

10. **Vaccinium praeces** P. F. Stevens, sp. nov.

A Vaccinio bulleyano, V. lamellato, et Agapetes dispar, quibus in facie plus minusve similibus sunt, in inflorescentiis, pedicellis floribusque pubescentibus, differt.

Epiphytic shrub. Twigs ± terete, 2.3–3 mm wide, with few multicellular glandular hairs, becoming lenticellate. Leaves pseudoverticillate, 2 to 4 per verticil, the intervening stem 2.5–10 cm long, with leaves reduced to ovate to obovate scales up to 10 × 5 mm; petiole 1–1.5 mm long; lamina ovate to elliptic, 7.5–ca. 14 × (3.3–)4–7.3 cm, acuminate at apex, rounded to slightly cordate at base, serrulate, subchartaceous, glabrous, with ca. 14 pairs of broadly ascending lateral veins, the upper surface drying gray-green, midrib depressed but raised in center, venation ± impressed, the lower surface drying olivaceous, midrib strongly raised, venation raised. Inflorescences from axils of reduced leaves, corymbose-umbellate, with ca. 20 flowers, the axis 2–2.5 cm long, with flowers restricted to distal part, subdensely pubescent; bracts subpersistent, ovate, 2–2.5 cm long, with marginal glandular hairs (bracts at base and along axis inconspicuous); pedicels 1–1.5 cm long, slightly broadened toward apex, pubescent, the bracteoles basal, ca. 1 mm long. Receptacle ca. 1 × 1 mm, slightly 5-angled, pubescent; calyx limb 3.5–4 mm long, divided almost to base into 5 narrowly triangular lobes, pubescent, each lobe with prominent midrib; corolla urceolate, ca. 7 × 3.5 mm (ca. 2.2 mm across at mouth), slightly angled, green, pubescent outside, with hairs only toward apex inside, the lobes 5, broadly triangular, ca. 0.7 mm long; stamens 8 or 10, the filaments ca. 1.2 mm long, flattened, widened toward base where ca. 0.6 mm across, glabrous, the anthers ca. 3.9 mm long, the thecae ca. 1.6 mm long, rounded at base, granulate, the tubules ca. 2.3 mm long, opening by introrse slits ca. 0.9 mm long, the spurs absent; disc glabrous; style ca. 6.3 mm long. Fruits unknown.

TYPE. Burma, North Triangle (Tagulam Bum), 2410 m, 15 Nov. 1953, *Kingdon-Ward 21605* (holotype, BM!).

DISTRIBUTION. Known only from the type collection.

Vaccinium praeces is closely related to the group of species straddling the dividing line between *Vaccinium* sect. *Epigynium* (to which *V. praeces* is assigned) and *Agapetes* subser. Coriacea. From all these species (*V. bulleyanum* (Diels) Sleumer, *V. lamellatum* P. F. Stevens, and *A. dispar* Airy Shaw) it can be separated by its densely pubescent inflorescences and flowers. From *V. bulleyanum* it also differs in its larger, thinner leaves that lack a submarginal vein. Although *V. praeces* and *V. bulleyanum* have similar inflorescences, *V. praeces* has stamens with much longer filaments, those of *V. bulleyanum* being only ca. 0.5 mm long. *Vaccinium lamellatum* has leaves much smaller than those of *V. praeces,* and it also has a lamellate, rather than slightly angled, receptacle. *Agapetes dispar* is perhaps most closely related to *V. praeces,* but in addition to differing in inflorescence pubescence, *A. dispar* has a longer (8–10 cm) inflorescence axis, longer (2–2.5 cm) pedicels, and somewhat pubescent stamen filaments.

There is possibly another taxon in this circle of affinity. *Kingdon-Ward 3050* (E; ridge above Laktang, 2453 m; specimen in young fruit) has the inflorescence type and length—as well as the indumentum—of *Vaccinium praeces,* but there are probably only about ten flowers per inflorescence, and the calyx lobes are up to 6.5 mm long. The leaves are falsely whorled, and the blades have a distinct submarginal vein.

11. **Vaccinium subdissitifolium** P. F. Stevens, sp. nov.

Vaccinium vacciniaceum (Roxb.) Sleumer var. *hispidum* (C. B. Clarke) Sleumer, Bot. Jahrb. Syst. **71:** 479. 1941, *pro majore parte, excl. spec. Assamica*; *V. venosum* Wight

var. *hispidum* C. B. Clarke *in* Hooker f. Fl. Brit. India **3:** 452. 1882. TYPE: Sikkim, 4000–7000 ft [1219–2143 m], *Hooker s.n., pro parte* (lectotype, K!; isolectotypes, E!, GH!, NY!). See also *V. vacciniaceum.*
Gaylussacia serrata auct. non Lindley: Griffith, Ic. Pl. Asiat. *pl. 507.* 1854.

A Vaccinio vacciniaceo in lamina basi plerumque late rotundata, non subcuneata vel anguste rotundata, foliis subdissitis, non pseudoverticillatis, perulis basi inflorescentiae persistentibus, non deciduis, et corolla 3–4.5 mm, non 5–7(–8.5) mm, longa, differt, et a V. leucobotrys in foliis subdissitis, non pseudoverticillatis, lamina plerumque suboblonga vel obovata, non ovata, antheris prominente granulatis, non sublaevibus, et corolla intus glabra, non pubescentia, differt.

Epiphytic shrub. Twigs terete, 1.5–2.5 mm wide, pubescent and with multicellular setular hairs to 1.7 mm long, rarely glabrous, becoming lenticellate. Leaves ± scattered along stem; petiole 1–2 mm long; lamina oblong to obovate, rarely ovate, (2–)3.3–8(–15) × (0.6–)1.2–2.3(–4) cm, subacuminate at apex, broadly to narrowly rounded at base, serrate, chartaceous, glabrous, drying greenish brown to blackish above and brown below, with 6 to 16 pairs of ascending lateral veins, midrib and venation ± raised above and below (venation sometimes inconspicuous below). Inflorescences from upper foliate axils, racemose or corymbo-racemose, with ca. 10 to numerous flowers, the axis 1.8–5.3 cm long, glabrous; bracts ovate, to 4 mm long, with setose margins (basal bracts persistent, scarious, conspicuous); pedicels 2.5–7 mm long, glabrous, the bracteoles subopposite, ovate to linear, to 3 mm long. Receptacle 1–1.5 × 1–1.5 mm, ± rugulose, glabrous; calyx limb 0.5–1.3 mm long, divided to base into 5 triangular lobes, glabrous; corolla urceolate, 3–4(–5) × ca. 2.5 mm (ca. 1.2 mm wide at mouth), greenish white, glabrous, sometimes minutely papillate inside at mouth, with 5 triangular lobes ca. 0.6 mm long; stamens 10, the filaments ca. 0.8 mm long, widened and slightly connate at base, glabrous, the anthers 3–3.2 mm long, the thecae ca. 1.4 mm long, narrowed and acute at base, strongly granulate, the tubules 1.6–1.8 mm long, opening by introrse slits for ½–⅓ their length, the spurs absent; disc glabrous; style ca. 4.5 mm long. Fruits ca. 1.5 × 1 mm, white or greenish white; seeds ovoid, ca. 1.5 × 1 mm, the testa cells thin walled, becoming mucilaginous on wetting, the embryo ca. 1 mm long, drying blackish.

TYPE. India, Sikkim, 4000–7000 ft [1219–2143 m], *Hooker s.n., pro parte* (holotype, GH!; isotypes, E!, K!, NY!).

DISTRIBUTION. Foothills of the Himalayas in Bhutan and India (Sikkim and Assam).

ADDITIONAL SPECIMENS SEEN. **Bhutan:** *sine loco, Griffith, Kew Dist. 2260* (BM, *pro parte,* E), *Kew Dist. 3641, pro parte* (BM, GH, K), *Nuttall s.n.* (K). **India.** ASSAM: SE of Apa Tani valley, Subansiri Div. of N.E.F.A., 2134 m, *Cox & Hutchinson 468* (E, K), 2377 m, *Cox & Hutchinson 409* (E, K); Mishmi Hills, Glo, Kamlang Valley, 1219 m, *Kingdon-Ward 18456* (A, K, NY). SIKKIM: Tumlong, 1981 m, *Clarke 27709A* (K), *27709C* (BM); Pasheeting, 1676 m, *Gamble 3666A* (K).

Vaccinium subdissitifolium can be separated from its two closest relatives, *V. vacciniaceum* (Roxb.) Sleumer and *V. leucobotrys,* by the characters given in the diagnosis. *Vaccinium subdissitifolium* is in some ways intermediate between these two species, although its consistently more or less scattered leaves are characteristic of neither. In flower *V. subdissitifolium* is most similar to *V. leucobotrys* but differs in corolla indumentum (*V. leucobotrys* has hairs on the inner surface of the corolla) and in its more granulate anthers. In these two features *V. subdissitifolium* approaches *V. vacciniaceum,* especially subsp. *glabritubum,* and in leaf characters it is also perhaps more similar to *V. vacciniaceum* than to *V. leucobotrys.* Ranking of these and other taxa related to *V. vacciniaceum* (*V. venosum, V. nuttallii,* and *V. kingdon-wardii*) is difficult.

The inflorescence axis possibly elongates after flowering, as the field notes of *Cox & Hutchinson 409* suggest.

Vaccinium subdissitifolium has been typified on the same collection as the type of *V. vacciniaceum* var. *hispidum.* However, in view of confusion surrounding the name *hispidum* (see *V. vacciniaceum*), a new name has been chosen at the species level. Specimens of *V. vacciniaceum* var. *vacciniaceum* are sometimes mounted with the type of *V. subdissitifolium.*

Kingdon-Ward 18456, from Assam, is a very robust specimen that has larger leaves than the others (measurements in the description in parentheses), and it also has twigs that are glabrous at maturity. However, it has persistent bracts at the base of the inflorescence and leaves that are scattered along the upper half of the innovation, so it is referred to this species.

12. **Vaccinium vacciniaceum** (Roxb.) Sleumer

12a. **Vaccinium vacciniaceum** (Roxb.) Sleumer subsp. **vacciniaceum**

Vaccinium vacciniaceum (Roxb.) Sleumer var. *vacciniaceum,* Bot. Jahrb. Syst. **71:** 479. 1941. *Ceratostem[m]a vacciniacea* Roxb. Fl. Indica, ed. 2. **2:** 412. 1932. TYPE: India, Assam, Garrow Hills, *Roxburgh s.n.,* 1813 (BM!).

V. vacciniaceum (Roxb.) Sleumer var. *hispidum* auct. non (Clarke) Sleumer: Sleumer, Bot. Jahrb. Syst. **71:** 479. 1941, *pro parte Assamica.*

Epiphytic or terrestrial shrub. Twigs terete, 1.4–2 mm wide, usually with setular hairs to 1 mm long at least at beginning of innovation, becoming lenticellate. Leaves pseudoverticillate, 5 to 10 together, the intervening stem 2–10 cm long, with leaves reduced to narrowly triangular scales to 7 mm long; petiole (1–)2–3(–4) mm long; lamina narrowly elliptic, 3–11 × 0.9–2.1 cm, acute at apex, narrowly cuneate to ± rounded at base, serrate, chartaceous, glabrous, with 7 to 13 pairs of lateral veins, the upper surface drying black to dull green, midrib narrowly raised, venation raised, the lower surface drying brown or brownish green, midrib broadly raised, venation slightly raised. Inflorescences from foliate axils, racemose or corymbo-racemose, with at least 10 flowers, the axis 1.7–6 cm long, glabrous or very rarely with long-stalked subcapitate hairs; bracts deciduous, narrowly triangular, to 3 mm long (basal bracts inconspicuous); pedicels 7–13 mm long, slightly expanded at apex, glabrous, the bracteoles ± basal, linear to narrowly triangular, 0.8–1.3 mm long. Receptacle 0.8–1 × 0.8–1 mm, smooth, glabrous; calyx limb 0.7–1 mm long, divided almost to base into 5 triangular lobes, glabrous; corolla urceolate, 5–7(–8.5) × ca. 2 mm (1 mm across at mouth), white to greenish white or pinkish yellow, with unicellular hairs inside especially toward mouth, the lobes triangular, ca. 0.6 mm long; stamens 10, the filaments 1.8–2.5 mm long, flattened and widened at base, subglabrous or with unicellular hairs, the anthers 3.3–3.7 mm long, the thecae 1–1.3 mm long, usually sharply verruculose, sometimes ± smooth, the tubules 2–2.5 mm long, dehiscing by long introrse slits, the spurs absent or minute; disc glabrous; style 5.5–7 mm long. Fruits ca. 2 mm long (immature?), glistening white or yellowish; seeds (immature) ca. 1 mm long, testa with thin-walled cells that become mucilaginous on wetting.

DISTRIBUTION. Meghalaya, Nagaland, and Manipur, India, and the Chin area of Burma.

SELECTED SPECIMENS SEEN. **Burma:** Haka, 1981 m, *Dickason 7371* (A). **India.** MANIPUR: Sirhoi, 1829–2438 m, *Kingdon-Ward 17269* (BM); Ukhrul, 1576 m, *Kingdon-Ward 17125* (A, BM); Japoo, 1829 m, *Watt 6226* (P); Khaujang, 2134–2438 m, *Kingdon-Ward 17395* (BM). MEGHALAYA: Khasia Hills, Shampung, 1524 m, *Badul Khan s.n.*, v.1980 (P); below Upper Shillong, 1372 m, *Cox & Hutchinson 553* (E, K); Pynursla, 1286 m, *Cox & Hutchinson 317* (E, K); Lushai Hills, Lakher Country, 2134 m, *Lorrain s.n.*, vi.1928 (K); Blue Mtns., 2100 m, *Koelz 33038* (E); Khasia and Jaintia Hills, Upper Shillong, 1829 m, *Ruse 61* (A); Cherrapunjee, 1200 m, *Chand 5341* (E). NAGALAND: Kohima, Naga Hills, 2100 m, *Koelz 25446* (E); Puhiratadza, 1981–2347 m, *Prain s.n.* (E); Pulebudze, 2286 m, *Bor 2998* (K); Kanku Range, 1981 m, *Bor 2943* (K).

Dickason 7533 (A; Haka, Burma) has bracts more conspicuous than those of the other specimens, and there are also numerous long-stalked, capitate hairs on the inflorescence axis. Although a conspicuously and subpersistently bracteate inflorescence is characteristic of *Vaccinium leucobotrys,* that species has an entirely glabrous inflorescence axis.

A few specimens (e.g., *Ruse 61*) have almost smooth anther thecae, but this seems to be uncorrelated with other variation.

12b. **Vaccinium vacciniaceum** (Roxb.) Sleumer subsp. **glabritubum** P. F. Stevens, subsp. nov.

V. vacciniaceum (Roxb.) Sleumer var. *vacciniaceum* Sleumer, Bot. Jahrb. Syst. **71:** 479. 1941, *pro parte.*

V. vacciniaceum auct. non (Roxb.) Sleumer: Sen Gupta, Rec. Bot. Surv. India **20:** 137. 1973.

V. serratum auct. non (Don) Wight: Biswas, Pl. Darj. Sikkim Himal. **1:** 498. 1966.

A subsp. vacciniacea in tubo corollae intus glabro, petiolo 1–2 mm longo, et in lamina basi plus minusve anguste rotundata, differt.

As in subsp. *vacciniaceum,* but corolla tube glabrous inside, petiole 1–2 mm long, and lamina ± narrowly rounded at base.

TYPE. Nepal, Arun Valley, Maghang Kola, E of Num, 9000 ft [2743 m], 30 April 1956, *Stainton 167* (holotype, A; isotype, BM).

DISTRIBUTION. Nepal and Bhutan; collected once in China (southern Tibet).

ADDITIONAL SPECIMENS SEEN. **Bhutan:** Chukka Timpu, 1219 m, *Cooper 3783* (BM); SW Wangdi Phodrang, 1829 m, *Bowes Lyon 6060* (BM), 2286 m, *Bowes Lyon 6058* (BM);

Kinga Rapden, Mangde Chu, 1219 m, *Ludlow et al. 18589* (BM, E); Rhine Lhakang, 1829 m, *Ludlow et al. 20142* (BM, E); Sichulu [Sichula], *Biswas 2014* (A); Mirik, 1676 m, *Biswas 3740* (A). **China.** TIBET: between Shakti and Pangshen, Nyam Jang Chu, 1825 m, *Ludlow & Sherriff 1240* (E). **India.** SIKKIM AND ADJACENT W BENGAL: Sureil, 1524 m, *Cave s.n.*, 19 April 1916 (A, E); Lebong, 1524 m, *Cave s.n.*, 8 May 1912 (E); Darjeeling, *Cowan s.n.* (K), *Polunin 9532* (BM), 2134 m, *Clarke 27535* (K); Senchal Forest, 2134 m, *Lace 2223* (E), Dhobijhna Nursery, 1829 m, *Gamble 10314* (K); below Darjeeling toward Jakaor, ca. 1829 m, *Herb. Lacaita H vii 452* (BM); Senchal, 2134 m, May 1879, *anon.* (NY); Gangtok, 1524 m, *Ludlow et al. 4003* (A, BM, E); Roro Chu, 1676 m, *Stainton 5306* (BM); Talung Chu, 914 m, *Bowes Lyon 6029* (BM); Yoksam, 1981 m, *Bowes Lyon 3003* (BM); Baboo Chola, 1219 m, *Griffith 6870A* (K); Kinseong [Kurseong], *Gamble 3663A* (K), *3665A* (K); Dikchu, 613 m, *Biswas 6739* (A); Singlik, 1366 m, *Biswas 6810* (A); Reinak, 1524 m, *Clarke 27917* (K); Kalimpong, 1372 m, *Ludlow & Sherriff 15834* (BM, E); *sine loco*, 1219–2143 m, *Hooker s.n., pro parte* (NY), 1829 m, *Cave s.n.*, 4 May 1920 (A). **Nepal:** Mechi Zone, Ilam Distr., Aulabari, 1700 m, *Nicolson 3247* (BM); Ilam, Chintapu, 2134 m, *Stainton 5780* (BM); W of Ilam, Mai Pokhari, 2134 m, *Williams 395* (BM); Arun Valley, Dhoje, N of Chainpur, 2286 m, *Stainton 120* (BM); Tamur Valley, Hellok, 1676 m, *Stainton 5827* (BM).

Within *Vaccinium vacciniaceum* Sleumer (1941) recognized vars. *vacciniaceum* and *hispidum*. The type of var. *hispidum* and some specimens that he cited as belonging to that variety are described above as *V. subdissitifolium*, while other specimens are to be referred to *V. leucobotrys* and to *V. vacciniaceum* subsp. *vacciniaceum*. Specimens that he cited under var. *vacciniaceum* are to be referred to both subspecies of *V. vacciniaceum* recognized above.

The basis for the recognition of *Vaccinium vacciniaceum* var. *hispidum* was the presence of setular hairs at the beginning of an innovation, but the presence or absence of such hairs seems to be a rather trivial character. Within *V. vacciniaceum* as here circumscribed, the correlation of the absence of unicellular hairs on the inside of the corolla with a shorter petiole, a more rounded leaf base, and the geographic provenance of the specimen is almost perfect. The sole exception, a possibly mislabeled specimen collected by Hooker and Thompson in Khasia (E, GH, K, P), lacks hairs on the inside of the corolla tube and has a short petiole and a rounded leaf base.

VACCINIUM SECTION UNCERTAIN

13. **Vaccinium brevipedicellatum** C. Y. Wu, Acta Phytotax. Sin. **19:** 107. 1981. TYPE: China, Yunnan, Mar-li-po [Malipo], 1200–1500 m, 22.xi.1947, *K. M. Feng 13561* (holotype, PE; isotype, A!).

Agapetes chapaënsis Dop *in* Lecomte, Fl. Gén. Indo-Chine **3:** 702. 1930; non *Vaccinium chapaënse* Merr. (1938). TYPE: Vietnam, massif de Za Yang Pueh, près de Chapa, 1 août 1926, *Poilane 12735* (holotype, P!).

Agapetes chapaënsis Dop var. *oblonga* Dop *in* Lecomte, *ibid.* TYPE: Vietnam, massif de Lo nu Tong, près de Chapa, 2200 m, 29 juillet 1926, *Poilane 12679* (holotype, P!; isotype, A!).

AMPLIFIED DESCRIPTION. Twigs with unicellular hairs borne on epidermal papillae. Leaves with lamina ovate to narrowly elliptic, 1.4–3 × 0.6–1.4 cm, obtusely acuminate at apex, cuneate to rounded at base, entire, with 2 glandular spots near base, subcoriaceous, the upper surface sharply and shallowly transversely corrugated, drying greenish to grayish brown, the lower surface smooth, drying brown, the lateral veins 2 pairs, arising near base, steeply ascending, the midrib raised, sparsely pubescent toward base. Inflorescences from foliate axils, with 3 flowers, the axis up to 2 mm long, with glandular-capitate hairs to 1 mm long; pedicels to 1.5 mm long, with glandular-capitate hairs at apex. Corolla unknown; stamens 9 (really 10?), the filaments ca. 0.6 mm long, flattened, fringed with hairs, the anthers ca. 2.2 mm long, the thecae 0.9–1 mm long, ± smooth, the tubules ca. 1.2 mm long, opening by introrse slits for about ½ their length, the spurs arising from tubule-theca junction, 0.5–0.7 mm long, minutely papillate; disc glabrous; style ca. 3.1 mm long. Fruits purple-black, ca. 2.5 by 2.5 mm, with 10 longitudinal ridges when dry; seeds ca. 1.2 × 0.9–1.05 mm, angled, brown, the testa cells with greatly thickened anticlinal walls and slightly thickened inner periclinal walls, the embryo ca. 0.75 mm long, ± pellucid.

DISTRIBUTION. Vietnam and southwestern China.

ADDITIONAL SPECIMENS SEEN. **China.** YUNNAN: Mar-li-po, Hwang-jin-in, 1300–1600 m, *K. M. Feng 13198* (A), 1400–1600 m, *K. M. Feng 13014* (A).

Specimens of *Agapetes chapaënsis* have unicellular hairs borne on epidermal papillae that are common in species of *Vaccinium* sect. *Conchophyllum,* and they apparently also have very small flowers (the stamens and the style remained attached on a young fruit of *Feng 13561*). *Agapetes chapaënsis* hence is best placed in *Vaccinium.* The epithet *chapaënse* is occupied in *Vaccinium* (*V. chapaënse* Merr.); the epithet *brevipedicellatum* chosen for this species alludes to the short pedicels.

Vaccinium brevipedicellatum cannot really be assigned to a section since its corolla is not known, but it has affinities with both sect. *Conchophyllum* (in which Wu placed the species—the stamens and the unicellular hairs grouped on epidermal papillae are similar) and sect. *Aëthopus* (the pedicel indumentum and the inflorescence type are similar, but the stamens are different, those of *V. paucicrenatum* Sleumer lacking spurs). However, it differs from both groups in that the vascular tissue in the petiole forms a closed circle. In all the small-leaved species of *Vaccinium* sects. *Aëthopus* and *Conchophyllum* that have been examined, the vascular tissue in the petiole is arcuate.

All the specimens of *Vaccinium brevipedicellatum* cited have characteristically corrugated leaves. Leaf shape is variable, and there is little difference between the types of *Agapetes chapaënsis* vars. *chapaënsis* and *oblonga.* The leaf blades on the two specimens from Vietnam seen are narrower than those on specimens from Yunnan, and if varieties based on leaf shape are to be recognized, specimens from Yunnan may form one variety, those from Vietnam another.

When Wu described *Vaccinium brevipedicellatum,* he was unaware of the earlier names for this taxon in *Agapetes.* He did not describe either stamens or styles.

ACKNOWLEDGMENTS

I am grateful to the directors of the institutions cited above for permission to examine material in their herbaria or for sending specimens on loan.

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A NOTE ON THE OCEANIC SPECIES OF MELICYTUS (VIOLACEAE)

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The genera *Melicytus* Forster and *Hymenanthera* R. Br. together comprise 13 species of shrubby violets with nearly actinomorphic flowers. The genera have been distinguished primarily by the number of seeds per carpel, but Beuzenberg (1961) has shown that this character varies both within and between species in such a way that the distinction between the two genera cannot be maintained. Furthermore, two species, *Melicytus lanceolatus* Hooker f. and *Hymenanthera chathamica* (F. Mueller) Kirk, produced a fully fertile hybrid, suggesting that there are no consistent breeding barriers between the genera. Although Beuzenberg suggested that species of *Hymenanthera* be included in *Melicytus,* he did not publish the relevant combinations. In this paper we will use the name *Melicytus* to refer to all members of *Melicytus sensu stricto* plus *Hymenanthera,* whether or not the combinations have been formally made.

Most species of *Melicytus* occur in New Zealand or Australia, but there are also representatives on the Kermadec Islands, Samoa, Tonga, Vanuatu, Norfolk Island, Lord Howe Island, Chatham Island, the southern Solomon Islands, and Fiji. This paper will consider the status of three oceanic taxa, *M. ramiflorus* J. R. & G. Forster subsp. *oblongifolius* (Cunn.) P. Green, *M. fasciger* Gillespie, and *M. samoensis* (Christoph.) A. C. Smith, in their relationship to each other and to *M. ramiflorus* subsp. *ramiflorus,* from New Zealand.

Since Beuzenberg's 1961 publication, the genus has received little attention. Jacobs (1966) and Jacobs and Moore (1971) mistook a specimen of *Melicytus fasciger* (*Kajewski 841*) from Vanuatu for *Rinorea bengalensis* (Wallich) Kuntze. In 1975 Van Steenis reported a specimen of *M. fasciger* (*Whitmore BSIP 1695*) from the Santa Cruz group of the Solomon Islands. In 1970 Green transferred the New Caledonian species *Hymenanthera latifolia* Endlicher to *Melicytus,* and in the same publication he reduced the Fijian *M. fasciger,* the Samoan *M. samoensis,* and the Norfolk Island *H. oblongifolia* Cunn. to subspecies of the New Zealand species, *M. ramiflorus.* He gave little evidence for reducing the oceanic species to subspecific status. He was countered in 1978 and 1981 by Smith, who claimed that *M. fasciger* and *M. samoensis* were sufficiently distinct from *M. ramiflorus* to warrant specific recognition. Smith distinguished the three species on the bases of leaf serration (conspicuously serrate, subentire to crenulate or serrate, or subentire to callose-crenulate), number of serrations per cm (3 to 5 or 4 to 7), and petal length (2 mm or less, 3–4 mm, or 4–7 mm). Smith expressed no opinion on the status of *M. ramiflorus* subsp. *oblongifolius* (Cunn.) P. Green.

Journal of the Arnold Arboretum **66**: 491–502. October, 1985.

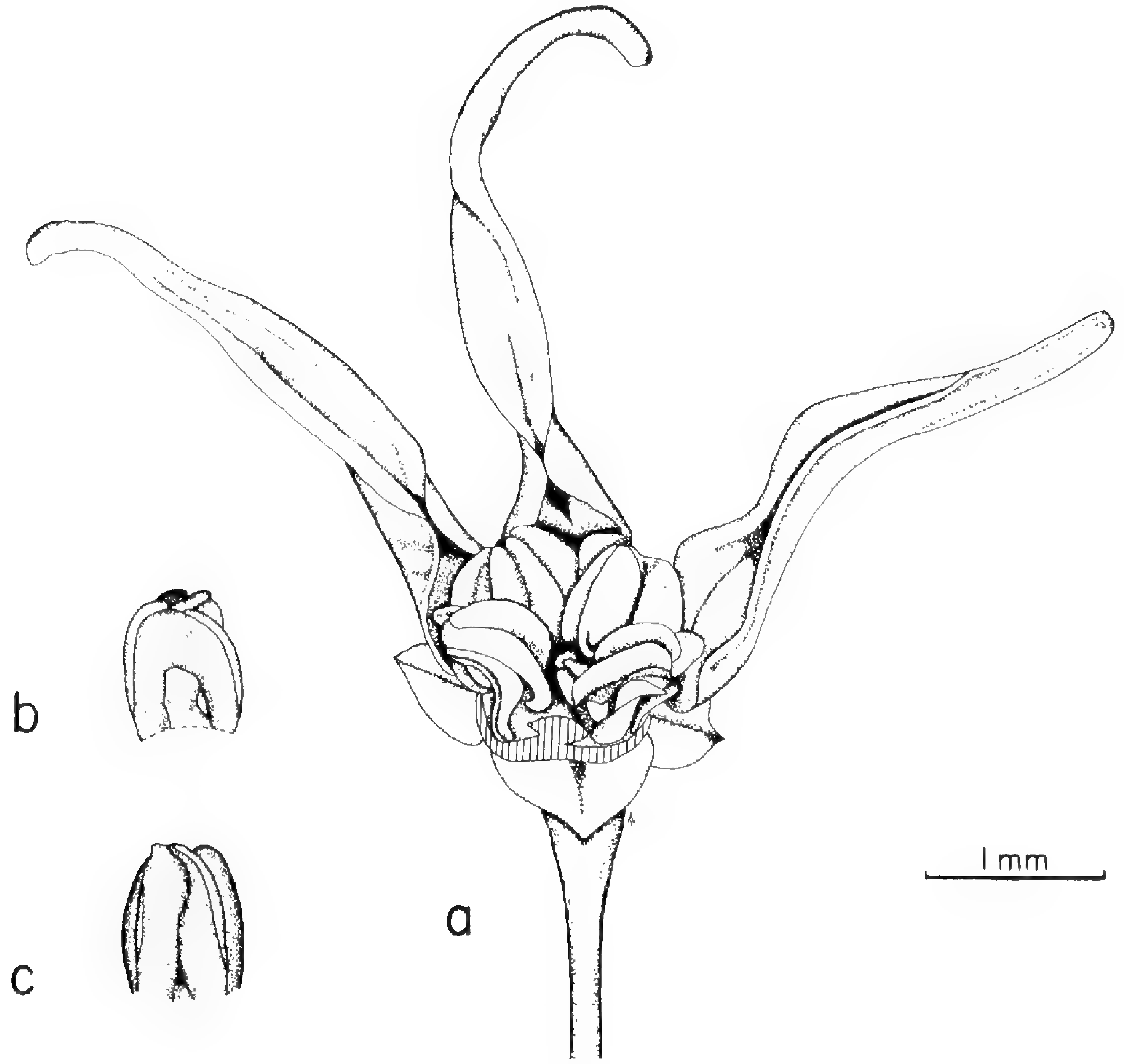

FIGURE 1. *Melicytus fasciger* (*Stauffer & Koroiveibau 5827*): a, flower with 1 stamen and 2 petals removed; b, stamen, abaxial side, note flaplike connective; c, stamen, adaxial side (stamens of other 3 species virtually identical).

CHARACTERS STUDIED AND THEIR DISTRIBUTIONS

We examined material of *Melicytus fasciger, M. ramiflorus* subspecies *oblongifolius* and *ramiflorus,* and *M. samoensis* collected throughout their ranges. All four are small trees with membranaceous, elliptic to ovate or obovate, glandular-toothed to subentire leaves. Stipules are triangular to lanceolate and caducous. Leaf scars show little variation in shape; there are always three vascular bundles. Leaf-venation pattern is similar throughout the genus: pinnate and eucamptodromous, with the free endings of veinlets generally single but sometimes branched. Flowers are in axillary fascicles with pedicels 3–12 mm long that appear to elongate soon after anthesis in the pistillate plants. Petals and sepals are inserted at the edge of a somewhat expanded receptacle (see FIGURES 1 and 2 for comparison of flowers of *M. fasciger,* a member of the study group, and *M. lanceolatus,* typical of the rest of the genus). The stamens, surprisingly uniform in these species, are free and have only a small appendage on the dorsal side (generally no more than half the length of the anther); the anthers are sessile or nearly so.

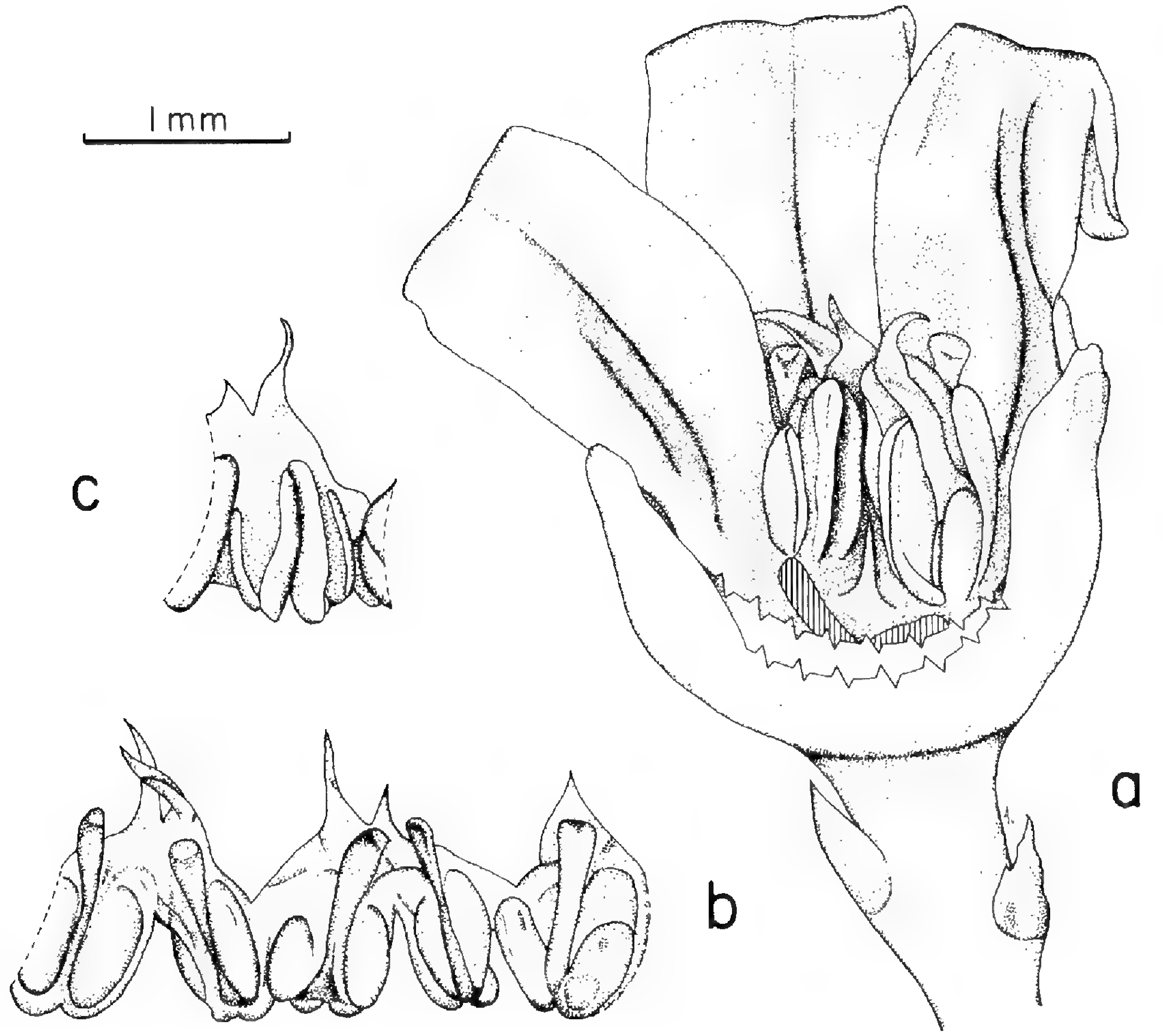

FIGURE 2. *Melicytus lanceolatus* (*Kirk s.n.*, A): a, flower with 1 stamen and 2 petals removed; b, stamen, abaxial side, note extended connective; c, stamen, adaxial side.

In an attempt to find discrete, concordant differences among the species, we began by testing the characters that Smith had used, particularly leaf serrations and petal length. We counted the number of teeth per centimeter and per side of the leaf for five to ten leaves on each of 136 specimens. These data are displayed in FIGURES 3 and 4. There are clearly no breaks in the distribution of either character. Describing the leaf margins as serrate, subentire, or crenulate also requires subjective division of a continuum. Although certain tendencies are observable in some groups of specimens, they are insufficient to allow consistent distinction among groups.

Stipules are generally glabrous, except in the New Zealand members of *Melicytus ramiflorus,* in which they are covered with stiff pubescence (as are the bud scales, and the pedicels and calyxes of pistillate flowers). Pubescence is present on all specimens of New Zealand *M. ramiflorus* examined, but it is absent from the Kermadec Islands specimens and from all other members of the genus, including the specimens from the Oceanian[1] islands.

We measured petal length on 49 specimens; pistillate flowers were measured if they were open, whereas staminate flowers were measured only if they were

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[1] As used here, Oceania does not include New Zealand or Australia.

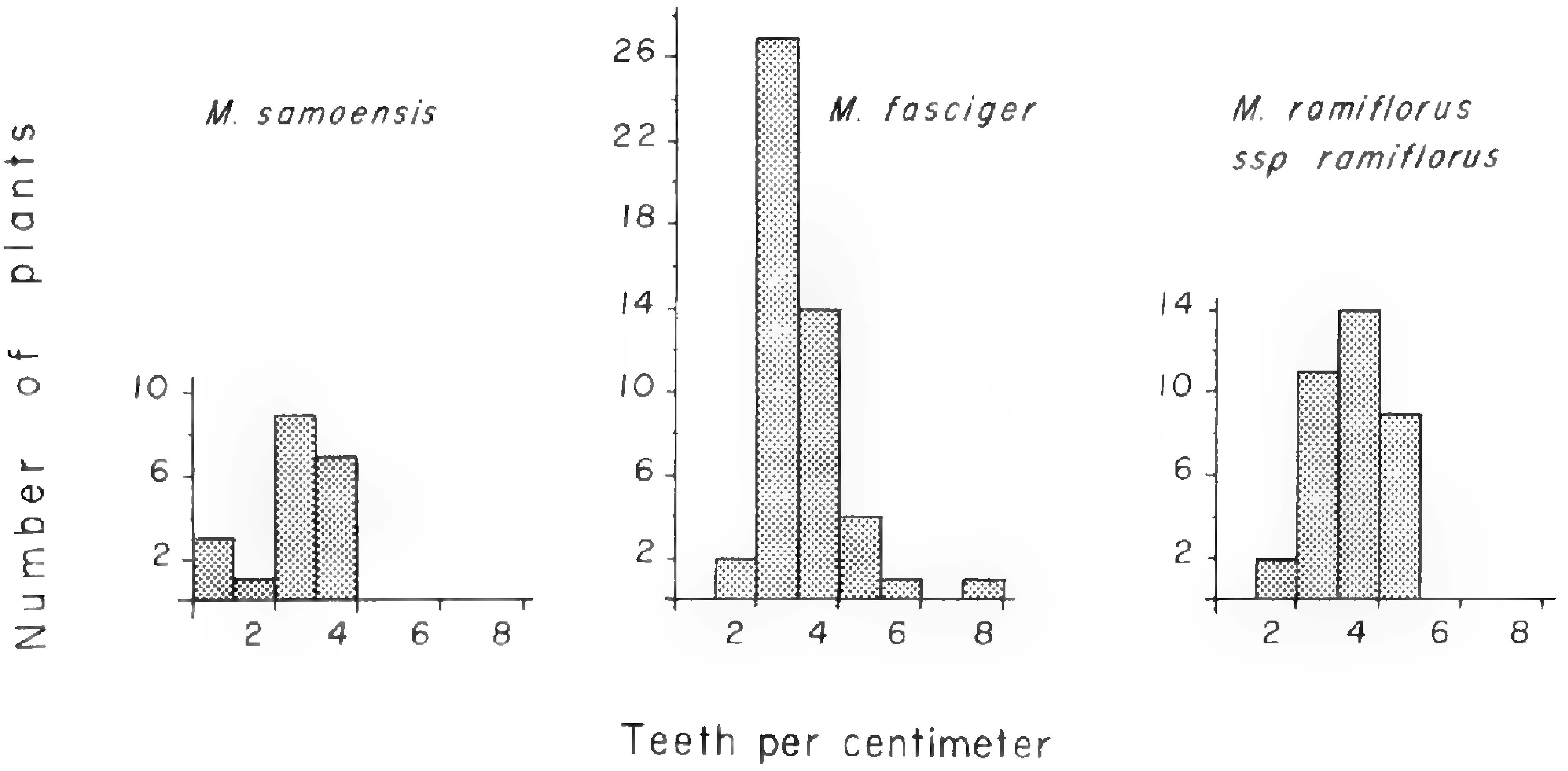

FIGURE 3. Leaf margins: number of teeth per centimeter of margin. Each graphed value = median of counts on 10 leaves per specimen. (*Melicytus ramiflorus* subsp. *oblongifolius* (obscurely crenate rather than dentate) not illustrated.)

past anthesis. (Smith (1978) noted that petals elongate rapidly prior to anthesis.) The measurements are graphed in FIGURE 5. Several conclusions are possible from these graphs. First, pistillate flowers appear to have smaller petals than staminate ones. Second, there is no break at 2 mm, as was suggested by Smith (1978); New Zealand and Oceanian specimens can therefore not be distinguished on the basis of this character. Third, there is a conspicuous break between 3.5 and 4.8 mm for the Fijian plants. The plants with very long petals are all staminate ones collected from Viti Levu (Fiji), but there are short-petaled specimens from that island as well (discussed in more detail below). Petal shape varies from short and rounded to more or less triangular to long and lanceolate, with the shape correlating roughly with the length; however, the variation is not consistently correlated with any other characters that we have been able to find, nor can it be divided into discrete character states.

Each flower is generally subtended by two bracteoles, but the position of these varies. They may be directly under the calyx, as in the long-petaled specimens from Fiji; about midway on the pedicel, as in *Melicytus ramiflorus*; at the base of the pedicel and indistinguishable from the bracts, as in the specimens from Samoa and Tonga; or variable in position, as in plants from Norfolk Island. Bracteole shape varies little. Pedicel length varies somewhat, but because elongation appears to occur soon after anthesis in the pistillate plants, this was a difficult character to use.

The fruit is a berry with several seeds. Seeds are of two distinct types: small (less than 3 mm long) and purplish black, or large (greater than 3.5 mm) and tan. The small, dark seeds are found in both subspecies of *Melicytus ramiflorus*, while the larger, tan ones occur throughout the genus, including *M. fasciger* and *M. samoensis*. Curiously, the large seeds are rarely filled with endosperm, whereas the smaller ones are nearly always filled with a white oily endosperm. The seeds of the Samoan specimens are substantially larger (all over 4 mm) than those of any other group of specimens, whereas the seeds of the other

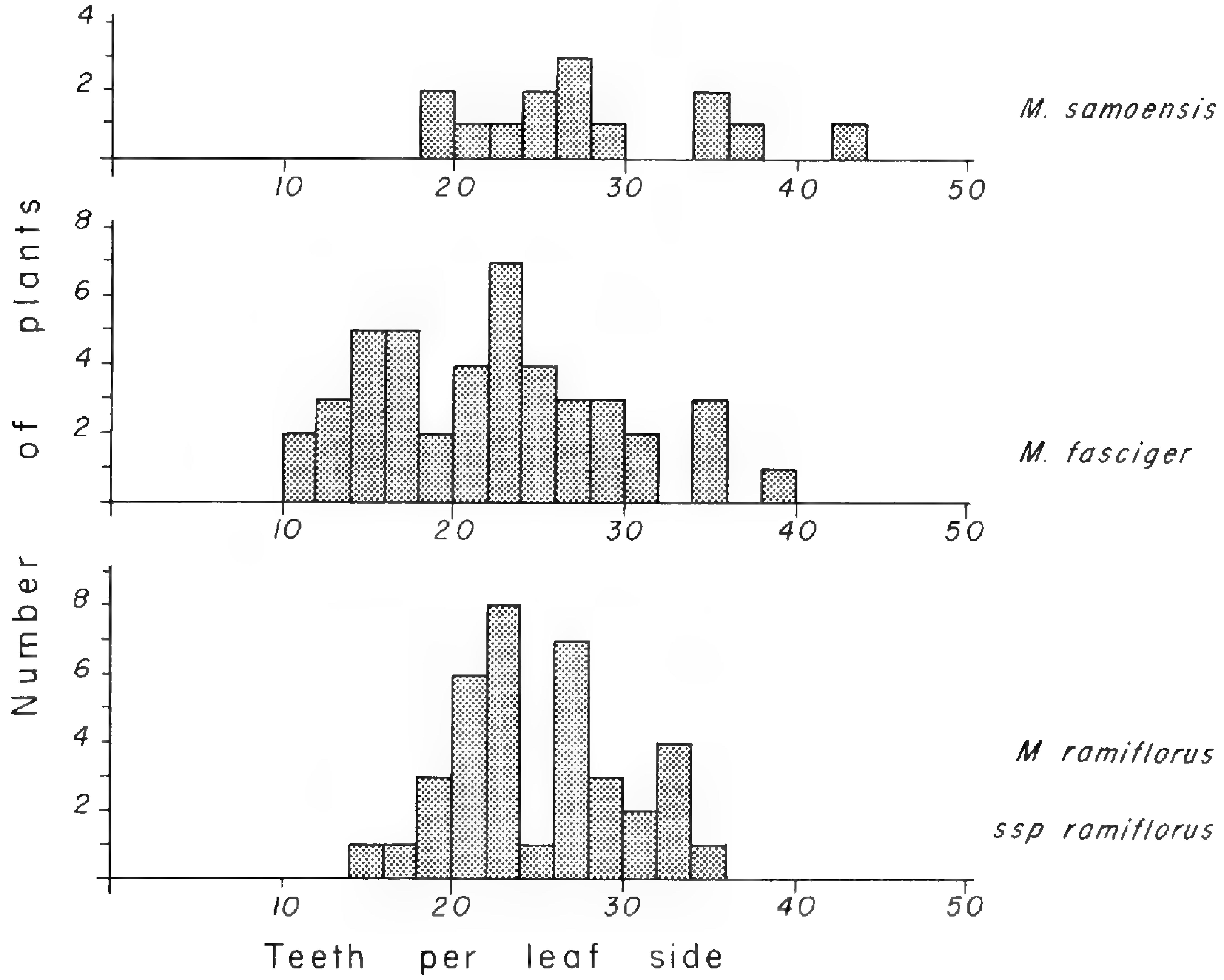

FIGURE 4. Leaf margins: number of teeth per side of leaf. See explanation under FIGURE 3.

Oceanian plants are intermediate in size between those of *M. samoensis* and those of *M. ramiflorus*.

The two basic seed types also have distinctive testa structures. The small seeds (FIGURE 6A) have a double or triple outer layer of large, open, irregular, thin-walled cells containing irregular bodies of dark-staining material that may be tannins; inside this tissue is a single or double layer of thick-walled lignified cells with prominent plasmodesmata. The innermost layer of cells is again thin walled and small. In these seeds a vascular bundle with a sclerenchymatous sheath is always visible at the chalazal end. The large seeds (FIGURE 6B) have a thin outer layer of more or less collapsed and indistinct cells around a single or double layer of thick-walled cells similar to those in the small seeds. Although some vascular tissue is apparent in the funicular region of these seeds, it is never surrounded by a sclerenchymatous sheath. In specimens of *Melicytus fasciger* and *M. samoensis*, there is considerable variation in the thickness of the various cell layers in the testa, but there are too few specimens available to determine whether this is due to the age of the seed or to variation within a plant, or whether it might delimit taxonomic groups.

DISCUSSION AND CONCLUSIONS

The data suggest that *Melicytus ramiflorus* from New Zealand can be distinguished from the Oceanian members of the genus by 1) stiffly pubescent

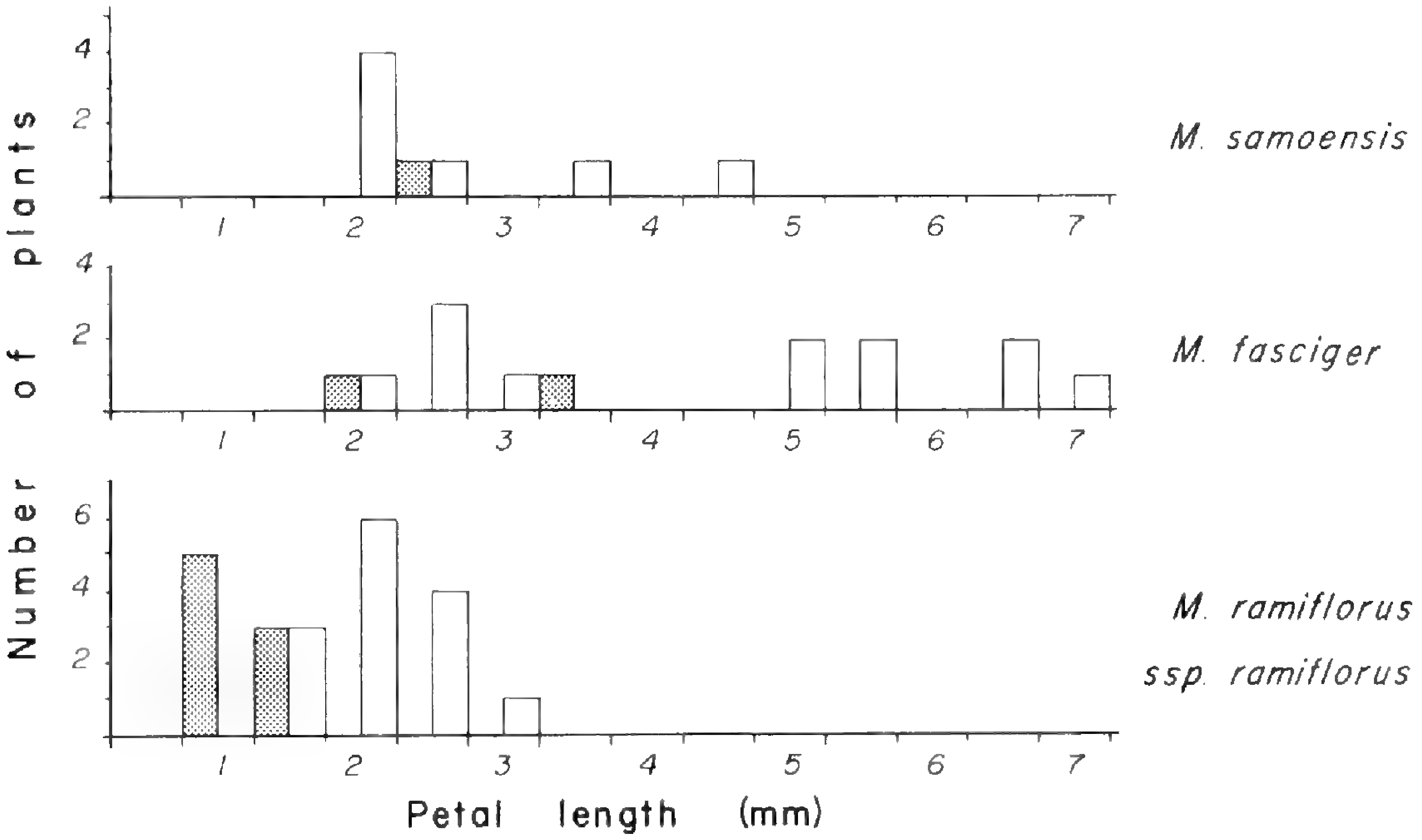

FIGURE 5. Petal length. Shaded bars = pistillate flowers (measured if open); open bars = staminate flowers (measured after anthesis). Flowers measured after rehydration. Each graphed value based on mean of 5 flowers per specimen, 5 petals per flower. Single flowering specimen seen of *Melicytus ramiflorus* subsp. *oblongifolius* was staminate, with petals 1.1–1.2 mm.

stipules and bud scales on all plants, and puberulent pedicels and sepals on pistillate ones; 2) bracteoles about midway along the pedicel; 3) seeds less than 2.5 mm long; and 4) testa dark, minutely and irregularly tuberculate, with a distinctive structure in cross section. Of these characters, numbers 1 and 3 appear to be unique in the genus, while 4 is shared only with *M. ramiflorus* subsp. *oblongifolius,* from Norfolk Island. The seed characters also appear in *Sykes 643* (L), from the Kermadec Islands, but the stipules on this plant are nearly glabrous. We conclude that the testa morphology serves as a unique character to unite the New Zealand, Kermadec Islands, and Norfolk Island plants as a single species.

The Norfolk Island plants, *Melicytus ramiflorus* subsp. *oblongifolius,* have seeds 2.3–3 mm long, intermediate between seeds of *M. fasciger* and those of *M. ramiflorus* subsp. *ramiflorus.* Unlike the latter subspecies, *M. ramiflorus* subsp. *oblongifolius* has leaf margins that are only obscurely crenate, rather than toothed. It is also intermediate between *M. fasciger* and *M. ramiflorus* subsp. *ramiflorus* in bracteole position, which varies from midway up the pedicel to immediately subtending the calyx. The endosperm of *M. ramiflorus* subsp. *oblongifolius* is crisp and fills the seed but appears to be less oily than that of *M. ramiflorus* subsp. *ramiflorus.*

Despite the lack of floral differences, the New Zealand, Kermadec Islands, and Norfolk Island plants should not be considered conspecific with those from the other Oceanian islands. The seed and stipule characters are sufficiently distinct and consistent to mark *Melicytus ramiflorus* as a strictly monophyletic taxon, separate from the other two species.

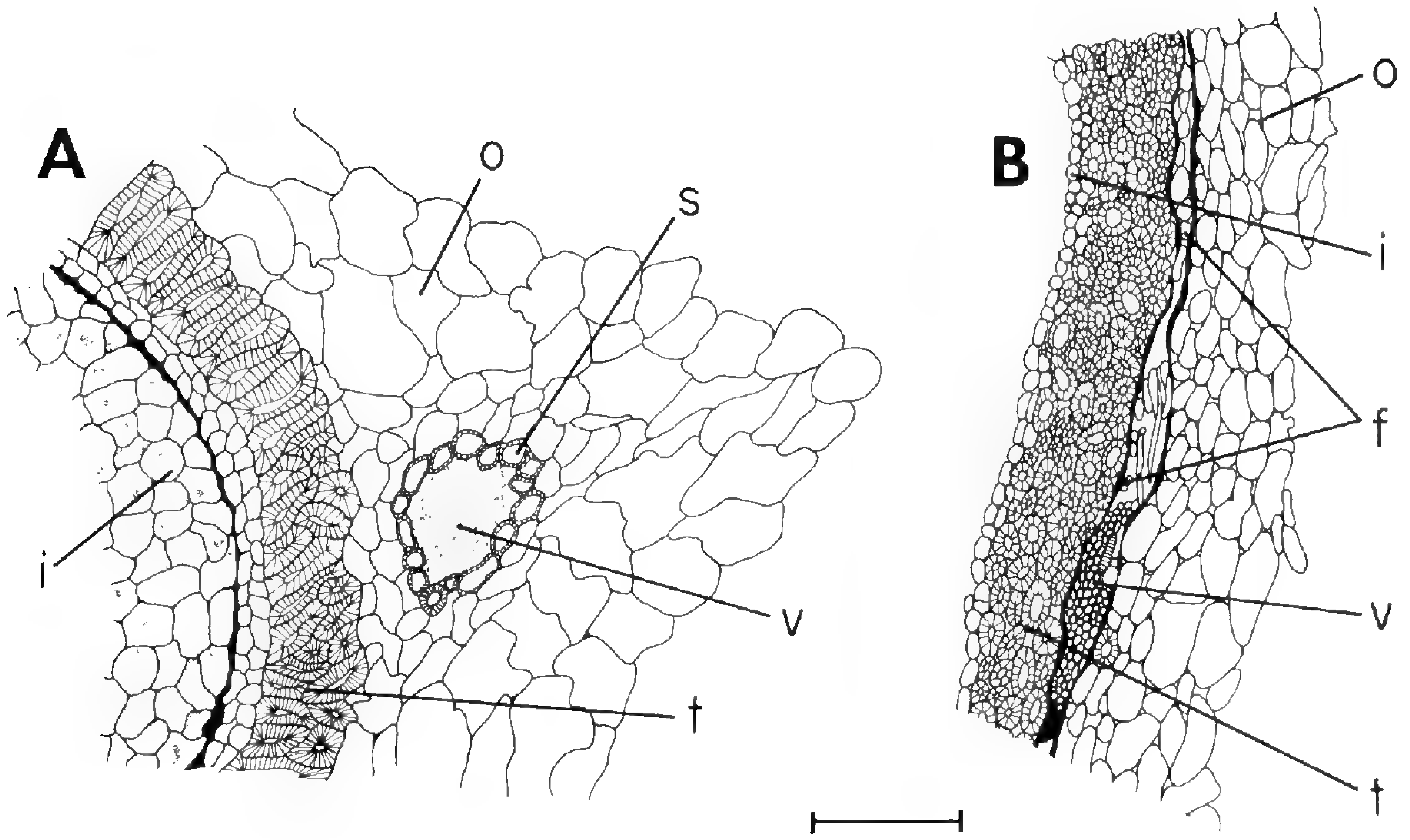

FIGURE 6. Cross sections of testa near chalazal end of seed: A, *Melicytus ramiflorus* subsp. *ramiflorus* (*Cooper 121932*); B, *M. fasciger* (*Bernardi 12944*). Camera lucida drawings of paraffin-embedded material stained with safranin and fast green. Key: o = outer layer of thin-walled cells, many highly crushed in B; v = vascular tissue; s = sclerenchymatous sheath; t = inner layer of thick-walled cells; i = innermost layer of thin-walled cells; f = layer of crushed thin-walled cells present only in funicular region of seeds of Oceanian species. Scale = 0.01 mm.

Among the Oceanian plants, the Samoan ones are distinctive in lacking bracteoles on the pedicels and in having pale brown seeds that are over 4 mm long. Although our material is insufficient to allow us to reach firm conclusions, it appears that representatives of *Melicytus* from Tonga are similar and should be included with the Samoan plants. Smith has applied the name *M. samoensis* to these plants.

Melicytus fasciger occurs on Fiji (Viti Levu, Taveuni, and Ngau) and Vanuatu; we have also seen one specimen from the Solomon Islands. These plants are distinguished from *M. ramiflorus* and *M. samoensis* in having brown seeds 3–4 mm long. Within this group of plants, there is a marked discontinuity in petal length of the mature staminate flowers. The average petal lengths in five collections (two from Vanuatu, two from Viti Levu, and one from Taveuni) are 1.4–2.6 mm; in another seven collections (all from Viti Levu), 4.8–6.6 mm. We have seen two collections of flowering pistillate plants, one from Viti Levu and the other from the small island of Ngau. These had average petal lengths of 1.7 and 3.2 mm, respectively. As noted above, in all taxa examined pistillate flowers tended to have shorter petals than did staminate ones. Thus the pistillate plant from Viti Levu could be conspecific with either the long- or the short-petaled staminate forms, whereas the plant from Ngau may be associated with longer-petaled staminate plants. However, we have seen no staminate plants from Ngau. We have seen two fruiting specimens from Fiji—one from Viti Levu, with seeds ca. 3 mm long, and one from Taveuni with seeds up to 3.9

mm. Lack of flowering material from Taveuni prevents connection of these plants with either of the two staminate forms from Viti Levu.

This evidence suggests that there may be two taxa in Fiji and Vanuatu—one relatively long-petaled one that may be endemic to Viti Levu, and a second, more widespread, short-petaled one. Only more collecting will determine whether this is the case or if petal length is simply very variable on Viti Levu. The type specimen of *Melicytus fasciger* (*Parks 20645*) is a long-petaled staminate plant from Viti Levu. If future workers decide that the short-petaled plants are indeed distinct, a new name will have to be provided.

The four taxa discussed here appear to be unusual within *Melicytus/Hymenanthera* because of their comparatively short, lanceolate to lance-ovate petals that are not at all imbricate at anthesis and their short stamen appendages. We think that they represent a monophyletic unit within the genus. Within this group, *M. ramiflorus* is also a monophyletic taxon based on the uniquely derived character of testa structure. Each of the other two taxa has unique characters, but we have found no character suggesting that *M. fasciger* and *M. samoensis* together constitute a monophyletic unit. This rules out the possibility of recognizing *M. samoensis* as a subspecies of *M. fasciger* to form a taxon distinct from *M. ramiflorus.* If the classification is to reflect the cladistic structure of the group, then *M. fasciger* and *M. samoensis* must be given the same rank as *M. ramiflorus.* Whether this rank should be variety, subspecies, or species is arbitrary. We have chosen the rank of species because the several distinguishing seed characters, although not easily observed, are consistent within geographic units.

TAXONOMIC TREATMENT

KEY TO THE OCEANIAN TAXA OF MELICYTUS

1. Bracteoles at base of pedicel; seeds ≥ 4 mm long; plants of Samoa and Tonga. . . . . 3. *M. samoensis.*
1. Bracteoles above base of pedicel; seeds < 4 mm long.
   2. Leaves crenate; seeds 2.5–3 mm long; plants of Norfolk Island. 2b. *M. ramiflorus* subsp. *oblongifolius.*
   2. Leaves dentate; seeds < 2.5 or > 3 mm long.
      3. Stipules stiff-pubescent (except on Kermadec Islands plants); bracteoles near middle of pedicel; seeds black, minutely and sparsely tuberculate, < 2.5 mm long; testa with vascular bundle with sclerenchymatous sheath; plants of New Zealand and Kermadec Islands. . . . . 2a. *M. ramiflorus* subsp. *ramiflorus.*
      3. Stipules glabrous; bracteoles variously located; seeds brown, smooth, > 3 mm long; testa without prominent sclerenchymatous vascular bundle; plants of Fiji, Vanuatu, and Solomon Islands. . . . . 1. *M. fasciger.*

1. **Melicytus fasciger** Gillespie, Bernice P. Bishop Mus. Bull. **91:** 20. *fig. 22.* 1932.

Melicytus ramiflorus J. R. & G. Forster subsp. *fasciger* (Gillespie) P. Green, Kew Bull. **23:** 345. 1969. TYPE: Viti Levu, Mba, Nandarivatu, May, June, July 1927, *Parks 20645* (holotype, BISH; isotypes, P!, SUVA, UC, US).

Shrubs or small trees to 10 m; bark whitish, smooth. Leaves with stipules deltate to lance-linear, 0.5–0.9 mm long, acute at apex, glabrous, caducous; petiole 5–13 mm long, adaxially bicarinate; blade elliptic, ovate, obovate, or oblanceolate, 8.5–17.5 × 3–6.7 cm, membranaceous, apex acuminate, base cuneate, margin serrate to dentate, with dentations 1 to 4 per cm and generally gland tipped. Inflorescences fascicles of 1 to 14 flowers. Pedicel 5–12 mm long in flower, becoming 8–21 mm in fruit; bracteoles variously located on pedicel, from below middle to just beneath calyx, ovate, erose; sepals deltate to ovate, 0.8–1.4 mm long, acute to obtuse at apex, 1-nerved, erose, green; petals lanceolate to lance-ovate, unequal, averaging 1.5–3 or 4.5–7 mm long in staminate flowers and 1.5–3.4 mm in pistillate, often apically thickened, white; anthers nearly sessile, ovate, the connective a short abaxial triangular or ovate flap, ≤ ½ length of anther; stigma flaring, crateriform. Fruits subglobose, 4.5–5.5 × 4.5–6 mm, becoming dark at maturity; placentae 3 to 5; seeds 2 per placenta, 3 or 4 developing, 3–3.5 mm long, tan to dark, smooth, with endosperm oily, shrunken in all specimens seen; embryo straight with orbicular cotyledons and straight hypocotyl.

SPECIMENS EXAMINED. **Fiji.** VITI LEVU. Road to Mavai, alt. 2700 ft, *Gibbs 749* (pistillate: BM). Mba, Nandarivatu: valley of Sigatoka, alt. 900 m, *Gillespie 3851* (sterile: BISH, 2 sheets); Mt. Lomalagi, alt. 2700–2900 ft, *Koroiveibau 13946* (short-petaled staminate: BISH, BRI); Mt. Koroyanitu, alt. 3850 ft, *Koroiveibau 14144* (short-petaled staminate: BISH), *Parks 20645* (long-petaled staminate: P); Tavua, upper part of W slopes of Mt. Lomalagi, alt. 950 m, *Stauffer & Koroiveibau 5827* (long-petaled staminate: A, BISH, BRI, K, P); by "Governor's Seat," *Im Thurn s.n.*, 31 Jan. 1906 (short-petaled staminate: K); Tavua, remnant woods on steep slopes at head of Savundamatau Creek, ca. 3 mi W of Nandarivatu, alt. 2900–3000 ft, *Webster & Hildreth 14258* (in fruit: BISH, GH). Mandrongo, Nausori Highlands, rain forest on W slopes of Mt. Mandrongo, alt. ca. 2000 ft, *Webster & Hildreth 14274* (short-petaled staminate: BISH). Mt. Victoria: alt. 800 m, *Lam 6856* (long-petaled staminate: L); lower slopes of mtn., alt. 3000 ft, *Vaughan 3415* (long-petaled staminate: BM). Nandronga and Navosa [formerly Tholo West]: near Koroneyalewa, alt. 1500 ft, on forest ridge, *Parham 1467* (sterile: A); N portion of Rairaimatuku Plateau, between Nandrau and Rewasu, alt. 725–925 m, *Smith 5647* (long-petaled staminate: A, BISH, K, US); alt. ca. 2700 ft, Vaturua, Nadrau, *Ranamu FD 1187* (long-petaled staminate: BISH, BRI). TAVEUNI: vic. of Waiyevo, stream banks, alt. 650 m, *Gillespie 4723* (short-petaled staminate: A, BISH, BRI, GH, US; sterile: K, P); slopes of Mt. Manuka, E of Wairiki, alt. 300–600 m, *Smith 3143* (in fruit: BISH, GH, US). NGAU: hills E of Herald Bay, inland from Sawaieke, alt. 300–450 m, *Smith 7746* (pistillate: BISH, GH, K, P). **Solomon Islands:** Santa Cruz Group, Vanikoro Is., S coast at Emwa, ridge forest, alt. ca. 1500 ft, *Whitmore BSIP 1695* (short-petaled staminate: L). **Vanuatu.** ANEITYUM: in vicinioribus Anawounamalo per semitam ad rivum Inwa Lelgey, alt. 10–180 m, *Bernardi 12944* (K); Anelgauhat Bay, *Kajewski 841* (A, 2 sheets), *Morrison s.n.*, 6 July 1896 (K). ESPIRÍTU SANTO. Mt. Tabwemasana: alt. 1460 m, *Chew RSNH 217* (K, L), alt. 5800 ft, *Gillison & Beveridge 3516* (K), alt. 1600–1800 m, *McKee 24170* (K); entre les deux sommets, alt. 1800 m, *Raynal RSNH 16342* (K, L, P). TANA: Mt. Tokosh Meru, alt. 600 m, *Kajewski 166* (A).

2a. **Melicytus ramiflorus** J. R. & G. Forster, Char. Gen. Pl. 124. 1776. TYPE: [New Zealand], *Forster 222* (holotype, BM!).

Shrubs or small trees to 4 m; bark smooth, gray, lenticellate. Leaves with stipules broadly asymmetric, triangular, tapering to acuminate point, covered with stiff erect trichomes, caducous; petiole 11–26 mm long, adaxially bicarinate; blade ovate, oblong, or elliptic, 7–14.4 × 2.6–5.8 cm, membranaceous, apex acute to acuminate (rarely obtuse), base rounded to cuneate, margin dentate, with dentations 1 to 7 per cm and generally gland tipped. Inflorescences fascicles of 1 to 20 flowers. Pedicel 2–6(–16) mm long in flower, becoming 6–11 mm in fruit, puberulent in pistillate flowers, glabrous in staminate; bracteoles usually near midpoint of pedicel, ovate, erose; sepals triangular, 0.6–1.2 mm long, acute to obtuse at apex, 1-nerved, erose, green, puberulent in pistillate flowers, glabrous in staminate; petals ovate to lanceolate, unequal, averaging 1–2.9 mm long in staminate flowers and 0.6–1.1 mm in pistillate, white, apically thickened; anthers nearly sessile, ovate, the connective an abaxial flap, shorter than anther; stigma flaring, crateriform. Fruits subglobose, 3–5 × 3–5.2 mm, blue-violet; placentae 3 (to 5); seeds 2 or 3 per placenta, up to 9 or 10 developing, 1.8–2.4 mm long, dark, lustrous, minutely and sparsely tuberculate, with endosperm oily, filling seed; embryo straight with ovate cotyledons and straight hypocotyl.

SPECIMENS EXAMINED. **New Zealand.** Without further locality, *Anonymous s.n., BRI 247133* (BRI), *Banks & Solander s.n.,* 1768–71 (US), *Sind s.n.* (BRI), *Wilkes Expedition s.n.,* 1838–42 (GH). NORTH ISLAND: Woodhill State Forest, ca. 50 km NW of Auckland, alt. 50–100 m, *Bernardi 12366* (US); Waiheke Is. in Hauraki Gulf, S coast at Rocky Bay, *Broek & Broek-Groen 51* (L, 2 sheets); Port Waikato, *Cooper 121932* (A); Swanson Reserve near Auckland, *Davis & Cooper s.n.,* 21 March 1950 (US); Urewera Natl. Park, Gisborned Distr., Aniwanewa, far E side of Lake Waikaremoana, just E of Waipai Swamp, Lake Ruapani track, *Edwards 32* (A); Waitakere Range W of Auckland, S end of Scenic Drive, alt. 300–450 m, *Fosberg 30255* (US); Orakei Basin, Auckland, *Gardner 859* (L); Taranaki, Mt. Egmont, in bush at 3000 ft, *Hunnewell 13534* (GH); Woodcocks N of Auckland, *Hynes s.n.,* 18 Oct. 1958 (US), *Kirk s.n.* (US); Auckland, *Leland et al. 224* (GH, 2 sheets; US); Manukau Co., ca. 10 km E-SE of Clevedon, *Orchard 3282* (A); Whangarei Co., ca. 1½ km SW of Oakura Bay settlement, alt. 60 m, *Orchard 3684* (A); Coromandel Co., ca. 5 km E of Coromandel on road to Te Rerenga, alt. 340 m, *Orchard 3949* (A); Auckland, Purewa Bush, *Powell s.n.,* 29 Nov. 1949 (A); Auckland Prov., Cascade Park, Waitakere range, W-NW of Auckland, *Walker 4246* (US); Wellington Prov., near The Spiral in Natl. Park near Raurimu, *Walker 4315* (US); Wellington Prov., near Waikane, 37 mi N of Wellington, *Walker 5168* (US); Auckland metropolitan area, Mt. Wellington lava fields, *Wright 503* (L); Northland, Mangamuku Gorge, *Zotov 84968* (A). SOUTH ISLAND: Akaroa, *Belligny s.n.* (GH); Nelson, *Dall s.n.,* 1882 (BRI); Greymouth, *Helms s.n.* (BRI); Westland, Franz Josef Glacier, *Hunnewell 13535* (GH), *Kirk s.n.* (A); Wellington, *Kirk 205* (GH), *Kirk 215* (US); Canterbury, Riccarton Bush, *Lothian s.n.,* Jan. 1937 (GH), *Von Mueller s.n.* (BRI); Canterbury, Pel Forest, *Philipson 10111* (A); Christchurch, Radcliffe Valley, *Stemmer s.n.,* 10 Dec. 1972 (L). KERMADEC ISLANDS. Raoul Is.: Low Flat, *Sykes 643/K* (L); above Low Flat, *Sykes 1084/K* (BRI).

2b. **Melicytus ramiflorus** J. R. & G. Forster subsp. **oblongifolius** (Cunn.) P. Green, J. Arnold Arbor. **51:** 220. 1970. TYPE: Norfolk Island, 1830, *Cunningham 127* (holotype, K!).

Hymenanthera oblongifolia Cunn. London J. Bot. **1:** 124. 1842.
Hymenanthera dentata R. Br. var. *oblongifolia* (Cunn.) Kirk, Trans. & Proc. New Zealand Inst. **28:** 511. 1896.

Shrubs or small trees to 8 m; bark whitish, smooth. Leaves with stipules lanceolate, deltate, or narrowly lanceolate, 0.5–0.8 mm long, acuminate at apex, hyaline and erose at margin, glabrous, caducous; petiole 10–14 mm, adaxially bicarinate; blade elliptic to ovate, obovate, or oblanceolate, 5.5–9.5 × 2.1–3.7 cm, membranaceous, apex acute, base cuneate, margin obscurely crenate with gland dots where veins meet margin, 1 to 4 gland dots per cm. Inflorescences fascicles of 1 to 7 flowers. Pedicel 2–7 mm long in flower, becoming 6–11 mm in fruit; bracteoles from near midpoint of pedicel to just beneath calyx, ovate, erose; sepals triangular, 1–1.8 mm long; petals ovate, 1.1–1.2 mm long in staminate flowers (pistillate flowers unknown), thickened on back; anthers nearly sessile, oblong to broadly deltate, the connective an abaxial flap, shorter than anther. Fruits subglobose, 4.2–4.7 × 2.8–3.7 mm, becoming mauve at maturity; placentae 3; seeds 2 per placenta, 3 to 6 developing, 2.3–3 mm long, pale to dark brown, smooth, with endosperm crisp and watery, filling seed; embryo straight with suborbicular cotyledons; hypocotyl pale greenish.

SPECIMENS EXAMINED. **Norfolk Island:** saddle between Mt. Pitt and Mt. Bates, alt. ca. 800 ft, *Hooglund 11361* (K); Mt. Pitt Reserve, *Lazarides 8073* (L), *Prior s.n.*, 1903 (K); *Ralston s.n.*, July 1969 (K); without further locality, *Backhouse 641* (K), *Cunningham s.n.* (Hb. Brown, K); *Cunningham 44* (K).

3. **Melicytus samoensis** (Christoph.) A. C. Smith, Allertonia **1:** 370. 1978. TYPE: Samoa, Savaii, 8 Aug. 1931, *Christophersen & Hume 2315* (holotype, BISH!; isotypes, K!, US).

Melicytus ramiflorus J. R. & G. Forster var. *samoensis* Christoph. Bernice P. Bishop Mus. Bull. **128:** 149. *fig. 21.* 1935.

Melicytus ramiflorus J. R. & G. Forster subsp. *samoensis* (Christoph.) P. Green, Kew Bull. **23:** 346. 1969.

Shrubs or small trees to 7 m; bark smooth. Leaves with stipules lanceolate to deltate, 1–1.5 mm long, acute at apex, glabrous, caducous; petiole 8–20 mm, adaxially bicarinate; blade elliptic, ovate, or obovate, the largest 10.5–18 × 3.8–7.5 cm, membranaceous, apex acuminate, base cuneate, margin crenate to minutely dentate, dentations < 1 to 3 per cm and generally with dark apical gland. Inflorescences fascicles of 1 to 13 flowers. Pedicel 3–9(–12) mm long in flower, becoming 7–12 mm in fruit; bracteoles generally basal, not clearly distinguishable from bracts; sepals deltate to ovate, 0.8–1.2 mm long, acute to obtuse at apex, 1-nerved, erose, green; petals lanceolate, lance-ovate, or ovate, unequal, 1.5–4.5 mm long in staminate flowers, averaging 2.4 mm in single pistillate plant seen, white, thickened apically, spreading at anthesis; anthers nearly sessile, ovate, the connective a short abaxial triangular flap, ca. ½ length of anther; stigma flaring, crateriform. Fruits irregular, 5.5–8 × 4.5–8 mm, thin walled, smooth; placentae generally 3; seeds 2 per placenta, usually 6 developing, ≥ 4 mm long, tan, smooth, with endosperm shrunken in all specimens seen; embryo straight, with orbicular cotyledons and straight hypocotyl.

SPECIMENS EXAMINED. **Tonga.** EUA: Powell Plantation, *Parks 16006* (BISH, K), *Parks 16307* (BISH), *Sister s.n.*, Dec. 1889 (K); ravine N of Riechelmann's Fuai plantation, near center of island, alt. ca. 120 m, *Yuncker 15349* (BISH, US). **Samoa.** SAVAII: forest above Matavanu crater, alt. ca. 800 m, *Christophersen 651* (BISH, K, P); above Salailua, alt. ± 1450 m, *Christophersen 3094* (BISH); forest at Olo, above Safotu, 700–800 m, *Christophersen & Hume 2315* (BISH, P); Olo, alt. ± 700 m, *Christophersen & Hume 2519* (BISH, K); Aopo-

Gagamalae, alt. 1000–1110 m, *Christophersen & Hume 3437* (BISH, US); Maungalsa, *Vaupel 201* (K, L); in forest W of Mt. Silisili, alt. 1600 m, *Whistler W2523* (BISH); in forest between Mauga Mu and Mauga Afi, alt. 1500 m, *Whistler W2621* (A, BISH, K). UPOLU: E of main road near Tiavi, alt. 700 m, *Whistler W1064* (BISH, US); near Mt. Le Pu'e, alt. 750 m, *Whistler W1189* (BISH, US).

ACKNOWLEDGMENTS

We would like to thank P. F. Stevens for suggesting this project and for his comments throughout. We also thank R. A. Howard for his comments on the manuscript, and A. Cronquist and P. S. Green for their reviews.

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THE "TRIPLARIS SCANDENS (VELL. CONC.) COCUCCI" COMPLEX (POLYGONACEAE)

RICHARD A. HOWARD

COCUCCI (1957a) published the combination *Triplaris scandens* (Vell. Conc.) Cocucci based on *Magonia scandens* Vell. Conc. (1829). *Magonia* Vell. Conc. is illegitimate, being a later homonym of *Magonia* A. St. Hil. (Sapindaceae). As synonyms of his *Triplaris scandens,* Cocucci listed *T. laurifolia* Cham. & Schldl. (1828), *T. macrocalix* Casar. (1845), *Ruprechtia lundii* Meisner (1855), *R. obidensis* Huber (1909), *R. macrocalix* Huber (1909), and *R. scandens* Rusby (1927). He later (1965) added to the synonymy *R. zernyi* (Standley) Howard, which I had transferred from the genus *Coccoloba.* A reexamination of the original descriptions, authentic specimens as available, and more recent collections indicates that this is a heterogeneous assemblage. I suggest that four species—*Ruprechtia crenata* (Casar.) Howard, *R. laurifolia* (Cham. & Schldl.) Meyer, *R. lundii,* and *R. obidensis*—be recognized within "*Triplaris scandens* (Vell. Conc.) Cocucci."

Cocucci's publications on species of *Ruprechtia* (1957a, 1957b, 1961, 1965) have established the vegetative characters of a hollow pith and persistent ocreae for distinguishing *Triplaris* from *Ruprechtia,* which has solid internodes and caducous ocreae. Brandbyge (1982), in an unpublished thesis I have been privileged to study, found that these characters are not exclusive. He described some species of *Triplaris* with solid stem internodes and some with nonpersistent ocreae. He also altered Cocucci's proposed interpretation of the inflorescence, as well as his emphasis on the narrowed hypanthium base in *Ruprechtia.* In general, the species of *Ruprechtia* are small trees or bushes of dry areas, while *Triplaris* is represented by larger trees with much larger leaves and is generally found in wetter areas. Although one can easily distinguish specimens of *Triplaris* from specimens of *Ruprechtia* by general appearance, assigning unambiguous key characters to separate the two genera is difficult. Relating the staminate and pistillate plants of a species is also difficult in both genera. Some species are represented in herbaria primarily by staminate specimens, others by pistillate specimens or fruiting material. Although perianth characters of pistillate plants and achene characters seem reliable, size and shape of the mature fruiting perianth have not been determined for all species.

Cocucci's "*Triplaris scandens* complex" presents additional problems. Some plants are described as lianas or vines, a growth form not previously recognized in either *Triplaris* or *Ruprechtia.* These may have either solid or hollow stems, and the ocreae are either persistent or caducous. In the specimens available for study, the leaves on the main stems are commonly larger than those on the

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terminal portions of the stem or on the axillary branches. The majority of staminate plants have the inflorescences on the main stem, which rarely has axillary branches. The specimens with pistillate flowers or fruits seem to represent either terminal portions of a main branch or axillary branches. Staminate inflorescences are branched from the base as fascicles of racemes or are paniculate. Pistillate inflorescences are infrequently paired and rarely branched above. The fruiting perianth is accrescent in both the hypanthium and the lobes. Fully mature fruiting perianths are not known for all species.

Brandbyge (1982) did not accept *Triplaris scandens* in his monographic treatment of *Triplaris*; in fact, he suggested that its proper position was in *Ruprechtia* and that more than one taxon was involved. I agree with Brandbyge that the component species involved in the circumscription of *Triplaris scandens* sensu Cocucci are better accommodated in *Ruprechtia*. Neither Cocucci or Brandbyge nor I have seen all of the types to establish beyond doubt the correct names for some of the more difficult taxa. None of us has assembled material from the many herbaria in Brazil; we hope our colleagues there will examine these conclusions and seek the necessary mature collections in future field work.

Ruprechtia crenata (Casar.) Howard, comb. nov.

Triplaris crenata Casar. Nov. Stirp. Brasil. Dec. **9:** 80. 1844.
Ruprechtia carpinoides Meisner *in* Martius, Fl. Brasil. **5**(1): 58. 1855.

Casaretto based *Triplaris crenata* on an unnumbered Riedel collection from Rio de Janeiro. It is not clear whether the holotype is in Turin, Genoa, or elsewhere. Correspondence on this problem has not been answered.

Meisner based *Ruprechtia carpinoides* on a staminate specimen in the De Candolle herbarium and suggested that it may be *Triplaris crenata* Casar. Cocucci (1961) placed it in the synonymy of *T. crenata*, stating that he had not the slightest doubt they were one and the same species, but he did not state whether he saw the material of Casaretto. A Field Museum photograph (neg. #7413, GH) of the "type" in the Delessert Herbarium shows a staminate plant that was collected "R. Jan. Jan. 1838, Brezil"; however, the name "Lund" as collector is crossed out and "Riedel" is written in. A Riedel specimen without number (NY) was collected in "Rio de Janeiro Jan. 1883 [*sic*]" and is probably a true isotype. Two Glaziou collections from Rio, *12115* (K) and *19761* (K), can be assigned here.

In his unpublished manuscript Brandbyge (1982, p. 70) concluded that *Triplaris crenata* "must belong to *Ruprechtia*." Descriptions refer to the plants as trees "40 pedalis ex Riedel" and to specimens of *R. carpinoides* as "a very high tree." Clearly this is not comparable to *Triplaris scandens* sensu Cocucci.

Ruprechtia laurifolia (Cham. & Schldl.) Meyer, Mém. Acad. Imp. Sci. Saint-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. **6**(2): 150. 1840.

Triplaris laurifolia Cham. & Schldl. Linnaea **3:** 55. 1828.
Triplaris macrocalyx Casar. Nov. Stirp. Brasil. Dec. **9:** 79. 1845.

For *Triplaris laurifolia,* Chamisso and Schlechtendal cited a collection made and sent by Sellow (*s.n., s.l.*). A collection of a staminate plant from Brasilia aequinoctialis, *Sellow 1395* (B), may be the holotype.

The type of *Triplaris macrocalyx* was described without location or collector and is therefore presumably a specimen collected by Casaretto from "Taypú" in the province of Rio de Janeiro. Brandbyge (1982) excluded both names from *Triplaris.*

Several collections by Riedel and by Riedel and Luschnatt bear a herbarium name honoring Riedel by "Hauk" as "spec. nov. with affinities to *R. laurifolia* det. E. Hassler." Neither "Hauk" nor any reference to a publication by Hassler can be traced.

ADDITIONAL SPECIMENS SEEN. **Brazil.** Without further locality, *Clausen s.n.* (US). EDO. RIO DE JANEIRO: without further locality, *Gardner 5593* (BM, K), *Glaziou 6703* (K), *8905* (K), *12116* (K), *13.134* (US, a collection of 2 sheets with different localities: on one "Province of Goyas" is printed and Goyas is crossed out; on the other "Province of" is printed, "Rio-Janeiro" is stamped on, and above this is written "Minas"), *Mrs. Graham s.n.* (K), *Martius 67* (K), *Miers 3753* (K), *Riedel 672* (A, GH), *s.n.* (K), *Riedel & Luschnatt 672* (NY, US), *1374* (US), *Sello 631* (BM, K), *s.n.* (BM, K), *St. Hilaire 104* (NY), *109* (K, NY), *Tweedie 110* (K), *Weddell 479* (A); Jacarépaguá, *Vidal s.n.* (A).

Ruprechtia lundii Meisner *in* Martius, Fl. Brasil. 5(1): 53. 1855.

Lund 578, photographed by Macbride among the types in the Delessert Herbarium (Field Mus. neg. #7416, GH), appears to consist of a leafless branch with staminate inflorescences, a leafless branch with large mature fruits, and a separate cluster of four leaves. One label states only "Bresil" as the location but bears the number *578* and the date 1839. A second label, without number, states, "R. Jan. Sept. 33" and "Bresil, ms Lund 1839." Two specimens at NY are possible isotypes: *Lund 578* was collected "in monte prope Brioca (Rio de Jan.)," and *Lund N 576* at "Vende Grande, prope Rio Janeiro 9/1833." Meisner did not indicate a type but cited several collections in W, DC, and M. Cocucci (1957a, p. 362) stated he saw "el isocótipo SCHOTT 4562" but did not indicate the herbarium or any label details, nor did he select a lectotype.

Ruprechtia lundii Meisner forma *minor* Meisner (*in* Martius, *ibid.*), with the type *Blanchet s.n.,* is based only on isolated fruits.

The large fruit of *Ruprechtia lundii* exemplified by *Lund 578* is matched by the recent collection *Prance & Ramos 6991* (A, US) made along the Pôrto Velho to Cuiabá highway, Territory of Rondônia, Brazil. A second collection, *Cordeiro 603* (A) from Estrada Belmonte, Terr. de Rondônia, appears to be the same, with younger pistillate flowers. The leaves of these collections are comparable to those of *Lund 578* (Field Mus. neg. #7416); they differ from those of the specimens I cite of *R. laurifolia* and *R. obidensis.* Rio de Janeiro and Territorio Rondônia are admittedly widely separated.

Ruprechtia obidensis Huber, Bol. Mus. Paraense Hist. Nat. 5: 344. 1909.

Magonia scandens Vell. Conc. Fl. Flumin. 165. 1825 [1829], Icones 4: *pl. 60.* 1827 [1831].

Triplaris scandens (Vell. Conc.) Cocucci, Rev. Fac. Ci. Exact. Fís. Nat. Univ. Nac. Córdoba **19:** 361. 1957.
Ruprechtia apetala Wedd. var. *sprucei* Meisner *in* DC. Prodr. Syst. Nat. Regni Veg. **14:** 182. 1857.
Ruprechtia scandens Rusby, Mem. New York Bot. Gard. **7:** 237, 238. 1927.
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Ruprechtia zernyi (Standley) Howard, J. Arnold Arbor. **41:** 357–390. 1960.

Vellozo's name *Magonia scandens* cannot be transferred to *Ruprechtia* because of *Ruprechtia scandens.* I do not know if a voucher specimen for *Magonia scandens* exists. Vellozo's plate with the dissection may typify the taxon. The plant was collected "Reg. Praedii S. Crucis." Cocucci expressed no doubt in transferring the specific name to *Triplaris.* Brandbyge thought that Cocucci's concept of *Triplaris* was in error and so excluded the Vellozo name from his treatment of *Triplaris.*

The first available name for this species is *Ruprechtia obidensis* (1909) based on *Ducke 2899* (staminate) and *Ducke 2901* (pistillate) from Óbidos, Edo. Pará, Brazil. Presumably a specimen exists in the herbarium of Museu Goeldi, and the pistillate/fruiting plant should be chosen as the lectotype. The original description clearly describes immature fruits, and Field Museum negative no. 8492 (GH) of an isotype in the Delessert Herbarium shows a pistillate plant without evident fruit. Huber compared this species with *Ruprechtia laurifolia,* stating it differed in the long, acute leaves. Cocucci (1957a) concluded that the differences were not of taxonomic value and placed the species in the synonymy of his *Triplaris scandens.*

Ducke accepted the name *Ruprechtia obidensis* and indicated that a synonym was *R. macrocalyx.* Huber described *R. macrocalyx* at the same time as *R. obidensis* and cited *Ducke 8540* (pistillate) and *Ducke 8539* (staminate) from Faro, Edo. Pará, Brazil. His description emphasizes the large fruiting calyx. The specific name "macrocalyx" would have been a preferable choice, had Ducke carefully considered the original descriptions. Loose specimens of *Ducke 8540* and *8539* in the Delessert Herbarium have been combined in one photograph (Field Mus. neg. #8493, GH), but the young fruits pictured are not the same size as those described by Huber. A lectotype for *R. macrocalyx* must be sought elsewhere.

Spruce 639, from Santarém, Edo. Pará, was described as *Ruprechtia apetala* Wedd. var. *sprucei* by Meisner. The specimen in the Delessert Herbarium (Field Mus. neg. #7414, GH) is staminate.

Ruprechtia scandens is based on material from head of Beni River, Edo. La Paz, Bolivia, 18 Aug. 1921, cited as *Rusby & White 972.* The holotype (NY) has a Rusby field label with "Rusby" crossed out and "White" written in. Among his observations, White noted that the stems were hollow but no ants were present in twelve staminate vines examined. An isotype (GH) collected on 18 August 1921 has a few young pistillate flowers just past the receptive stage and is credited to Rusby and White. A second sheet, with a larger quantity of mature fruits, was credited to O. E. White as number 972, collected 17 August 1921. Rusby admitted that he was sick most of the trip and that White did a large part of the collecting. It cannot be determined if these two collections are from the same plant.

Ruprechtia zernyi was originally described as a species of *Coccoloba* and is known from a single staminate collection that has very small leaves. It was made at Taperinha, near Santarém, Pará, Brazil. Comparable small leaves are found on many other specimens.

ADDITIONAL SPECIMENS SEEN. **Bolivia.** EDO. LA PAZ: Prov. S. Yungas, Basin Río Bopi, San Bartolomé (near Calisaya), *Krukoff 10126* (A, US). **Brazil.** EDO. PARÁ: Municipio de Oriximina, estrada Oriximina-Óbidos, *Cid, Ramos, Mota, & Rosas 2493* (A); Rio Trombetas, Oriximina, *M. Silva 1.702* (A); Óbidos, *Ducke 19542* (US); Santarém, *Spruce 903* (K); Belterra, *Baldwin 2751* (US). EDO. AMAZONAS: Urucará, São Sebastião, *M. Silva 1820* (US), *1824* (A); Manáos, Estrada do Aleixo, *Ducke 738* (NY, US), *Guédès 38* (US); Serra near Namorado Novo watershed between Rio Curuqueté & Rio Madeira at Abunã, *Prance et al. 14709* (A, K); Manaus, *Ducke 25.627* (US); Terr. Acre, near mouth of Rio Macauhan (tributary of Rio Yaco), *Krukoff 5791* (A, BM, K, M, NY, US); Rio Acre, *Ule 9350* (K); Rondônia, trail from W bank of Rio Madeira, 2 km below mouth of Rio Abunã, *Prance et al. 6043* (A, GH, K, NY, US). **Colombia.** EDO. MAGDALENA: Santa Marta, Río Frío, Quebrada Rodríguez, *F. Walker 1212* (US); Poponte, *C. Allen 929* (K). **Peru:** Río Acre, Seriugal Auristella, *Ule 9350* (US). **Venezuela.** DPTO. TRUJILLO: Quebrada Seca bridge & R. Motatán, *Pittier 13299* (A, US), *13302* (A, M, US).

UNPLACED COLLECTIONS

Two collections from Venezuela have not been adequately placed. *Wurdack & Monachino 41230* (A, US), from Edo. Bolívar, northernmost slopes of Cerro Baraguán, and *Bunting & Aristeguieta 6111* (A), from Edo. Zulia, carretera Maracaibo–Carora, are both staminate plants described as small trees to 6 m or less. Neither collection fits any known species of *Ruprechtia*, and each may represent a new species. I prefer to delay applying any names to this material until fruiting material is known.

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