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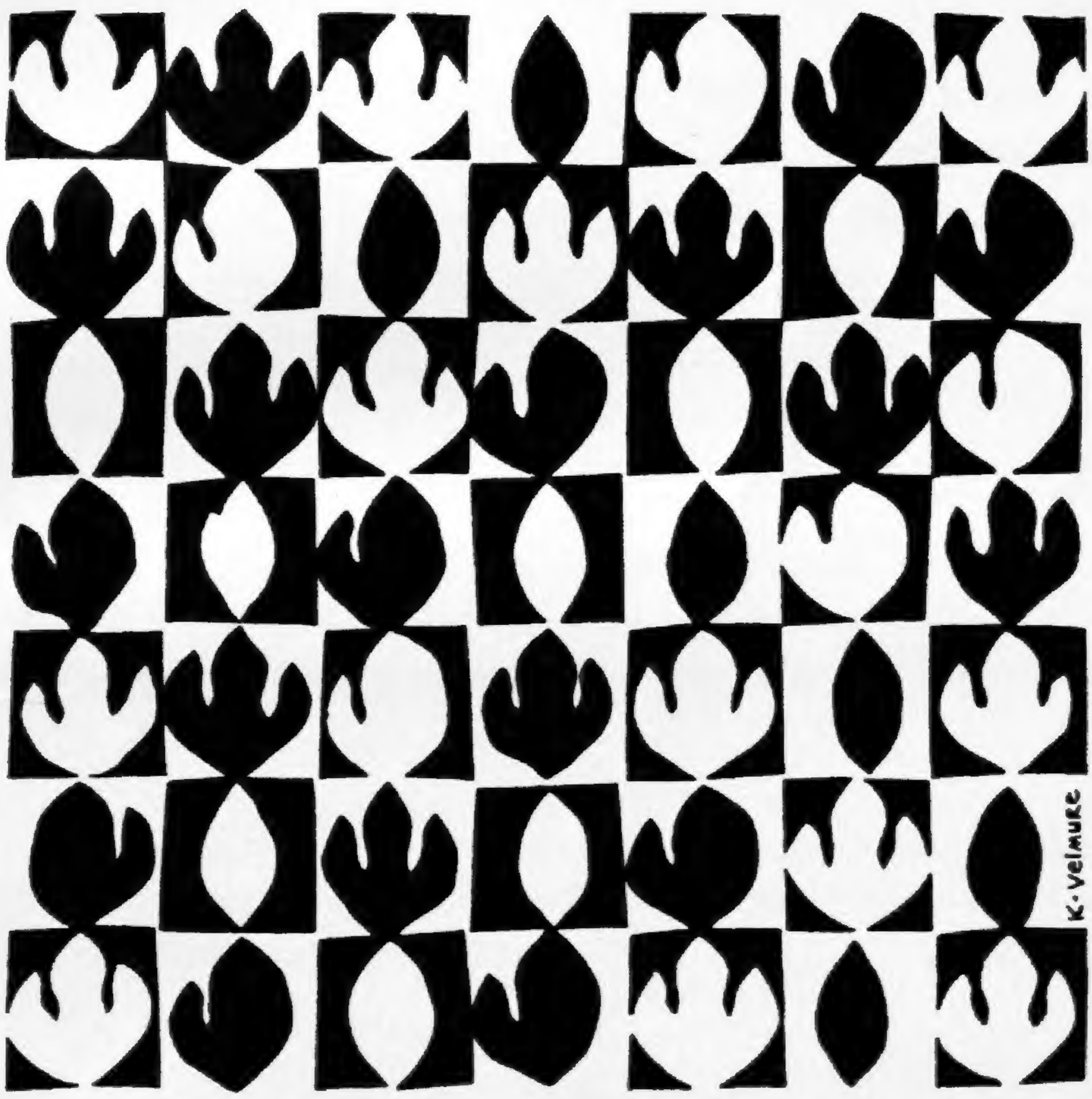

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LILY MAY PERRY

On January 5, DR. LILY MAY PERRY *observed her eightieth birthday. The staff of the Arnold Arboretum, with admiration, appreciation, and affection, dedicates this number of the* Journal of the Arnold Arboretum *to her. Miss Perry arrived at Harvard fifty years ago. With an absence of only five years, she served under two directors at the Gray Herbarium before transferring to the Arnold Arboretum, where she has helped the three directors who succeeded Charles Sargent. Although Miss Perry officially retired in 1964, she has rarely missed a day of "work" since that time, completing her studies of the Myrtaceae of Papua New Guinea, revising a large manuscript on medicinal plants of Southeast Asia, participating in regular seminars, serving as unofficial historian of systematic botany at Harvard, and aiding anyone who asks her help. She obviously enjoys each day, and we join in wishing her a happy birthday and many more.*

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LAURACEAE HARDY IN TEMPERATE NORTH AMERICA

STEPHEN A. SPONGBERG

THE TREATMENT OF the five genera of Lauraceae presented below is an initial contribution towards a projected manual of cultivated ligneous plants, the preparation of which is a project of the Arnold Arboretum, and the purpose of which is to provide a modern, accurate account of woody plants encountered in cultivation in the cooler temperate regions of North America. It is planned that additional treatments of selected families, groups of families, individual genera, or taxa of other ranks will be published as they are completed. This decision has been made for several reasons. Through publication the information assembled will be made available immediately. It is hoped that errors, omissions, and supplemental information, particularly concerning hardiness, will be brought to our attention; moreover, we will welcome constructive criticisms and suggestions from our colleagues and other interested individuals. In addition, nomenclatural and taxonomic problems and proposals that would be inappropriate in the manual can be presented and discussed more easily in the pages of a botanical journal. It is also hoped that the periodic appearance of these treatments will stimulate further interest in the taxonomy, encourage continued investigations, result in additional collections, and promote further ornamental use of a wider variety of cultivated woody plants.

That there is a need for a modern manual of cultivated woody plants has become increasingly evident within the last decade. While the indigenous or spontaneous flora of most areas of North America is relatively well known and has been treated in numerous readily available regional and/or local manuals or floras, cultivated plants generally have not received equal attention. As a result, many of the species that comprise our cultivated flora are poorly known, and few manuals or guides that can be used to identify cultivated and exotic material are available. The absence of a modern, standard reference treating cultivated plants constitutes a noticeable gap in our total floristic knowledge of North America, especially since ornamental cultivated plants are prominent in the environment of our increasingly urbanized society. As a result of this prominence, not only has the American public become more interested in plants in general, but botanists, teachers, nurserymen, and professional and ama-

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teur horticulturists, among others, have expressed need for an accurate and current reference dealing with the woody members of this large cosmopolitan group of plants.

As with any taxonomic study, our work in compiling a manual treating cultivated woody plants will be partially original, but it must be based upon and must draw information from previous scientific investigations and publications; the most recent North American work of the type now envisioned, and the model upon which our work will largely be based, was prepared by Alfred Rehder (1863–1949). Rehder's monumental contributions to our knowledge of the taxonomy of cultivated trees and shrubs are for the most part incorporated in his *Manual of Cultivated Trees and Shrubs Hardy in North America, Exclusive of the Subtropical and Warmer Temperate Regions*, which was written while Rehder was a member of the staff of the Arnold Arboretum, and in his *Bibliography of Cultivated Trees and Shrubs Hardy in the Cooler Temperate Regions of the Northern Hemisphere*. Since their publication, these two works have remained the standard references of their kind for the area covered. The work presently under way will attempt to update and correct the information included in Rehder's *Manual*. However, our current investigations will eventually result in a new manual, not a new, revised edition of Rehder's work.

The first edition of Rehder's *Manual* appeared in 1927 and was followed by a second, revised and enlarged edition in 1940. Currently in its twelfth printing, the *Manual* is available only periodically and never in great enough quantity to satisfy the continued demand. As a result, it has been increasingly difficult to obtain. The *Bibliography*, which gives complete bibliographic citations and almost complete synonymy for the names accepted in the second edition (including a few not in the *Manual*), was prepared at and published by the Arboretum during Rehder's retirement and appeared just before his death in 1949. The supply of copies, however, has long been depleted.

Since the publication of the second edition of the *Manual* and the *Bibliography* thirty-four and twenty-five years, respectively, have elapsed, and, as a consequence of numerous experimental and systematic studies published during these years, changes in the interpretations and understanding of many of the taxa treated in Rehder's works have resulted. Furthermore, the results of these studies have often necessitated nomenclatural changes. Additional nomenclatural alterations are required under the provisions of the current (1972) edition of the International Code of Botanical Nomenclature (Regnum Vegetabile vol. 82), since Rehder prepared the second edition and the *Bibliography* following the 1935 edition of the International Code. Moreover, expanded provisions for the nomenclature of cultivated plants, in particular, and the official adoption of the old concept but new term cultivar were incorporated in the 1953 edition of the International Code of Nomenclature of Cultivated Plants. The current edition of that code, which includes additional modifications, was adopted in 1969 (Regnum Vegetabile vol. 64).

These nomenclatural considerations and the advance of our knowledge

of many groups have often rendered Rehder's treatments of these groups outmoded and inaccurate. Also, the continued introduction into cultivation of new plants that are not treated in the second edition of the *Manual* (e.g., *Metasequoia*) has further diminished the usefulness of that work.

Our work, therefore, will be based on a complete re-examination of herbarium material and botanical and horticultural literature; living specimens will be studied whenever possible and herbarium specimens of cultivated plants will be studied and compared with specimens of the same taxa from their native areas. New information, such as chromosome numbers and indications of plants known to be poisonous to man, will be incorporated. Keys for identification will be strictly dichotomous throughout, and selected references to recent, as well as standard, taxonomic and horticultural publications will be included under families and genera to increase the usefulness and value of each treatment. Except when known for taxa new to cultivation, dates of introduction will not be included, nor will expanded references to illustrations, but it is hoped that the inclusion of drawings, at least for critical groups, will be possible.

Continuity with Rehder's works will be achieved, since it has been decided that all of the accepted taxa included in Rehder's *Bibliography* will either be treated or accounted for in the new manual. Taxa treated in Rehder's *Manual* and *Bibliography* for which no records in cultivation exist will be handled in one of two ways.[1] Either the name will be listed as undocumented in cultivation, or, if confusion exists between a taxon known in cultivation and an undocumented taxon, the undocumented taxon will be keyed and/or described in order to clarify its status and prevent continued confusion. Changes in taxonomic interpretation that result in the inclusion of taxa recognized by Rehder within the concepts of other taxa will be indicated by the addition of major synonymy.

Documentation will be based on three sources but except in rare instances will not be included in the treatments. Herbarium specimens will constitute the primary evidence of a taxon's occurrence in cultivation; yet literature reports (including selected nursery catalogs) and the published inventories of various botanical gardens and arboreta from within the range outlined below will also be accepted as valid. Several of the inventories to be consulted are available in computerized form from the Plant Records Center of the American Horticultural Society. It will be assumed that the published and inventory records are correct, and the names therein will be treated so that misidentifications, if they have occurred, can be corrected.

In determining which newly cultivated taxa are to be added to those included in Rehder's *Bibliography*, Rehder's broad concept of woodiness, outlined in the Introduction to the first edition of his *Manual*, will be employed. Additionally, documentation will be required from within an arbitrary range that roughly coincides with the area outlined in the seventh and eighth editions of Gray's *Manual*. Our area will include all

[1] For the most part, these taxa comprise Rehder's "related species" and those included in anticipation of their introduction and/or success in cultivation.

of northeastern North America west to the western boundaries of Minnesota, Iowa, and Missouri, and south to the southern boundaries of Missouri, Kentucky, and Virginia. In Canada, the western boundary will be a hypothetical line extending northward to the Arctic Ocean from the northwestern corner of Minnesota. Although this area is arbitrary and artificial, it has been defined for the following reasons. The majority of North American botanical gardens and arboreta in the Temperate Zone are located within this area. Secondly, the greatest representation of cultivated woody plants in the Arnold Arboretum herbarium is from the same region. Additionally, it will be feasible for us to visit major living collections within this area, and if new species of woody plants are in cultivation in temperate North America, it is expected that the majority will occur here.

Two problems, one of major concern to horticulturists and the second of interest and concern to both horticulturists and taxonomists, center around the potential range of species in cultivation and the treatment and concept of cultivar and ranks below the level of species. Both of these multifarious problems have received considerable attention and thought in the planning of the new manual and deserve mention here.

Plant hardiness is the factor most often considered in discussions of the potential range of cultivated woody species, and the information usually sought is the northern limit at which a particular species will tolerate the severity of winter climate. But when one considers northern species in cultivation, the question must also be asked from the reverse position, i.e., how far south will a northern species tolerate the changing, more southern environmental conditions. Additionally, a northern species grown primarily for its flowers may survive a southern Virginia winter, but the more southern climate and photoperiod may affect adversely or eliminate its ability to bloom and, therefore, also affect its ornamental value. The same circumstances in reverse may prove true for a southern species at more northern latitudes.

Only the repeated efforts of trial and error will determine with accuracy the possible ranges of species in cultivation, and the range of a particular species may require modification through the discovery of physiological and ecological variation within that species. As a consequence of such variation, nursery stock originating from seed collected from plants native to the Virginia Coastal Plain may not prove hardy in Boston, while plants of the same species grown from seed collected in the Mississippi Embayment region of Arkansas might flourish in the Arnold Arboretum.

With problems such as these in mind, it has been decided that the inclusion of zonal designations of hardiness will be postponed until publication of the treatments in manual form. Although the absence of these data will temporarily limit the usage of the published treatments, it is hoped that enough new data can be accumulated and tabulated from herbarium collections, botanical garden and arboreta inventories, commercial nursery offerings, and personal and communicated observations so that the final zonal designations in the manual will be more accurate

and dependable than if given provisionally now. It is also intended that a notation will be developed to include information for at least some species on "reverse hardiness" as well as "useful range." In our initial work towards these goals the Plant Hardiness Zone Map prepared by the United States Department of Agriculture (Miscellaneous Publ. No. 814. 1965) is being used for zonal designations. By allowing for more exacting designations due to zone subdivisions, this map has an advantage over previously published hardiness zone maps.

The primary intent of this work is to provide modern taxonomic treatments in manual form that will facilitate the determination of the botanical entities and provide the correct names of the genera and species of ligneous plants cultivated within our area. Thus, the treatment of cultivars is not a primary concern. Moreover, it would be impossible within the scope of the work presently envisioned to treat all of the cultivars now being grown. Such a work would necessarily be encyclopedic in length, and its value questionable, inasmuch as new cultivars, many of which replace and eclipse the popularity of other cultivars, are constantly being named and introduced.

Being without rank, cultivars may be selected from within a botanical taxon at any infraspecific rank, may comprise the entire ranked category, may cut across botanical categories of the same or a different rank, or may even cut across the limits of biological species, i.e., they may include elements of two distinct gene pools. When it can be determined that a named cultivar is coextensive with an accepted botanical taxon, or that a taxon as it is known in cultivation is represented primarily by a particular cultivar, we will attempt to list the correct alternative cultivar name. For some groups we will endeavor to indicate the characters that distinguish widely grown cultivars, and whenever known, published compilations of cultivars will be included under generic references.

In many instances horticulturally significant variations have been recognized in a botanical context, usually at the rank of *forma*. In those instances where evidence suggests that the plants comprising these categories are not worthy of taxonomic recognition, a cultivar name may be desirable so that the particular variants can be referred to in a horticultural context. In this respect, our concern with cultivars is primarily restricted, except as outlined above, to accounting for variants recognized by botanical combinations in Rehder's *Bibliography* but no longer considered worthy of taxonomic recognition. We have decided that in our treatments infraspecific taxa that are of dubious taxonomic status will be handled in a special manner. The correct botanical name will be given in a distinctive type face (SMALL CAPITALS), the presumed distinguishing characters will be stated, and the alternative cultivar name will be listed if one has been designated previously. The choice of name, either botanical or cultivar, is open and dependent upon the context in which the reader is working. If a cultivar name has not been proposed for the dubious taxon, we will not designate one. If in the future there is need for a cultivar name, we hope that one will be given in accordance with the then cur-

rent provisions of the International Code of Nomenclature of Cultivated Plants.

ACKNOWLEDGMENTS

The entire professional staff of the Arnold Arboretum is due thanks for freely given time and knowledgeable suggestions during the initial planning of the manual project. The responsibility for the final decisions based on the variety of opinions and diversity of viewpoints expressed during these discussions, however, is mine. For their continued help, advice, interest, and encouragement in the project, special thanks are extended to Drs. R. A. Howard, B. G. Schubert, C. E. Wood, Jr., and R. E. Weaver, Jr., and Mr. R. S. Hebb and Miss M. Gilmore. I am also indebted to Dr. E. A. Shaw, with whom I have had several constructive discussions concerning cultivars, and to Miss K. Clagett for editorial assistance.

Special thanks and gratitude are also extended to an anonymous donor whose generous gift to the Arnold Arboretum for this project has made and continues to make this work possible.

LAURACEAE A. L. de Jussieu, Gen. Pl. 80. 1789, nom. cons.

(LAUREL FAMILY)

Evergreen or deciduous trees or shrubs, the leaves, bark, and wood usually containing aromatic oils. Leaves exstipulate, simple, mostly alternate, entire, unlobed or occasionally lobed; venation pinnate or 3-veined from the base. Inflorescences usually axillary, cymose, racemose, or reduced and umbelliform, sometimes subtended by a deciduous involucre. Flowers small, perfect or imperfect (and the plants dioecious or rarely polygamodioecious). Perianth of (4 or) 6 yellowish or greenish tepals in 2 similar whorls, the tepals free nearly to the base, forming a very shallow perianth tube below. Stamens in 4 whorls of 3 stamens each, inserted on the rim of the perianth tube, 1 or more whorls often absent or reduced to staminodia; functional stamens of the third whorl usually associated with stalked or sessile glands; anthers 2- or 4-locular, introrsely to extrorsely dehiscent by valvular flaps. Ovary superior or ± adnate to the perianth tube, 1-locular, with a single pendulous, anatropous ovule; style and stigma 1. Fruit a fleshy or rarely dry, usually indehiscent, 1-seeded drupe, the perianth tube (if persistent) and the pedicel often thickened to form a cupule beneath the drupe; seeds lacking endosperm, the straight embryo with large, fleshy cotyledons. TYPE GENUS: *Laurus* L.

Between 2,000 and 2,500 species in 30 to 40 genera, primarily of tropical and warm-temperate regions, particularly of Central and South America and eastern Asia. Several species of this family are the sources of well-known spices and herbs. Notable among those not mentioned below is

the cinnamon of commerce, the dried bark of *Cinnamomum zeylanicum* Nees and/or *C. cassia* Blume.

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KEY TO GENERA OF LAURACEAE IN CULTIVATION

1. Inflorescence subtended and enclosed in bud by a deciduous involucre of bracts; flowers arranged in pedunculate or subsessile (often appearing fasciculate) umbelliform clusters. ..... 2.
   2. Umbelliform flower clusters distinctly pedunculate, the clusters subtended by an involucre of 5 or 6 caducous bracts; flowers perfect; anthers 4-locular. ..... 1. *Umbellularia.*
   2. Umbelliform flower clusters subsessile (often appearing fasciculate) to distinctly pedunculate, the clusters subtended by an involucre of 4 caducous bracts; flowers imperfect and the plants dioecious or occasionally polygamodioecious; anthers 2-locular. ..... 3.
      3. Perianth of 4 bractlike tepals in 2 whorls; staminate flowers with 12(–16) stamens, all associated with pairs of stipitate glands or rarely the outer 2 whorls eglandular. ..... 2. *Laurus.*
      3. Perianth of 6 petaloid tepals in 2 whorls; staminate flowers with 9 stamens, the outer 2 whorls eglandular, the inner whorl associated with pairs of stipitate glands. ..... 3. *Lindera.*
1. Inflorescence neither subtended nor enclosed in bud by an involucre of bracts; flowers arranged in small racemes or pedunculate cymose or subumbelliform inflorescences. ..... 4.
   4. Plants deciduous; inflorescence a small raceme; flowers imperfect and the plants dioecious (or occasionally polygamodioecious); anthers 4-locular, dehiscing introrsely. ..... 4. *Sassafras.*
   4. Plants evergreen; inflorescence a pedunculate subumbel or cyme; flowers perfect; anthers 4-locular, the inner whorl dehiscing extrorsely, the outer whorls dehiscing introrsely. ..... 5. *Persea.*

1. **Umbellularia** (Nees) Nuttall, N. Am. Sylva 1: 87. 1842.

Evergreen trees or shrubs with naked winter buds. Leaves strongly aromatic when bruised, short petiolate, alternate, involute in bud, pinnately veined. Flowers perfect, 4–5 mm. long, arranged in pedunculate umbelliform clusters in the axils of upper leaves or appearing to be in short, bracteate, terminal, compound-racemose inflorescences; each flower cluster enclosed in bud by a caducous involucre of 5 or 6 bracts. Perianth of 6, pale yellow, bractlike tepals. Functional stamens 9, the inner 3 with stipitate orange glands on each side of the filaments at base, alternating with an inner whorl of 3 scalelike staminodia; anthers 4-locular, the inner 3 with extrorse dehiscence, the outer 6 dehiscing introrsely. Ovary subglobose, small, tapering into a slender style; stigma capitate. Fruits subglobose or ovoid purplish-brown drupes borne on slightly thickened pedicels. (*Oreodaphne* subg. *Umbellularia* Nees, Syst. Laurin. 462. 1836.) TYPE SPECIES: *Tetranthera californica* Hooker & Arnott = *U. californica* (Hooker & Arnott) Nuttall. (Name Latin, diminutive of *umbella*, a little umbel.) — CALIFORNIAN LAUREL, OREGON MYRTLE, PEPPERWOOD.

A monotypic genus native to the Pacific Coast of North America.

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1. **U. californica** (Hooker & Arnott) Nuttall, N. Am. Sylva 1: 87. 1842.

Aromatic trees or shrubs of various habit to 45 m., the trees usually with a dense crown of erect, slender branches; bark greenish to reddish brown. Leaves oblong to oblong-lanceolate, 3–8(–10) cm. long, 1.5–3 cm. wide, with obtusely acuminate apices and cuneate to subrounded bases; surfaces of the blades finely reticulate, shining dark green above, paler green and dull beneath. Flower clusters 1.5–2 cm. in diameter, with 4–9 flowers; involucre of caducous bracts leaving conspicuous scars at the summit of the peduncle. One, 2, or 3 subglobose or ovoid drupes developing per flower cluster, each drupe 2–2.5 cm. long, greenish, becoming brownish purple when mature. $2n = 24$. *Tetranthera ? californica* Hooker & Arnott; *Oreodaphne californica* Nees.)

Indigenous to the Pacific Coast of the United States from southwestern Oregon (Coos County) south to San Diego County, California, and occurring in both the Coast Ranges and the Sierra Nevada. Plants with the peduncles and lower surfaces of the leaves finely tomentulose have been recognized as var. *fresnensis* Eastwood (Leafl. West. Bot. **4**: 166. 1945), while of the various growth forms, the trees with wide-spreading branches forming a crown broader than high and with slender pendulous branchlets have been designated as f. PENDULA Rehder (Jour. Arnold Arb. 1: 143. 1919). Often harvested and sold for flavoring in cooking as California bay leaf, the leaves of this species should not be confused with those of the true bay leaf, the foliage of *Laurus nobilis*.

2. Laurus Linnaeus, Sp. Pl. 1: 369. 1753; Gen. Pl. ed. 5. 173. 1754.

Evergreen shrubs or small trees with glabrous or pubescent reddish- or purplish-brown branchlets. Leaves ovate or obovate to narrowly elliptic, alternate, with pinnate venation. Flowers imperfect and the plants dioecious; flowers small, 3–4 mm. long, short pedicellate in pedunculate umbelliform clusters, the clusters occurring singly, fascicled, or in racemose inflorescences in the axils of leaves; each flower cluster subtended by an involucre of 4 deciduous bracts. Perianth of 4 yellowish, persistent, bractlike tepals in 2 whorls. Staminate flowers with 12 (rarely up to 16) stamens in 3 (or 4) whorls; filaments of all stamens associated with a pair of stipitate glands, or rarely the filaments of the first 2 whorls eglandular; anthers 2-locular, dehiscing introrsely. Carpellate flowers usually with 4 staminodia with sagittate filaments, often with small glands; ovary subglobose with a short style. Drupes ovoid, black, borne on the persistent and slightly enlarged perianth tube and pedicel. LECTOTYPE SPECIES: *L. nobilis* L.; typified by the removal of the other species attributed to *Laurus* by Linnaeus and their placement in other genera of Lauraceae. (Name an ancient one applied to the Laurel.) — LAUREL, SWEET BAY.

Two closely related species, *Laurus azorica* (Seub.) J. Franco (*L. canariensis* Webb & Berth.), $2n = 36$, of the Canary Islands and the Azores, and *L. nobilis* L. of the Mediterranean region, which is occasionally cultivated in our area.

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1. **L. nobilis** Linnaeus, Sp. Pl. 1: 369. 1753.

Evergreen shrubs or trees to 10 or rarely 20 m. with resinous winter buds, glabrous reddish-brown branchlets, and smooth brown or black bark. Petioles short, 3–6 mm. long, narrowly winged; leaf blades coriaceous, ovate to obovate or elliptic, (3–)5–10(–12) cm. long, (1.5–)2–4 cm. wide, with entire margins, acute to obtuse apices, and cuneate bases; both surfaces of the blades glabrous and finely reticulate, grayish green and shining above, pale and with the midvein elevated beneath. Flowers borne on finely pubescent pedicels in umbelliform cymose clusters, the clusters distinctly pedunculate, 1 to several in the axils of leaves or leaf scars. Drupes black and shining, ovoid to ellipsoid, 1–1.5 cm. long. $2n = 42$. — GRECIAN LAUREL, SWEET BAY.

Native to and characteristic of the Mediterranean region from Asia Minor west to Spain and Portugal. Cultivated since ancient times, this species is the laurel of mythology, history, and poetry and the source of bay leaf commonly used in cooking for flavoring. Easily trimmed into various shapes, the pruned plants are often grown in tubs for formal ornamental purposes. Aside from the typical form, f. *angustifolia* (Nees) Markgraf (in Hegi, Illus. Fl. Mittel-Europa ed. 2. 4(1): 15. 1958) (= cv. Angustifolia; var. *salicifolia* Hort.), with very narrow lanceolate leaves only 6–20 mm. wide, and f. *crispa* (Nees) Markgraf (loc. cit., 1958) (= cv. Undulata; var. *undulata* Meisner), with margins of leaf blades conspicuously wavy, may be encountered in cultivation.

3. **Lindera** Thunberg, Nov. Gen. Pl. 64. 1783, nom. cons.

Aromatic, deciduous or evergreen trees and shrubs, the leaves of deciduous species sometimes persistent over winter; buds absent or with few to numerous imbricated scales. Leaves petiolate, alternate to subopposite, unlobed with pinnate venation or 3-lobed and 3-veined from the base. Flowers imperfect and the plants dioecious or occasionally polygamodioecious; flowers small, yellow, short pedicellate in subsessile or short-pedunculate umbelliform clusters above the axils of leaves or of leaf scars; each flower cluster subtended by 4 deciduous bracts. Perianth of 6 or rarely more tepals in 2 whorls. Staminate flowers with 9 stamens in 3 whorls, the 3 innermost stamens with pairs of conspicuous stalked glands at the base of the filaments; anthers 2-locular. Carpellate flowers with stamens variously developed; ovary globose, with a short style. Fruits borne on slightly or obviously thickened pedicels, fleshy and indehiscent or dry and irregularly dehiscent. (*Benzoin* Schaeffer; including *Daphnidium* Nees, *Aperula* Blume, and *Parabenzoin* Nakai.) TYPE SPECIES: *L. umbellata* Thunberg. (Name commemorating John Linder, 1676–1723, an early Swedish botanist.)

A genus of about 100 species of temperate and tropical areas of eastern Asia and two species indigenous to the eastern United States. *Lindera*

triloba (Sieb. & Zucc.) Blume and *L. cercidifolia* Hemsley, both listed by Rehder, have been deleted from the present treatment since no documentation for their cultivation in our area has been found.

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KEY TO THE SPECIES OF LINDERA IN CULTIVATION

1. Flowers appearing in spring before the leaves; plants deciduous, the leaves (or most of them) not persistent over winter. . . . . 2.
   2. Pedicels and abaxial surfaces of the subtending bracts densely silky pubescent; leaf blades unlobed or 3-lobed, 3-veined from the base; drupes subglobose, black. . . . . 1. *L. obtusiloba*.
   2. Pedicels and abaxial surfaces of the subtending bracts finely pubescent or glabrous; leaf blades unlobed with pinnate venation; drupes subglobose or ellipsoid, red, reddish brown, or rarely yellowish. . . . . 3.
      3. Flower clusters subsessile, not noticeably pedunculate at anthesis, usually 4 clusters per node; drupes indehiscent, red, reddish brown, or rarely yellowish. . . . . 4.
         4. Winter buds glabrous or ± villous; pedicels of staminate flowers glabrous, pedicels of carpellate flowers 1–1.5 mm. long; drupes borne on slender pedicels 3–4 mm. long, not conspicuously enlarged at summit; mature drupes 8–10 mm. long. . . 2. *L. benzoin*.
         4. Winter buds villous; pedicels of staminate flowers finely pubescent, pedicels of carpellate flowers 2.5 mm. long; drupes borne on stout pedicels 9–12 mm. long, conspicuously enlarged at summit; mature drupes 10–11.5 mm. long. . . . . 3. *L. melissifolia*.
      3. Flower clusters distinctly stalked on peduncles 3–5 mm. long at anthesis, usually 2 clusters per node; drupes dehiscent into 5 or 6 irregular segments, yellowish. . . . . 4. *L. praecox*.
1. Flowers appearing in spring with the current season's leaves, the persistent foliage of the previous season, or the plants evergreen. . . . 5.
   5. Plants deciduous, the leaves dropping in fall or persistent over winter; terminal buds glabrous, with 3 or 4 imbricated scales. . . . . 6.
      6. Leaves chartaceous, elliptic, oblong-elliptic, or oblanceolate, not persistent over winter; flower clusters distinctly pedunculate and umbelliform, the peduncles and/or pedicels densely silky pubescent. . . . 7.
         7. Branchlets yellowish brown with sessile winter buds; peduncles at anthesis 3–5 mm. long, glabrous; pedicels pubescent, in fruit 10–

12 mm. long; drupes red. ..... 5. *L. erythrocarpa.*[2]

7. Branchlets dark green with stipitate winter buds; peduncles at anthesis 4–8 mm. long, pubescent; in fruit, the pubescent pedicels 15–22 mm. long; drupes black. ..... 6. *L. umbellata.*

6. Leaves subcoriaceous, narrowly lanceolate to oblong, persistent over winter, falling in spring; flower clusters subsessile, often appearing fasciculate in the axils of the persistent leaves; pedicels sparingly pubescent. ..... 7. *L. angustifolia.*

5. Plants evergreen; terminal buds large with 8–10 silky-pubescent imbricated scales. ..... 8. *L. megaphylla.*

1. **L. obtusiloba** Blume, Mus. Bot. Lugd.-Bat. 1: 325. 1851.

Shrubs or small, slender trees to ca. 10 m.; winter buds glabrous with 3 or 4 outer scales, the young branchlets pale yellowish green, often with conspicuous lenticels. Petioles pubescent, 1–2 cm. long; leaf blades 6–12 cm. long, 3–12 cm. wide, variable in shape, usually broadly ovate or subcordate with acute apices or 1–3-lobed, the lateral lobes short and obtuse, bases broadly cuneate or subcordate and 3-veined from the base; blades dark green and glabrescent above, pale bluish green and silky pubescent beneath, at least along the veins. Flowers borne on densely silky-pubescent pedicels in subsessile, umbelliform clusters, several clusters together in the axils of leaf scars from the previous season's leaves. Drupes black, subglobose, 7–8 mm. in diameter on pubescent pedicels ca. 1 cm. long. $2n = 24$. (*Benzoin obtusilobum* (Blume) Kuntze; *Lindera triloba* Hort., non (Sieb. & Zucc.) Blume.)

Native to eastern Asia in China, Japan, and Korea.

2. **L. benzoin** (L.) Blume, Mus. Bot. Lugd.-Bat. 1: 324. 1851.

Bushy, many-branched aromatic shrubs to 4.5 m. with small, glabrous, vegetative buds and larger, subglobose floral buds; young branchlets grayish black. Leaves short petiolate, the blades erect or ascending, becoming clear yellow in fall, oblong to obovate, 7–12 cm. long, 2–3.5 cm. wide, with acute or short-acuminate apices and cuneate bases; upper surfaces light green, pale green beneath. Flowers in dense, subsessile or sessile clusters, the clusters of staminate flowers ca. 5 mm. in diameter, larger than the clusters of carpellate flowers, usually several together above the scars of the previous season's leaves; carpellate flower clusters often single or paired at the nodes. Drupes scarlet, elliptic-oblong, 8–10 mm. long, 5–7 mm. wide, on slender pedicels 3–4 mm. long, not conspicuously enlarged at the summit, deciduous. $2n = 24$. (*Laurus benzoin* L.; *Benzoin aestivale* Nees.) — SPICE BUSH.

[2] Considerable taxonomic and nomenclatural confusion centers around *Lindera erythrocarpa*, *L. umbellata*, and other eastern Asiatic species of this group. Plants of the complex are variable, and the species are difficult to delimit; the treatment adopted here is essentially that of J. Ohwi, Fl. Japan, English ed., F. G. MEYER & E. H. WALKER, *eds*. 1965.

Widespread in eastern North America from Maine to southern Michigan and Illinois, southward to North Carolina, Kentucky, Missouri, and Kansas. Plants with finely pubescent branchlets, petioles, lower leaf surfaces (pubescent at least along the veins), and ciliate leaf margins have been recognized as var. *pubescens* (Palmer & Steyerm.) Rehder (Jour. Arnold Arb. 20: 412. 1939) (*Benzoin aestivale* var. *pubescens* Palmer & Steyerm.). More southern in distribution, var. *pubescens* extends into Florida and Texas. *Lindera benzoin* f. *xanthocarpa* (G. S. Torrey) Rehder (Jour. Arnold Arb. 20: 413. 1939) (*Benzoin aestivale* f. *xanthocarpa* G. S. Torrey), with yellow rather than red drupes, is known from wild populations in Massachusetts and is occasionally cultivated.

3. **L. melissifolia** (Walter) Blume, Mus. Bot. Lugd.-Bat. 1: 324. 1851.

Low deciduous shrubs to ca. 2 m., similar to the preceding but with villous winter buds and reddish brown branchlets. Petioles short, finely pubescent; leaf blades drooping, chartaceous, narrowly oblong, broadly lanceolate, or ovate, 5–15 cm. long, 1.5–6 cm. wide, with acute to acuminate apices, finely ciliate margins, and broadly cuneate, rounded, or obtuse bases; blades green, smooth and glabrous above, finely reticulate and pubescent, particularly along the elevated midvein, beneath. Flowers in dense, subsessile clusters, usually several clusters together above the leaf scars of the previous season's leaves. Mature drupes red, elliptic-oblong, 10–11.5 mm. long, 7–8 mm. wide, borne on pedicels 9–12 mm. long, the pedicels conspicuously enlarged at the summit and persistent. (*Laurus melissaefolia* Walter.)

One of the rarest native North American shrubs, known from a few scattered localities from Florida to Louisiana and northward to eastern North Carolina, Arkansas, and southern Missouri; known in cultivation at the Henry Foundation for Botanical Research, Gladwyne, Pennsylvania. See Steyermark (1949) for a valuable discussion and comparison of this species and its close ally, *L. benzoin*.

4. **L. praecox** (Siebold & Zuccarini) Blume, Mus. Bot. Lugd.-Bat. 1: 324. 1851.

Deciduous shrubs or small trees of bushy habit to 8 m.; vegetative buds small, conical, with 3 or 4 scales, floral buds globose; branchlets dark brown or silvery brown with conspicuous white lenticels when young. Leaves chartaceous, with petioles 1–2 cm. long; leaf blades elliptic, ovate, or broadly ovate, 4–9 cm. long, 2–5 cm. wide, with acute apices and broadly cuneate to subrounded bases; blades green above, glaucescent, often with soft hairs along the veins beneath. Flowers borne on short finely pubescent pedicels in small umbelliform clusters, the clusters on peduncles 3–5 mm. long, 2 or 3 clusters per node. Fruits dry, subglobose, 1.5–2 cm. in diameter, yellowish or yellowish brown, borne on thickened pedicels ca. 1 cm. long and dehiscing into 5 or 6 irregular segments to expose the single

seed. $2n = 24$. (*Benzoin praecox* Sieb. & Zucc.; *Parabenzoin praecox* (Sieb. & Zucc.) Nakai.)

Indigenous to Japan where it is relatively common in mountainous regions. Along with a few other Asiatic species of *Lindera*, *L. praecox* has been segregated into the genus *Parabenzoin* by Nakai because of its dry fruits that dehisce into five or six irregular segments. Carpellate plants are rarely encountered in cultivation, probably because their flower clusters are smaller and less showy than those of staminate plants.

5. **L. erythrocarpa** Makino, Bot. Mag. Tokyo 11: 219. 1897.

Large deciduous shrubs to ca. 6 m. (?) with yellowish brown branchlets and sessile winter buds. Petioles 6–10 mm. long; leaf blades chartaceous, oblanceolate to oblong, 6–13 cm. long, 1.5–2.5 cm. wide, with acute or ± obtuse apices and cuneate bases; upper surfaces of the blades glabrous, dark green, the lower surfaces glaucescent with sparse deciduous pubescence. Flowers borne on pubescent pedicels in pedunculate, umbelliform clusters, the glabrous peduncles 3–5 mm. long. Drupes red, globose, 5–6 mm. in diameter, on pedicels 10–12 mm. long.

Native to China, Korea, and Japan; reported in cultivation at Longwood Gardens.

6. **L. umbellata** Thunberg, Nov. Gen. Pl. 64. *tab.* 1783.

Erect deciduous shrubs or small trees to ca. 3 m. with dark green branchlets and short stipitate winter buds. Leaves thinly chartaceous with slender petioles 10–15 mm. long; blades narrowly oblong to ovate-oblong, 5–9 cm. long, 1.5–3.5 cm. wide, with acute apices and cuneate bases; blades glabrous above, the lower surfaces whitish pubescent when young, becoming glabrous. Flowers borne on pubescent pedicels in pedunculate umbelliform clusters, the pubescent peduncles 4–8 mm. long. Drupes black, globose, ca. 6 mm. in diameter, on pedicels 15–22 mm. long. (Including *L. umbellata* var. *hypoglauca* (Maxim.) Makino; *L. hypoglauca* Maxim.)

Native to China and Japan.

7. **L. angustifolia** Cheng in C. P'ei, Contr. Biol. Lab. Sci. Soc. China, Bot. Ser. 8: 294. *fig. 21.* 1933.

Deciduous shrubs to ca. 3 m. (?) with small conical vegetative buds and larger, subglobose floral buds; young branchlets reddish brown or reddish green. Leaves short petiolate, subcoriaceous, oblong to narrowly lanceolate, 5–10 cm. long, 1–2.5 cm. wide, with acute apices and cuneate bases; blades dark shining green above, pale green and glaucous below, turning pastel shades of orange and pink in fall; leaves persistent over winter and deciduous after anthesis in spring. Flowers on distinct, sparse-

ly pubescent pedicels in subsessile umbelliform clusters, several clusters together in the axils of the persistent leaves. Drupes black at maturity, globose, 5–6 mm. in diameter, borne on persistent pedicels, 1–1.5 cm. long, terminated by small discs or cupules, the drupes often appearing fasciculate on the branchlets.

Native to Central China. This species, not previously recorded as cultivated in our area, has promise as an ornamental plant, particularly since its foliage turns attractive pastel shades of pink and orange in fall and persists on the shrubs over winter. Specimens of this species (some misidentified as *Lindera umbellata* var. *hypoglauca*, others unidentified) have been examined from the Barnes Arboretum, the Garden Center of Greater Cleveland, and the Cole Nursery Company, Inc.; it is apparently also grown at the Holden Arboretum.

8. **L. megaphylla** Hemsley, Jour. Linn. Soc. Bot. **26**: 389. 1891.

Evergreen shrubs or small trees to 20 m.; branchlets purplish brown or purplish black with scattered white lenticels and large terminal buds 1–2 cm. long with numerous, finely white-pubescent, imbricated scales. Petioles 1–2.5 cm. long; leaf blades coriaceous, oblong to oblanceolate, 6–20 cm. long, (1.5–)2.5–6 cm. wide, with acuminate apices and cuneate bases; upper surfaces dark green and lustrous, the midveins prominently elevated on the dull green, glaucous, and glabrous or finely pubescent lower surfaces. Flowers borne on densely silky-pubescent pedicels in pedunculate umbelliform clusters above the axils of the leaves or leaf scars. Drupes black, globose to ovoid, ca. 1.5 cm. long, on stout pedicels ca. 1 cm. long; the pedicels terminated by discs ca. 8 mm. in diameter. (*Benzoin grandifolium* Rehder.)

Native to Taiwan, southern and southwestern China.

4. **Sassafras** T. F. L. Nees & Ebermaier, Handb. Med.-Pharm. Bot. **2**: 418. 1831.

Dioecious deciduous trees with thick, furrowed bark; winter buds with several imbricated scales. Leaves petiolate, involute in bud; leaf blades ovate to elliptic in outline, unlobed or 1–3(–5)-lobed at apex, with a prominent midvein and 2 prominent lateral veins from near the base. Flowers appearing before the leaves and/or as the leaves expand in spring, imperfect (or occasionally appearing perfect, but functionally imperfect), arranged in lax, drooping, several-flowered racemes in the axils of the scales of terminal buds. Perianth yellowish green, 6-parted nearly to base. Staminate flowers with 9 stamens in 3 whorls, each stamen of the inner whorl with a pair of stalked glands at the base of the filament; anthers 4-locular (2-locular in one species not in cultivation) with introrse dehiscence; staminodia and pistillodia variously present or absent. Carpel-

late flowers with a rudimentary androecium of 6 stamens or 9 stamens and 3 staminodia; ovary ovoid, the slender style terminated by a slightly expanded stigma. Fruit an ovoid, dark blue drupe borne on the club-shaped, enlarged, fleshy pedicel and perianth base. (Including *Pseudosassafras* Lecomte.) TYPE SPECIES: *Laurus sassafras* L. = *S. albidum* (Nuttall) Nees. (Name apparently a vernacular one used by early European settlers in Florida and later adopted by Trew.) — SASSAFRAS.

Three species, of which two, *Sassafras tzuma* Hemsley of China and *S. randaiense* Rehder of Taiwan, are not known in cultivation, while the third, *S. albidum*, is widely distributed and sometimes cultivated in the eastern United States and southern Canada.

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1. **S. albidum** (Nuttall) C. G. Nees, Syst. Laurin. 490. 1836.

Trees to 20 m. or rarely to 38 m., often suckering from the roots and forming colonies; branchlets and buds glabrous and glaucous, the bark on young branchlets green or brownish; leaves and bark aromatic. Petioles 1.5–3 cm. long; leaf blades ovate to elliptic, 8–12(–18) cm. long, 2–8 cm. wide, cuneate at base, unlobed or usually 1–3-(rarely 4- or 5-)lobed, characteristically mitten-shaped, the lobes subacute or obtuse; upper surfaces bright green, glabrous and glaucous beneath; foliage becoming bright orange or yellowish in fall; leaf scars with a single, linelike bundle scar. Flowers in small racemes 3–5 cm. long; staminate flowers with 9 stamens, the anthers 2-locular; staminodia and pistillodia absent; carpellate flowers with 6 rudimentary stamens in 2 whorls. Drupes ovoid, ca. 1 cm. long, borne on bright red fleshy pedicels. $2n = 48$. (*Sassafras officinale* Nees & Eberm. var. *albidum* Blake.)

Widespread in eastern North America from southern Maine and southern Ontario to Iowa and southward to Florida and Texas. Plants with finely pubescent or puberulent branchlets and the mature leaves silky pubescent beneath have been recognized as var. *molle* Fernald (Rhodora **38**: 179. 1936) (*Sassafras officinale* Nees & Eberm.; *S. variifolium* (Salisb.) Kuntze). This variety is generally of more southern distribu-

tion than var. *albidum*. Recently, f. *moldenkei* Oswald (Phytologia 7: 321. 1961) (plants with leaves pubescent beneath and the branchlets bright red purple instead of green or brownish) has been described from Long Island, and if introduced into cultivation may become valuable as an ornamental. It should be noted, however, that *S. albidum* is a very difficult species to transplant.

Filé, a powder prepared from the dried, young, mucilaginous leaves and pith, sometimes mixed with thyme, is used to thicken gumbo and as a condiment in the southern United States. Sassafras tea is brewed using the bark of the roots, while an oil used to flavor carbonated beverages (root beer) is obtained from the roots and bark.

5. **Persea** Miller, Gard. Dict. Abr. ed. 4. 1754, nom. cons.

Evergreen trees and shrubs with naked buds. Leaves petiolate, revolute in bud, chartaceous to coriaceous, pinnately veined, and usually pubescent. Flowers perfect, arranged in pedunculate, cymose or subumbelliform inflorescences in the axils of leaves. Perianth lobes 6, nearly free to the base, hairy, persistent in fruit. Androecium of 9 functional stamens and 3 inner staminodia, the first 2 whorls of functional anthers with introrse dehiscence, the third whorl with extrorse dehiscence; anthers 4-locular; filaments with paired stalked or basally sessile glands. Ovary subglobose, the style slender and often pubescent. Drupes baccate, small and subglobose or globose or large and ellipsoid, sometimes fleshy, borne on the spreading, persistent perianth lobes. (*Borbonia* Miller; *Tamala* Raf.) TYPE SPECIES: *P. americana* Miller. (Name an ancient one used by Theophrastus for an oriental tree and later adopted by Linnaeus.) — SWEET BAY.

Approximately 150 species primarily of tropical America but extending southward to Chile and northward to Delaware and Arkansas; one species in the Canary Islands. As accepted here, two species are infrequently cultivated in our area, while outside our region additional species are native to the southeastern United States, and *Persea americana* Miller, the American avocado, and its var. *drymifolia* (Schlecht. & Cham.) Blake, the Mexican avocado, are cultivated in warmer regions of the United States and often grown as house plants.

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KEY TO THE SPECIES OF PERSEA IN CULTIVATION

1. Peduncles shorter than the petioles of the leaves subtending the inflorescences; pubescence of branchlets and leaves appressed. . . . . 1. *P. borbonia.*
1. Peduncles longer than the petioles of the leaves subtending the inflorescences; pubescence of branchlets and leaves crisped and erect. . . . . 2. *P. palustris.*

1. **P. borbonia** (L.) Sprengel, Syst. **2**: 268. 1825.

Shrubs or small trees to ca. 12 m. with thick, deeply furrowed, aromatic bark; branchlets reddish brown with angular tips and sparse to dense appressed pubescence. Petioles 1–3 cm. long, the leaf blades coriaceous, elliptic to lanceolate, 4–10(–13) cm. long, 1–4(–6.5) cm. wide, with acute to rounded apices, remotely revolute margins, and cuneate bases; both surfaces thinly pilose when young, bright green, lustrous, and becoming glabrous above, pale green, often appearing glabrous but sparsely appressed pubescent with coppery-brown hairs, primarily along the veins, below. Flowers inconspicuous, 3–3.5 mm. long, in pedunculate, several-flowered cymes, the peduncles slender, 0.8–2.5 cm. long, shorter than the petiole of the subtending leaf. Drupes subglobose, 8–12 mm. in diameter, black, glaucous, borne on reddish pedicels. $2n = 24$. (Excluding *P. humilis* Nash; including *P. littoralis* Small.) — RED BAY.

Native to the Coastal Plain and Piedmont of the southeastern United States from North Carolina to Florida and westward into Texas.

2. **P. palustris** (Rafinesque) Sargent, Bot. Gaz. **67**: 229. 1919.

Shrubs or small trees to 15 m. with thin, fissured, gray bark; branchlets angular, reddish brown, densely to sparsely pubescent with crisped, erect, rusty-brown hairs. Petioles 0.8–2.5 cm. long, the leaf blades subcoriaceous to coriaceous, obovate, ovate, or lanceolate, (5–)6.5–18 cm. long, 1.5–5.5 cm. wide, with acute to slightly rounded apices, remotely revolute margins, and cuneate bases; upper surfaces glabrescent, lustrous green, lower surfaces grayish white, finely pubescent with rusty-brown, crisped hairs, particularly along the veins. Flowers small, 4.5–5 mm. long, in pedunculate, several-flowered cymes, the peduncles slender, 1–7.5 cm. long, usually longer than the petioles of the subtending leaves. Drupes subglobose to ellipsoid, 7–8 mm. in diameter, black. $2n = 24$. (*P. borbonia* f. *pubescens* (Pursh) Fern.; *P. pubescens* (Pursh) Sarg.; *Laurus caroliniensis* β *pubescens* Pursh; *Tamala palustris* Raf.) — SWEET BAY, RED BAY, SWAMP BAY.

Native to the Coastal Plain from southeastern Virginia to southern Florida and west into Texas; also known from the Bahama Islands.

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SYSTEMATIC ANATOMY OF THE XYLEM AND COMMENTS ON THE RELATIONSHIPS OF FLACOURTIACEAE

REGIS B. MILLER

SLEUMER (1954) HAS STATED that ". . . no single character exists wherewith to distinguish Flacourtiaceae from other families or to recognize them in the field." However, the combination of simple generally alternate leaves, numerous stamens, a unilocular ovary with parietal placentation, copious endosperm, and often a glandular receptacle unites this complex of genera into a loosely organized family. This loose organization has resulted in a variety of taxonomic treatments. The wood anatomy of selected Flacourtiaceae has been studied previously, but a comprehensive investigation of the secondary xylem has never been undertaken. Therefore, in an effort to understand more completely the classification of the Flacourtiaceae, this anatomical study, focusing mainly upon tribal and generic relationships, was initiated. Hopefully it will lead to the definition of a more natural taxon. In addition, the validity of previously proposed ordinal and familial alliances is examined to help clarify phylogenetic problems and evolutionary trends. Generic descriptions together with an anatomical circumscription of the family presented in this work will be useful in the identification of unknown wood specimens, in the construction of keys, and in the classification of new taxa.

TAXONOMIC HISTORY

Early taxonomists, such as De Candolle (1824, 1825), Endlicher (1839), and Lindley (1853), treated many of the tribes of the modern Flacourtiaceae as separate "orders," which are equivalent to the modern rank of family. Gradually the genera of these families (orders) and other genera were united by taxonomists such as Clos (1855, 1857) and Bentham and Hooker (1862, 1867) until the all-inclusive Bixaceae of Baillon (1875) was erected. In 1894 Warburg proposed the segregation of the *Bixa* complex (i.e., those genera usually assigned to the modern concept of Bixaceae and Cochlospermaceae) from the rest of the flacourtiaceous genera. From Warburg to the present this segregation is generally followed. In 1925 Gilg revised Warburg's Flacourtiaceae, suggesting the union of the tribe Erythrospermeae with the tribe Oncobeae and proposing the new tribe Trichostephaneae.

In contemporary times three major phylogenetic systems have been proposed. Hutchinson (1967) saw the Flacourtiaceae as the largest and most dominant family in the Bixales, an order of only eight families. Some of Hutchinson's proposed changes within the Flacourtiaceae include the union of Gilg's (1925) tribes Abatieae and Phyllobotryeae with

the tribes Casearieae and Scolopieae, respectively; the exclusion of Gilg's tribe Trichostephaneae from the Flacourtiaceae; the removal of the tribe Paropsieae to the Passifloraceae; and the removal of the subtribe Prockiinae (tribe Scolopieae) to the Tiliaceae. Hutchinson saw the phyletic position of the Flacourtiaceae as an intermediate group of plants between orders Dilleniales and Tiliales. There seems to be little doubt that Hutchinson pictured the Flacourtiaceae (Bixales) not only as an intermediate group, but also as a primitive group giving rise to orders such as the Thymelaeales, Pittosporales, and Passiflorales.

Cronquist (1968) and Takhtajan (1969) treated the Flacourtiaceae similarly. Takhtajan positioned the family at the base of his Violales, from which he derived the other families in the order. He proposed that members of the Violales were derived from dillenialean forebears and that they were closely related to the Theales. Takhtajan also derived order Passiflorales from the Flacourtiaceae through the Passifloraceae, the basal family of the former order. The tribe Paropsieae, included earlier by some botanists in the Flacourtiaceae, was transferred to the family Passifloraceae.

Cronquist also placed the Flacourtiaceae in order Violales; however, he did not consider the family to be a basal group as did Takhtajan. Cronquist believed that although the Flacourtiaceae was primitive in the order, other families in the Violales did not arise from it directly. In contrast to Takhtajan, Cronquist considered the Violales to be derived from order Theales. He circumscribed the Violales more broadly than Takhtajan and included 20 families to form a somewhat heterogeneous group. Nevertheless, Cronquist stated that these families still belong "to the same general circle of affinity. . . ."

ANATOMICAL REVIEW

Several anatomical studies on segments of Flacourtiaceae have been directed toward clarifying relationships among the genera. In studying the Indonesian Flacourtiaceae Den Berger (1928) noted that the formation of the segregate families Bixaceae and Samydaceae was not consistent with the wood anatomy. He also stated that *Paropsia* differs very strongly from the other genera of Flacourtiaceae, even at first glance. Other pertinent observations made by Den Berger suggest similarities between the Flacourtiaceae and certain Euphorbiaceae, the genus *Siphonodon* (Celastraceae), and the Elaeocarpaceae (Tiliaceae). He also maintained that there is no special link between the Flacourtiaceae and Theaceae. Tupper (1934) concluded that the wood anatomy of Flacourtiaceae was "remarkably and strikingly constant and similar." Taylor (1938) also suggested that the Flacourtiaceae formed a homogeneous unit. Like Den Berger, Taylor concluded that the tribe Paropsieae should be included in the Passifloraceae. In 1964 Ayensu and Stern studied the anatomy of the Passifloraceae and also concluded that the Paropsieae belong in that family.

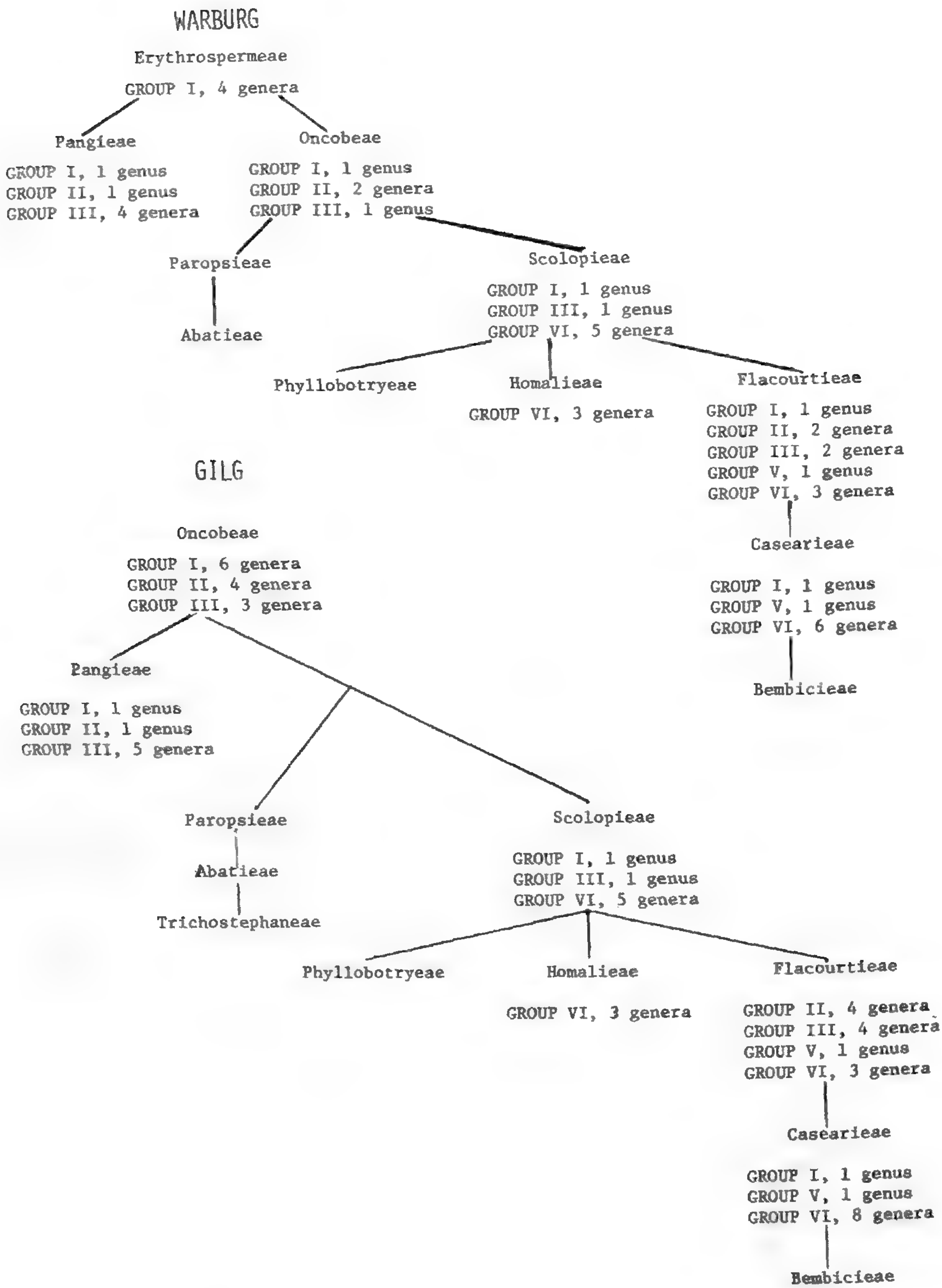


FIGURE 1. The phylogenetic sequences of tribes of Flacourtiaceae as proposed by Warburg (1894) and Gilg (1925). For each tribe the number of genera in each anatomical group is shown.

According to James and Ingle (1956), Flacourtiaceae of the Southwest Pacific area can be divided into two distinct structural groups. One of the groups generally corresponds to Gilg's Oncobeae and Pangieae, while the other corresponds to Gilg's Scolopieae, Homalieae, Flacourtieae, and Casearieae.

Major anatomical studies of families closely related to Flacourtiaceae include investigations of the Hypericaceae and Guttiferae by Vestal (1937), Dioncophyllaceae and Peridiscaceae by Metcalfe (1952, 1962), Bixaceae by Williams (1962), Cochlospermaceae by Keating (1968), and Violaceae by Taylor (1972). Many of these authors report some degree of relationship with Flacourtiaceae. Pertinent results of these studies will be discussed later.

Other anatomical studies generally have included only descriptions of selected genera or are contained in general reference works. These include studies by Record (1941), Record and Hess (1943), Metcalfe and Chalk (1950), Solereder (1908), Desch (1941), Reyes (1938), Bannan (1943), Miller (1966), and others.

MATERIALS AND METHODS

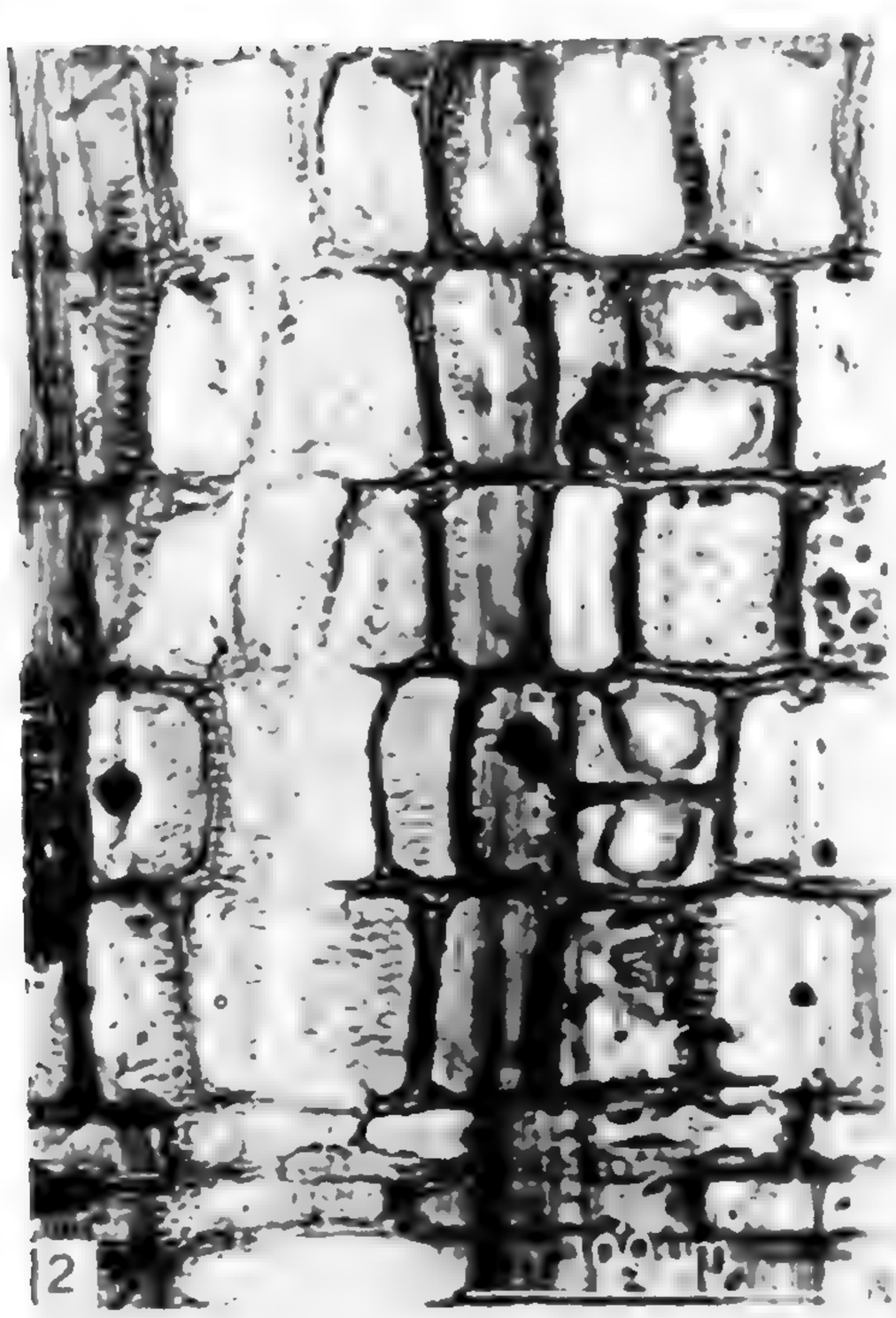
TABLE 1 lists the 241 wood specimens examined. These represent 153 species in 64 genera, approximately 61 per cent of the genera of Flacourtiaceae. The scientific names that accompanied the wood specimens were generally used. Sources for name changes that resulted from synonymy are cited in TABLE 1.

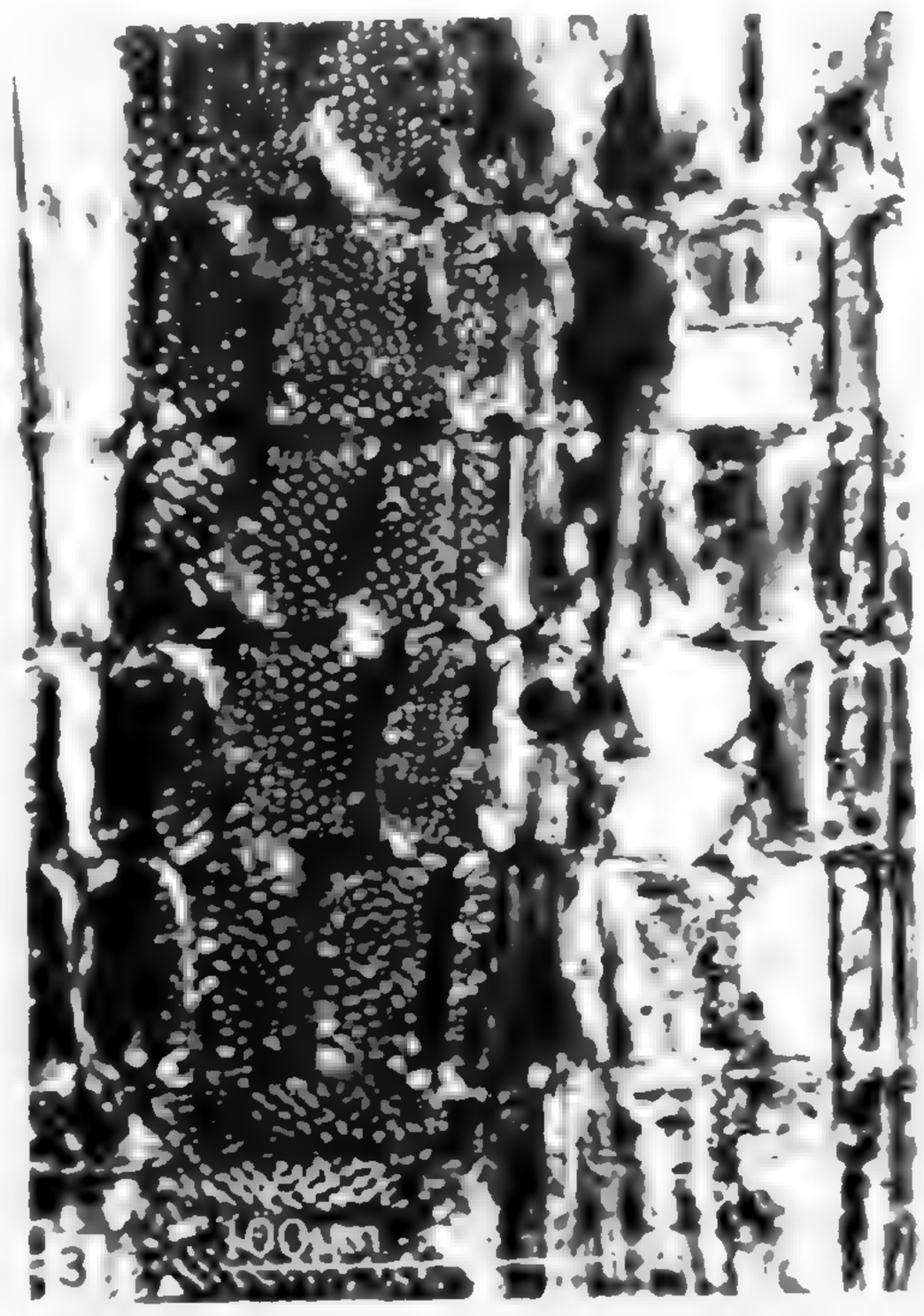
Sectioning and staining techniques were generally standard and have been described fully elsewhere (Miller 1973).

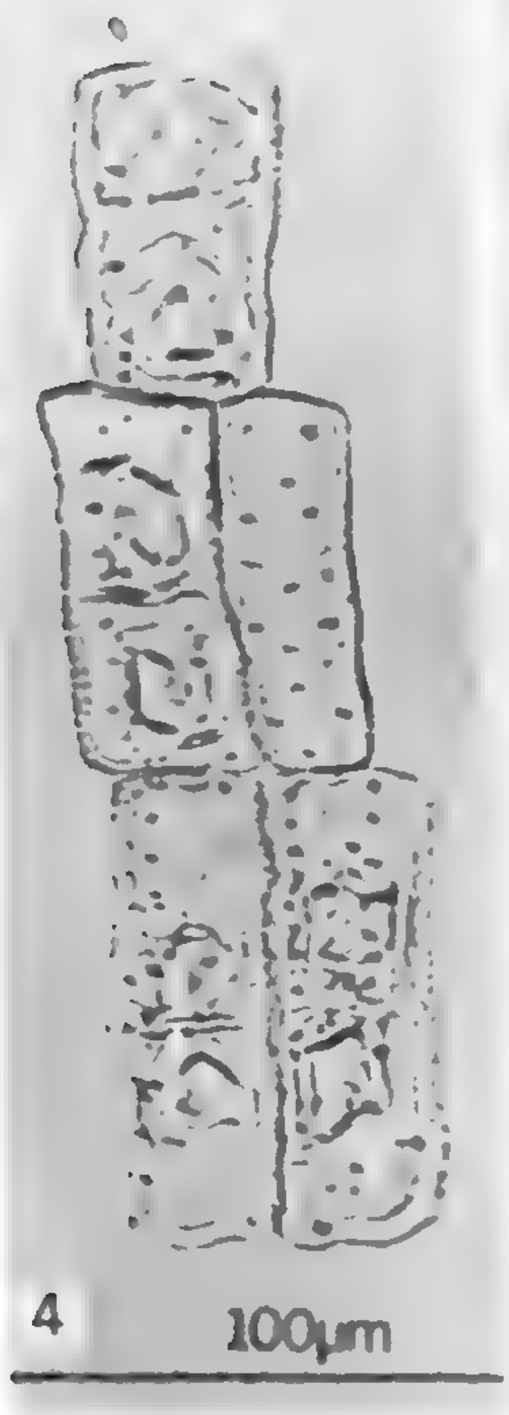
Nomenclature and terminology generally conform to the recommendations of the Committee on Nomenclature, International Association of Wood Anatomists (1957). Standard terms for size classification follow those of Chattaway (1932); the Committee on the Standardization of Terms of Cell Size, International Association of Wood Anatomists (1937, 1939); and Record and Chattaway (1939).

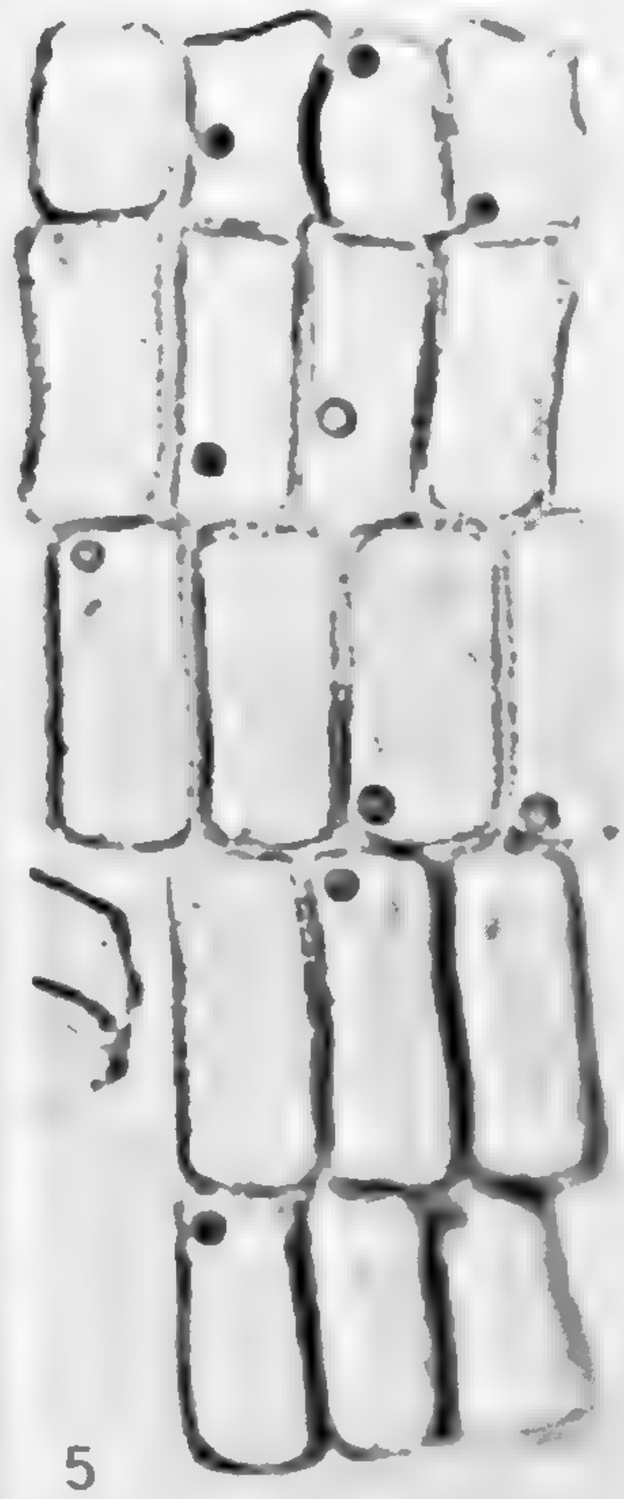
Pore diameters were measured in the tangential direction, and the average was based on 25 measurements. Only the larger pores were included. The percentage of solitary pores and the number of pores per square millimeter were determined by examining an area of "1, 2, 4, or 5 square millimeters, such that it [contained] about 50 to 100 vessels" (Rendle & Clark 1934). In this study, descriptions of radial multiples that exceeded 10 per cent of the total percentage of pores are referred to as "mostly" (e.g., radial multiples mostly 2 and 3). Descriptions of those radial multiples that are less than 10 per cent of the total percentage of pores are referred to as "occasionally" (e.g., occasionally to 5).

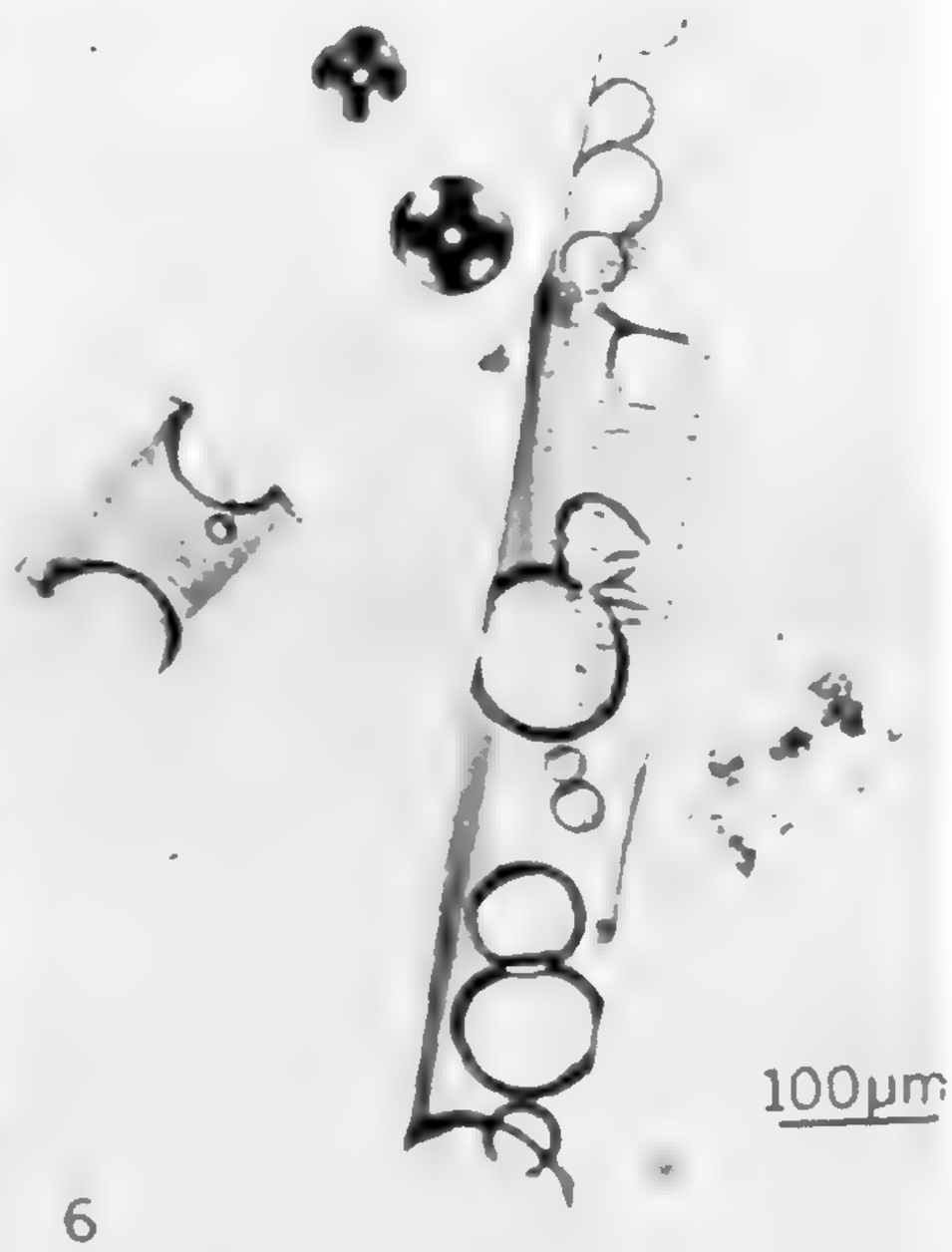
Vessel-element lengths were measured from tip to tip. These and fiber (imperforate tracheary elements) lengths are based on 50 measurements. A ratio of the fiber length to vessel-element length (developed by Chattaway, 1936) was computed for each specimen from the average. (This ra-











FIGURES 2–6: 2, radial section of *Calantica cerasifolia* showing prismatic crystals in upright ray cells; 3, same prismatic crystals under polarized light; 4, *Homalium pallidum*, maceration showing the integuments left behind after the prismatic crystals are decomposed; note chambered upright ray cells; 5, *Mayna amazonica*, maceration showing granular type silica in ray cells; 6, dried macerated material of *Hydnocarpus gracilis* treated with concentrated sulfuric acid to show vitreous silica; photographed under polarized light; note birefringence of partially decomposed cells.

tio is hereinafter referred to as "fiber length to vessel length ratio," F/V.) Chattaway's ratio, which varies from 1.1 to 9.5 in woody dicots, theoretically shows the relative specialization of wood. The closer the value approaches 1.00, the less specialized the wood. This indicates that in primitive species, as a whole, there is little elongation of the cambial derivatives.

The minimum and maximum size of intervascular and vessel-ray pits is reported. Maximum size was determined by measuring the pits in the largest dimension. Where the intervascular and vessel-ray pits are similar in size, the size classification for intervascular pits is given.

Because of the long uniseriate extensions of the heterocellular rays and the vertical fusion of rays, total ray height varied considerably. Consequently, only the multiseriate portion was measured for 25 of the larger rays. The measurements of the 10 largest rays were then averaged. By this method an average ray height for each specimen is obtained which is more easily reproducible and more reliable for comparison and identification purposes than an average obtained by randomly measuring any size ray. The shape and size of ray cells of the multiseriate portion are of diagnostic value. The shape of these individual cells as observed on the radial surface was noted to be elongate, rectangular, or square. The height of individual cells from the multiseriate portion of rays was determined from the tangential section by dividing the number of cells counted over a given distance (at least 150 μm.) into that distance to give an average cell measurement. Only the minimum and maximum values for multiseriate ray-cell height are reported.

The presence of prismatic or druse crystals, presumed to be a form of calcium oxalate (Al-Rais *et al.* 1971; Scurfield, Michell, and Silva 1973), was determined by observing the crystals with polarized light (FIGURE 3). The cell types and the relative abundance in which crystals occurred were recorded for each specimen. In some cases crystals in the upright ray cells are in short chains of two to eight crystals (FIGURES 2, 8, 22). This type of arrangement, in which two to eight crystals in an upright cell are separated from one another by a septum, is called "chambered." An arrangement of two crystals in an upright cell is called two-chambered, three crystals three-chambered, and so forth. Specimens with prismatic crystals that were surrounded by a sheath or integument were also recorded. These integuments can be readily observed, since in macerated preparations the crystal decomposes, leaving the integument as a mold of the crystal (FIGURE 4). When no integuments were found in macerated material and yet crystals were observed in section, a radial free-hand section in which there were at least a few crystals was cut in order to verify the observation. Jeffrey's macerating fluid was then drawn under the cover slip and the crystals were observed with and without polarized light. After 5 to 10 minutes, the crystals completely disappeared and the presence or absence of integuments was determined. When crystals were so infrequent that it could not be determined with

TABLE 1. **Wood specimens examined.**

SPECIES [a]	COLLECTOR [b]	COLLECTION LOCALITY	HERBARIUM [c]	XYLARIUM [d]
AHERNIA				
glandulosa Merr.	CLPw Mus. Pl. 176	Philippines	None [e]	SJRw[f] 2296
glandulosa	R. Rosenblyth & F. Tamesis *s.n.*	Philippines	US?	CLPw 11674[g]
glandulosa	Whitford 73w	Philippines	US?	CLPw 12683[g]
ANCISTROTHYRSUS				
tessmanii Harms	A. Ducke 290	Brazil	MAD [h]	SJRw 33817
APHLOIA				
myrtiflora Galp.	A. A. Pardy *s.n.*	S. Rhodesia	None	USw 21257
theiformis (Willd.) Benn.	H. Browne 52–1897	East Africa	None	K–Jw
theiformis	For. Dep.	Mauritius	None	SJRw 15517
theiformis	For. Dep.	Mauritius	None	SJRw 32941
ASTEROPEIA				
micraster Hallier	CTFw 149	Madagascar	None	SJRw 29785
rhopaloides (Baker) Baill.	R. Block 21	Madagascar	None	SJRw 10759
rhopaloides	CTFw 46	Madagascar	None	SJRw 33869
AZARA				
integrifolia R. & P.	D. S. Bullock 70	Chile	None	USw 18895
microphylla Hook. f.	M. Rothkugel & H. Curran 597	Argentina	BAFC?	SJRw 1768
serrata R. & P.	F. G. Meyer 9635	Juan Fernandez Is.	US	USw 34027
serrata		Chile	None	SJRw 34064
uruguayensis (Speg.) Sleum.	W. Herter 1396d	Uruguay	MAD	SJRw 34146
BANARA				
axilliflora Sleum.	Krukoff 5175	Brazil	F	MADw 18988
guianensis Aubl.	B. Maguire & Stahel 22781	Surinam	NY	MADw 11755

guianensis	Ll. Williams 5321	Peru	F	MADw 16421
guianensis	P. Shank 124	Nicaragua	MAD	SJRw 46910
mollis (Poepp. & Endl.) Tul.	Ll. Williams 7031	Peru	F	MADw 23635
nitida Spruce ex Benth.	Ll. Williams 6986	Peru	F	MADw 16424
regia Sandwith	Acosta-Solís 6934	Ecuador	F	MADw 23705
roigii P. Wils.	J. T. Roig 4997; Col. No. 111	Cuba	NY?	SJRw 26541
vellozii Gardn.	H. S. Irwin 2121	Brazil	MAD	SJRw 53071
BARTERIA				
fistulosa Mast.	Breteler 1404	West Africa	WAG	UW 9321
BARTHOLOMAEA				
sessiliflora Steyerm.	Ortiz 109	Guatemala	F	(i)
BENNETTIODENDRON				
leprosipes (Clos) Merr.	SiBoeeca 3788	Sumatra	MICH	USw 28357
leprosipes	Koorders 2085	Java	BZF?	SJRw 30093
BERBERIDOPSIS				
corallina Hook. f.	F. G. Meyer 9766	Chile	US	USw 34057
BUCHNERODENDRON				
speciosum Gürke	Carrington 508	Congo	BR	TERVw[j] 24319
CALANTICA				
cerasifolia Tul.	Thouvenot 74	Madagascar	F	MADw 25421
CALONCOBA				
brevipes (Stapf) Gilg	Cooper 89	Liberia	MAD	USw 4518
brevipes	Cooper 173	Liberia	MAD	USw 4811
brevipes	Cooper 331	Liberia	MAD	SJRw 15237
brevipes	Cooper 470	Liberia	MAD	SJRw 15329
echinata (Oliv.) Gilg	C. Vigne 2804	Ghana	K?	FHOw 8466
echinata	Cooper 122	Liberia	MAD	SJRw 13772
flagelliflora (Mildbr.) Gilg	Devred 1262	Congo	P	(k)
gilgiana (Sprague) Gilg	C. Vigne 2751	Ghana	K?	FHOw 7935

TABLE 1. Wood specimens examined (*continued*).

SPECIES [a]	COLLECTOR [b]	COLLECTION LOCALITY	HERBARIUM [c]	XYLARIUM [d]
CALONCOBA (*con'd*)				
glauca (P. Beauv.) Gilg	Escherich 340	Cameroon	B	Bw
glauca	FHI 7718	Nigeria	FHI?	PRFw 23105
schweinfurthii Gilg	Uganda For. Dep. 207; Herb. 1152	Uganda	ENT	FHOw 8245
schweinfurthii Gilg	Uganda For. Dep. 168; Herb. 11	Uganda	ENT	FHOw 13889
welwitschii (Oliv.) Gilg	Sargos 827	Congo	P?	PRFw 15281
welwitschii	Zenker 783	Cameroon	B?	USw 31300
CAMPTOSTYLUS				
aristatus (Oliv.) Gilg	Zenker 1637	Cameroon	B?	Bw
mannii (Oliv.) Gilg	Dechamps 36; wood 522	Congo	BR	TERVw
mannii	Zenker 2860	Cameroon	B?	Bw
CARPOTROCHE				
brasiliensis Endl.	Tatto 35	Brazil	MAD	SJRw 40639
platyptera Pittier	Cooper T. 11	Costa Rica	MAD	SJRw 10473
platyptera	Cooper 377	Panama	MAD	SJRw 11970
platyptera	Terrill 187	Nicaragua	MAD	SJRw 12436
CARRIEREA				
calycina Franch.	Cheng 46	China	?	BWCw 10731
calycina	Chow *s.n.*	China	None	SJRw 42572
CASEARIA [1]				
DASYLEPIS (Sleumer 1972e)				
brevipedicellata Chipp	C. Vigne 2750	Ghana	K	SJRw 23989
DOVYALIS (Sleumer 1972b)				
caffra (Hook. f. & Harv.) Hook. f.	Opdyke 589	Ohio (Cult.)	None	MADw 12235
caffra	Ferreira *s.n.*	S. Africa	None	USw 20714

ELEUTHERANDRA				
pes-cervi Sloot.	For. Dep. of Java 3499	Indonesia	L?	SJRw 15445
pes-cervi	For. Dep. of Java 4115	Indonesia	L?	SJRw 15446
ERYTHROSPERMUM (Smith 1936)				
acuminatissimum (A. Gray) A. C. Smith	Gillespie 4667	Fiji	BISH	SJRw 25976
acuminatissimum	A. C. Smith 1470	Fiji	MAD	SJRw 28238
candidum (Becc.) Becc.	FPAw 20250	New Guinea	L	USw 24084
FLACOURTIA				
cataphracta Roxb. ex Willd.	W. L. Stern & Wasshausen 2421	Dominica	MAD	USw 35472
indica (Burm. f.) Merr.	A. J. Fors 310	Cuba	SV?	MAD 13915
indica	Schlieben 5464; wood 437	Tanzania	MAD	SJRw 13915
indica	Schlieben 5416; wood 422	Tanzania	MAD	SJRw 33954
rukam Zoll. and Mor.	Krukoff 306	Sumatra	F	USw 31377
rukam	Kanehira 352; wood A1816	Micronesia	FU?	SJRw 20339
rukam	Kanehira 1294; wood A2053	Micronesia	FU?	SJRw 26782
subintegra A. C. Smith	A. C. Smith 1700	Fiji	MAD	SJRw 28328
subintegra	A. C. Smith 1939	Fiji	MAD	SJRw 28426
GOSSYPIOSPERMUM (Wilson 1930)				
praecox (Griseb.) P. Wils.	A. J. Fors 70	Cuba	MAD	MADw 13780
praecox	Rose 8	Venezuela	US	SJRw 2663

TABLE 1. Wood specimens examined (*continued*).

SPECIES [a]	COLLECTOR [b]	COLLECTION LOCALITY	HERBARIUM [c]	XYLARIUM [d]
GYNOCARDIA				
odorata R. Br.	DD 39643	E. Pakistan	DD	DDw 6177
odorata	G. Gillett 1866	Hawaii (Cult.)	BISH	MADw 25466
HASSELTIA				
floribunda H.B.K.	Christopherson 122	Panama	US	MADw 5747
floribunda	Englesing 152	Nicaragua	MAD	SJRw 12427
cf. *guatemalensis* Warb.	Little 6063	Panama	MAD	MADw 10338
lateriflora Rusby	Espina & Giacometto A116	Colombia	MAD	SJRw 20891
lateriflora	Espina & Giacometto A149	Colombia	MAD	SFRw 20924
laxiflora (Benth.) Eichl.	Ll. Williams 588	Peru	F	MADw 15062
HECATOSTEMON				
guazumaefolius (H.B.K.) Sleum.	Ll. Williams 9943	Venezuela	F	MADw 23752
HOMALIUM				
foetidum (Roxb.) Benth.	BZFw 6929	Java	?	SJRw 8182
grandiflorum Benth.	For. Dep. of Java 3498	Indonesia	L	SJRw 22357
grandiflorum Benth. var. *javanicum* (Koord. & Valet.) Sleum.	Koorders 1131c	Java	BZF?	SJRw 30985
guianensis (Aubl.) Warb.	Stahel 372	Surinam	MAD	MADw 19878
hainanense Gagnep.	McClure 18345; wood 11	China	LU?	SJRw 26708
letestui Pellegr.	Cooper 229	Liberia	MAD	SJRw 15155
longifolium Benth.	KEPw 1289; KEP 4784	Malaya	KEP	SJRw 28970
pallidum A. C. Smith	A. C. Smith 1221	Fiji	MAD	SJRw 28136
racemosum Jacq.	Krukoff 6088	Brazil	F	MADw 12297
racemosum	A. J. Fors 1265	Cuba	SV?	MADw 14451
racemosum	RPPRw Tree No. 48	Puerto Rico	RPPR	MADw 17485
smythei Hutch. & Dalz.	Cooper 324	Liberia	MAD	SJRw 15231
smythei	Cooper 469	Liberia	MAD	SJRw 15328
stenophyllum Merr.	Sun Yat Sen U. 70384; wood 834	China	NSM	SJRw 29563
tomentosum (Vent.) Benth.	Col. No. 1890	Burma	DD	SJRw 13178
trichostemon Blake	Ll. Williams 9469	Mexico	MAD	MADw 9877
HYDNOCARPUS (Sleumer 1938)				
gracilis (Sloot.) Sleum.	Krukoff 4164	Sumatra	F	MADw 25423
gracilis	For. Dep. of Java 4308	Indonesia	L?	SJRw 15442
heterophylla Blume	Koorders 1269a	Java	BZF?	SJRw 30098
kunstleri (King) Warb.	For. Dep. of Java 3955	Indonesia	L?	SJRw 22353
kunstleri	KEPw 4033; KEP 46109	Malaya	KEP	SJRw 38716
macrocarpus (Bedd.) Warb.		Burma	None	SJRw 12705
macrocarpus	Col. No. 2913	Burma	DD	SJRw 13111
saigonensis Pierre	Col. No. 3	Burma	DD	SJRw 13182
sumatrana (Miq.) Koord.	CLPw 433	Philippines	CLP	MADw 22588
sumatrana	Koorders 1253c	Java	BZF?	SJRw 30097
venenata Gaertn.	Broadway *s.n.*	Trinidad	F	SJRw 10940
yatesii Merr.	Krukoff 4165	Sumatra	F	MAD 25422
IDESIA				
polycarpa Maxim.	K. Ogata *s.n.*	Japan (Cult.)	TOFO	TWTw 155

TABLE 1. Wood specimens examined (*continued*).

SPECIES [a]	COLLECTOR [b]	COLLECTION LOCALITY	HERBARIUM [c]	XYLARIUM [d]
IDESIA (*con'd*)				
polycarpa	H. H. Hu 46	China	PE?	SJRw 21462
polycarpa	Fan Mem. Inst. of Biol. 127	China	PE	SJRw 21739
polycarpa	Fan Mem. Inst. of Biol. 377	China	PE	SJRw 21863
ITOA				
stapfii (Koord.) Sleum.	Schram (B. W. 7779)	New Guinea	L	MADw 2569
stapfii	For. Dep. of Java 5425	Indonesia	L	SJRw 15447
KIGGELARIA				
africana L.	PFPw 5410	S. Africa	PRE	SJRw 50377
flavo-velutina Sleum.	Schlieben 3528 (Type); wood 179	Tanzania	MAD	SJRw 27529
LAETIA				
apetala Jacq.	Capucho 466	Brazil	F	MADw 23725
apetala	G. C. Bucher 302	Cuba	NY	SJRw 21437
calophylla Eichl.	Krukoff 7241	Brazil	F	MADw 23669
cupulata Spruce ex Benth.	Ll. Williams 14194	Venezuela	F	MADw 23726
micrantha A. Robyns	Stern *et al.* 206	Panama	MO	SJRw 54698
micrantha	Stern *et al.* 513 (Type)	Panama	MO	SJRw 54946
procera (Poepp.) Eichl.	Stahel 124	Surinam	MAD	MADw 19646
procera	Maguire 48294	Brazil	NY	MADw 20267
procera	Maguire 51753	Brazil	NY	MADw 21447
suaveolens (Poepp. & Endl.) Benth.	Ll. Williams 8035	Peru	F	MADw 16436
ternstroemioides Griseb.	Bucher 20	Cuba	NY	SJRw 14737

ternstroemioides	J. G. Jack 5878	Cuba	A	SJRw 16706
thamnia L.	Madera del Trop., Tree No. 49	Yucatán	F	MADw 14988
LETHEDON (= *Microsemma* Labillardière) (Kostermans 1963)				
le-ratii (Guill.) Kosterm.	McKee 4329	New Caledonia	?	FPAw 14222
setosa (C. T. White) Kosterm.	L. S. Smith 3368	Australia	?	FPAw 11038
LINDACKERIA				
dentata (Oliv.) Gilg	Zenker 879	Cameroon	B?	Bw
dentata	C. Vigne 2468	Ghana	FHO?	SJRw 23251
latifolia Benth.	Ll. Williams 14896	Venezuela	F	MADw 23727
laurina Presl.	H. Pittier 5228	Panama	US	MADw 5778
maynensis Poepp. & Endl.	Krukoff 6159	Brazil	F	MADw 12330
paludosa (Benth.) Gilg	Krukoff 1648	Brazil	F	MADw 23677
paraensis Kuhlm.	A. Ducke 190	Brazil	MAD	SJRw 23652
LUDIA (Sleumer 1972a)				
mauritiana Gmelin	Capuron SF 27114	Madagascar	L	(i)
scolopioides Capuron & Sleum.	M. G. Cours 2768	Madagascar	L	(i)
LUNANIA				
cubensis Turcz.	Bucher 132	Cuba	MAD	SJRw 16841
cubensis	Bucher 257	Cuba	NY	SJRw 21428
parviflora Spruce ex Benth.	Ll. Williams 1895	Peru	F	MADw 15244
parviflora	Krukoff 5275	Brazil	F	MADw 19018
MACROHASSELTIA (Williams 1961)				
macroterantha (Standl. & L. Wms.) L. Wms.	Barbour 1016	Costa Rica	MAD	MADw 10286
macroterantha	Dayton 3125	Costa Rica	MAD	MADw 10305

TABLE 1. Wood specimens examined (*continued*).

SPECIES [a]	COLLECTOR [b]	COLLECTION LOCALITY	HERBARIUM [c]	XYLARIUM [d]
MAYNA				
amazonica (Mart.) Macbr.	Krukoff 9001	Brazil	F	MADw 23681
echinata Spruce & Triana	Ll. Williams 4892	Peru	F	MADw 16445
grandifolia (Karst.) Warb.	Dugand, 1014; wood 468	Colombia	MAD	SJRw 33759
longicuspis (Standl.) Standl.	Cooper & Slater 234 (Type)	Panama	MAD	SJRw 10587
longicuspis	Cooper 638	Panama	MAD	SJRw 12271
longifolia Poepp. & Endl.	Ll. Williams 2711	Peru	F	SJRw 17987
odorata Aubl.	Krukoff 4629	Brazil	F	MADw 23685
pacifica Cuatr.	Cuatrecasas 16562	Colombia	US	MADw 23738
zuliana (Pittier) A. Robyns	Stern *et al.* 908	Panama	MO	SJRw 55120
NEOPTYCHOCARPUS (Buchheim 1959)				
apodanthus (Kuhlm.) Buchheim	A. Ducke 416	Brazil	MAD	SJRw 44330
apodanthus	Pires & Silva 11239	Brazil	IAN	IANw
OLMEDIELLA				
betschleriana (Goepp.) Loes.	Salas *s.n.*	Guatemala	F	SJRw 22081
ONCOBA				
spinosa Forsk.	Schlieben 4133; wood 236	Tanzania	MAD	RBHw 1671
OPHIOBOTRYS				
zenkeri Gilg	Ghana For. Dep. 2056	Ghana	None	SJRw 20025
OSMELIA				
grandistipulata Sloot.	For. Dep. of Java 6285	Indonesia	L?	SJRw 16046
grandistipulata	For. Dep. of Java 6190	Indonesia	L?	SJRw 16047
grandistipulata	For. Dep. of Java 5528	Indonesia	L?	SJRw 16048
philippina (Turcz.) Benth.	SiBoeeca 6752	Sumatra	MICH	USw 28880
philippina	Bartlett 7272	Sumatra	MICH	USw 29390
philippina	Krukoff 4003	Sumatra	F	SJRw 34299
PANGIUM				
edule Reinw.	CLPw 315	Philippines	CLP	MADw 18439
edule	For. Dep. of Java 3315	Indonesia	L?	SJRw 15443
PAROPSIA (Sleumer 1970)				
braunii Gilg	Schlieben 5442; wood 429	Tanzania	MAD	RBHw 1830
guineensis Oliv.	Zenker 727	Cameroon	B?	Bw
madagascariensis (Baill.) Perr.	TEFw 716.R.182	Madagascar	P?	USw 27402
vareciformis (Griff.) Mast.	KEP No. 32695	Malaya	KEP	PRFw 9008
PERIDISCUS				
lucidus Benth.	A. Ducke 113	Brazil	MAD	SJRw 22573
PINEDA				
weberbaueri Irmscher	Iltis & Ugent 539	Peru	WIS	MADw 193
PLEURANTHODENDRON (Williams 1961)				
mexicana (A. Gray) L. Wms.	Ll. Williams 8660	Mexico	F	MADw 9855
mexicana	Ll. Williams 8504	Mexico	MAD	MADw 9869
mexicana	Record G.46	Guatemala	MAD	MADw 10991
mexicana	Kuylen G.59	Guatemala	MAD	MADw 11004
mexicana	Winzerling III.5	Br. Honduras	MAD	MADw 11255
mexicana	Record & Kuylen H.43	Honduras	MAD	SJRw 9989
POLIOTHYRSIS				
sinensis Hook. f.	Kew Gardens	Kew (Cult.)	K	K–Jw

TABLE 1. Wood specimens examined (*continued*).

SPECIES [a]	COLLECTOR [b]	COLLECTION LOCALITY	HERBARIUM [c]	XYLARIUM [d]
PROCKIA				
crucis P. Br. ex L.	Reitz & Klein 7559	Brazil	WIS	MADw 21831
crucis	H. Pittier 11936	Venezuela	MAD	SJRw 8400
RAWSONIA				
ulugurensis Sleum.	Schlieben 3948; wood 221	East Africa	B	Bw
RYANIA (Monachino 1949)				
angustifolia (Turcz.) Monachino	Froes 12528	Brazil	NY	MADw 21104
angustifolia	Krukoff 7643	Brazil	F	SJRw 34111
angustifolia	Froes 15386	Brazil	NY	SJRw 40678
pyrifera (L. C. Rich.) Uitt. & Sleum.	Krukoff 15402	Trinidad	NY	MADw 21105
speciosa Vahl var. *chocoensis* (Triana & Planch.) Monachino	Cuatrecasas 15716	Colombia	US	MADw 17541
RYPAROSA				
javanica (Blume) Kurz ex Koord. & Val.	Koorders 30291B; wood 1339c	Java	BZF?	SJRw 30100
kunstleri King	For. Dep. of Java 4167	Indonesia	L?	SJRw 15444
kunstleri	Krukoff 4155	Sumatra	F	SJRw 34374
SAMYDA				
dodecandra Jacq.	G. S. Miller 1676	Puerto Rico	US?	USw 6101
macrantha P. Wils.	J. G. Jack 5893	Cuba	MAD	SJRw 16707
SCAPHOCALYX				
spathacea Ridl.	Selvaraj *s.n.*	Malaya	KEP	KEPw 11179
SCOLOPIA (Sleumer 1972c)				
luzonensis (Presl.) Warb.	Bartlett 13492	Philippines	MICH	USw 29824
mundii (Nees) Warb.	PFPw 5414	S. Africa	PRE	SJRw 50380
spinosa (Roxb.) Warb.	SiBoeeca 4830	Sumatra	MICH	USw 28616
spinosa	SiBoeeca 5077	Sumatra	MICH	USw 28688
spinosa	For. Dep. of Java 5158	Indonesia	L?	SJRw 22356
spinosa	For. Dep. of Java 5159	Indonesia	L?	SJRw 22888
spinosa	Koorders 2046a	Java	BZF?	SJRw 30086
thouvenotii H. Perrier	Thouvenot 84 (lectotype)	Madagascar	P	MADw 25424
zeyheri (Nees) Harvey	PRFw 5050	S. Africa	PRE?	USw 11945
SCOTTELLIA (Sleumer 1972d)				
klaineana Pierre	Zenker 3018	Cameroon	BR, B	Bw
klaineana	PRFw 7193	Nigeria	FHO?	MADw 16827
klaineana	Cooper 292	Liberia	MAD	SJRw 15204
klaineana	Cooper 369	Liberia	MAD	SJRw 15261
klaineana	Cooper 420	Liberia	MAD	SJRw 15284
klaineana Pierre var. *mimfiensis* (Gilg) Pellegrin	C. Vigne 2502	Ghana	FHO	SJRw 23261
SOYAUXIA (Brenan 1953)				
grandifolia Gilg & Stapf	Cooper 233	Liberia	MAD	USw 4843
STREPTOTHAMNUS				
moorei F. Muell.	Webb & Tracey 10267	Australia	BRI	(m)
TETRATHYLACIUM				
johansenii Standl.	Curran 329	Colombia	MAD	MADw 10684
macrophyllum Poepp.	Ll. Williams 2713	Peru	F	MADw 16447
TRICHADENIA				
philippinensis Merr.	W. H. Wetmore 9	Philippines	US?	MADw 5270
philippinensis	CLPw 10065[g]	Philippines	US?	SJRw 2298

TABLE 1. Wood specimens examined (*continued*).

SPECIES [a]	COLLECTOR [b]	COLLECTION LOCALITY	HERBARIUM [c]	XYLARIUM [d]
TRIMERIA				
tropica Burkill	Schlieben 5072; wood 345	Tanzania	MAD	SJRw 2945
TRIPHYOPHYLLUM (Shaw 1952)				
peltatum (Hutch. & Dalz.) Shaw	Cooper 303	Liberia	MAD	SJRw 15213
XYLOSMA				
benthamii Griseb.	Ll. Williams 12509	Venezuela	F	MADw 23696
congestum Merr.	Fan Mem. Inst. of Biol. 283	China	PE	SJRw 20046
flexuosa (H.B.K.) Hemsl.	Madera del Trop., Tree No. 58	Yucatán	F	MADw 15706
flexuosa	Record BH. 38	Br. Honduras	MAD	SJRw 8806
longifolium Clos	Col. No. C3690	Burma	DD?	SJRw 12530
nelsonii Merr.	Kanehira 3630; wood A2259	Mariana Is.	FU?	SJRw 33238
panamensis Turcz.	Cooper 548	Panama	MAD	MADw 23697
pilosum Macbr.	Ll. Williams 4977 (Type)	Peru	F	SJRw 18640
prunifolium Griseb.	R. Espina 49	Colombia	MAD	SJRw 20498
prunifolium	Dugand 233; wood 70	Colombia	MAD	SJRw 22522
salzmanni (Clos) Eichl.	Ll. Williams 4487	Peru	F	MADw 23744
salzmanni	Hoehne 28203; wood 47	Brazil	MAD	SJRw 23792
venosum N. E. Brown	Col. No. 59	Argentina	MAD	SJRw 15015
ZUELANIA				
guidonia (Sw.) Britt. & Millsp.	H. Pittier 2710 (Type)	Panama	US	MADw 5771
guidonia	Ll. Williams 8777	Mexico	MAD	MADw 9882
guidonia	Ll. Williams 9164	Mexico	MAD	MADw 9883
guidonia	Ll. Williams 8651	Mexico	MAD	MADw 15688
guidonia	J. G. Jack 5659	Cuba	MAD	SJRw 16644

[a] Names cited are those that initially accompanied the specimens, except for names based upon recent taxonomic revisions. When there are appropriate generic monographs, author and date follow names of the genera. Authorities for other synonymies are as follows: Blake (1919), Dale and Greenway (1961), Hutchinson (1967), Hutchinson and Dalziel (1954), Kao (1959), Kuhlmann (1928), Macbride (1941), Pellegrin (1952), Robyns (1968), Shultes (1945), Sleumer (1934, 1938, 1950, 1953, 1954), Williams (1961), and Tisserant and Sillans (1954).

[b] Usually refers to the collector and his number, but in some cases refers to the catalog number of an institution.

[c] Abbreviations follow those recommended by Lanjouw and Stafleu (1964) in the *Index Herbariorum*.

[d] Abbreviations follow those recommended by Stern and Chambers (1960) and Stern (1967) in the *Index Xylariorum*.

[e] Refers to specimens collected without accompanying herbarium material.

[f] SJRw refers to the Samuel J. Record Memorial Wood Collection formerly cited as Yw and formerly at Yale University School of Forestry; now maintained at the U. S. Forest Products Laboratory, Madison, Wisc.

[g] Number refers to former Philippine Bureau of Forestry; abbreviated B.F.

[h] MAD refers to the herbarium maintained at the U. S. Forest Products Laboratory, Madison, Wisc., which combines the pre-existent U. S. Forest Products Laboratory herbarium with the herbarium formerly at Yale University School of Forestry (Y).

[i] Specimen from herbarium sheet.

[j] Unofficial abbreviation of Musée Royal de l'Afrique Centrale, Service d'Anatomie des Bois Tropicaux de la Section d'Economie Agricole et Forestière at Tervuren, Belgium.

[k] Slide from Dr. P. Baas and Dr. H. Sleumer at Rijksherbarium, Leiden, Netherlands.

[l] Genus examined for Master's Thesis (Miller 1966).

[m] Specimen obtained through Dr. S. L. Everist, Botanic Museum and Herbarium, Brisbane, Queensland, Australia.

certainty whether integuments were absent, the notation "no integuments observed" is applied.

Silica deposits, which are chemically unconfirmed *in situ*, occur in the form of dark amorphous granules or glassy casts (vitreous silica). The granular type of silica was observed in maceration (FIGURE 5). The vitreous silica was observed by treating dried macerated material with concentrated sulfuric acid. This process removes most cellulosic and lignin material, leaving the silica casts which appear as a glassy replica of the decomposed cell. Confusion between a silica cast and a partly decomposed cell may be dispelled by observation with polarized light. The silica cast is nonbirefringent, whereas the cellulose cell is birefringent (FIGURE 6). Other deposits are not quantified or qualified and are only classified according to color and relative abundance.

ANATOMICAL DESCRIPTIONS

APPENDIX I lists the more important secondary xylem characters for each genus and may be used as a key to the woods of Flacourtiaceae. The genera in APPENDIX I and in the generic descriptions are arranged in accordance with the scheme of Hutchinson (1967). The tribe Prockieae, which is in Hutchinson's Tiliaceae, follows the tribe Casearieae. After the Prockieae, there is a group labeled "Anomalous Genera" which includes many taxa previously incorporated in Flacourtiaceae.

FAMILY DESCRIPTION

The secondary xylem of Flacourtiaceae is somewhat variable, yet some characters are common to most genera. The wood is diffuse porous with poorly defined to rarely distinct growth rings. Pores are generally rounded or circular in cross-sectional outline, but in *Azara*, *Bennettiodendron*, *Berberidopsis*, *Buchnerodendron*, *Camptostylus*, *Carpotroche*, *Erythrospermum*, *Hydnocarpus*, *Idesia*, *Mayna*, *Osmelia*, *Ryania*, and *Scaphocalyx* the pores are angular. The overall average pore diameter (i.e. the average of individual specimen averages) varies from 34 μm. in *Neoptychocarpus* to 212 μm. in *Streptothamnus*; however, pore diameters are mostly moderately small (50–100 μm.). Generally pores are 50–80 per cent solitary. *Berberidopsis* and *Streptothamnus* have pores that are essentially 100 per cent solitary. Radial multiples consist mostly of two to four pores. Although the overall average number of pores per square millimeter varies from 6 in *Pangium* to over 100 in some species of *Azara*, in most genera the overall average number of pores per square millimeter is numerous to very numerous (20 to over 40) (FIGURES 11, 12, 13).

Vessel elements are usually ligulate and vessel walls are 1–8 μm. thick. The overall average length of vessel elements varies from 478 μm. in *Poliothyrsis* to 1794 μm. in *Hydnocarpus*. Spiral thickenings occur throughout the vessels in all species of *Berberidopsis*, *Kiggelaria*, *Olmediella*, *Poliothyrsis*, and *Carrierea* (FIGURE 18). Also, some species of

Appendix I --Summary of anatomical features in Flacourtiaceae and other selected genera

NOTE: Characters enclosed by parentheses are either rare for the genus or characteristic of only some species of the genus. Refer to generic descriptions for more complete detail.

LEGEND:

End wall: Simp. = Exclusively simple perforation plates
Scal. = Exclusively scalariform perforation plates
S&S = Simple and scalariform perforation plates

Intervessel pitting: Opp. = Opposite intervessel pitting
Alt. = Alternate intervessel pitting
O-A = Opposite to alternate intervessel pitting

Spirals: +Vessel = Spirals present throughout vessel
+Tails = Spirals present only in vessel element tails

F/V ratio: F/V = Fibrous element length to vessel element length ratio

+ = Character present
- = Character absent

Fibers: T = Tracheid
F = Fiber-tracheid
L = Libriform fiber

Rays: L = Over 1 cm.
M = 1,000-10,000µm
S = 500-1,000µm
VS = Up to 500µm
Ht. - Heterogeneous } Kribs (1935)
Ho. = Homogeneous

Crystals: P = Prismatic
D = Druse
A = Axial parenchyma
M = Multiseriate ray cell
U = Upright ray cell
F = Fibrous element

Silica: G = Granular
V = Vitreous
M = Multiseriate ray cell
U = Upright ray cell
F = Fibrous
V = Vessel element

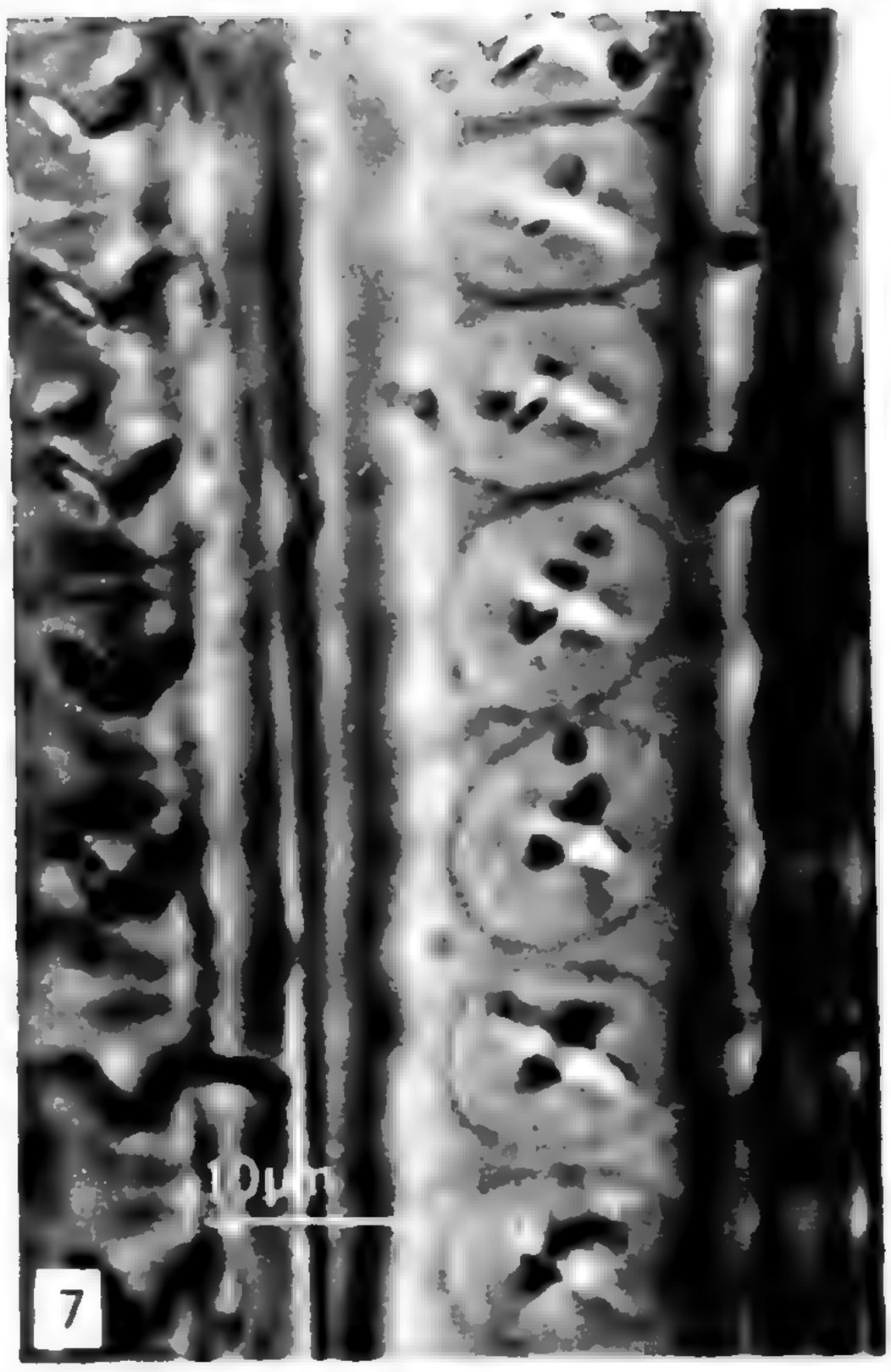
Genera	Group	Vessel elements: End wall	Vessel elements: Pitting: Intervessel: Opp. Alt. O-A	Vessel elements: Pitting: Vessel-ray: Size (µm)	Vessel elements: Pores: Size (µm)	Vessel elements: Pores: percent solitary	Vessel elements: Spirals	F/V ratio	Fibers: Type	Fibers: Septate	Ray: Height	Ray: Width in cells	Ray: Type	Axial parenchyma	Crystals: Type	Crystals: Location	Crystals: In chambered up-right ray cells	Crystals: Integumented	Silica: Type	Silica: Location
BERBERIDOPSIDEAE																				
Streptothamnus	I	Scal.	O-A	8-10	10-40	100	-	1.34	T	-	L	3-5	Ht.-I	-	(P)	M	-	-	-	-
Berberidopsis	I	Scal.	Opp.	8-20	10-30	99	+Vessel	1.37	T	-	L	15-25	Ht.-I	-	-	-	-	-	-	-
Erythrospermum	I	Scal.	O-A	7-24	8-34	77	-	1.38	F	+	M	2-6	Ht.-I	-	P	M&U	-	+	-	-
Camptostylus	II	S&S	Alt.	8-10	8-36	79	(+Tails)	1.79	F&L	+	M	2-5	Ht.-I	-	P&(D)	M&U	(+)	-	-	-
Ahernia	III	Simp.	Alt.	8-10	8-30	37	-	1.84	F	+	S	2-6	Ht.-I	-	P	U	+	+	-	-
Dasylepis	I	Scal.	Alt.	8-20	10-22	84	-	1.54	F	+	M	4-6	Ht.-I	-	P	M	-	-	-	-
Scottellia	I	Scal.	Alt.	8-26	8-30	63	+Tails	1.64	F	+	M	3-7	Ht.-I	-	P	M&U	-	+	(G)	M
Rawsonia	I	Scal.	Alt.	9-26	8-25	50	-	1.73	F	+	M	2-12	Ht.-I	-	(P)	M&(U)	-	+	-	-
ONCOBEAE																				
Carpotroche	I	Scal.	O-A	7-36	8-30	72	-	1.55	F&L	+	M	2-5	Ht.-I	-	P	M&U	-	-	-	-
	(II)	(S&S)																		
Mayna	I,	Simp.,	O-A	7-34	8-26	69	(+Vessel)	1.56	F&L	+	M	3-5	Ht.-I	-	P	M&U	-	-	(G)	M&U
	II,	S&S, &					(+Tails)													
	III	Scal.																		
Oncoba	III	Simp.	Alt.	7-8	6-25	49	-	1.68	F	+	VS	2	Ht.-I	-	P	U	+	+	-	-
Caloncoba	II	S&S	Alt.	8-10	10-36	61	-	2.07	F&L	+	M	2-7	Ht.-I	-	P	M	-	-	-	-
Lindackeria	III	Simp.	Alt.	6-10	7-32	49	(+Tails)	1.70	F&L	+	M	2-7	Ht.-I	-	P&(D)	M	(+)	+	(G)	M&U
	(II)	(S&S)																		
Buchnerodendron	II	S&S	Alt.	8-9	8-13	66	-	1.63	F	+	M	3-6	Ht.-I	-	P&(D)	M&U	-	-	-	-
SCOLOPIEAE																				
Scolopia	VI	Simp.	Alt.	4-6	4-6	59	+Tails	1.84	L	+	VS-S	2-5	Ht.-I	-	P	U&(M)	+	+	-	-
	(V)	(S&S)					(+Vessel)									&(F)				
Bartholomaea	V	S&S	Alt.	4-6	4-6	-	-	1.46	F	+	-	1-2	Ht.-I	-	P	M&U	+	+	-	-
BANAREAE																				
Banara	VI	Simp.	Alt.	4-7	4-7	46	(+Tails)	1.84	F&L	+	VS	2-4	Ht.-I	-	P&(D)	U&(F)	+	+	-	-
				(2-4)	(2-4)															
Pineda	VI	Simp.	Alt.	6-9	6-20	49	-	1.83	F	+	VS	2	Ht.-I	-	P	U&(M)	+	+	-	-
Trimeria	VI	Simp.	Alt.	6-8	6-8	57	-	1.73	L	+	VS-S	2-4	Ht.-I	-	P	U&(M)	+	+	-	-
HOMALIEAE																				
Calantica	VI	Simp.	Alt.	3-5	3-5	42	-	1.93	F&L	+	VS-S	2-3	Ht.-I	-	P	U&(M)	+	+	-	-
Homalium	VI	Simp.	Alt.	4-6	4-6	45	-	1.70	F&L	+	VS-S	2-5	Ht.-I	-	P	U&(M)	+	+	-	-
	(V)	(S&S)		(8)	(8)											&(F)				
PANGIEAE																				
Hydnocarpus	I	Scal.	O-A	8-10	8-44	76	(+Tails)	1.56	F	+	M	2-3	Ht.-I	-	P	M&U	-	-	(V)	V&F
				(14)																
Eleutherandra	III	Simp.	Alt.	6-8	8-38	36	-	2.13	F&L	+	M	1-3	Ht.-I	-	P	M&U	-	+	-	-
Gynocardia	III	Simp.	Alt.	10-14	10-40	63	-	1.70	F	+	VS-S	1-2	Ht.-I	-	(P)	M&U	-	-	-	-
	(II)	(S&S)																		
Pangium	III	Simp.	Alt.	8-10	10-56	56	-	2.40	F	+	M	3-5	Ht.-I	-	P	M&U	-	+	-	-
Trichadenia	III	Simp.	Alt.	8-11	10-45	40	-	2.41	F&L	+	M	2-5	Ht.-I	-	P	M&U	-	+	-	-
Scaphocalyx	III	Simp.	Alt.	8-25	7-35	78	-	1.80	F&L	+	M	2	Ht.-I	-	P	M&(U)	-	-	-	-
Ryparosa	II	S&S	Alt.	10-14	12-50	58	-	1.93	F&L	+	M	3-8	Ht.-I	-	P	M&U	-	-	-	-
Kiggelaria	III	Simp.	Alt.	8-10	7-26	52	+Vessel	2.00	F&L	+	S-M	3-4	Ht.-I	-	(P)	M	-	-	-	-
FLACOURTIAEAE																				
Olmediella	II	S&S	Alt.	10-34	10-32	61	+Vessel	2.23	F&L	(+)	M	4-6	Ht.-I	-	P	M&U	-	+	-	-
Bennettiodendron	II	S&S	Alt.	8-14	8-25	70	+Tails	1.46	F&L	+	VS	2	Ht.-I	-	P	U&(M)	+	+	-	-
							(+Vessel)													
Flacourtia	VI	Simp.	Alt.	4-6	4-6	41	(+Tails)	1.78	F&L	+	VS	2-6	Ht.-I	-	P	U&(M)	+	+	-	-
	(V)	(S&S)					(+Vessel)													
Dovyalis	V	S&S	Alt.	4-6	4-6	63	-	1.95	F	+	VS	2-3	Ht.-I	-	P	M&U	-	+	-	-
Azara	II	S&S	O-A	8-12	8-28	45	(+Vessel)	1.73	F	+	VS	2-4	Ht.-I	-	P	M&U	(+)	+	-	-
	(I)	(Scal.)																		
Ludia	V	S&S	Alt.	4-5	4-5	-	(+Vessel)	1.61	F	+	VS	2-3	Ht.-I	-	P	M&U	+	+	-	-
Xylosma	VI	Simp.	Alt.	4-6	4-6	52	(+Vessel)	1.73	F&L	+	VS-S	2-5	Ht.-I	-	P	U&(M)	(+)	+	-	-
				6-8	6-8															
Poliothyrsis	III	Simp.	Alt.	8-11	8-16	50	+Vessel	1.83	F	+	VS	2-3	Ht.-I	-	-	-	-	-	-	-
Carrierea	II	S&S	Alt.	10-14	8-20	54	+Vessel	1.84	F&L	(+)	VS	2-3	Ht.-I	-	(P&D)	M&U	-	+	-	-
~~Itoa~~	~~III~~	~~Simp.~~	~~Alt.~~	~~10-15~~	~~10-36~~	~~39~~	~~-~~	~~2.08~~	~~F&L~~	~~(+)~~	~~VS~~	~~2-4~~	~~Ht.-I~~	~~-~~	~~P~~	~~U&(M)~~	~~-~~	~~+~~	~~-~~	~~-~~
Idesia	III	Simp.	Alt.	10-12	8-12	55	-	1.68	F	-	VS-S	2-4	Ht.-I	-	(P)	U	-	+	-	-
	(II)	(S&S)																		
CASEARIEAE																				
Casearia	VI	Simp.	Alt.	2-4	2-4	46	-	1.54	F&L	+	S-M	2-3	Ht.-I	-	P	M&U	-	+	-	-
				(5-6)	(5-6)						(L)	(12)								
Gossypiospermum	VI	Simp.	Alt.	3-4	3-4	53	-	1.73	L	+	S	3	Ht.-I	-	P	M&U	-	+	-	-
Laetia	VI	Simp.	Alt.	2-5	2-5	50	-	1.72	F&L	+	M	2-7	Ht.-I	-	P&(D)	M&U	-	+	-	-
	(V)	(S&S)		(5-7)	(5-7)						(L)	(15)								
Hecatostemon	VI	Simp.	Alt.	3-4	3-4	53	-	1.80	F&L	+	VS	2-3	Ht.-I	-	P	U&(M)	(+)	+	-	-
Ryania	VI	Simp.	Alt.	4-6	4-6	70	-	1.60	F&L	+	M	5-20	Ht.-I	-	(P)	M&U	-	-	-	-
	(V)	(S&S)																		
Zuelania	VI	Simp.	Alt.	4-5	4-5	50	-	1.62	F&L	+	S-M	2-4	Ht.-I	-	P	M&U	-	+	-	-
Osmelia	V	S&S	Alt.	3-5	3-5	58	-	1.62	F&L	+	M	1-4	Ht.-I	-	P	M&(U)	-	-	-	-
Ophiobotrys	VI	Simp.	Alt.	2-4	2-4	65	-	1.53	L	+	S	2-4	Ht.-I	-	P	U&(M)	-	+	-	-
Lunania	VI	Simp.	Alt.	3-6	3-6	55	-	1.57	F&L	+	M	2-4	Ht.-I	-	P	M&U	-	+	-	-
Tetrathylacium	I	Scal.	Alt.	8-10	8-26	58	-	1.67	F&L	+	M	2-5	Ht.-I	-	P	M&U	(+)	+	-	-
Samyda	VI	Simp.	Alt.	2-4	2-4	65	-	1.69	F&L	+	S	2	Ht.-I	-	P	M&(U)	-	+	-	-
Neoptychocarpus	IV	Scal.	Alt.	2-4	2-4	58	-	1.60	L	S	M	2-3	Ht.-I	-	P	M&(U)	-	+	-	-
			Opp?																	
PROCKIEAE																				
Prockia	VI	Simp.	Alt.	4-7	4-7	38	-	1.66	F&L	+	VS	2-3	Ht.-I	-	P	U&(M)	+	+	-	-
Hasseltia	III	Simp.	Alt.	4-7	4-30	60	(+Tails)	1.70	F&L	+	VS-S	2-3	Ht.-I	-	P	U&(M)	+	+	-	-
	(II)	(S&S)																		
Pleuranthodendron	II	S&S	Alt.	8-10	8-32	49	+Tails	1.74	F&L	+	VS-S	2-5	Ht.-I	-	P	U&(M)	+	+	-	-
Macrohasseltia	II	S&S	Alt.	10-14	10-22	48	+Tails	1.75	F&L	+	VS	2-3	Ht.-I	-	P	U	+	+	-	-
							(+Vessel)													
ANOMALOUS GENERA																				
Ancistrothyrsus	-	S&S	Alt.	8-10	8-14	89	-	1.95	T	-	M	3-7	Ht.-I	+	P	A&M	-	-	-	-
													& II							
Barteria	-	S&S	Alt.	5-8	5-8	34	-	2.11	L	-	S	1-3	Ht.-I	+	-	-	-	-	-	-
Paropsia	-	Simp.	Alt.	3-5	3-5	52	-	2.82	F&L	-	M	2-5	Ht.-I	+	P	M&(U)	-	-	-	-
				6-8	6-8								Ho.-I			&(A)				
Soyauxia	-	Scal.	?	6-10	8-36	100	-	1.34	T	-	VS-S	1	Ht.-	+	-	-	-	-	G	M&U
													III							
Peridiscus	-	Scal.	Opp.	14-18	10-25	45	-	1.41	L	(+)	M	1-2	Ht.-I	+	-	-	-	-	-	-
Aphloia	-	Scal.	Alt.	6-7	4-20	97	+Tails	1.80	F	+	M	4-30	Ht.-I	+	-	-	-	-	-	-
		(S&S)					(+Vessel)													
Asteropeia	-	Simp.	Alt.	2-4	2-4	97	-	1.61	F	-	VS	1-2	Ho.-	+	-	-	-	-	-	-
													III							
Lethedon	-	Simp.	Alt.	4-7	4-7	56	-	2.44	T	-	S-M	1-2	Ho.-I	+	(P)	M&(U)	-	-	-	-
													Ht.-II							
Triphyophyllum	-	Simp.	Alt.	8-12	8-12	95	-	2.09	F	-	S	1	Ho.-	+	-	-	-	-	-	-
													III							

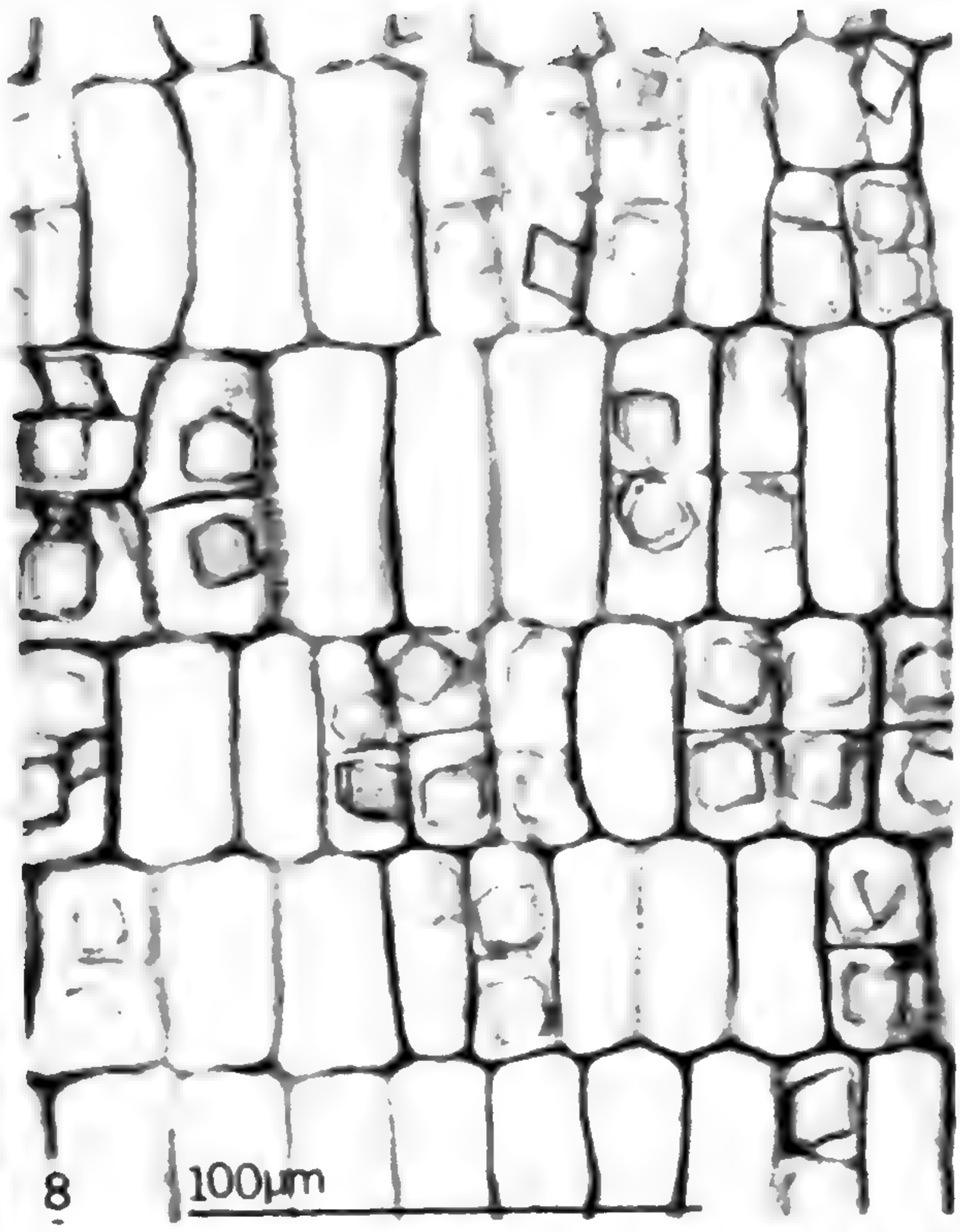
Mayna, Scolopia, Bennettiodendron, Flacourtia, Azara, Ludia, Xylosma, and *Macrohasseltia* have spirals throughout their vessels. Species with spirals only in the vessel-element tails (ligules) occur in the following genera: *Camptostylus Scottellia, Mayna, Lindackeria, Scolopia, Banara, Hydnocarpus, Bennettiodendron, Flacourtia, Hasseltia, Pleuranthodendron,* and *Macrohasseltia* (FIGURE 14). Tyloses are frequent in species of *Berberidopsis, Buchnerodendron, Caloncoba, Lindackeria,* and *Mayna.* Sclerotic tyloses occur in one specimen of *Eleutherandra.* Perforation plates are exclusively scalariform, simple and scalariform, or exclusively simple in different taxa (FIGURES 15, 16, 17). The end-wall angles are usually oblique. Intervascular pitting is alternate (FIGURES 24, 26), but it is opposite in some species of *Azara, Erythrospermum, Carpotroche, Hydnocarpus, Mayna,* and possibly *Neoptychocarpus* (FIGURE 23). The size of the intervascular and vessel-ray pits varies from very small to very large (FIGURES 24–27). Intervascular and vessel-ray pits are frequently unilaterally compound when the pit size is small or very small (FIGURE 27); however, when the pit size is large or very large, unilaterally compound pits are rare.

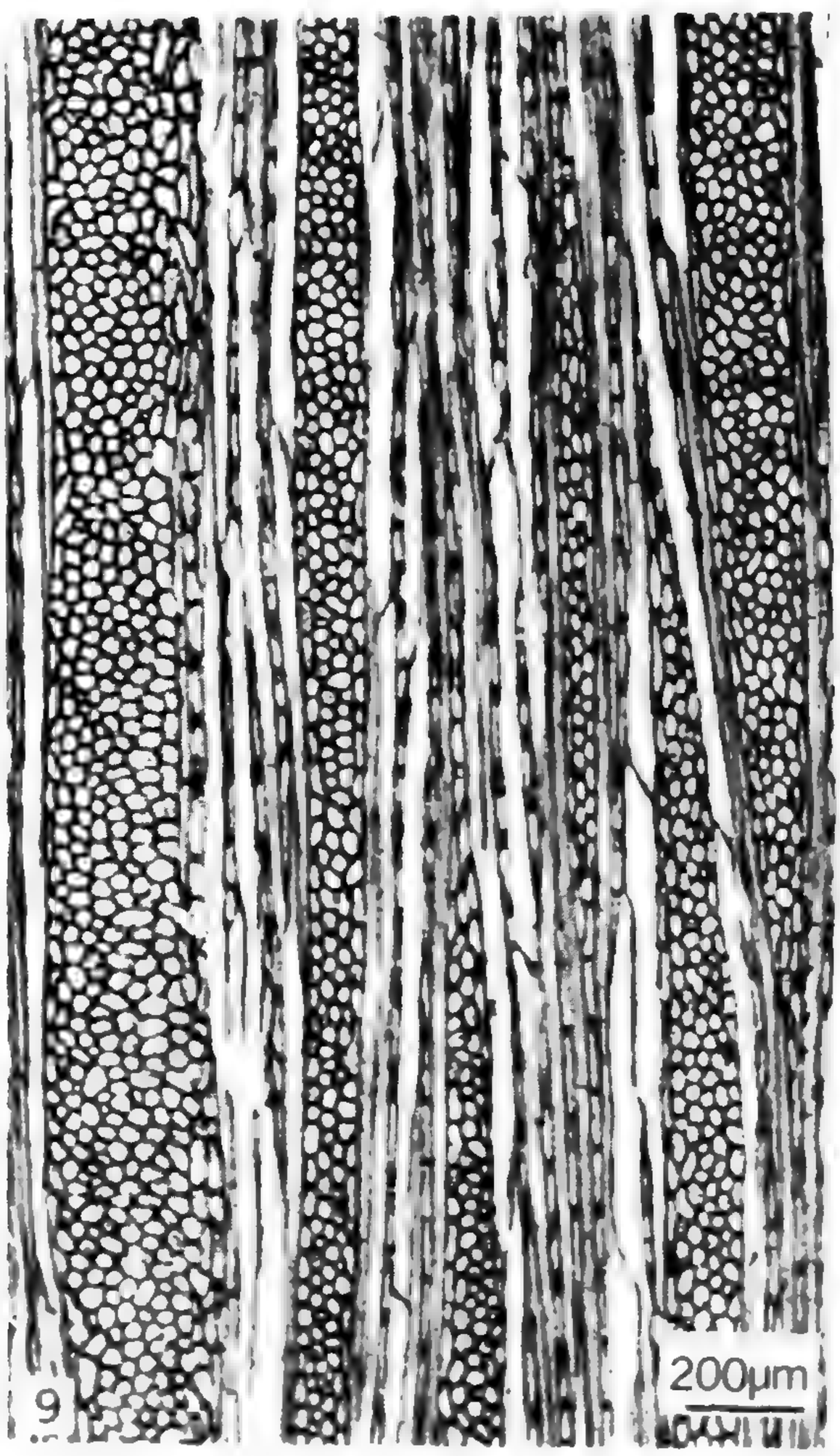
Rays are of two kinds: uniseriate homocellular rays entirely composed of upright cells and multiseriate heterocellular rays typically with long uniseriate extensions (Heterogeneous Type I, Kribs 1935) (FIGURES 9, 10). Ray height is variable. *Berberidopsis, Streptothamnus,* and species of *Casearia* and *Laetia* have rays over 1 cm. in height. On the other hand, some genera have an average ray height of less than 500 μm. Most genera have a ray width of less than 8 cells. Individual cells of the multiseriate portion of the rays as observed on the radial surface are elongate, rectangular, or square. Simply or scalariformly perforated ray cells occur sporadically in a number of genera (FIGURES 19, 20). Axial parenchyma is absent or scanty.

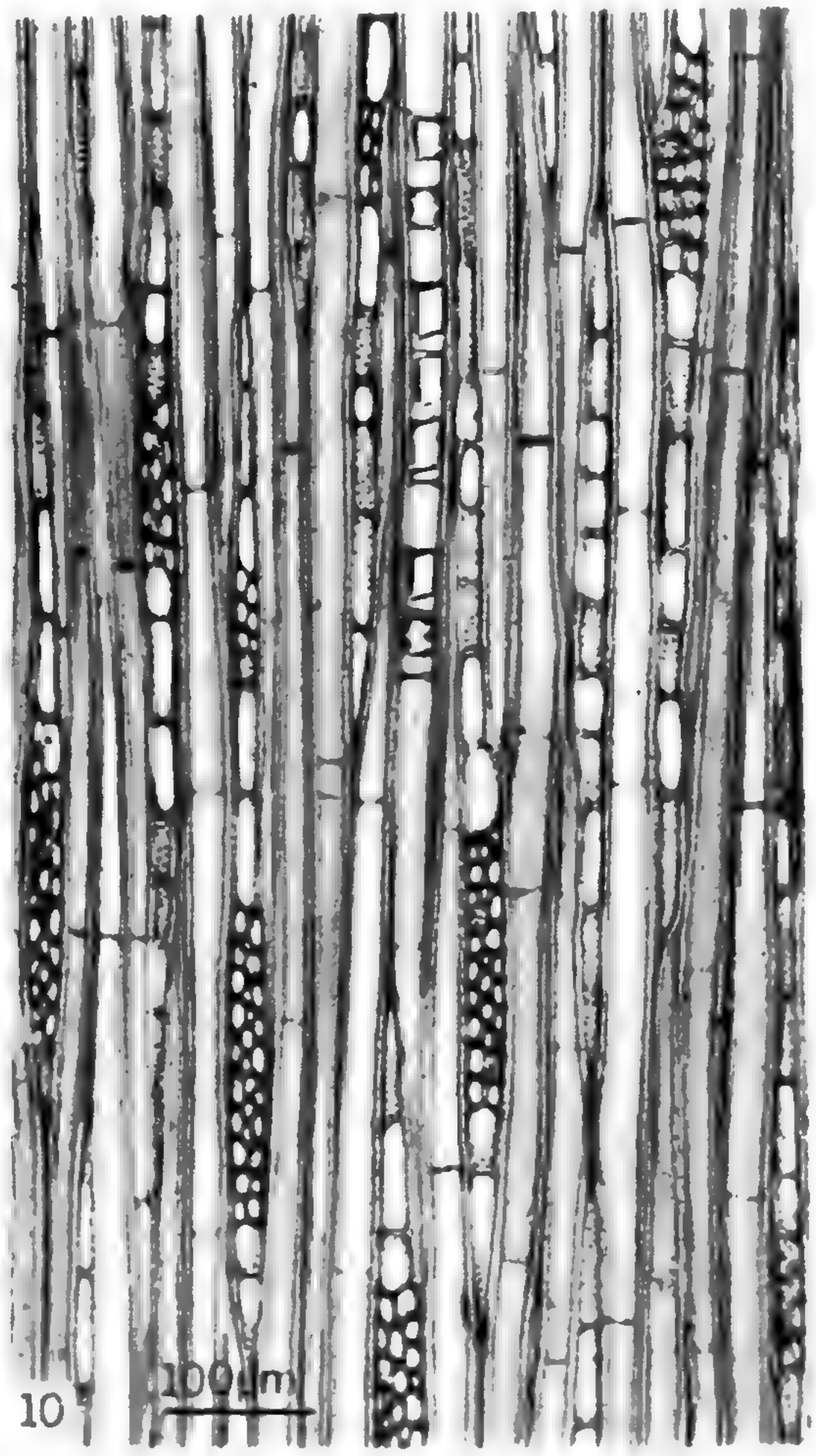
Fibrous elements (= imperforate tracheary elements) are usually septate (FIGURE 10). They are nonseptate in *Berberidopsis, Streptothamnus,* and *Idesia.* Both septate and nonseptate fibrous elements occur in *Carrierea, Itoa,* and *Olmediella.* Pits between fibrous elements are simple and slitlike (libriform wood fibers) or bordered with an extended aperture (fiber-tracheids). *Berberidopsis* and *Streptothamnus* are the only genera in which the fibrous elements are tracheids (FIGURE 7). The shortest fibrous elements occur in *Poliothyrsis* (overall average 874 μm.) and the longest in *Ryparosa* (overall average 3075 μm.). Wall thicknesses of fibrous elements vary from very thin to very thick. The fiber length to vessel length ratio varies from under 1.4 in *Berberidopsis, Erythrospermum,* and *Streptothamnus* to 2.4 in *Pangium* and *Trichadenia.*

Prismatic crystals are present in the ray cells of all genera except *Berberidopsis* and *Poliothyrsis.* Prismatic crystals also occur in the fibrous elements of some species of *Banara, Homalium,* and *Scolopia* (FIGURE 10). Genera in which prismatic crystals occur in chambered upright ray cells include *Ahernia, Banara, Bartholomaea, Bennettiodendron, Camptostylus, Calantica, Flacourtia, Hecatostemon, Homalium, Lindackeria,*









FIGURES 7–10: 7, radial section of *Streptothamnus moorei* showing bordered pits in tracheids; 8, radial section of *Ahernia glandulosa* showing prismatic crystals in chambered upright ray cells; 9, tangential section of *Ryania angustifolia* showing heterocellular rays typically with long uniseriate extensions (Heterogeneous Type I, Kribs 1935); 10, tangential section of *Banara regia* showing heterocellular rays typically with long uniseriate extensions (Heterogeneous Type I, Kribs 1935) and prismatic crystals in septate fibrous elements.

Ludia, Oncoba, Pineda, Scolopia, Tetrathylacium, Trimeria, Hasseltia, Macrohasseltia, Pleuranthodendron, and *Prockia* (FIGURES 2, 8, 22). Genera with crystals not encased by an integument include *Buchnerodendron, Caloncoba, Camptostylus, Carpotroche, Dasylepis, Gynocardia, Hydnocarpus, Kiggelaria, Mayna, Osmelia, Ryania, Ryparosa, Scaphocalyx,* and *Streptothamnus*. Druse crystals have been found in some species of *Camptostylus, Carrierea, Banara, Buchnerodendron, Laetia, Lindackeria,* and *Hasseltia* (FIGURES 21, 22). Granular silica occurs in some species of *Lindackeria, Mayna,* and *Scottellia* (FIGURE 5) and vitreous silica occurs in most species of *Hydnocarpus* (FIGURE 6).

GENERIC DESCRIPTIONS

In the generic descriptions numerical measurements which follow pore diameter, vessel-element length, etc. are minimum and maximum individual specimen averages followed by an average of all the specimen averages for a particular genus. When only one specimen of a genus is examined or when no variation in the average exists among a few specimens, the numbers reported are the minimum and maximum individual measurements followed by a specimen average. When variation within a genus is reported, only the species name is cited if an exception applies to all the specimens of a given species. When an exception applies to only part of the specimens of a given species, the xylarium designation and number follow the species cited. The number of species reported for each genus was taken from Willis (1966) and Hutchinson (1967).

Tribe Berberidopsideae

Streptothamnus F. Mueller. Two species endemic in the states of New South Wales and Queensland, Australia. One specimen.

Pore diameter medium-sized to moderately large (176–248 μm.; average 212 μm.); pores 100 per cent solitary; pores per square millimeter moderately numerous (18 pores/mm.^{2}). Vessel elements very long to extremely long (1159–2745 μm.; average 1976 μm.); perforation plates exclusively scalariform, 6 to 15 bars which are 4–6 μm. thick and 8–14 μm. apart; end-wall angles 10° to 30°. Intervascular pits absent except on overlapping vessel-element ligules; opposite to alternate; medium-sized, 8–10 μm. Vessel-ray pits circular to linear; coarse, 10–40 μm. Height of multiseriate portion of rays mostly over 1.5 cm.; width 3 to 5 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly square; cell height 25–37 μm. Tracheids moderately long to extremely long (2074–3416 μm.; average 2644 μm.) with thin to very thin walls, 4–6 μm.; nonseptate. F/V ratio 1.34. Prismatic crystals rare in ray cells of multiseriate portion and absent in upright ray cells; no integuments observed; not in chambered cells.

Berberidopsis Hooker f. Monotypic genus from Chile. One specimen.

Pore diameter moderately small (64–80 μm.; average 72 μm.); pores

99 per cent solitary; pores per square millimeter very numerous (92 pores/mm.^{2}). Vessel elements medium-sized to extremely long (530–2040 μm.; average 1389 μm.); perforation plates exclusively scalariform, mostly over 15 bars which are 2 μm. thick and 4–8 μm. apart, end-wall angles 10° to 25°. Fine spiral thickenings occur throughout the vessel body. Tyloses are occasionally to rarely present. Intervascular pitting very rare or absent except on overlapping vessel-element ligules; opposite; medium-sized to very large, 8–20 μm. Vessel-ray pits circular to linear; coarse, 10–30 μm. Height of multiseriate portion of rays mostly over 1.5 cm.; width 15 to 25 cells or 240–340 μm. Individual ray cells of multiseriate portion as observed on the radial surface are square to elongate; cell height 20–35 μm. Tracheids medium-sized to moderately long (1550–2200 μm.; average 2644 μm.) with thin walls, 4–6 μm.; nonseptate. F/V ratio 1.37. Crystals absent.

Erythrospermum Lambert. Six to 30 species from Madagascar, Mascarene Islands, Ceylon, India, Burma, Indonesia, and Melanesia. Three specimens representing two species.

Pore diameter moderately small (50–85 μm.; average 62 μm.); pores average 77 per cent solitary, range 69 to 85 per cent; radial multiples mostly 2, occasionally to 4; pores per square millimeter numerous to very numerous (34–61 pores/mm.^{2}; average 52 pores/mm.^{2}). Vessel elements very long (1217–1852 μm.; average 1545 μm.); perforation plates exclusively scalariform, mostly over 15 bars which are 1–3 μm. thick and 4–8 μm. apart; end-wall angles 10° to 15°. Occasional tyloses occur in *E. candidum*. Intervascular pitting opposite to alternate; pits circular to occasionally linear; medium-sized to very large, 7–24 μm. Vessel-ray pits circular to linear; medium to mostly coarse, 8–34 μm. Height of multiseriate portion of rays averages 4753 μm., range 3645–5581 μm.; width 2 to 6 cells. Individual ray cells of multiseriate portion as observed on the radial surface are square to elongate; cell height 20–50 μm. Simply and scalariformly perforated ray cells in *E. acuminatissimum* (SJRw 25976). Fiber-tracheids moderately long to very long (1786–2344 μm.; average 2110 μm.) with very thin to thick walls, 3–8 μm.; septate. F/V ratio averages 1.38, range 1.27 to 1.47. Prismatic crystals abundant in ray cells of multiseriate portion and abundant to rare in upright ray cells; integumented except in *E. acuminatissimum* (SJRw 25976); not in chambered cells. Reddish-brown deposits frequent in ray cells.

Camptostylus Gilg. Four species from west tropical Africa. Three specimens representing two species.

Pore diameter mostly moderately small (57–105 μm.; average 77 μm.); pores average 79 per cent solitary, range 70 to 91 per cent; radial multiples mostly 2, occasionally to 4; pores per square millimeter numerous to very numerous (31–77 pores/mm.^{2}; average 53 pores/mm.^{2}). Vessel elements moderately long to very long (982–1453 μm.; average 1193 μm.); perforation plates mostly simple to occasionally scalariform, up to 10

bars which are 2 μm. thick and 4–6 μm. apart; end-wall angles 25° to 35°. Spiral thickenings occur in vessel tails of *C. mannii* (TERVw). Intervascular pitting alternate; pits circular to occasionally linear; mostly medium-sized, 8–10 μm.; in *C. mannii* (TERVw) occasionally very large, up to 46 μm. Vessel-ray pits circular to linear; medium to mostly coarse, 8–36 μm. Height of multiseriate portion of rays averages 1308 μm., range 1075–1660 μm.; width mostly 2 to 5 cells. Individual ray cells of multiseriate portion as observed on the radial surface are square to elongate; cell height 16–35 μm. Fiber-tracheids and libriform fibers moderately long to very long (1877–2532 μm.; average 2128 μm.) with mostly thin walls, 3–6 μm.; septate. F/V ratio averages 1.79, range 1.72–1.91. Prismatic crystals rare to abundant in ray cells of multiseriate portion and absent to frequent in upright ray cells; not integumented; not in chambered cells. Druse crystals in 2- to 4-chambered upright ray cells of *C. mannii* (TERVw). Brown or dark reddish-brown deposits occasionally in ray cells.

Ahernia Merrill. Monotypic genus from Hainan Island and the Philippines. Three specimens.

Pore diameter medium-sized (100–160 μm.; average 123 μm.); pores average 37 per cent solitary, range 29 to 46 per cent; radial multiples mostly 2, occasionally to 5; pores per square millimeter moderately numerous (14–16 pores/mm.^{2}; average 15 pores/mm.^{2}). Vessel elements moderately long (880–1052 μm.; average 980 μm.); perforation plates exclusively simple; end walls somewhat oblique, 30° to 40°. Intervascular pitting alternate; pits circular to oval; medium-sized, 8–10 μm. Vessel-ray pits circular to linear; medium to mostly coarse, 8–30 μm. Height of multiseriate portion of rays averages 897 μm., range 534–1383 μm.; width 2 to 6 cells. Individual ray cells of multiseriate portion as observed on the radial surface are elongate to rectangular; cell height 15–27 μm. Fiber-tracheids moderately long (1684–1909 μm.; average 1739 μm.) with thin walls, 3–6 μm.; septate. F/V ratio averages 1.84, range 1.81–1.91. Prismatic crystals abundant in upright ray cells and usually absent in ray cells of multiseriate portion; integumented; mostly in 2-, occasionally in 4-chambered upright ray cells.

Dasylepis Oliver. Seven to 10 species from tropical Africa. One specimen.

Pore diameter moderately small (56–80 μm.; average 67 μm.); pores average 84 per cent solitary; radial multiples mostly 2; pores per square millimeter numerous (38 pores/mm.^{2}). Vessel elements moderately long to very long (915–1556 μm.; average 1331 μm.); perforation plates exclusively scalariform, mostly 6 to 13 bars which are 4 μm. thick and 10–14 μm. apart; end-wall angles 10° to 20°. Intervascular pitting alternate; pits circular to linear; medium-sized to very large, 8–20 μm. Vessel-ray pits circular to linear; coarse, 10–22 μm. Height of multiseriate portion of rays averages 2250 μm., maximum 2850 μm., width 4 to 6 cells. Indi-

vidual ray cells of multiseriate portion as observed on the radial surface are square to rectangular; cell height 20–27 μm. Fiber-tracheids medium-sized to very long, mostly moderately long (1434–2592 μm.; average 2053 μm.) with thick to very thick walls, 5–8 μm., septate. F/V ratio 1.54. Prismatic crystals abundant in ray cells of multiseriate portion and rare in upright ray cells; not integumented; not in chambered cells.

Scottellia Oliver. Eight to 10 species from tropical Africa. Six specimens representing one species.

Pore diameter mostly moderately small (66–103 μm.; average 83 μm.); pores average 63 per cent solitary, range 47 to 78 per cent; radial multiples mostly 2, occasionally to 5; pores per square millimeter numerous to very numerous (33–59 pores/mm.^{2}; average 42 pores/mm.^{2}). Vessel elements moderately long to very long (1046–1582 μm.; average 1348 μm.); perforation plates exclusively scalariform, mostly 5 to 15 bars which are 2–6 μm. thick and 8–18 μm. apart; end-wall angles 15° to 30°. Spiral thickenings occasionally in vessel tails; absent in *S. klaineana* (Bw). Intervascular pitting mostly alternate; pits circular to linear; medium-sized to very large, 8–26 μm. Vessel-ray pits circular to linear; medium to mostly coarse, 8–30 μm. Height of multiseriate portion of rays averages 2346 μm., range 1548–3148 μm.; width 3 to 7 cells. Individual ray cells of the multiseriate portion as observed on the radial surface are square to elongate; cell height 20–30 μm. Fiber-tracheids moderately long to very long (1850–2483 μm.; average 2191 μm.) with thin to thick walls, 3–8 μm.; septate. F/V ratio averages 1.64, range 1.46–1.79. Prismatic crystals frequent to abundant in both types of ray cells, in *S. klaineana* (Bw) rare in ray cells of multiseriate portion and absent in upright ray cells; integumented; not in chambered cells. Very small silica bodies, mostly 6 μm. or less, are rare to frequent in ray cells of multiseriate portion of *S. klaineana*.

Rawsonia Harvey & Sonder. Seven to eight species from tropical Africa and South Africa. One specimen.

Pore diameter moderately small (56–80 μm.; average 68 μm.); pores average 50 per cent solitary; radial multiples mostly 2, occasionally to 6; pores per square millimeter very numerous (83 pores/mm.^{2}). Vessel elements medium-sized to mostly moderately long (589–1140 μm.; average 889 μm.); perforation plates exclusively scalariform, mostly 4 to 10 bars which are 2–4 μm. thick and 10–14 μm. apart; end-wall angles 15° to 30°. Intervascular pitting alternate; pits circular to linear; mostly large to very large, 9–26 μm. Vessel-ray pits circular to linear; medium to mostly coarse, 8–25 μm. Height of multiseriate portion of rays averages 4429 μm., maximum 6100 μm.; width up to 12 cells. Individual ray cells of multiseriate portion as observed on the radial surface are square to elongate; cell height 15–24 μm. Fiber-tracheids medium-sized to moderately long (1220–1860 μm.; average 1474 μm.) with thin to thick walls, 3–5 μm.; septate. F/V ratio 1.73. Prismatic crystals occasional in ray cells of

multiseriate portion and rare in upright ray cells; integumented; not in chambered cells. Reddish-brown deposits abundant in ray cells.

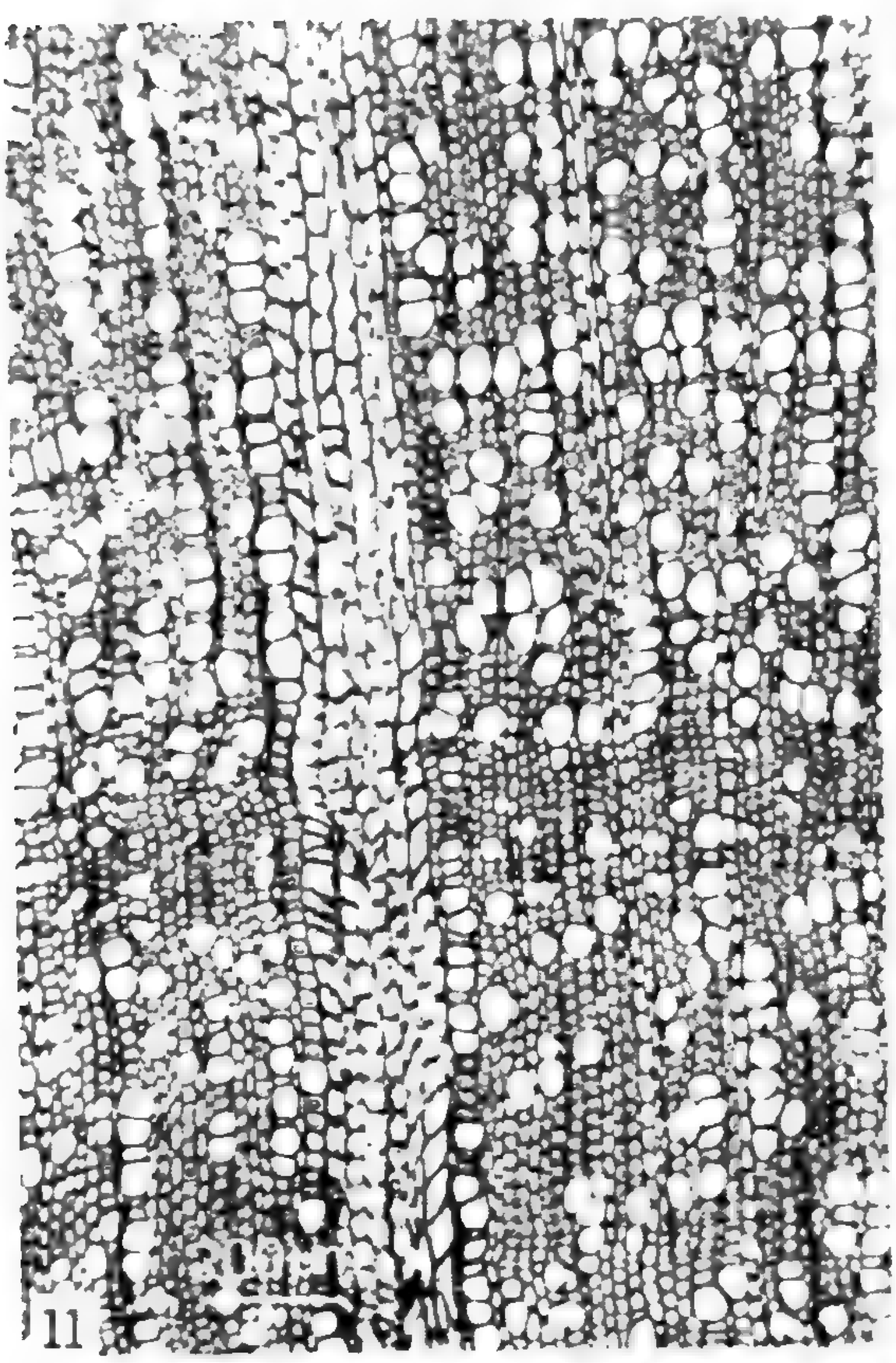
Tribe Oncobeae

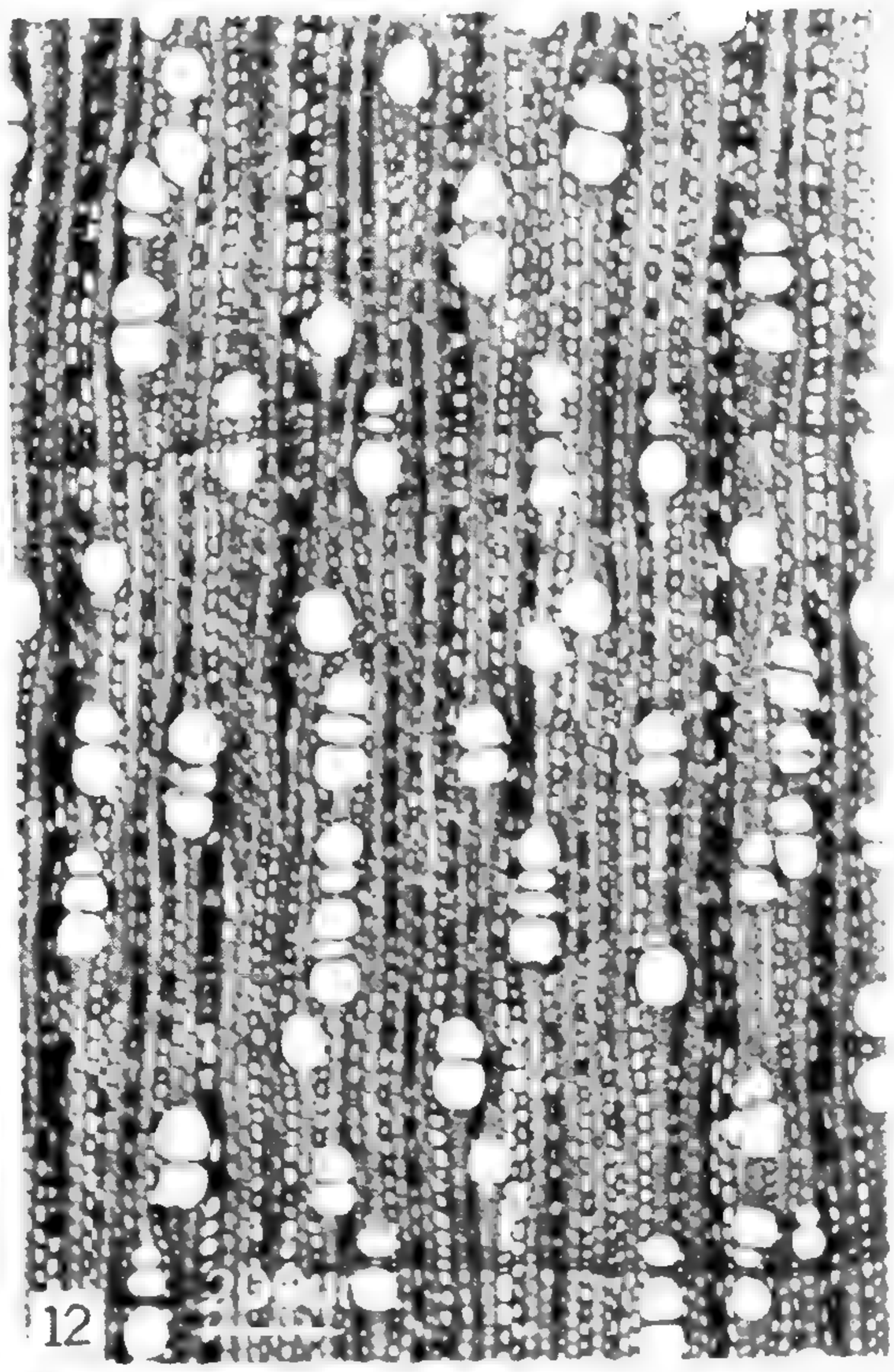
Carpotroche Endlicher. Fifteen to 20 species from Central America and tropical South America. Four specimens representing two species.

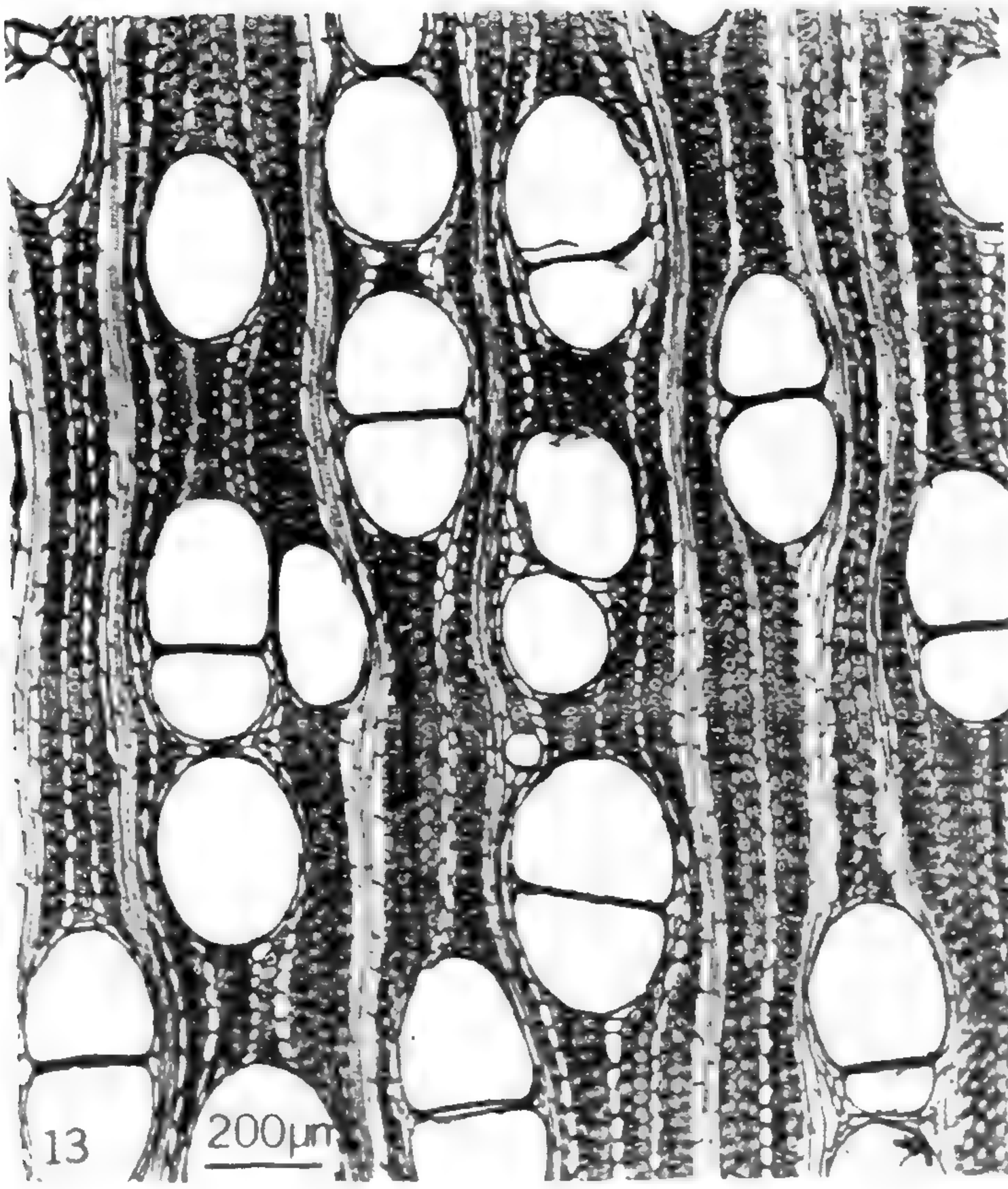
Pore diameter very small (42–49 μm.; average 44 μm.); pores average 72 per cent solitary, range 66 to 77 per cent; radial multiples mostly 2, occasionally to 7; pores per square millimeter numerous to very numerous (36–98 pores/mm.^{2}; average 79 pores/mm.^{2}). Vessel elements moderately long (920–1030 μm.; average 993 μm.); perforation plates in *C. platyptera* are exclusively scalariform with 7 to 15 or more bars which are 1–3 μm. thick and 3–8 μm. apart; in *C. brasiliensis* perforation plates are mostly simple and occasionally scalariform (up to 5 bars); end-wall angles 20° to 35°. Occasional tyloses in *C. platyptera* (SJRw 10473 and SJRw 11970). Intervascular pitting mostly alternate to occasionally opposite; pits circular to linear; mostly medium-sized to very large, 7–36 μm. Vessel-ray pits circular to linear; medium to coarse, 8–30 μm. Height of multiseriate portion of rays averages 2363 μm., range 1979–2653 μm.; width 2 to 5 cells. Individual ray cells of multiseriate portion as observed on the radial surface are square to rectangular; cell height 23–50 μm. Simply perforated ray cells in *C. brasiliensis*. Mostly fiber-tracheids, occasionally libriform fibers, medium-sized to moderately long (1387–1889 μm.; average 1535 μm.) with mostly thin to very thin walls, 3–5 μm.; septate. F/V ratio averages 1.55, range 1.38–1.84. Prismatic crystals abundant to occasional in ray cells of multiseriate portion and abundant to rare in upright ray cells; not integumented; not in chambered cells. Reddish-brown deposits frequent to sporadic in ray cells.

Mayna Aublet. Fifteen species from tropical America. Nine specimens representing eight species.

Pore diameter very small to moderately small (38–69 μm.; average 47 μm.); pores average 69 per cent solitary, range 39 to 85 per cent; radial multiples mostly 2, occasionally to 9; pores per square millimeter numerous to very numerous (28–87 pores/mm.^{2}; average 65 pores/mm.^{2}). Vessel elements mostly moderately long to very long (774–1319 μm.; average 974 μm.); perforation plates in *M. longifolia* and *M. pacifica* are exclusively scalariform with 7 to 15 or more bars which are 2–4 μm. thick and 4–10 μm. apart; perforation plates are mostly simple and occasionally scalariform (up to 4 bars) in *M. amazonica, M. echinata, M. longicuspis* (SJRw 10587), and *M. zuliana*; perforation plates are exclusively simple in *M. grandifolia, M. longicuspis* (SJRw 12271), and *M. odorata*; end-wall angles 15° to 55°. Occasional tyloses occur in *M. amazonica, M. echinata, M. grandifolia, M. longicuspis* (SJRw 12271), and *M. zuliana*. Fine spiral thickenings occur throughout the vessel elements of *M. amazonica* and in vessel tails of *M. zuliana*. Intervascular pitting mostly alternate to occasion-







FIGURES 11–14: 11, transverse section of *Ryania angustifolia* showing poorly defined growth rings, little or no axial parenchyma, angular pores, very numerous pores per square millimeter, and an average pore diameter of less than 50 μm.; 12 *Lindackeria latifolia*, typical transverse section of Flacourtiaceae with poorly defined growth rings, little or no axial parenchyma, rounded pores,

ally opposite; pits circular to linear; medium-sized to very large, 7–34 μm. Vessel-ray pits circular to linear; medium to coarse, 8–26 μm. Height of multiseriate portion of rays averages 3622 μm., range 2535–4307 μm.; width 3 to 5 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly square; cell height 20–40 μm. Simply perforated ray cells in *M. amazonica, M. echinata, M. longicuspis* (SJRw 10587), *M. pacifica,* and *M. zuliana.* Fiber-tracheids and libriform fibers medium-sized to moderately long (1263–1990 μm.; average 1517 μm.) usually with thin to very thin walls, 2–6 μm., thick to very thick, 5–8 μm., in *M. amazonica*; septate. F/V ratio averages 1.56, range 1.51–1.66. Prismatic crystals abundant to occasional in ray cells of multiseriate portion and frequent to rare in upright ray cells; absent in *M. amazonica*; not integumented; not in chambered cells. Large silica bodies (10–16 μm.) abundant in ray cells of *M. amazonica.* Reddish-brown deposits abundant to occasional in ray cells and fibrous elements.

Oncoba Forskåll. Five to 40 species from tropical Africa and South Africa. One specimen.

Pore diameter mostly moderately small (72–104 μm.; average 85 μm.); pores average 49 per cent solitary; radial multiples mostly 2 and 3, occasionally to 5; pores per square millimeter numerous (31 pores/mm.^{2}). Vessel elements medium-sized to moderately long (518–1128 μm.; average 855 μm.); perforation plates exclusively simple; end-wall angles 30° to 45°. Intervascular pitting alternate; pits circular to oval; medium-sized, 7–8 μm. Vessel-ray pits circular to linear; fine to coarse, 6–25 μm. Height of multiseriate portion of rays averages 345 μm.; maximum 416 μm.; width mostly 2 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly elongate; cell height 13–16 μm. Simply perforated ray cells present. Fiber-tracheids medium-sized to moderately long (1159–1800 μm.; average 1435 μm.) with mostly thin walls, 4–6 μm.; septate. F/V ratio 1.68. Prismatic crystals frequent in upright ray cells and absent in ray cells of multiseriate portion; integumented; mostly in 2-, occasionally in 4-chambered upright ray cells. Reddish-brown deposits occasional in ray cells.

Caloncoba Gilg. Fifteen to 20 species from tropical Africa. Thirteen specimens representing seven species.

Pore diameter moderately small to medium-sized (52–122 μm.; average 90 μm.); pores average 61 per cent solitary, range 47 to 84 per cent; radial multiples mostly 2, occasionally to 5; pores per square millimeter

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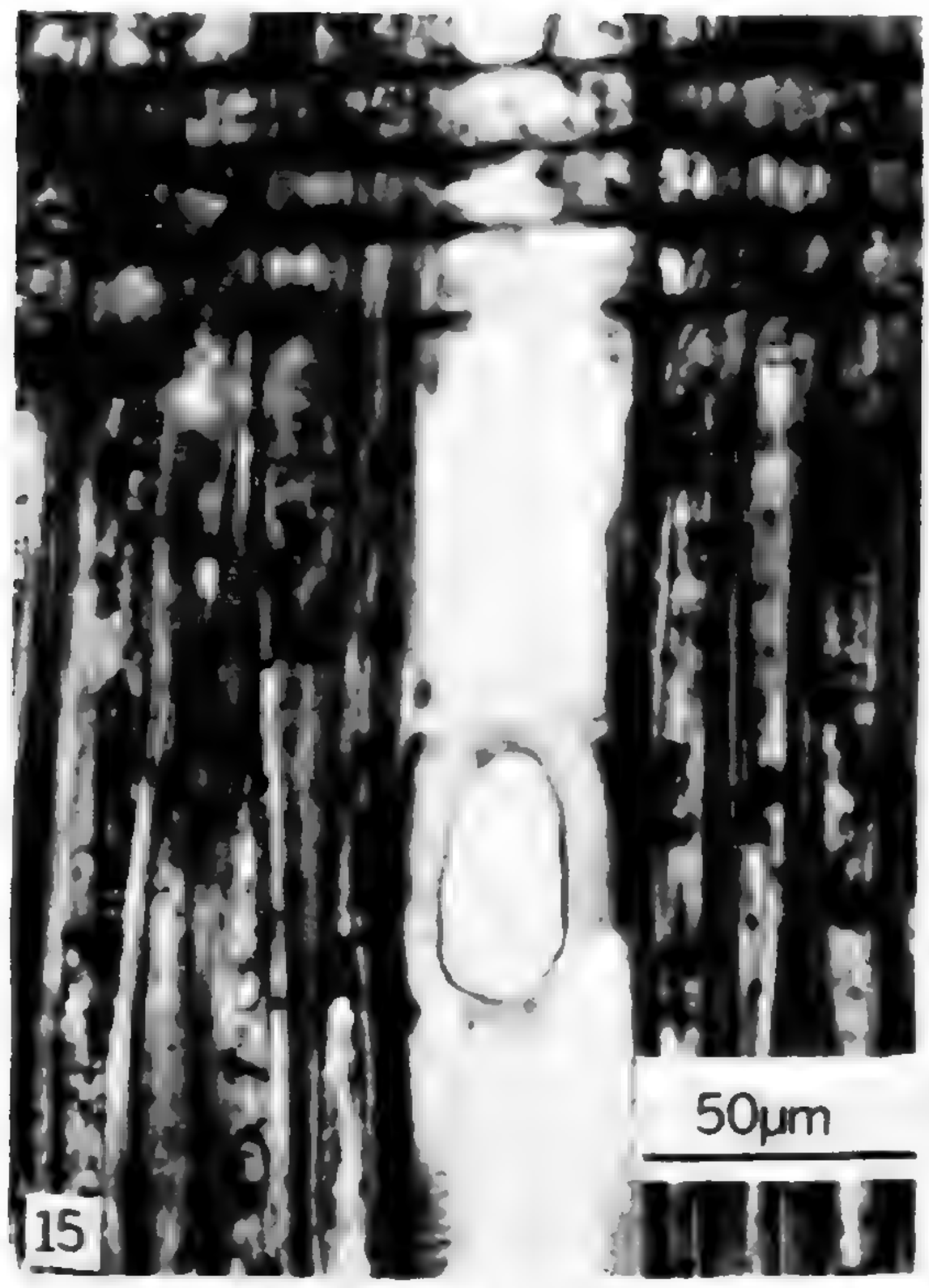
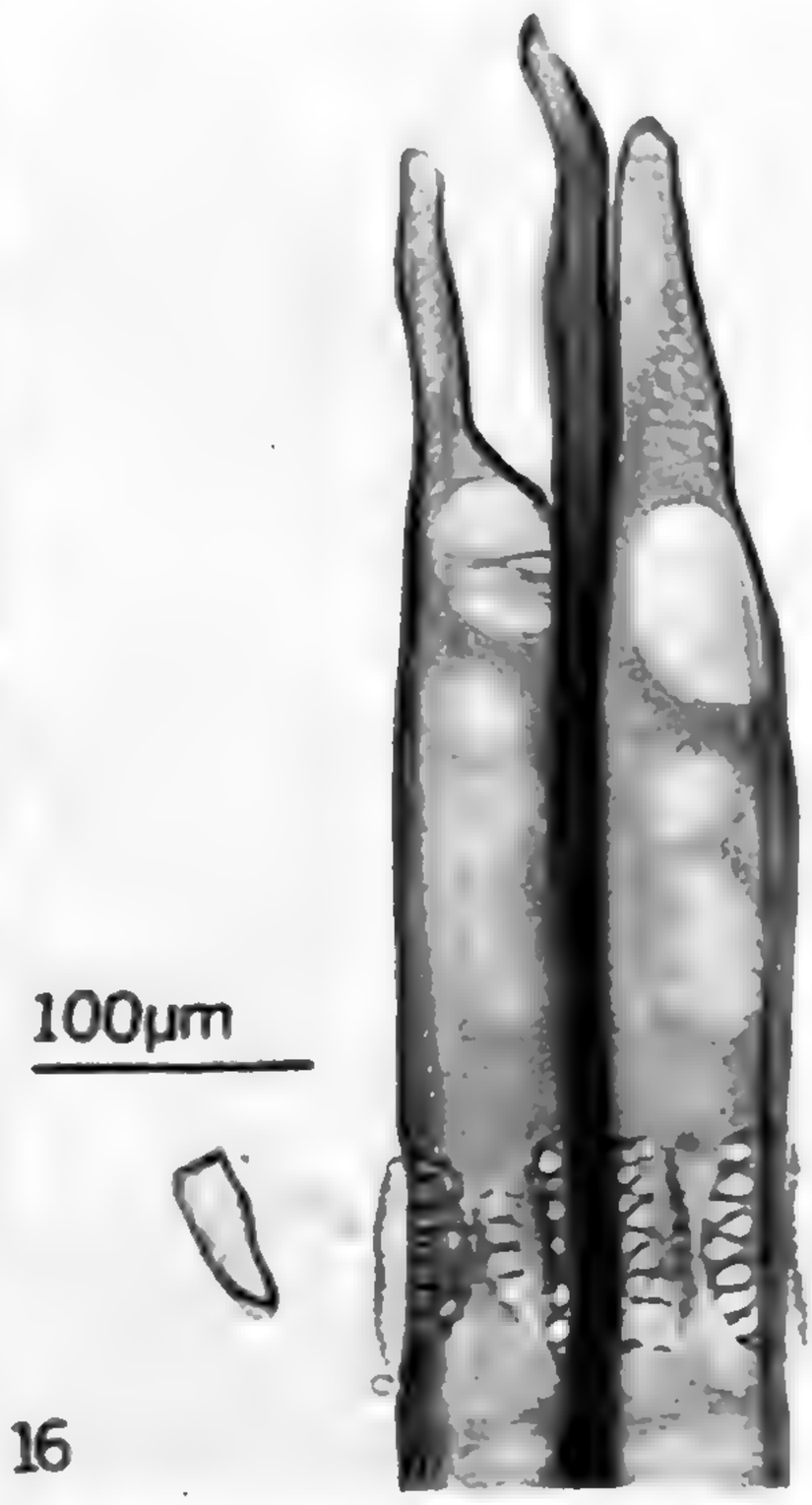
numerous pores per square millimeter, and an average pore diameter of 78 μm.; 13, transverse section of *Laetia procera* showing no growth rings, little or no axial parenchyma, rounded pores, moderately few pores per square millimeter, and an average pore diameter of more than 200 μm.; 14, *Pleuranthodendron mexicana,* maceration showing spiral thickenings in the vessel-element tails (ligules); photographed under partially crossed nicols.

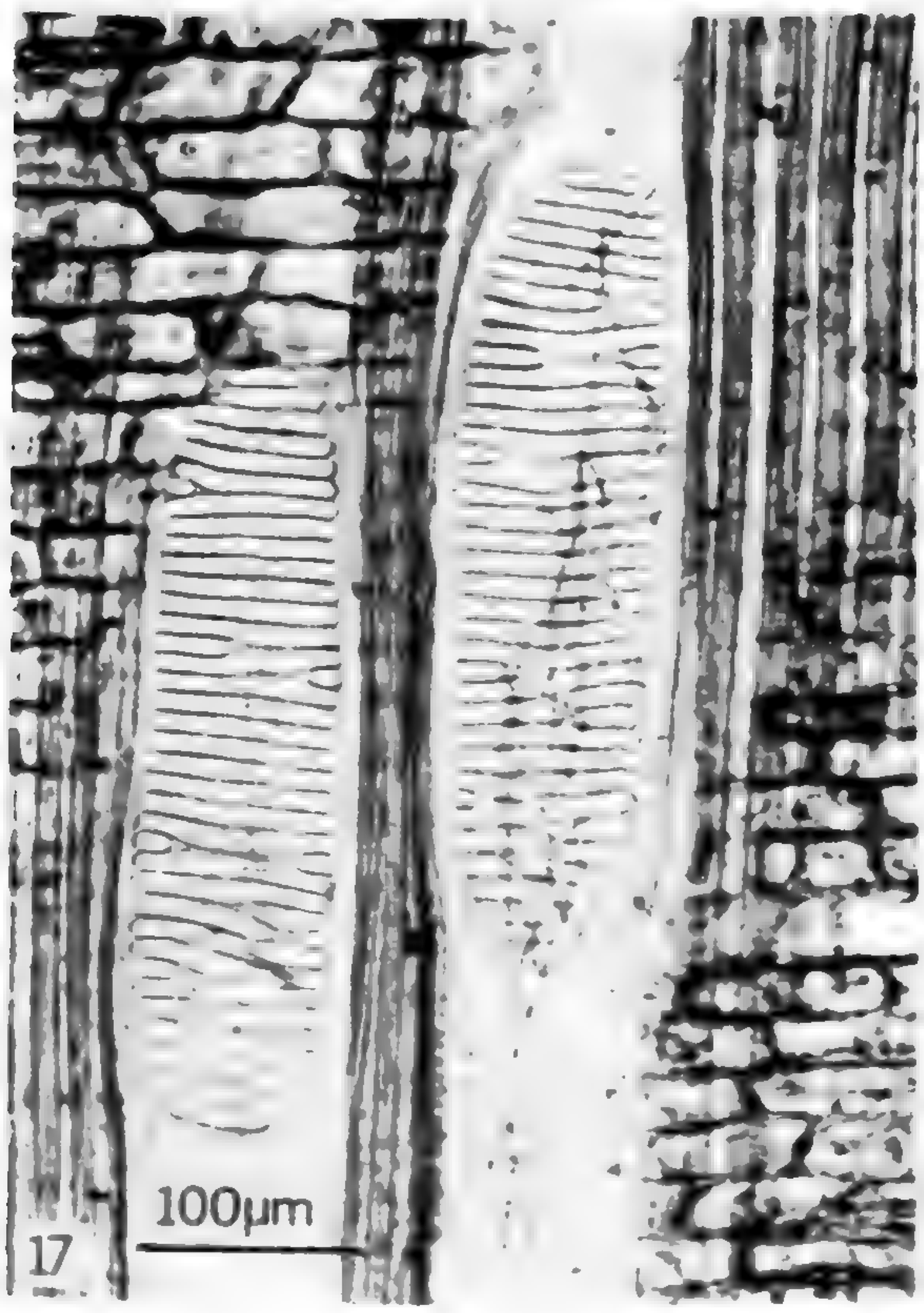
moderately numerous to very numerous (11–85 pores/mm.^{2}; average 29 pores/mm.^{2}). Vessel elements mostly moderately long to very long (797–1269 μm.; average 1056 μm.); perforation plates mostly simple and occasionally scalariform with 1 to 10 bars which are 1–4 μm. thick and 4–14 μm. apart; end-wall angles 30° to 45°. Intervascular pitting alternate; pits circular to oval; mostly medium-sized, 8–10 μm. Vessel-ray pits circular to linear; mostly coarse, 10–36 μm. Height of multiseriate portion of rays averages 1387 μm., range 941–3065 μm.; width mostly 2 to 3 cells, but 3 to 5 cells in *C. echinata* (FHOw 8466) and *C. glauca* (PRFw 23105) and 4 to 7 cells in *C. welwitschii* (PRFw 15281). Individual ray cells of multiseriate portion as observed on the radial surface are mostly square; elongate in *C. flagelliflora*; cell height 23–40 μm. Simply and scalariformly perforated ray cells are usually present; absent in *C. brevipes* and *C. welwitschii* (PRFw 15281). Fiber-tracheids and libriform fibers moderately long to very long (1692–2655 μm.; average 2174 μm.) with very thin to very thick walls, 3–9 μm. F/V ratio averages 2.07, range 1.60–2.30. Prismatic crystals generally more abundant in ray cells of multiseriate portion than in upright ray cells; not integumented; not in chambered cells. Reddish-brown or yellowish deposits abundant to absent in ray cells and fibrous elements.

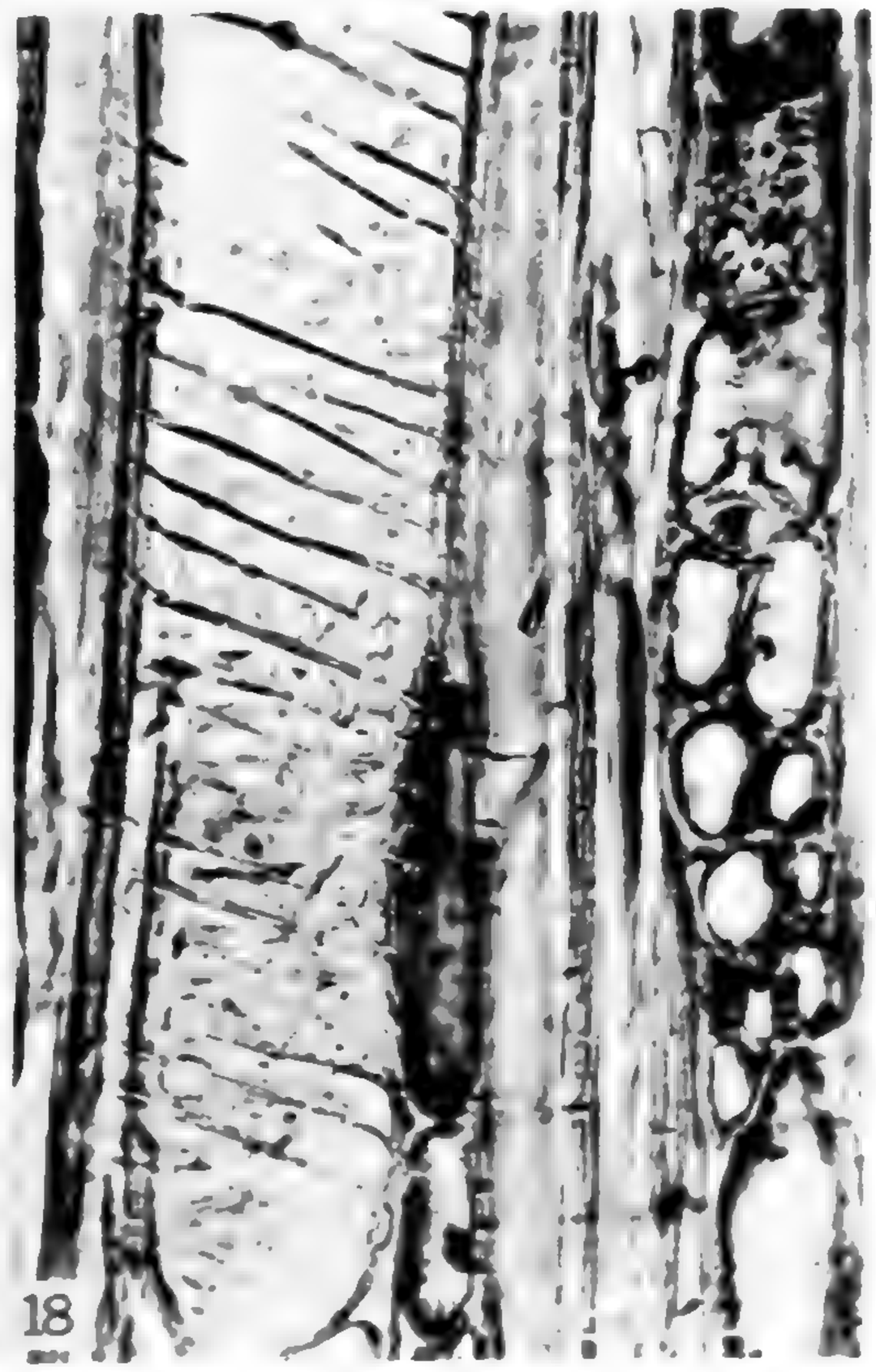
Lindackeria Presl. Eighteen to 25 species from tropical America and tropical Africa. Seven specimens representing six species.

Pore diameter moderately small (54–89 μm.; average 71 μm.); pores average 49 per cent solitary, range 36 to 61 per cent; radial multiples mostly 2 and 3, occasionally to 9; pores per square millimeter numerous to very numerous (20–47 pores/mm.^{2}; average 33 pores/mm.^{2}). Vessel elements medium-sized to mostly moderately long (705–1182 μm.; average 940 μm.); perforation plates exclusively simple; in *L. dentata* (Bw) perforation plates are mostly simply and rarely scalariform (up to 3 bars); end-wall angles 30° to 50°. Tyloses are occasionally present in all specimens of *Lindackeria* except *L. dentata* (Bw), in which tyloses are absent. Fine spiral thickenings occasionally occur in vessel tails of *L. dentata* (Bw). Intervascular pitting alternate; pits circular to oval; mostly medium-sized, 6–10 μm. Vessel-ray pits circular to linear; medium to coarse, 7–32 μm. Height of multiseriate portion of rays averages 2106 μm., range 1621–3183 μm.; width 2 to 7 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly square; cell height 20–40 μm. Simply perforated ray cells in *L. maynensis*. Fiber-tracheids and libriform fibers medium-sized to moderately long (1297–1990 μm.; average 1588 μm.) with thin to thick walls, 3–8 μm.; septate. F/V ratio averages 1.70, range 1.42–1.84. Prismatic crystals abundant to rare in ray cells of multiseriate portion and mostly rare to absent in upright ray cells; integumented; not in chambered cells. In *L. dentata* (Bw) druse crystals occasionally occur in 2-, 3-, or 4-chambered ray cells. Silica bodies abundant in both types of ray cells of *L. laurina*. Reddish-brown deposits abundant to occasional in ray cells and fibrous elements.









FIGURES 15–18: 15, radial section of *Buchnerodendron speciosum* showing a simple perforation plate; 16, *Olmediella betschleriana*, maceration showing simple and scalariform perforation plates; note spiral thickenings in vessel element; 17, radial section of *Erythrospermum candidum* showing scalariform perforation plates with many bars; 18, tangential section of *Carrierea calycina* showing spiral thickenings in vessel element.

Buchnerodendron Gürke. Five or six species from tropical Africa. One specimen.

Pore diameter mostly moderately small (48–64 μm.; average 57 μm.); pores average 66 per cent solitary; radial multiples mostly 2, occasionally to 11; pores per square millimeter very numerous (57 pores/mm.^{2}). Vessel elements medium-sized to mostly moderately long (629–1199 μm.; average 942 μm.); perforation plates mostly simple and occasionally scalariform (up to 5 bars); end-wall angles 20° to 40°. Tyloses occasionally present. Intervascular pitting alternate; pits circular to polygonal; medium-sized, 8–9 μm. Vessel-ray pits circular to linear; medium to coarse, 8–13 μm. Height of multiseriate portion of rays averages 1632 μm., maximum 2160 μm.; width 3 to 6 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly square; cell height 25–35 μm. Simply and scalariformly perforated ray cells common. Fiber-tracheids medium-sized to moderately long (1081–1945 μm.; average 1536 μm.) with very thin to thin walls, 3–4 μm.; septate. F/V ratio averages 1.63. Prismatic crystals frequent to occasional in ray cells of multiseriate portion and in upright ray cells; not integumented; not in chambered cells. Druse crystals present in ray cells of suspected wounded area.

Tribe Scolopieae

Scolopia Schreber. Forty-five to 55 species from the Old World tropics and subtropics. Nine specimens representing five species.

Pore diameter mostly moderately small (54–105 μm.; average 76 μm.); pores average 59 per cent solitary, range 47 to 71 per cent; radial multiples mostly 2, occasionally to 6; pores per square millimeter numerous to very numerous (20–44 pores/mm.^{2}; average 31 pores/mm.^{2}). Vessel elements medium-sized to very long (617–1279 μm.; average 881 μm.); perforation plates exclusively simple except in *S. zeyheri*, which has perforation plates that are mostly simple and rarely scalariform; end-wall angles 20° to 45°. Spiral thickenings generally present in the vessel tails; occasional to rare throughout the vessel elements; absent in *S. zeyheri*. Intervascular and vessel-ray pitting alternate; pits circular to polygonal; small, 4–6 μm. Height of multiseriate portion of rays averages 476 μm., range 226–722 μm.; width 2 to 5 cells. Individual ray cells of multiseriate portion as observed on the radial surface are elongate; cell height 12–23 μm. Simply perforated ray cells occur in *S. luzonensis*, *S. zeyheri*, and *S. spinosa* (SJRw 22356 and SJRw 30086). Libriform fibers medium-sized to moderately long (1278–2090 μm.; average 1582 μm.) with thin to very thick walls, 3–8 μm.; septate. F/V ratio averages 1.84, range 1.62–2.10. Prismatic crystals abundant in upright ray cells and rare to absent in ray cells of multiseriate portion; in *S. zeyheri* crystals are occasional in both types of ray cells; integumented; mostly in 2- to 4-chambered upright ray cells, occasionally in 6- to 8-chambered cells. Prismatic crystals occasionally in the fibrous elements of *S. spinosa* (USw 28688).

Dark reddish-brown deposits abundant in the ray cells and occasionally in the fibrous elements.

Bartholomaea Standley & Steyermark. Two species from Central America. One specimen from a herbarium sheet.

Pore structure not examined since the twig specimen was very small. Vessel elements medium-sized to moderately long (580–1037 μm.; average 785 μm.); perforation plates mostly simple and rarely scalariform, up to 5 bars which are 2 μm. thick and 4 μm. apart; end-wall angles 20° to 35°. Intervascular and vessel-ray pitting alternate; pits circular, small, 4–6 μm. Rays uniseriate to biseriate; individual ray cells of multiseriate portion as observed on the radial surface are mostly square. Fiber-tracheids medium-sized (946–1403 μm.; average 1144 μm.); septate. F/V ratio 1.46. Prismatic crystals frequent to abundant in both types of ray cells; integumented; mostly in 2- or 4-chambered upright ray cells.

Tribe Banareae

Banara Aublet. Thirty-five to 50 species from the West Indies and Central America to southern Brazil and Paraguay. Nine specimens representing seven species.

Pore diameter very small to medium-sized (42–139 μm.; average 93 μm.); pores average 46 per cent solitary, range 11 to 65 per cent; radial multiples mostly 2 and 3, occasionally to 9; pores per square millimeter moderately numerous to very numerous (14–97 pores/mm.^{2}; average 37 pores/mm.^{2}). Vessel elements medium-sized to moderately long (553–1026 μm.; average 766 μm.); perforation plates exclusively simple; end-wall angles 25° to 60°. Spiral thickenings are rare to occasional in the vessel tails of *B. guianensis* (MADw 11755), *B. roigii*, and *B. vellozii*. Intervascular and vessel-ray pitting alternate; pits circular to polygonal; small, 4–7 μm.; in *B. axilliflora* very small, 2–4 μm. Height of the multiseriate portion of rays averages 276 μm., range 199–349 μm.; width 2 to 4 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly elongate; cell height 10–23 μm. Fiber-tracheids and libriform fibers medium-sized to moderately long (1025–2000 μm.; average 1414 μm.) with thin to very thick walls, 2–8 μm.; septate. F/V ratio averages 1.84, range 1.47–2.15. Prismatic crystals abundant to rare in upright ray cells, usually absent or rare in ray cells of multiseriate portion; integumented; mostly in 2- to occasionally 4-chambered upright ray cells; in *B. nitida* and *B. roigii* the cells are mostly 4- to 8-chambered. Druse crystals occasionally in upright ray cells of *B. mollis* and *B. regia*. Prismatic crystals occasionally in the fibrous elements of *B. nitida*, *B. regia*, and *B. roigii*.

Pineda Ruiz & Pavon. One to two species from Peru. One specimen.

Pore diameter very small to moderately small (40–56 μm.; average 45 μm.); pores average 49 per cent solitary; radial multiples mostly 2 and

3, occasionally to 10; pores per square millimeter very numerous (86 pores/mm.^{2}). Vessel elements medium-sized to moderately long (400–1102 μm.; average 659 μm.); perforation plates exclusively simple; end-wall angles 20° to 45°. Intervascular pitting alternate; pits circular or oval to polygonal; small to mostly medium-sized, 6–9 μm. Vessel-ray pits mostly circular to oval, occasionally oblong to linear; fine to coarse, 6–20 μm. Height of multiseriate portion of rays averages 223 μm. or 10 cells, maximum 320 μm. or 16 cells; width 2 cells. Individual ray cells of multiseriate portion as observed on the radial surface are square to rectangular; cell height 18–23 μm. Simply perforated ray cells present. Fiber-tracheids medium-sized (932–1498 μm.; average 1203 μm.) with thin to thick walls, 3–6 μm.; septate. F/V ratio averages 1.83. Prismatic crystals abundant in upright ray cells and occasional in ray cells of multiseriate portion; integumented; mostly in 2- to occasionally 4-chambered upright ray cells.

Trimeria Harvey. Five to eight species from tropical and South Africa. One specimen.

Pore diameter very small (32–50 μm.; average 39 μm.); pores average 57 per cent solitary; radial multiples mostly 2 and 3, occasionally to 9; pores per square millimeter very numerous (69 pores/mm.^{2}). Vessel elements medium-sized to moderately long (518–1067 μm.; average 816 μm.); perforation plates exclusively simple; end-wall angles 25° to 35°. Intervascular and vessel-ray pitting alternate; pits circular or oval; small to medium-sized, 6–8 μm. Height of multiseriate portion of rays averages 582 μm., maximum 760 μm.; width 2 to 4 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly elongate; cell height 14–18 μm. Simply perforated ray cells present. Libriform fibers mostly medium-sized (1067–1647 μm.; average 1415 μm.) with thin walls, 4–6 μm.; septate in normal fibers, but nonseptate in gelatinous fibers. F/V ratio averages 1.73. Prismatic crystals abundant in upright ray cells and occasional in ray cells of multiseriate portion; integumented; mostly in 2- to occasionally 4-chambered upright ray cells.

Tribe Homalieae

Calantica Jaubert ex Tul. Five species from tropical East Africa and Madagascar. One specimen.

Pore diameter mostly moderately small (72–104 μm.; average 83 μm.); pores average 42 per cent solitary; radial multiples mostly 2, occasionally to 4; pores per square millimeter moderately numerous (14 pores/mm.^{2}). Vessel elements mostly moderately long to very long (762–1555 μm.; average 1165 μm.); perforation plates exclusively simple; end-wall angles 25° to 35°. Intervascular and vessel-ray pitting alternate; pits circular to polygonal; small, 3–5 μm. Height of multiseriate portion of rays averages 452 μm., maximum 680 μm.; width 2 to 3 cells. Individual ray cells of multiseriate portion as observed on the radial surface are rectangular to elongate; cell height 20–30 μm. Fiber-tracheids and libriform

fibers moderately long to very long (1860–2592 μm.; average 2245 μm.) with very thick walls, 8–11 μm.; septate. F/V ratio averages 1.93. Prismatic crystals abundant in upright ray cells and occasional in ray cells of multiseriate portion; integumented; mostly in 2-, occasionally in 3- or 4-chambered upright ray cells. Reddish-brown deposits frequent in ray cells.

Homalium Jacquin. Over 200 species from the tropics and subtropics. Sixteen specimens representing 12 species.

Pore diameter moderately small to medium-sized (77–146 μm.; average 97 μm.); pores average 45 per cent solitary, range 22 to 80 per cent; radial multiples mostly 2 and 3, occasionally to 7; pores per square millimiter moderately few to numerous (8–38 pores/mm.^{2}; average 22 pores/mm.^{2}). Vessel elements medium-sized to very long (560–1362 μm.; average 1056 μm.); perforation plates exclusively simple in most species; in *H. longifolium* and *H. pallidum* perforation plates are mostly simple and occasionally scalariform with few or vestigial bars; end-wall angles 15° to 60°. Intervascular and vessel-ray pitting alternate; pits circular to polygonal; small, mostly 4–6 μm., occasionally 6–8 μm. Height of multiseriate portion of rays averages 524 μm., range 350–973 μm.; width 2 to 5 cells. Individual ray cells of multiseriate portion as observed on the radial surface are elongate; cell height mostly 13–23 μm.; in *H. grandiflorum* cell height 18–27 μm. Fiber-tracheids and libriform fibers medium-sized to moderately long (1115–2247 μm.; average 1776 μm.) with mostly thick to very thick walls, 4–11 μm.; septate. F/V ratio averages 1.70, range 1.27–2.00. Prismatic crystals abundant in upright ray cells, but rare to occasional in *H. stenophyllum*; mostly occasional to absent in ray cells of multiseriate portion, but abundant in *H. longifolium*, *H. pallidum*, and *H. racemosum* (MADw 14451); integumented; mostly in 2- to 4-chambered upright ray cells or cells appearing to be chambered, and frequently more than 1 crystal per chamber; not in chambered cells in *H. letestui*. Prismatic crystals occasionally in scanty paratracheal parenchyma and in the fibrous elements of *H. foetidum*, *H. pallidum*, *and H. racemosum* (MADw 14451). Reddish-brown deposits abundant in the ray cells and fibrous elements of *H. grandiflorum* var. *javanicum*, *H. hainanense*, and *H. trichostemon*; absent in the ray cells of *H. letestui*, *H. smythei*, and *H. tomentosum*; sporadic in the ray cells of the remaining specimens.

Tribe Pangieae

Hydnocarpus Gaertner. Thirty to 40 species from India, Malay Archipelago, and Indo-China. Twelve specimens representing eight species, including the species of *Asteriastigma* and *Taraktogenos*.

Pore diameter moderately small to medium-sized (55–146 μm.; average 86 μm.); pores average 76 per cent solitary, range 45 to 93 per cent; radial multiples mostly of 2, occasionally to 4; pores per square millimeter moderately numerous to very numerous (13–72 pores/mm.^{2}; average 38 pores/mm.^{2}). Vessel elements very long to extremely long (1296–2361

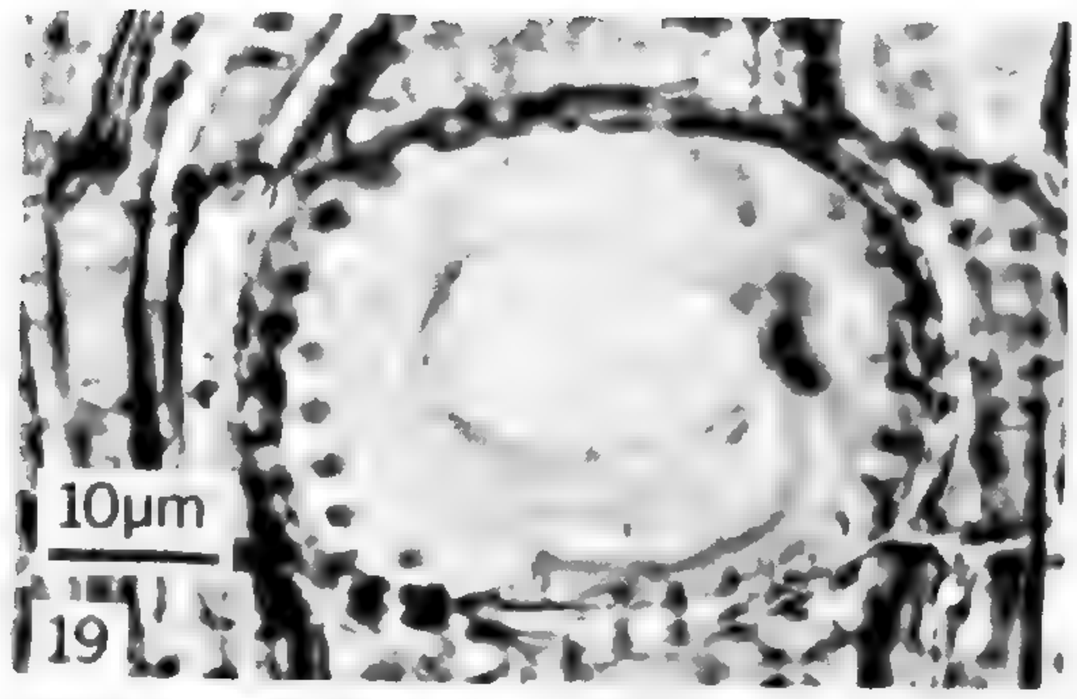
μm.; average 1794 μm.); perforation plates exclusively scalariform, mostly over 15 bars which are 1–6 μm. thick and 4–16 μm. apart; end-wall angles 10° to 25°. Tyloses occasional to rare in *H. gracilis* (MADw 25423), *H. kunstleri* (SJRw 22353), *H. sumatrana* (MADw 22588), and *H. yatesii*. Spiral thickenings occur in the vessel tails and occasionally throughout vessel elements of *H. kunstleri* (SJRw 38716). Intervascular pitting opposite to alternate; pits circular to oval; medium-sized, mostly 8–10 μm. in *H. gracilis* (MADw 25423), *H. macrocarpus*, *H. sumatrana*, and *H. venenata*; large, mostly 10–14 μm. in the remaining specimens. Vessel-ray pits circular to linear; medium to coarse, 8–44 μm. Height of multiseriate portion of rays averages 1218 μm., range 348–3273 μm.; width 2 to 3 cells. Individual ray cells of multiseriate portion as observed on the radial surface are square to elongate; cell height 23–53 μm. Simply perforated ray cells in *H. kunstleri* (SJRw 38716). Fiber-tracheids moderately long to extremely long (1982–3628 μm.; average 2793 μm.) with thin to very thick walls, 3–15 μm.; septate. F/V ratio averages 1.56, range 1.46–1.81. Prismatic crystals abundant to occasional in both types of ray cells, usually more prevalent in ray cells of multiseriate portion, absent in *H. kunstleri* (SJRw 22353), *H. macrocarpus*, *H. saigonensis*, and *H. yatesii*; not integumented; not in chambered cells. Vitreous silica in the vessel elements and occasionally fibrous elements of all species except *H. sumatrana*. Reddish-brown or brownish-orange deposits in the ray cells of *H. macrocarpus* and *H. sumatrana*.

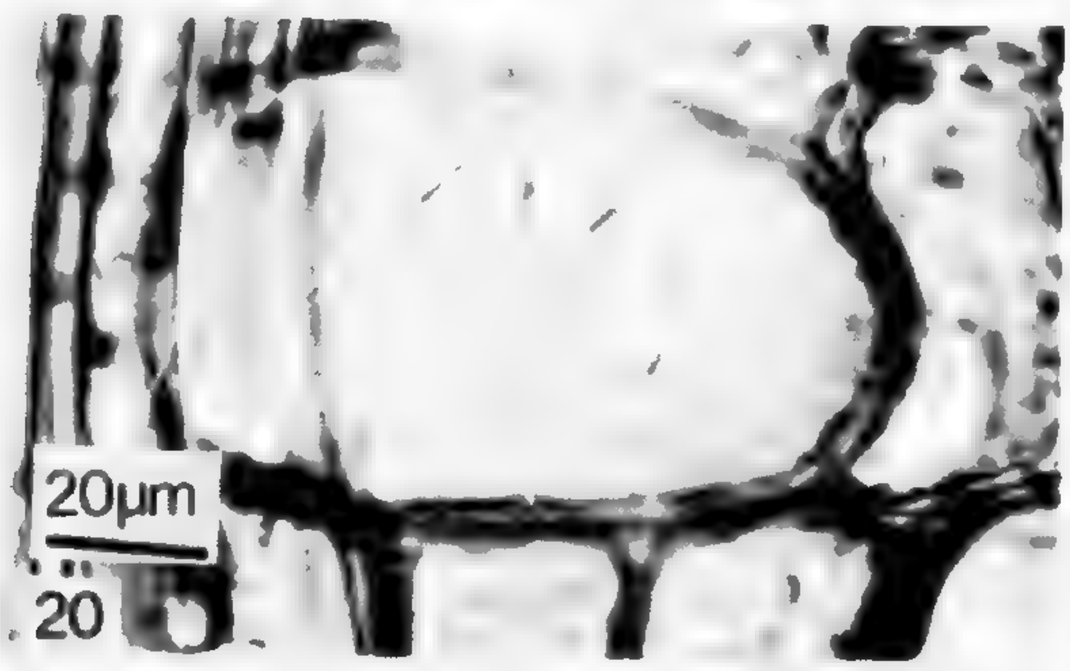
Eleutherandra Van Slooten. One or two species from Sumatra and Borneo. Two specimens representing one species.

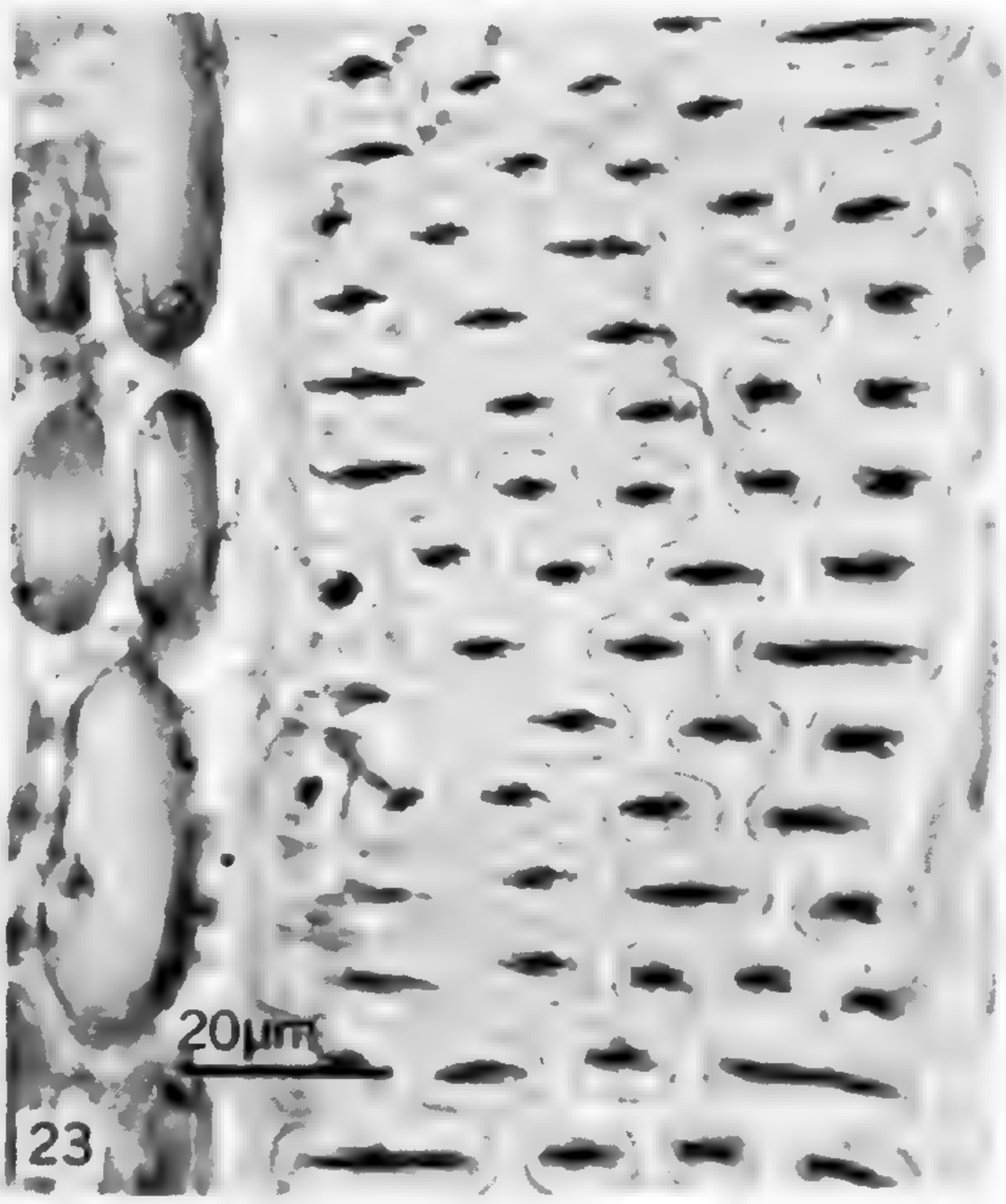
Pore diameter medium-sized (119–126 μm.; average 122 μm.); pores average 36 per cent solitary, range 24 to 48 per cent; radial multiples mostly 2 and 3, occasionally to 7; pores per square millimeter moderately few (7–8 pores/mm.^{2}; average 8 pores/mm.^{2}). Vessel elements very long (1103–1252 μm.; average 1177 μm.); perforation plates exclusively simple; end-wall angles 20° to 35°. Sclerotic tyloses occur occasionally in *E. pes-cervi* (SJRw 15445). Intervascular pitting alternate; pits circular to polygonal; small to medium-sized, 6–8 μm. Vessel-ray pits circular to linear; medium to coarse, 8–38 μm. Height of multiseriate portion of rays averages 1640 μm., range 1630–1650 μm.; width 1 to 3 cells. Individual ray cells of multiseriate portion as observed on the radial surface are square to elongate; cell height 28–40 μm. Fiber-tracheids and occasionally libriform fibers are very long (2306–2736 μm.; average 2521 μm.) with very thick walls, 10–16 μm.; septate. F/V ratio averages 2.13, range 2.09–2.16. Prismatic crystals abundant in both types of ray cells; integumented; not in chambered cells.

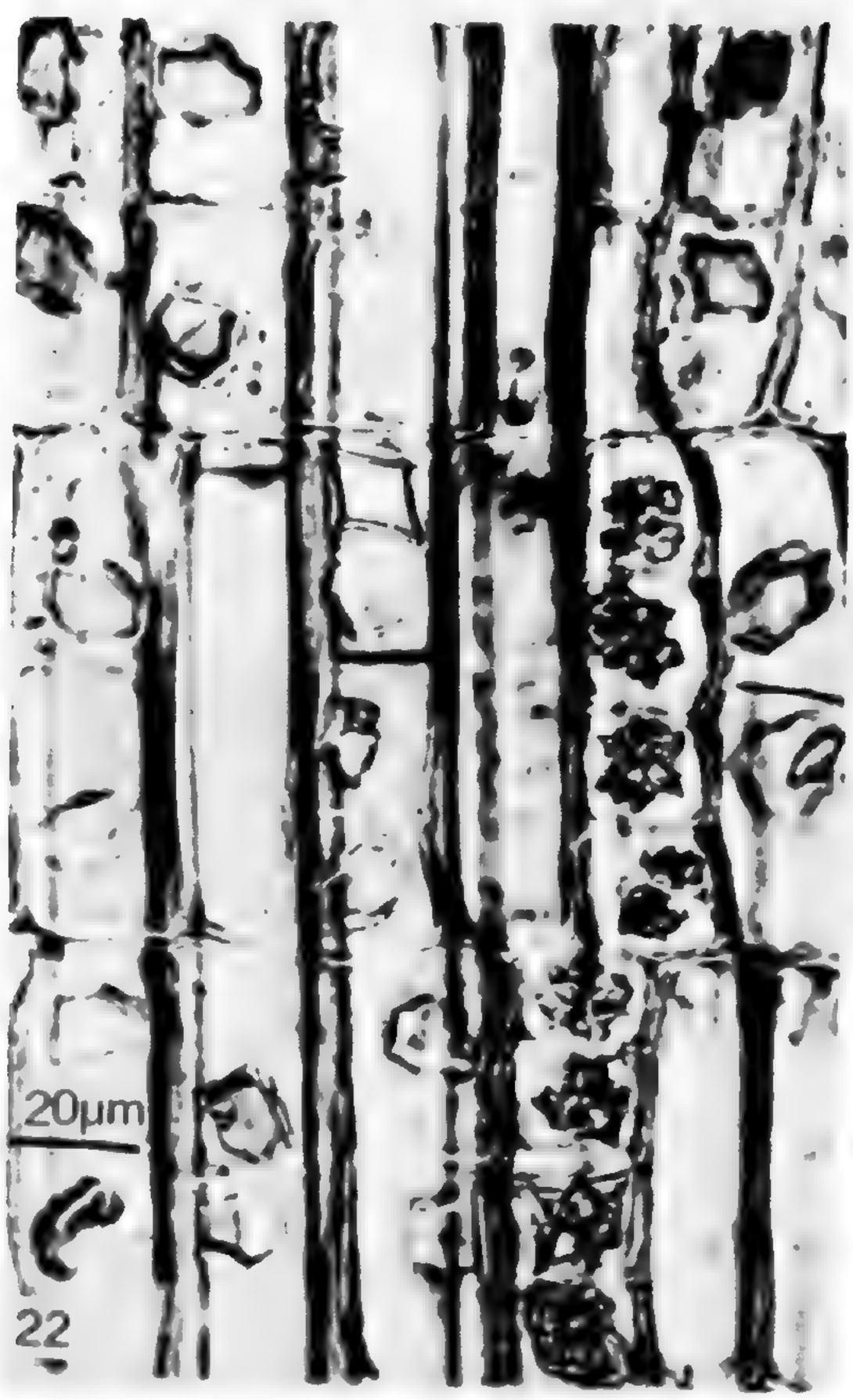
Gynocardia R. Brown. Monotypic genus from India and Burma. Two specimens.

Pore diameter moderately small to medium-sized (64–117 μm.; average 91 μm.); pores average 63 per cent solitary, range 60 to 65 per cent;









FIGURES 19–23: 19, radial section of *Buchnerodendron speciosum* showing simply perforated ray cell; 20, radial section of *Carpotroche brasiliensis* showing modified scalariformly perforated ray cell; 21, radial section of *Laetia procera* showing druse crystals in "paired" upright ray cells; 22, radial section of *Hasseltia floribunda* showing prismatic and druse crystals in chambered upright ray cells; 23, tangential section of *Erythrospermum candidum* showing opposite and transitional intervascular pitting.

radial multiples mostly 2, occasionally to 3; pores per square millimeter moderately numerous (13–19 pores/mm.^{2}; average 16 pores/mm.^{2}). Vessel elements moderately long (1086–1096 μm.; average 1091 μm.); perforation plates mostly simple and occasionally to rarely scalariform with vestigial and few bars, up to 5 bars which are 2 μm. thick and 6 μm. apart; end-wall angles 30° to 45°. Intervascular pitting alternate; pits circular to polygonal; large, 10–14 μm. Vessel-ray pits circular to linear; coarse, 10–40 μm. Height of multiseriate portion of rays averages 560 μm. or 11 cells, maximum 800 μm. or 15 cells; width 1 to 2 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly square; cell height 40–80 μm. Scalariformly perforated ray cells present. Fiber-tracheids moderately long (1782–1934 μm.; average 1858 μm.) with thin to very thin walls, 3–6 μm.; septate. F/V ratio averages 1.70, range 1.64–1.76. Prismatic crystals occasional in either upright ray cells or ray cells of multiseriate portion; no integuments observed; not in chambered cells.

Pangium Reinwardt. One to three species from Malay Archipelago, Philippine Islands, Solomon Islands, and New Guinea. Two specimens representing one species.

Pore diameter medium-sized (139–148 μm.; average 143 μm.); pores average 56 per cent solitary, range 54 to 58 per cent; radial multiples mostly 2, occasionally to 3; pores per square millimeter moderately few (6 pores/mm.^{2}). Vessel elements moderately long (930–1000 μm.; average 965 μm.); perforation plates exclusively simple; end-wall angles 25° to 60°. Intervascular pitting alternate; pits circular to polygonal; medium-sized, 8–10 μm. Vessel-ray pits circular to linear; coarse, 10–56 μm. Height of multiseriate portion of rays averages 2482 μm., range 1952–3212 μm.; width 3 to 5 cells. Individual ray cells of multiseriate portion as observed on the radial surface are square to elongate; cell height 30–50 μm. Fiber-tracheids moderately long to very long (2037–2713 μm.; average 2375 μm.) with thin to thick walls, 5–8 μm.; septate. F/V ratio averages 2.40, range 2.19–2.71. Prismatic crystals abundant to frequent in both types of ray cells; integumented; not in chambered cells.

Trichadenia Thwaites. One to two species from Ceylon, Philippine Islands, New Guinea, and Melanesia. Two specimens representing one species.

Pore diameter medium-sized (149–170 μm.; average 160 μm.); pores average 40 per cent solitary, range 34 to 46 per cent; radial multiples mostly of 2 and 3, occasionally to 4; pores per square millimeter moderately few (8–9 pores/mm.^{2}; average 8 pores/mm.^{2}). Vessel elements very long (1194–1196 μm.; average 1195 μm.); perforation plates exclusively simple; end-wall angles 30° to 50°. Intervascular pitting alternate; pits circular to polygonal; mostly medium-sized, 8–11 μm. Vessel-ray pits circular to linear; mostly coarse, 10–45 μm. Height of multi-

seriate portion of rays averages 2316 μm., range 2006–2625 μm.; width 2 to 5 cells. Individual ray cells of multiseriate portion as observed on the radial surface are square to rectangular; cell height 26–55 μm. Fiber-tracheids and occasionally libriform fibers are very long to extremely long (2635–3112 μm.; average 2874 μm.) with thick to very thick walls; 6–15 μm.; septate. F/V ratio averages 2.41, range 2.21–2.60. Prismatic crystals abundant to occasional in both types of ray cells; integumented; not in chambered cells.

Scaphocalyx Ridley. Two species from the Malay Peninsula. One specimen.

Pore diameter moderately small (72–88 μm.; average 78 μm.); pores average 78 per cent solitary, radial multiples mostly 2, occasionally to 4; pores per square millimeter numerous (38 pores/mm.^{2}). Vessel elements moderately long to very long (915–1708 μm.; average 1324 μm.) perforation plates exclusively simple; end-wall angles 15° to 25°. Intervascular pitting alternate; pits circular to linear; medium-sized to very large, 8–25 μm. Vessel-ray pits circular to linear; medium to coarse, 7–35 μm. Height of multiseriate portion of rays averages 1847 μm., maximum 2299 μm.; width mostly 2 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly square; cell height 28–38 μm. Simply perforated ray cells present. Fiber-tracheids and libriform fibers moderately long to very long (1708–2776 μm.; average 2385 μm.) with mostly thick walls, 6–8 μm.; septate. F/V ratio averages 1.80. Prismatic crystals abundant to frequent in ray cells of multiseriate portion and occasional in the upright ray cells; not integumented; not in chambered cells.

Ryparosa Blume. Eighteen to 25 species from Andamans, Indo-China, Malay, and New Guinea. Three specimens representing two species.

Pore diameter medium-sized (108–154 μm.; average 130 μm.); pores average 58 per cent solitary, range 33 to 74 per cent; radial multiples mostly 2, occasionally to 5; pores per square millimeter moderately few to moderately numerous (7–17 pores/mm.^{2}; average 13 pores/mm.^{2}). Vessel elements very long (1445–1678 μm.; average 1592 μm.); perforation plates mostly simple and occasionally scalariform with vestigial and up to 15 or more bars which are 1 μm. thick and 2–4 μm. apart; end-wall angles 15° to 25°. Intervascular pitting alternate; pits mostly circular; large, 10–14 μm. Vessel-ray pits circular to linear; coarse, 12–50 μm. Height of multiseriate portion of rays averages 3423 μm., range 1955–4197 μm.; width 3 to 8 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly square to occasionally elongate; cell height 25–40 μm. Simply perforated ray cells in *R. kunstleri* (SJRw 15444). Fiber-tracheids and libriform fibers very long to extremely long (2762–3246 μm.; average 3075 μm.) with thick to very thick walls, 7–17 μm.; septate. F/V ratio averages 1.93, range 1.91–1.94.

Prismatic crystals frequent to occasional in ray cells of multiseriate portion and occasional to absent in upright ray cells; not integumented; not in chambered cells.

Kiggelaria Linnaeus. One to four species from tropical Africa and South Africa. Two specimens representing two species.

Pore diameter moderately small (72–96 μm.; average 83 μm.); pores average 52 per cent solitary; radial multiples mostly 2 and 3, occasionally to 4; pores per square millimeter numerous (22–37 pores/mm.^{2}; average 30 pores/mm.^{2}). Vessel elements medium-sized (642–797 μm.; average 720 μm.); perforation plates exclusively simple; end-wall angles 20° to 45°. Spiral thickenings occur throughout the vessel elements. Intervascular pitting alternate; pits circular to polygonal; medium-sized, 8–10 μm. Vessel-ray pits circular to linear; medium to coarse, 7–26 μm. Height of multiseriate portion of rays averages 1008 μm., range 872–1145 μm.; width 3 to 4 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly square; cell height 23–35 μm. Fiber-tracheids and libriform fibers medium-sized (1291–1583 μm.; average 1437 μm.) with mostly thin walls, 3–6 μm.; septate. F/V ratio averages 2.00, range 1.99–2.01. Prismatic crystals rare in ray cells of multiseriate portion and absent in upright ray cells; no integuments observed; not in chambered cells.

Tribe Flacourtieae

Olmediella Baillon. Monotypic genus known only in cultivation, generally from Mexico and Honduras. One specimen.

Pore diameter moderately small (64–120 μm.; average 94 μm.); pores average 61 per cent solitary; radial multiples mostly 2 and 3, occasionally to 6; pores per square millimeter numerous (36 pores/mm.^{2}). Vessel elements moderately long (549–1189 μm.; average 844 μm.); perforation plates mostly simple and rarely scalariform; end-wall angles 20° to 35°. Coarse spiral thickenings common throughout the vessels. Intervascular pitting alternate; pits circular to linear; large to very large, 10–34 μm. Vessel-ray pits circular to linear; coarse, 10–32 μm. Height of multiseriate portion of rays averages 1606 μm., maximum 2161 μm.; width 4 to 6 cells. Individual ray cells of multiseriate portion as observed on the radial surface are very elongate; cell height 20–35 μm. Simply perforated ray cells. Fiber-tracheids and libriform fibers moderately long (1828–1951 μm.; average 1890 μm.) with thin to very thick walls, 4–10 μm.; mostly septate, some nonseptate fibrous elements. F/V ratio 2.23. Prismatic crystals abundant in both types of ray cells; integumented; not in chambered cells; occasionally many small crystals in one cell.

Bennettiodendron Merrill. Three species from India, southern China, and Malay Archipelago. Two specimens representing one species.

Pore diameter mostly moderately small (47–67 μm.; average 58 μm.); pores average 70 per cent solitary; radial multiples mostly 2 and 3, occasionally to 6; pores per square millimeter very numerous (61–94 pores/mm.^{2}; average 76 pores/mm.^{2}). Vessel elements moderately long (847–1094 μm.; average 970 μm.); perforation plates mostly simple and occasionally to rarely scalariform with up to 5 bars; end-wall angles 10° to 20°. Fine spiral thickenings occasionally throughout the vessel elements or more commonly in vessel tails. Intervascular pitting alternate; pits circular to occasionally linear; mostly medium-sized to large, 8–14 μm.; occasionally very large, up to 25 μm. Vessel-ray pits circular to linear; medium to coarse, 8–25 μm. Height of multiseriate portion of rays averages 308 μm., range 263–354 μm.; width 2 cells. Individual ray cells of multiseriate portion as observed on the radial surface are square to elongate; cell height 18–30 μm. Fiber-tracheids and libriform fibers medium-sized to moderately long (1092–1780 μm.; average 1436 μm.) with thin walls, 2–4 μm.; septate. F/V ratio averages 1.46, range 1.30–1.63. Prismatic crystals abundant in upright ray cells and occasional in ray cells of multiseriate portion; integumented; mostly in 2-, occasionally in 3- or 4-chambered upright ray cells. Yellowish-brown deposits common in rays.

Flacourtia Commerson ex L'Héritier. Fifteen to 60 species from tropical Africa, Southeast Asia, Malaysia, and Fiji Islands. Nine specimens representing four species.

Pore diameter mostly moderately small (48–77 μm.; average 66 μm.); pores average 41 per cent solitary, range 28 to 66 per cent; radial multiples mostly 2 and 3, occasionally to 7; pores per square millimeter moderately numerous to numerous (17–32 pores/mm.^{2}; average 23 pores/mm.^{2}). Vessel elements medium-sized to very long (616–1201 μm.; average 876 μm.); perforation plates exclusively simple; however, in *F. subintegra* (SJRw 28328), a few vestigial bars occur; end-wall angles 25° to 55°. Spiral thickenings throughout vessel elements or in the vessel tails of *F. indica* (MADw 13915). Intervascular and vessel-ray pitting alternate; pits circular to polygonal; small, 4–6 μm. Height of multiseriate portion of the rays averages 350 μm., range 256–408 μm.; width mostly 2 to 3 cells, occasionally 6. Individual ray cells of multiseriate portion as observed on the radial surface are rectangular to elongate; cell height mostly 13–23 μm.; in *F. subintegra* (SJRw 28426) cell height 16–26 μm. Simply perforated ray cells common; absent in *F. indica* (MADw 13915 and SJRw 33954) and *F. rukam* (USw 31377). Fiber-tracheids and libriform fibers medium-sized to moderately long (1018–2194 μm.; average 1545 μm.) with thin to very thick walls, 3–11 μm.; septate. F/V ratio averages 1.78, range 1.60–2.00. Prismatic crystals abundant to occasional in upright ray cells and rare to absent in ray cells of multiseriate portion; in *F. indica* (MADw 13915) and *F. subintegra* crystals are abundant in both types of ray cells; integumented; mostly in 2- to 4-chambered upright ray cells. Reddish-brown deposits common in the rays and fibrous elements.

Dovyalis E. Meyer ex Arnott. Twenty to 30 species from tropical Africa and South Africa, Ceylon, and New Guinea. Two specimens representing one species.

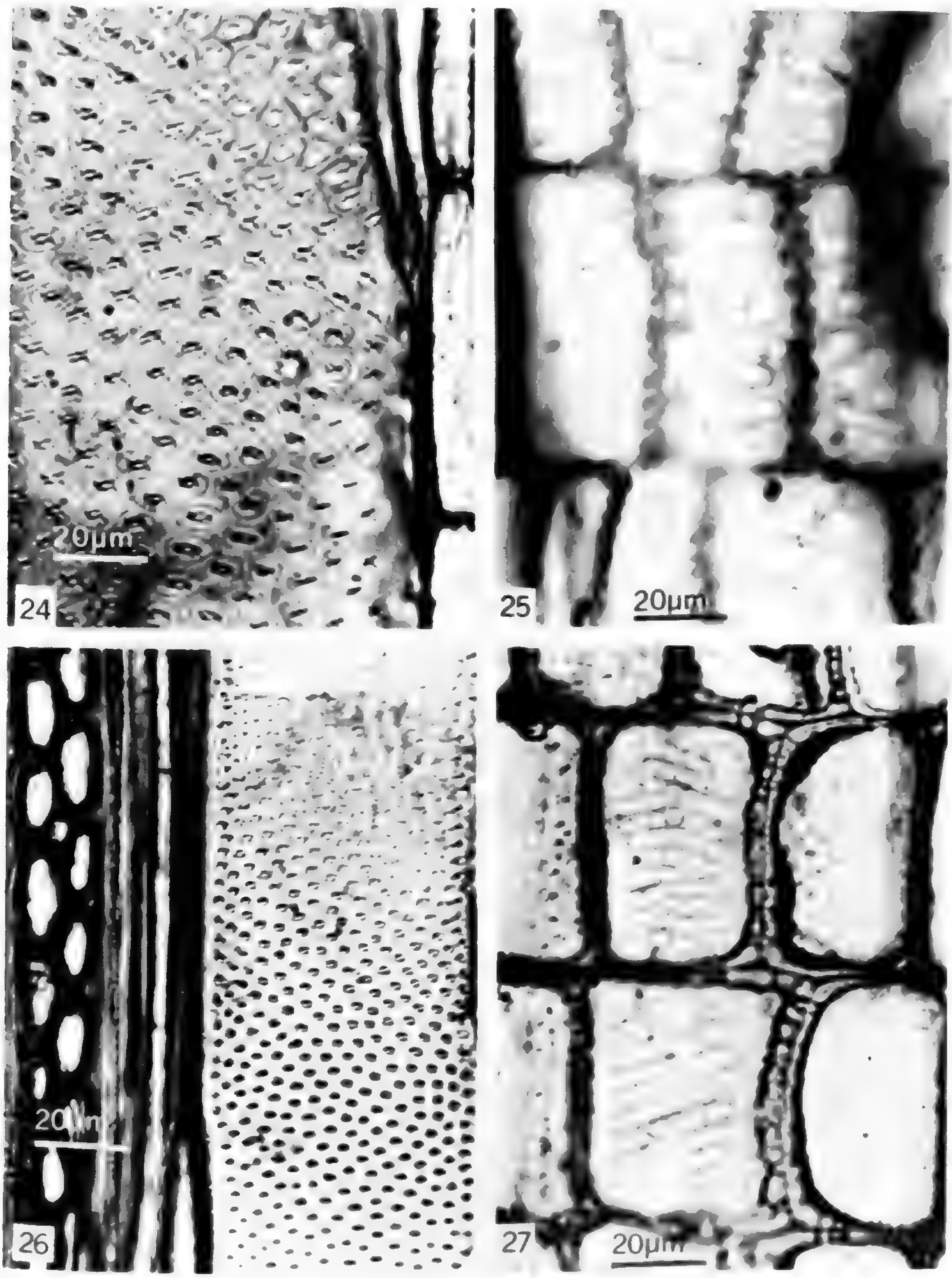
Pore diameter very small (36–49 μm.; average 43 μm.); pores average 63 per cent solitary, range 60 to 65 per cent; radial multiples mostly 2 and 3, occasionally to 6; pores per square millimeter very numerous (46–51 pores/mm.^{2}; average 49 pores/mm.^{2}). Vessel elements medium-sized (485–508 μm.; average 496 μm.); perforation plates mostly simple and occasionally scalariform with vestigial and up to 8 bars which are 2–3 μm. thick; end-wall angles 15° to 45°. Intervascular and vessel-ray pitting alternate; pits circular to polygonal; small, 4–6 μm. Height of multiseriate portion of the rays averages 373 μm., range 326–420 μm.; width 2 to 3 cells. Individual ray cells of multiseriate portion as observed on the radial surface are square to elongate; cell height 15–23 μm. Simply perforated ray cells in *D. caffra* (USw 20714). Fiber-tracheids medium-sized (945–983 μm.; average 964 μm.) with mostly thin walls, 2–4 μm.; septate. F/V ratio averages 1.95, range 1.86–2.03. Prismatic crystals abundant in both types of ray cells; integumented; not in chambered cells.

Azara Ruiz & Pavon. Eleven to 28 species from western Argentina, Chile, and Juan Fernandez Islands. Five specimens representing four species.

Pore diameter very small to moderately small (37–96 μm.; average 58 μm.); pores average 45 per cent solitary, range 28 to 70 per cent; radial multiples mostly 2 and 3, occasionally to 16; pores per square millimeter very numerous (56–121 pores/mm.^{2}; average 83 pores/mm.^{2}). Vessel elements medium-sized (404–704 μm.; average 526 μm.); perforation plates mostly simple and occasionally scalariform with up to 4 bars; in *A. serrata* (USw 34027) perforation plates are exclusively scalariform with 6 to 15 bars which are 2–3 μm. thick and 4–6 μm. apart; end-wall angles 10° to 30°. Very coarse spiral thickenings common throughout the vessels of *A. microphylla*. Intervascular pitting alternate to occasionally opposite; pits circular to oval; medium-sized to large, 8–12 μm.; in *A. serrata* (USw 34027) intervascular pitting is opposite; pits circular to linear and large to very large, 10–44 μm. Vessel-ray pits circular to linear; medium to coarse, 8–28 μm. Height of multiseriate portion of rays averages 257 μm., range 229–277 μm.; width 2 to 4 cells. Individual ray cells of multiseriate portion as observed on the radial surface are square to elongate; cell height 15–25 μm., in *A. serrata* (USw 34027) cell height is 20–35 μm. Fiber-tracheids moderately short to medium-sized (687–1029 μm.; average 901 μm.) with thin walls, 2–5 μm.; septate. F/V ratio averages 1.73, range 1.46–1.88. Prismatic crystals frequent to occasional in both types of ray cells; absent in *A. serrata* (USw 34027); integumented; mostly not in chambered cells, occasionally in 2-chambered cells in *A. integrifolia*. Reddish-brown deposits common in rays.

Ludia Commerson ex Jussieu. Six or seven species from East Africa, Madagascar, and Mascarene Islands. Two specimens, both from herbarium sheets, representing two species.

Pore structure not examined since the twig specimens were very small. Vessel elements medium-sized (373–712 μm.; average 543 μm.); per-



FIGURES 24–27: 24, tangential section of *Ahernia glandulosa* showing medium-sized intervascular pits; 25, radial section of *A. glandulosa* showing coarse vessel-ray pits; 26, tangential section of *Calantica cerasifolia* showing small intervascular pits; 27, radial section of *C. cerasifolia* showing fine vessel-ray pits and unilaterally compound pitting.

foration plates mostly simple, occasionally scalariform with a few bars or with vestigial bars; end-wall angles 10° to 45°. Fine spiral thickenings occasionally present throughout the vessels of *L. scolopioides*. Intervascular and vessel-ray pitting alternate; pits circular to oval; small, 4–5 μm. Height of multiseriate portion of rays averages 452 μm., range 224–680 μm.; width mostly 2 cells. Individual ray cells of multiseriate portion as observed on the radial surface are square; cell height 16–23 μm. Simply and scalariformly perforated ray cells present. Fiber-tracheids moderately short to medium-sized (627–1088 μm.; average 858 μm.) with mostly thin walls, 2–5 μm.; septate. F/V ratio averages 1.61, range 1.53–1.68. Prismatic crystals abundant in upright ray cells, occasional in ray cells of multiseriate portion; integumented; mostly in 2- to 4-chambered upright ray cells.

Xylosma G. Forster. About 100 species from the American and Asian tropics and warm temperate regions, absent in Africa. Thirteen specimens representing 10 species.

Pore diameter very small to medium-sized (37–111 μm.; average 76 μm.); pores average 52 per cent solitary, range 31 to 74 per cent; radial multiples mostly 2 and 3, occasionally to 21; pores per square millimeter moderately numerous to very numerous (17–103 pores/mm.^{2}; average 37 pores/mm.^{2}). Vessel elements medium-sized to moderately long (633-1143 μm.; average 851 μm.); perforation plates exclusively simple; end-wall angles 40° to 50°. Fine spiral thickenings common throughout the vessels of *X. benthamii*, *X. congestum*, *X. flexuosa* (SJRw 8806), *X. longifolium*, *X. pilosum*, *X. salzmanni*, and *X. venosum*. Intervascular pitting alternate; pits circular to polygonal and small, 4–6 μm., in *X. flexuosa* (SJRw 8806), *X. longifolium*, *X. nelsonii*, *X. panamensis*, *X. pilosum*, and *X. prunifolium*; pits small to medium-sized, 6–8 μm., in *X. benthamii*, *X. congestum*, *X. flexuosa* (MADw 15706), *X. salzmanni*, and *X. venosum*. Vessel-ray pits circular to oval; similar in size to their respective intervascular pits. Height of multiseriate portion of rays averages 581 μm., range 318–1270 μm.; width 2 to 5 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly elongate and the cell height is 13–20 μm. in *X. benthamii*, *X. congestum*, *X. longifolium*, *X. pilosum*, *X. prunifolium*, and *X. salzmanni* (MADw 23744); the ray cell type is square to elongate and the cell height is 20–35 μm. in *X. flexuosa*, *X. nelsonii*, *X. panamensis*, *X. salzmanni* (SJRw 23792), and *X. venosum*. Simply perforated ray cells occur in *X. flexuosa* (SJRw 8806), *X. longifolium*, *X. prunifolium* (SJRw 22522) and *X. salzmanni* (SJRw 23792). Fiber-tracheids and libriform fibers medium-sized to moderately long (1128–1802 μm.; average 1457 μm.) with mostly thin to very thin, occasionally thick, walls, 2–6 μm.; septate. F/V ratio averages 1.73, range 1.50–2.37. Prismatic crystals abundant to frequent in upright ray cells, mostly occasional to rare in ray cells of multiseriate portion; in *X. flexuosa* (MADw 15706) crystals are abundant in both types of ray cells; integumented; generally in 2-chambered upright ray cells, not in chambered cells in *X. congestum* and *X. flexuosa* (MADw 15706).

Reddish-brown deposits generally common in rays and fibrous elements; absent in *X. congestum*, *X. panamensis*, and *X. salzmanni* (SJRw 23792).

Poliothyrsis Oliver. One to three species from China and Celebes. One specimen.

Pore diameter very small to moderately small (40–56 μm.; average 46 μm.); pores average 50 per cent solitary; radial multiples mostly 2 and 3, occasionally to 11; pore clusters common; pores per square millimeter very numerous (79 pores/mm.^{2}). Vessel elements moderately short to medium-sized (278–695 μm.; average 478 μm.); perforation plates exclusively simple; end-wall angles 15° to 30°. Fine spiral thickenings frequent throughout vessel. Intervascular pitting alternate; pits circular to oval; medium-sized to large, 8–11 μm. Vessel-ray pits circular to linear; medium to coarse, 8–16 μm. Height of multiseriate portion of rays averages 213 μm. or 14 cells, maximum 227 μm. or 17 cells; width 2 to 3 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly elongate; cell height 12–18 μm. Fiber-tracheids moderately short to medium-sized (669–1086 μm.; average 874 μm.) with mostly very thin walls, 2–3 μm.; septate. F/V ratio averages 1.83. Prismatic crystals absent.

Carrierea Franchet. Three or four species from southern and western China and Indo-China. Two specimens representing one species.

Pore diameter moderately small (63–68 μm.; average 66 μm.); pores average 54 per cent solitary, range 51 to 56 per cent; radial multiples mostly 2 and 3, occasionally to 5; pores per square millimeter mostly very numerous (39–49 pores/mm.^{2}; average 44 pores/mm.^{2}). Vessel elements medium-sized (705–730 μm.; average 718 μm.); perforation plates mostly simple and occasionally scalariform with vestigial and up to 3 bars which are 2 μm. thick; end-wall angles 15° to 40°. Very coarse spiral thickenings common throughout the vessel. Intervascular pitting alternate; pits mostly circular, occasionally to linear; mostly large, 10–14 μm.; occasionally very large, up to 16 μm. Vessel-ray pits circular to linear; medium to mostly coarse, 8–20 μm. Height of multiseriate portion of the rays averages 164 μm. or 8.5 cells, range 110 μm. (5 cells) to 217 μm. (12 cells); width 2 to 3 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly elongate; cell height 15–20 μm. Fiber-tracheids and libriform fibers medium-sized (1291–1354 μm.; average 1322 μm.) with mostly very thin walls, 2–3 μm.; only septate in nongelatinous and latewood fibrous elements. F/V ratio averages 1.84, range 1.83–1.84. Prismatic and druse crystals occasional to rare in both types of ray cells; integumented; not in chambered cells, but druse crystals generally occur in "paired" upright ray cells.

Itoa Hemsley. Two species from eastern Asia and New Guinea. Two specimens representing one species.

Pore diameter medium-sized (171–186 μm.; average 178 μm.); pores average 39 per cent solitary, range 30 to 48 per cent; radial multiples

mostly 2, occasionally to 4; pores per square millimeter moderately few (6–8 pores/mm.^{2}; average 7 pores/mm.^{2}). Vessel elements moderately long (847–887 μm.; average 867 μm.); perforation plates exclusively simple; end-wall angles 60° to 80°. Intervascular pitting alternate; pits mostly circular to polygonal; mostly large, 10–15 μm.; occasionally linear and very large (up to 120 μm.) in *I. stapfii* (MADw 2569). Vessel-ray pits circular to linear; coarse, 10–36 μm. Height of multiseriate portion of rays averages 462 μm., range 454–470 μm.; width 2 to 4 cells. Individual ray cells of multiseriate portion as observed on the radial surface are elongate; cell height 18–23 μm. Fiber-tracheids and libriform fibers moderately long (1770–1836 μm.; average 1803 μm.) with thin to very thin walls, 2–4 μm.; septate in normal wood, but nonseptate in gelatinous fibers. F/V ratio averages 2.08, range 2.07–2.08. Prismatic crystals abundant in upright ray cells, rare or absent in ray cells of multiseriate portion; integumented; not in chambered cells.

Idesia Maximowicz. Monotypic genus from China and Japan. Four specimens.

Pore diameter moderately small (65–82 μm.; average 74 μm.); pores average 55 per cent solitary, range 46 to 61 per cent; radial multiples mostly 2 and 3, occasionally to 8; pores per square millimeter very numerous (44–61 pores/mm.^{2}; average 55 pores/mm.^{2}). Vessel elements medium-sized to moderately long (764–930 μm.; average 870 μm.); perforation plates mostly exclusively simple; in *I. polycarpa* (TWTw 155) mostly simple and rarely scalariform with up to 5 bars which are 2 μm. thick; end-wall angles 15° to 50°. Occasional tyloses in *I. polycarpa* (TWTw 155). Intervascular pitting alternate; pits circular, large, 10–12 μm. Vessel-ray pits circular to oval, medium to coarse, 8–12 μm. Height of multiseriate portion of the rays averages 447 μm., range 383–543 μm.; width 2 to 4 cells. Individual ray cells of multiseriate portion as observed on the radial surface are elongate; cell height 18–25 μm. Fiber-tracheids medium-sized (1246–1626 μm.; average 1466 μm.) with thin to very thin walls, 2–4 μm.; nonseptate. F/V ratio averages 1.68, range 1.62–1.75. Prismatic crystals frequent to rare in upright ray cells, absent in ray cells of multiseriate portion; completely absent in *I. polycarpa* (SJRw 21863); integumented; not in chambered cells.

Tribe Casearieae

Casearia Jacquin. About 160 to 250 species from both the New and Old World tropics and subtropics. Eighty-six specimens representing 27 species from the New World. Description condensed from unpublished Master's thesis, entitled "Systematic wood anatomy of the American *Casearia* Jacq." (Miller 1966).

Pore diameter mostly moderately small (46–108 μm.; average 75 μm.); pores average 46 per cent solitary, range 22 to 78 per cent; radial multiples mostly 2, occasionally to 6; pores per square millimeter moderately

numerous to very numerous (10–96 pores/mm.^{2}; average 31 pores/mm.^{2}). Vessel elements medium-sized to very long (550–1350 μm.; average 937 μm.); perforation plates exclusively simple; end-wall angles 15° to 70°. Intervascular and vessel-ray pitting alternate, pits circular to polygonal; mostly very small, 2–4 μm.; occasionally 5–6 μm. Height of multiseriate portion of rays variable, approximate range 300–2000 μm. and as high as 3000–7000 μm. in *C. javitensis* and *C. iquitosensis*; width mostly 2 to 3 cells and as wide as 12 cells in *C. javitensis* and *C. iquitosensis*. Individual ray cells of multiseriate portion as observed on the radial surface are square in some species and elongate in others; cell height less than 20 μm. in some species and more than 20 μm. in others. Simply perforated ray cells present in some species. Fiber-tracheids and libriform fibers moderately short to moderately long (882–1960 μm.; average 1444 μm.) with mostly thin to thick walls; septate. F/V ratio averages 1.54. Prismatic crystals common in ray cells of most species, but variable in frequency and location; integumented; not in chambered cells. Reddish-brown deposits common in some species.

Gossypiospermum Urban. Two to three species from Cuba and tropical South America. Two specimens representing one species.

Pore diameter very small (35–48 μm.; average 42 μm.); pores average 53 per cent solitary, range 50 to 56 per cent; radial multiples mostly 2 and 3, occasionally to 7; pores per square millimeter very numerous (70–77 pores/mm.^{2}; average 74 pores/mm.^{2}). Vessel elements medium-sized (546–698 μm.; average 622 μm.); perforation plates exclusively simple; end-wall angles 30° to 50°. Intervascular and vessel-ray pitting alternate; pits circular to polygonal; very small, 3–4 μm. Height of multiseriate portion of rays averages 634 μm., range 451–818 μm.; width mostly 3 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly elongate; cell height 11–16 μm. Libriform fibers medium-sized (1031–1097 μm.; average 1064 μm.) with thick to very thick walls, 4–6 μm.; septate. F/V ratio averages 1.73, range 1.57–1.89. Prismatic crystals in *G. praecox* (MADw 13780) abundant in both types of ray cells, in *G. praecox* (SJRw 2663) crystals abundant in upright ray cells and occasionally in ray cells of multiseriate portion; both have integumented crystals and both do not have crystals in chambered cells.

Laetia Loefling ex Linnaeus. Ten to 20 species from West Indies and Mexico to tropical South America. Thirteen specimens representing eight species.

Pore diameter very small to moderately small (45–98 μm.; average 73 μm.); in *L. procera* medium-sized to moderately large (112–217 μm.; average 175 μm.); pores average 50 per cent solitary, range 28 to 84 percent; radial multiples mostly 2 and 3, occasionally to 9; pores per square millimeter moderately numerous to very numerous (16–92 pores/mm.^{2}; average 40 pores/mm.^{2}); in *L. procera*, mostly moderately few (6–11 pores/mm.^{2}; average 8 pores/mm.^{2}). Vessel elements medium-sized to

very long (729–1400 μm.; average 1007 μm.); perforation plates exclusively simple in all *Laetia* except *L. calophylla*, which has perforation plates that are mostly simple and occasionally scalariform with up to 15 or more bars which are 2 μm. thick and 4 μm. apart; end-wall angles 15° to 65°. Intervascular and vessel-ray pitting alternate; pits circular to polygonal; mostly very small, 2–5 μm.; in *L. calophylla* and *L. procera* small, 5–7 μm. Height of multiseriate portion of rays averages 1771 μm., range 878–4647 μm.; in *L. cupulata* rays are over 5 cm. high. Ray width 2 to 7 cells; in *L. cupulata* up to 15 cells or 240 μm. Individual ray cells of multiseriate portion as observed on the radial surface are square to elongate; cell height 16–40 μm.; in *L. micrantha* very elongate and 11–16 μm. in height. Simply perforated ray cells in *L. apetala* (SJRw 21437), *L. calophylla*, *L. micrantha* (SJRw 54698), *L. suaveolens*, and *L. ternstroemioides* (SJRw 16706). Fiber-tracheids and libriform fibers medium-sized to very long (1262–2522 μm.; average 1727 μm.) with mostly thick to very thick walls, 3–14 μm.; septate. F/V ratio averages 1.72, range 1.53–2.09. Prismatic crystals abundant to frequent in both types of ray cells; in *L. micrantha* and *L. procera* crystals frequent in upright ray cells and rare in ray cells of multiseriate portion; crystals absent in *L. calophylla* and *L. cupulata*; integumented and not in chambered cells in all *Laetia*. Stalked and stalkless druse crystals in "paired" upright ray cells of *L. procera* (MADw 19646, MADw 21447). Reddish-brown deposits abundant to frequent in ray cells and occasionally in fibrous elements of *L. cupulata*, *L. micrantha*, and *L. suaveolens*.

Hecatostemon Blake. Monotypic genus from Venezuela. One specimen.

Pore diameter moderately small (56–80 μm.; average 60 μm.); pores average 53 per cent solitary; radial multiples mostly 2, occasionally to 3; pores per square millimeter numerous (25 pores/mm.^{2}). Vessel elements medium-sized to very long (397–1220 μm.; average 838 μm.); perforation plates exclusively simple; end-wall angles 35° to 45°. Intervascular and vessel-ray pitting alternate; pits circular to polygonal; very small, 3–4 μm. Height of multiseriate portion of rays averages 328 μm., maximum 368 μm.; width 2 to 3 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly elongate; cell height 13–18 μm. Simply perforated ray cells observed. Fiber-tracheids and libriform fibers medium-sized to moderately long (1250–1891 μm.; average 1512 μm.) with mostly thin walls, 3–5 μm.; septate. F/V ratio averages 1.80. Prismatic crystals frequent in upright ray cells and rare in ray cells of multiseriate portion; integumented; rarely in chambered upright ray cells.

Ryania Vahl. Eight to 14 species from northern tropical South America and Trinidad. Five specimens representing three species.

Pore diameter very small to moderately small (39–75 μm.; average 54 μm.); pores average 70 per cent solitary, range 56 to 84 per cent; radial multiples mostly 2, occasionally to 7; pores per square millimeter very

numerous (47–98 pores/mm.^{2}; average 72 pores/mm.^{2}). Vessel elements mostly moderately long (864–1155 μm.; average 987 μm.); perforation plates exclusively simple in *R. pyrifera* and *R. speciosa* var. *chocoensis*; mostly simple and rarely scalariform with vestigial or few bars in *R. angustifolia*; end-wall angles 20° to 40°. Intervascular and vessel-ray pitting alternate; pits circular to oval; small, 4–6 μm. Height of multiseriate portion of rays averages 5878 μm., range 5157–6817 μm.; width mostly 5 to 10 cells, up to 20 cells wide in *R. pyrifera*. Individual ray cells of multiseriate portion as observed on the radial surface are square to elongate; cell height 17–40 μm. Simply perforated ray cells in *R. angustifolia* (SJRw 34111). Fiber-tracheids and libriform fibers moderately long (1320–1836 μm.; average 1578 μm.) with very thin to thick walls, 3–7 μm.; septate. F/V ratio averages 1.60, range 1.42–1.82. Prismatic crystals occasional to absent in both types of ray cells; no integuments observed; not in chambered cells. Reddish-brown deposits common in rays and fibrous elements.

Zuelania A. Richard. Four or five species from Central America, West Indies, and Venezuela. Five specimens representing one species.

Pore diameter moderately small (64–91 μm.; average 78 μm.); pores average 50 per cent solitary, range 31 to 62 per cent; radial multiples mostly 2, occasionally to 9; pores per square millimeter mostly numerous to very numerous (19–54 pores/mm.^{2}; average 29 pores/mm.^{2}). Vessel elements medium-sized to moderately long (770–1088 μm.; average 964 μm.); perforation plates exclusively simple; end-wall angles 20° to 45°. Intervascular and vessel-ray pitting alternate; pits circular to polygonal; small, 4–5 μm. Height of multiseriate portion of rays averages 1276 μm., range 537–1637 μm.; width mostly 2 to 4 cells. Individual ray cells of multiseriate portion as observed on the radial surface are square to elongate; cell height 20–35 μm. Simply perforated ray cells in *Z. guidonia* (MADw 5771, MADw 9882, and SJRw 16644). Fiber-tracheids and libriform fibers medium-sized to moderately long (1168–1790 μm.; average 1569 μm.) with mostly thin to thick walls, 3–7 μm.; septate. F/V ratio averages 1.62, range 1.52–1.73. Prismatic crystals usually abundant in both types of ray cells; integumented; not in chambered cells.

Osmelia Thwaites. Four to 12 species from Ceylon, Malay Peninsula and Archipelago, Philippine Islands, and New Guinea. Six specimens representing two species.

Pore diameter mostly moderately small (56–105 μm.; average 79 μm.); pores average 58 per cent solitary, range 32 to 82 per cent; radial multiples mostly 2, occasionally to 6; pores per square millimeter moderately numerous to mostly numerous (17–42 pores/mm.^{2}; average 28 pores/mm.^{2}). Vessel elements very long to extremely long (1249–2029 μm.; average 1607 μm.); perforation plates mostly simple and rarely scalariform with up to 15 or more bars; end-wall angles 10° to 65°. Intervascular and vessel-ray pitting alternate; pits circular to polygonal; very

small to small, 3–5 μm. Height of multiseriate portion of rays averages 1415 μm., range 971–2293 μm.; width 1 to 4 cells. Individual ray cells of multiseriate portion as observed on the radial surface are square to elongate; cell height 17–40 μm. Simply and scalariformly perforated ray cells in *O. grandistipulata* (SJRw 16046 and SJRw 16048) and *O. philippina* (USw 29390). Fiber-tracheids and libriform fibers very long (2317–2991 μm.; average 2583 μm.) with thin to thick walls, 4–8 μm.; septate. F/V ratio averages 1.62, range 1.47–1.86. Prismatic crystals usually abundant or frequent in ray cells of multiseriate portion and occasional or absent in upright ray cells; not integumented; not in chambered cells.

Ophiobotrys Gilg. Monotypic genus from tropical West Africa. One specimen.

Pore diameter moderately small (64–88 μm.; average 74 μm.); pores average 65 per cent solitary; radial multiples mostly 2, occasionally to 3; pores per square millimeter numerous (21 pores/mm.^{2}). Vessel elements moderately long to extremely long (854–2257 μm.; average 1462 μm.); perforation plates exclusively simple; end-wall angle 20° to 35°. Intervascular and vessel-ray pitting alternate; pits circular to polygonal; very small, 2–4 μm. Height of multiseriate portion of rays averages 802 μm., maximum 1160 μm.; width 2 to 4 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly elongate; cell height 17–24 μm. Libriform fibers moderately long to very long (1830–2745 μm.; average 2231 μm.) with mostly very thick walls, 6–9 μm.; septate. F/V ratio averages 1.53. Prismatic crystals abundant in upright ray cells and frequent to occasional in ray cells of multiseriate portion; integumented; not in chambered cells.

Lunania Hooker. Eighteen to 20 species from West Indies, Central America, and tropical South America. Four specimens representing two species.

Pore diameter moderately small (54–97 μm.; average 70 μm.); pores average 55 per cent solitary, range 44 to 77 per cent; radial multiples mostly 2 and 3, occasionally to 6; pores per square millimeter numerous to very numerous (35–42 pores/mm.^{2}; average 38 pores/mm.^{2}). Vessel elements moderately long to very long (1034–1388 μm.; average 1207 μm.); perforation plates exclusively simple; end-wall angles 30° to 45°. Intervascular and vessel-ray pitting alternate; pits circular to polygonal; very small to small, 3–6 μm. Height of multiseriate portion of rays averages 1386 μm., range 758–2124 μm.; width 2 to 4 cells. Individual ray cells of multiseriate portion as observed on the radial surface are square to rectangular; cell height 20–35 μm. Fiber-tracheids and libriform fibers moderately long (1715–2111 μm.; average 1889 μm.) with thin to very thick walls, 3–7 μm.; septate. F/V ratio averages 1.57, range 1.50–1.75. Prismatic crystals abundant or frequent in both types of ray cells; integumented; not in chambered cells.

Tetrathylacium Poeppig & Endlicher. Four to five species from Central America and west tropical South America. Two specimens representing two species.

Pore diameter moderately small (64–84 μm.; average 74 μm.); pores average 58 per cent solitary, range 43 to 72 per cent; radial multiples mostly 2, occasionally to 6; pores per square millimeter numerous (24–38 pores/mm.^{2}; average 31 pores/mm.^{2}). Vessel elements very long (1278–1334 μm.; average 1251 μm.); perforation plates exclusively scalariform with up to 15 or more bars which are 2–4 μm. thick and 4–16 μm. apart; end-wall angles 10° to 25°. Occasional tyloses occur in *T. johansenii.* Intervascular pitting alternate; pits circular to polygonal, occasionally oblong; mostly medium-sized, 8–10 μm.; occasionally very large, up to 18 μm. in *T. macrophyllum.* Vessel-ray pits circular to linear; medium to coarse, 8–26 μm. Height of multiseriate portion of rays averages 1432 μm., range 1077–1787 μm.; width 2 to 5 cells. Individual ray cells of multiseriate portion as observed on the radial surface are square to elongate; cell height 20–35 μm. Fiber-tracheids and libriform fibers moderately long (2010–2158 μm.; average 2084 μm.) with very thin to thin walls, 3–6 μm.; septate. F/V ratio averages 1.67, range 1.56–1.76. In *T. johansenii* prismatic crystals abundant in both types of ray cells; integumented; occasionally in 2-chambered upright ray cells. In *T. macrophyllum,* prismatic crystals abundant in upright ray cells and occasional in ray cells of multiseriate portion; integumented; not in chambered cells.

Samyda Jacquin. Sixteen to 30 species from Mexico and West Indies. Two specimens representing two species.

Pore diameter very small (29–38 μm.; average 34 μm.); pores average 65 per cent solitary, range 56 to 74 per cent; radial multiples mostly 2, occasionally to 6; pores per square millimeter very numerous (72–120 pores/mm.^{2}; average 96 pores/mm.^{2}). Vessel elements medium-sized (548–649 μm.; average 599 μm.); perforation plates exclusively simple; end-wall angles 20° to 45°. Intervascular and vessel-ray pitting alternate; pits circular to polygonal; very small, 2–4 μm. Height of multiseriate portion of rays averages 601μm., range 633–669 μm.; width 2 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly square; cell height 20–28 μm. Fiber-tracheids and libriform fibers mostly medium-sized (874–1161 μm.; average 1013 μm.) with thin to thick walls, 3–5 μm.; septate. F/V ratio averages 1.69, range 1.58–1.79. Prismatic crystals frequent in ray cells of multiseriate portion and occasional to rare in upright ray cells; integumented; not in chambered cells.

Neoptychocarpus Buchheim. Two species from tropical South America. Two specimens representing one species.

Pore diameter very small (31–38 μm.; average 34 μm.); pores average 58 per cent solitary; radial multiples mostly 2, occasionally to 7; pores per square millimeter very numerous (73–81 pores/mm.^{2}; average 76

pores/mm.^{2}). Vessel elements moderately long to very long (966–1327 μm.; average 1146 μm.); perforation plates exclusively scalariform with up to 15 or more bars which are 2 μm. thick and 3–5 μm. apart; end-wall angles 10° to 20°. Intervascular and vessel-ray pitting alternate to sometimes opposite; pits circular to oval; very small, 2–4 μm. Height of multiseriate portion of rays averages 1882 μm., range 1128–2635 μm.; width 2 to 3 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly square; cell height 28–40 μm. Libriform fibers moderately long (1669–1953 μm.; average 1811 μm.) with thick walls, 10–14 μm.; septate. F/V ratio averages 1.60, range 1.47–1.73. Prismatic crystals abundant in ray cells of multiseriate portion and occasional to absent in upright ray cells; integumented; not in chambered cells. Reddish-brown deposits abundant in ray cells.

Tribe Prockieae (Tiliaceae)

Prockia P. Browne ex Linnaeus. Three to 18 species from the West Indies, tropical America, and Argentina. Two specimens representing one species.

Pore diameter very small to moderately small (42–56 μm.; average 49 μm.); pores 38 per cent solitary, range 23 to 53 per cent; radial multiples and/or radial pore chains mostly 2, 3, and 4, occasionally to 14; pores per square millimeter very numerous (42–92 pores/mm.^{2}; average 67 pores/mm.^{2}). Vessel elements medium-sized (695–740 μm.; average 718 μm.); perforation plates exclusively simple; end-wall angles 15° to 45°. Intervascular and vessel-ray pits alternate; circular to polygonal; small, 4–7 μm. Height of multiseriate portion of rays averages 310 μm., range 270–350 μm.; width 2 to 3 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly elongate; cell height 12–16 μm. Fiber-tracheids and libriform fibers medium-sized (1102–1282 μm.; average 1192 μm.) with mostly thin walls, 3–5 μm.; septate. F/V ratio averages 1.66, range 1.59–1.73. Prismatic crystals abundant to frequent in upright ray cells and occasional to absent in ray cells of multiseriate portion; integumented; mostly in 2-chambered to rarely 4-chambered upright ray cells. Reddish-orange deposits abundant in rays of *P. crucis* (MADw 21831).

Hasseltia H.B.K. Ten to 12 species from Mexico, Central America, and tropical South America. Six specimens representing four species.

Pore diameter moderately small (51–95 μm.; average 63 μm.); pores average 60 per cent solitary, range 38 to 71 per cent; radial multiples mostly 2, occasionally to 5; pores per square millimeter numerous to very numerous (32–110 pores/mm.^{2}; average 54 pores/mm.^{2}). Vessel elements moderately long to very long (832–1250 μm.; average 1073 μm.); perforation plates in *H. floribunda* mostly simple and occasionally scalariform with vestigial and up to 6 bars; exclusively simple in all other specimens of *Hasseltia*; end-wall angles 20° to 35°. Tyloses occur occasionally in

H. floribunda (MADw 12427), *H. lateriflora* (SJRw 20891), and *H. laxiflora*. Fine spiral thickenings rarely occur in the vessel tails of *H. floribunda* (SJRw 12427), *H. lateriflora*, and *H. cf. guatemalensis*. Intervascular pitting alternate; pits circular to polygonal; small, 4–7 μm. Vessel-ray pits circular to linear; fine to coarse, 4–30 μm. Height of multiseriate portion of rays averages 544 μm., range 298–765 μm.; width 2 to 3 cells. Individual ray cells of multiseriate portion as observed on the radial surface are square to elongate; cell height 15–27 μm. Simply perforated ray cells in *H. floribunda* (SJRw 12427), *H. lateriflora*, and *H. laxiflora*. Fiber-tracheids and libriform fibers medium-sized to moderately long (1416–2014 μm.; average 1821 μm.) with very thin to thin walls, 3–6 μm.; septate. F/V ratio averages 1.70, range 1.43–1.91. Prismatic crystals usually abundant to frequent in upright ray cells and occasional to rare in ray cells of multiseriate portion; in *H. laxiflora* crystals are abundant in both types of ray cells; in *H. cf. guatemalensis* crystals are rare in upright ray cells and absent in ray cells of multiseriate portion; all specimens of *Hasseltia* have prismatic crystals that are integumented and mostly in 2- to occasionally 4-chambered upright ray cells. Druse crystals rarely to occasionally in procumbent and 4-chambered upright ray cells of *H. floribunda* (MADw 5747). Reddish-yellow deposits frequent in ray cells of *H. laxiflora*.

Pleuranthodendron L. O. Williams. One to four species from Mexico, Central America, and tropical South America. Six specimens representing one species.

Pore diameter moderately small (52–84 μm.; average 70 μm.); pores average 49 per cent solitary, range 30 to 74 per cent; radial multiples mostly 2 and 3, occasionally to 8; pores per square millimeter numerous to very numerous (32–68 pores/mm.^{2}; average 44 pores/mm.^{2}). Vessel elements medium-sized to moderately long (739–1067 μm.; average 971 μm.); perforation plates simple and scalariform with up to 7 bars which are 2–4 μm. thick and 4–20 μm. apart; end-wall angles 20° to 50°. Fine spiral thickenings occur in the vessel tails. Intervascular pitting alternate; pits circular, occasionally linear; mostly medium-sized, 8–10 μm., occasionally very large, up to 40 μm. Vessel-ray pits circular to linear; medium to coarse, 8–32 μm. Height of multiseriate portion of rays averages 585 μm., range 301–838 μm.; width 2 to 5 cells. Individual ray cells of multiseriate portion as observed on the radial surface are square to elongate; cell height 13–23 μm.; in *P. mexicana* (MADw 11004) cell height 18–28 μm. Scalariformly perforated ray cells common. Fiber-tracheids and libriform fibers medium-sized to moderately long (1436–1907 μm.; average 1684 μm.) with thin to thick walls, 3–6 μm.; septate. F/V ratio averages 1.74, range 1.57–1.94. Prismatic crystals more abundant in upright ray cells than in ray cells of multiseriate portion; integumented; mostly in 2-chambered upright ray cells, not in chambered cells in *P. mexicana* (MADw 11004). Reddish-brown deposits common in ray cells.

Macrohasseltia L. O. Williams. Monotypic genus from Central America. Two specimens.

Pore diameter moderately small (86–90 μm.; average 88 μm.); pores average 48 per cent solitary, range 36 to 60 per cent; radial multiples mostly 2 and 3, occasionally to 6; pores per square millimeter moderately numerous (17–20 pores/mm.^{2}; average 18 pores/mm.^{2}). Vessel elements moderately long (816–1121 μm.; average 968 μm.); perforation plates mostly simple and occasionally scalariform with vestigial and up to 6 bars; end-wall angles 25° to 50°. Tyloses frequent in *M. macroterantha* (MADw 10286). Fine spiral thickenings occur in the vessel tails and occasionally throughout the vessel elements. Intervascular pitting alternate; pits circular to occasionally linear; mostly large, 10–14 μm., occasionally very large, up to 40 μm. Vessel-ray pits circular to linear; coarse, 10–22 μm. Height of multiseriate portion of rays averages 223 μm. or 10 cells, range 220–226 μm.; width 2 to 3 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly elongate; cell height 17–28 μm. Simply perforated ray cells in *M. macroterantha* (MADw 10286). Fiber-tracheids and libriform fibers medium-sized to moderately long (1491–1877 μm.; average 1684 μm.) with thin walls, 3–5 μm.; septate. F/V ratio averages 1.75, range 1.67–1.83. Prismatic crystals abundant to occasional in upright ray cells and absent in ray cells of multiseriate portion; integumented; mostly in 2-chambered upright ray cells. Reddish-brown deposits abundant in ray cells of *M. macroterantha* (MADw 10305).

Anomalous Genera

The genera described in this category were once placed in the Flacourtiaceae, but now are not considered by most taxonomists as belonging to this family. The following descriptions are complete descriptions and no characters are deleted.

Ancistrothyrsus Harms (Passifloraceae). Monotypic genus from western tropical America. One specimen.

Growth rings poorly defined to somewhat distinct. Pores mostly circular in outline; tangential diameter medium-sized to moderately large (174–260 μm.; average 228 μm.); pores average 89 per cent solitary; radial multiples mostly 2; pores per square millimeter moderately few (6 pores/mm.^{2}). Vessel elements medium-sized to moderately long (366–1037 μm.; average 728 μm.); perforation plates mostly simple and occasionally scalariform with a few vestigial bars; end-wall angles 30° to 90°. Vessel-wall thickness 6 μm. Tyloses present, occasionally sclerotic; sometimes prismatic crystals in tyloses. Intervascular pitting alternate; pits mostly circular; medium-sized, 8–10 μm. Vessel-ray pits circular to somewhat oblong; medium to coarse, 8–14 μm. Rays of two types, uniseriate homocellular rays composed entirely of upright ray cells and multiseriate heterocellular rays with long uniseriate extensions (Heterogeneous

Types I and IIA, Kribs 1935). Height of multiseriate portion of rays averages 2157 μm., maximum 5185 μm.; width 3 to 7 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly square; cell height 30–40 μm. Imperforate tracheary elements are tracheids; medium-sized to moderately long (1037–1738 μm.; average 1418 μm.) with thin to thick walls, 5–7 μm.; nonseptate. F/V ratio 1.95. Axial parenchyma abundant; vasicentric to somewhat aliform and apotracheal diffuse. Prismatic crystals occasional in axial parenchyma; frequent in ray cells of multiseriate portion and rare in upright ray cells; not integumented; not in chambered cells. Brown to reddish-brown deposits frequent to occasional in axial and ray parenchyma.

Barteria Hooker f. (Passifloraceae). Five to seven species from tropical Africa. One specimen.

Growth rings poorly defined. Pores circular to oval in outline; tangential diameter medium-sized (144–192 μm.; average 164 μm.); pores average 34 per cent solitary; radial multiples mostly 2, 3, and 4, occasionally to 6; pores per square millimeter moderately few (6 pores/mm.^{2}). Vessel elements moderately long to very long (793–1708 μm.; average 1190 μm.); perforation plates mostly simple and occasionally scalariform with vestigial and up to 12 bars which are 2–4 μm. thick and 4–10 μm. apart; end-wall angles 35° to 50°. Vessel-wall thickness 2–6 μm. Intervascular and vessel-ray pitting alternate; pits circular to oval; small to medium-sized, 5–8 μm. Rays of two types, uniseriate homocellular rays composed entirely of upright ray cells and multiseriate heterocellular rays with long uniseriate extensions (Heterogeneous Type I, Kribs 1935). Height of multiseriate portion of rays averages 624 μm., maximum 840 μm.; width 1 to 3 cells. Individual ray cells of multiseriate portion as observed on the radial surface are square to elongate; cell height 35–55 μm. Imperforate tracheary elements are libriform fibers; moderately long to extremely long (1860–3263 μm.; average 2511 μm.) with very thick walls, 9–12 μm.; nonseptate. F/V ratio 2.11. Axial parenchyma abundant; vasicentric and apotracheal in short tangential lines (reticulate). Prismatic crystals absent. Reddish to yellowish-brown deposits abundant in rays.

Paropsia Noronha ex Thouars (Passifloraceae). Thirteen to 20 species from tropical Africa, Madagascar, Sumatra, and the Malay Peninsula. Four specimens representing four species.

Growth rings poorly defined to absent. Pores circular to oval in outline; tangential diameter moderately small to medium-sized (79–138 μm.; average 111 μm.); pores average 52 per cent solitary, range 37 to 70 per cent; radial multiples mostly 2 and 3, occasionally to 10; pores per square millimeter few to moderately numerous (4–18 pores/mm.^{2}; average 12 pores/mm.^{2}). Vessel elements medium-sized to very long (655–1735 μm.; average 966 μm.); perforation plates exclusively simple; end-wall angles 30° to 50°. Vessel-wall thickness 4–6 μm. Intervascular and vessel-ray

pitting alternate; pits circular to oval; very small to small, 3–5 μm., in *P. braunii* and *P. guineensis* and small to medium-sized, 6–8 μm., in *P. madagascariensis* and *P. vareciformis*. Rays variable; mostly multiseriate homocellular rays or occasionally heterocellular rays with short uniseriate extensions (Heterogeneous Types I and IIA or Homogeneous Type I, Kribs 1935). Height of multiseriate portion of rays averages 2077 μm., range 979–3327 μm.; width 2 to 5 cells. Individual ray cells of multiseriate portion as observed on the radial surface are square to occasionally elongate; cell height 23–55 μm. Simply perforated ray cells in *P. braunii*. Imperforate tracheary elements fiber-tracheids and libriform fibers; mostly very long to extremely long (2115–3884 μm.; average 2570 μm.) with very thick walls, 5–14 μm.; nonseptate. F/V ratio averages 2.82, range 2.24–3.23. Axial parenchyma abundant, apotracheal in short tangential lines (reticulate). Large prismatic crystals (≈ 40 μm.) occur occasionally in axial parenchyma of *P. braunii* and *P. vareciformis*. Prismatic crystals generally more frequent in ray cells of multiseriate portion than in upright ray cells; no integuments observed; not in chambered cells. Reddish-brown deposits abundant in the axial and ray parenchyma of *P. guineensis* and *P. vareciformis*.

Soyauxia Oliver (Medusandraceae or Passifloraceae). One to seven species from tropical West Africa. One specimen.

Growth rings poorly defined. Pores angular in outline; tangential diameter moderately small (64–80 μm.; average 72 μm.); pores average 100 per cent solitary; pores per square millimeter numerous (21 pores/mm.^{2}). Vessel elements very long to mostly extremely long (1769–2653 μm.; average 2168 μm.); perforation plates exclusively scalariform, mostly over 15 bars which are 2–3 μm. thick and 6–10 μm. apart; end-wall angles 10° to 25°. Vessel-wall thickness 3–4 μm. Intervascular pits absent except on overlapping vessel-element ligules; no definite arrangement observed; medium-sized, 6–10 μm. Vessel-ray pits circular to linear; medium to mostly coarse; 8–36 μm. Rays uniseriate and heterocellular (Heterogeneous Type III, Kribs 1935); height averages 471 μm. or 17 cells, maximum 720 μm. or 27 cells. Individual ray cells as observed on the radial surface are square toward the middle of the rays and upright toward the end of the rays; square cell height 25–35 μm. Imperforate tracheary elements are tracheids; very long to extremely long (2318–2660 μm.; average 2912 μm.) with mostly very thick walls, 7–10 μm.; nonseptate. F/V ratio 1.34. Axial parenchyma apotracheal in short tangential lines (reticulate) and diffuse. Prismatic crystals absent. Silica bodies abundant in square ray cells and occasionally in upright ray cells; 10–14 μm. in diameter. Reddish-brown deposits abundant in rays and fibrous elements.

Peridiscus Bentham (Peridiscaceae). Monotypic genus from Venezuela and Brazil. One specimen.

Growth rings absent. Pores circular to somewhat angular in outline;

tangential diameter mostly medium-sized (96–120 μm.; average 109 μm.); pores 45 per cent solitary; radial multiples mostly 2 and 3, occasionally to 5; pores per square millimeter moderately numerous (14 pores/mm.^{2}). Vessel elements very long to extremely long (1550–2978 μm.; average 2218 μm.); perforation plates exclusively scalariform, up to 15 or more bars which are 4–6 μm. thick and 8–12 μm. apart; end-wall angles 15° to 30°. Vessel-wall thickness 4–6 μm. Tyloses abundant to frequent. Intervascular pitting opposite; pits circular to oval; large to mostly very large, 14–18 μm. Vessel-ray pits circular to linear; coarse, 10–20 μm. Rays of two types: uniseriate homocellular rays composed entirely of upright cells and multiseriate heterocellular rays with long uniseriate extensions (Heterogeneous Type I, Kribs 1935). Height of multiseriate portion of rays averages 1707 μm., maximum 2947 μm.; width 1 to 2 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly square; cell height 33–53 μm. Imperforate tracheary elements libriform fibers; very long to extremely long (2448–3794 μm.; average 3134 μm.) with very thick walls, 9–15 μm.; septate in part. F/V ratio 1.41. Axial parenchyma abundant; apotracheal in short tangential lines (reticulate) and diffuse. Prismatic crystals absent. White deposits occasionally occur in vessels and reddish-brown deposits are frequent in rays.

Aphloia (DC.) Bennett (= *Neumannia*, Neumanniaceae). Four to six species from tropical East Africa, Madagascar, Seychelles Islands, and Mascarene Islands. Four specimens representing two species.

Growth rings poorly defined. Pores circular to angular in outline; tangential diameter moderately small to medium-sized (78–120 μm.; average 94 μm.); pores average 97 per cent solitary; radial multiples occasionally to 2; pores per square millimeter numerous to very numerous (32–61 pores/mm.^{2}; average 43 pores/mm.^{2}). Vessel elements mostly very long to extremely long (1051–2416 μm.; average 1452 μm.); perforation plates exclusively scalariform; in *A. theiformis* (SJRw 32941) mostly scalariform and occasionally simple, mostly over 15 bars which are 2–4 μm. thick and 2–8 μm. apart; end-wall angles 15° to 25°. Vessel-wall thickness 2–4 μm. Fine spiral thickenings present in vessel-element tails; occasionally to rarely throughout the vessel elements. Intervascular pitting alternate; pits circular to oval; small, 6–7 μm. Vessel-ray pits circular to occasionally linear; medium to coarse, 4–20 μm. Rays of two types: uniseriate homocellular rays composed entirely of upright cells and heterocellular multiseriate rays with long uniseriate extensions (Heterogeneous Type I, Kribs 1935). Height of multiseriate portion of rays averages 3666 μm., range 2711–4795 μm.; width 4 to 30 cells or 96–520 μm. (mostly 191–349 μm.). Individual ray cells of multiseriate portion as observed on the radial surface are mostly elongate; cell height 19–32 μm. Scalariformly perforated ray cells occur in *A. theiformis* (SJRw 32941). Imperforate tracheary elements fiber-tracheids; medium-sized to moderately long (1329–2214 μm.; average 1860 μm.) with mostly

thin to thick walls, 5–8 μm.; in *A. theiformis* (SJRw 32914), thick to very thick, 11–13 μm.; septate. F/V ratio averages 1.80, range 1.72–1.85. Axial parenchyma rare to frequent; vasicentric and apotracheal diffuse. Prismatic crystals absent. Reddish-brown deposits abundant in rays.

Asteropeia Thouars (Theaceae or Asteropeiaceae). Six to seven species from Madagascar. Three specimens representing two species.

Growth rings absent. Pores circular to oval in outline; tangential diameter moderately small to mostly medium-sized (91–190 μm.; average 156 μm.); pores average 97 per cent solitary; range 93 to 100 per cent; radial multiples occasionally to 2; pores per square millimeter in *A. rhopaloides* moderately few (5–7 pores/mm.^{2}); in *A. micraster* numerous (24 pores/mm.^{2}). Vessel elements medium-sized (556–670 μm.; average 627 μm.); perforation plates exclusively simple; end-wall angles 60° to 70°. Vessel-wall thickness 4–6 μm. Intervascular pits essentially absent except on the vessel-element ligules; alternate; very small, 2–4 μm. Vessel-ray pits circular to oval; fine, 2–4 μm. Rays mostly uniseriate, rarely biseriate, and homocellular (Homogeneous Type III, Kribs 1935); height averages 194 μm. or 7 cells, range 122–241 μm. or 6 to 9 cells. Individual procumbent cells as observed on the radial surface are elongate; cell height 12–25 μm. Imperforate tracheary elements fiber-tracheids; very short to medium-sized (828–1146 μm.; average 1015 μm.) with very thick walls, 4–10 μm.; nonseptate. F/V ratio averages 1.61, range 1.49–1.71. Axial parenchyma abundant; aliform to confluent. Prismatic crystals absent. Yellowish deposits abundant to occasional in vessels; in *A. micraster* and *A. rhopaloides* (SJRw 33869) deposits occur in axial and ray parenchyma.

Lethedon Sprengel (= *Microsemma* Labillardière Thymelaeaceae). Eleven species from New Caledonia and Queensland, Australia. Two specimens representing two species.

Growth rings poorly defined. Pores circular to oval in outline; tangential diameter moderately small to medium-sized (72–121 μm.; average 96 μm.); pores average 56 per cent solitary, range 33 to 79 per cent; radial multiples mostly 2, occasionally to 8; pores per square millimeter moderately numerous to numerous (13–22 pores/mm.^{2}; average 18 pores/mm.^{2}). Vessel elements medium-sized (447–625 μm.; average 536 μm.); perforation plates exclusively simple; end-wall angles 25° to 70°. Vessel-wall thickness 4–6 μm. Intervascular and vessel-ray pitting alternate; pits circular to oval; small, 4–7 μm. Rays uni- or biseriate and homocellular or heterocellular with 1 to 3 rows of upright cells (Heterogeneous Type IIA and Homogeneous Type I, Kribs 1935). Excluding upright ray cells, ray height averages 928 μm., range 734–1122 μm.; individual ray cells as observed on the radial surface are square to elongate; cell height 26–40 μm. Imperforate tracheary elements tracheids; medium-sized (1175–1420 μm.; average 1298 μm.) with thin to thick walls, 5–8 μm.; nonseptate. F/V ratio averages 2.44, range 2.27–2.62. Axial paren-

chyma frequent; aliform to confluent. Prismatic crystals rare in upright ray cells and occasional to frequent in other ray cells; no integuments observed; not in chambered cells. Crystals absent in *L. setosa*.

Triphyophyllum Airy Shaw (= *Dioncophyllum*, Dioncophyllaceae). Monotypic genus from Sierra Leone, Liberia, and Ivory Coast. Description based on work by Metcalfe (1952) and one specimen.

Growth rings absent. Pores mostly circular in outline; tangential diameter medium-sized to very large (165–350 μm.; average 300 μm.); pores mostly solitary; radial multiples occasionally to 2; pores per square millimeter very few to few (about 2 pores/mm.^{2}). Vessel elements moderately short to medium-sized (286–530 μm.; average 412 μm.); perforation plates exclusively simple; end-wall angles slightly oblique to transverse. Vessel-wall thickness 12–16 μm. Intervascular pits rare and similar to vessel-ray pits; mostly alternate; circular to oval; medium-sized to large, 8–12 μm.; often with coalescent apertures. Rays uniseriate and homocellular, entirely composed of square or upright cells (Homogeneous Type III, Kribs 1935); height short to moderately high. Imperforate tracheary elements fiber-tracheids; very short to medium-sized (653–1102 μm.; average 861 μm.) with thin to thick walls; nonseptate. F/V ratio 2.09. Axial parenchyma frequent; vasicentric and apotracheal diffuse. Prismatic crystals absent.

DISCUSSION

Comparative Anatomy of the Secondary Xylem within Flacourtiaceae

The xylem anatomy of Flacourtiaceae supports Dr. Hermann Sleumer's contention (personal communication) that the "Flacourtiaceae as a family is a fiction; only the tribes are homogeneous." Morphologically and anatomically, only a combination of characters can be used to circumscribe and define Flacourtiaceae. Features of the wood common to most genera include the absence of axial parenchyma, presence of septate fibrous elements, heterocellular rays with long uniseriate extensions, moderately small to medium-sized pore diameters, medium-sized to very long vessel and fibrous elements, a fibrous-element length to vessel-element length ratio of less than two, and prismatic crystals in the ray cells. Two of the more conspicuous features which vary are the vessel pits and perforation plates. By combining these two variable features, I have been able to define six anatomical categories or groups into which the genera of Flacourtiaceae can be placed. Genera in groups I, II, and III have medium-sized to very large (7– over 15 μm.) intervascular pits and medium to coarse (7– over 10 μm.) vessel-ray pits. In addition, the intervascular and vessel-ray pits do not have similar shapes. These combinations of pitting are called *large vessel pitting* throughout the remainder of the text (Figures 24, 25). Genera in group I have exclusively scalariform perforation plates; genera in group II have simple and scalariform perforation

plates; and genera in group III have exclusively simple perforation plates. Groups IV, V, and VI have intervascular pits that are similar in size and shape to the vessel-ray pits. Since the intervascular and vessel-ray pits are generally very small or small (< 8 μm.), this pitting is called *small vessel pitting* throughout the remainder of the text (FIGURES 26, 27). Genera of Group IV have exclusively scalariform perforation plates; genera of group V have simple and scalariform perforation plates; and genera of group VI have exclusively simple perforation plates. In APPENDIX I each genus of the Flacourtiaceae is assigned to one or two of the six groups just described.

For the most part, the two different pit sizes are specific for the tribes of Flacourtiaceae. The tribes Berberidopsideae, Pangieae, and Oncobeae contain genera with large vessel pits (groups I, II, and III); whereas the tribes Scolopieae, Homalieae, Banareae, and Casearieae (except *Tetrathylacium*) have genera with small vessel pits (groups IV, V, VI).

The tribe Flacourtieae has seven genera with large vessel pits and four with small vessel pits. Although there are other features in the secondary xylem which further separate these genera, no single taxonomic character or combination of characters suggests that the genera of tribe Flacourtieae with large vessel pitting should be separated from those genera with small vessel pitting. Thus, anatomically the Flacourtieae appears to be a transitional group linking the tribes with large vessel pits to the tribes with small vessel pits. Since there appears to be a continuum, the Flacourtiaceae must be considered as a large heterogeneous family. However, future investigations in chemotaxonomy, morphology, palynology, and other fields may help to define more precisely the subfamilial or familial rankings of the tribes comprising the Flacourtiaceae.

EVOLUTIONARY TRENDS WITHIN FLACOURTIACEAE

For the most part, the secondary xylem supports the phylogenetic sequences of tribes of Flacourtiaceae that were proposed by Warburg (1894) and Gilg (1925). Since the six anatomical groups generally conform to the tribes of Flacourtiaceae, I attempted to determine the phylogeny of the anatomical groups independently of the sequences of Warburg and Gilg. The only assumption which guided my comparisons is that the family Flacourtiaceae is monophyletic in origin.

Bailey and Tupper (1918) established conclusively that within a given taxon simple perforation plates were more specialized than scalariform perforation plates. Consequently, genera of group I which have many bars, or genera of group IV which have small vessel pits and exclusively scalariform perforation plates with many bars appear to be the most primitive. When the floral characteristics and other features of the secondary xylem (APPENDIX I) are examined in the genera of group I (mostly in the Berberidopsideae), characters such as spirally arranged flower parts, numerous sepals and stamens, occasionally opposite intervascular pitting, and generally very long vessel elements are found to be present.

In contrast, *Neoptychocarpus* (tribe Casearieae), the only genus of group IV, has more specialized structures, such as whorled flower parts, four sepals and no petals, eight stamens, and moderately long vessel elements. Therefore, group I is potentially the most primitive of the six anatomical groups.

Frost (1930b) demonstrated evolutionary trends from exclusively scalariform perforation plates with many bars to exclusively scalariform perforation plates with fewer bars, to simple and scalariform perforation plates, to exclusively simple perforation plates. Thus group I, which has exclusively scalariform perforation plates, may have given rise to group II, which has simple and scalariform perforation plates. Also, group III, which has exclusively simple perforation plates, is more specialized than either groups I or II. Groups with small vessel pits also could have evolved in a like manner, but *Neoptychocarpus*, the only genus of group IV, is morphologically rather specialized for the Flacourtiaceae. In addition, the wood anatomy of *Neoptychocarpus* appears to show affinities with the family Lacistemaceae, which is discussed later. It seems that unless *Neoptychocarpus* is derived from some nonflacourtiaceous group, it probably evolved from the genera in group I, since the genera of both these groups have exclusively scalariform perforation plates. Whether the genera of groups V and VI evolved from *Neoptychocarpus* or directly from group I or II cannot be determined with certainty. However, assuming a monophyletic origin for Flacourtiaceae, genera with large vessel pits appear to have given rise to genera with small vessel pits.

If we compare the generic composition of the six anatomical groups to the flacourtiaceous tribes of Gilg (1925), Warburg (1894), and Hutchinson (1967), many similarities are noted. In FIGURE 1 the phylogenetic sequence of Gilg's tribes is shown along with the number of genera represented by each anatomical group. Basing his conclusions primarily on gross morphology, Gilg considered the tribe Oncobeae to be the most primitive. Anatomically, Gilg's Oncobeae has several genera with exclusively scalariform perforation plates and large vessel pits (group I). Thus the wood anatomy substantiates the primitive position of Oncobeae. Warburg (1894) and Hutchinson (1967) considered the genera of Gilg's Oncobeae to constitute the base for two separate tribes. Warburg called his tribes Erythrospermeae and Oncobeae and considered the Erythrospermeae to be the most primitive (FIGURE 1). Hutchinson's two tribes are the Oncobeae and Berberidopsideae, the latter of which he considered the most primitive. The genera of Berberidopsideae or Erythrospermeae belong mainly to group I, while the genera of Oncobeae belong mainly to group II (APPENDIX I). Consequently, the wood anatomy not only supports the splitting of Gilg's tribe Oncobeae into two separate tribes, but it also supports the phylogenetic specialization from group I (Warburg's Erythrospermeae) to group II (Warburg's Oncobeae) (FIGURE 1).

As shown in FIGURE 1, the tribe Pangieae is more specialized than either of its possible ancestors, the Erythrospermeae or Oncobeae. Both these primitive tribes are characterized by genera in group I, but tribe

Pangieae is characterized by genera mostly in groups II and III. As proposed, genera of group I probably gave rise to genera in groups II and III. Thus, the wood structure confirms this part of the sequences.

The tribe Scolopieae is derived from the tribe Oncobeae. The genera of Gilg's Scolopieae belong to groups I, II, III, V, and VI; however, Hutchinson (1967) placed most of these genera elsewhere. Genera in Hutchinson's Scolopieae and Banareae (formed from genera in Gilg's Scolopieae) are in groups V and VI. As proposed, group VI is the most specialized group, since genera with small vessel pits are derived from genera with large vessel pits and group VI has exclusively simple perforation plates. Thus, the xylem anatomy cannot negate the evolution of the Scolopieae (genera with small vessel pits) from the Oncobeae (genera with large vessel pits).

The tribe Homalieae is derived from the Scolopieae. Since the genera of Homalieae belong mostly to group VI, the secondary xylem cannot negate the derivation of tribe Homalieae from the Scolopieae. As discussed later, the wood of Homalieae, Banareae, and Scolopieae suggest a close alliance.

As previously mentioned, the Flacourtieae is the only tribe in which some genera have large vessel pits and some have small vessel pits. The phylogenies of Warburg (1894) and Gilg (1925) show tribe Scolopieae as the origin of the Flacourtieae. If Hutchinson's Scolopieae and Banareae replace the Scolopieae of Warburg and Gilg, then the derivation of tribe Flacourtieae from the Scolopieae suggests an interruption in the continuum from large to small vessel pits. Tribe Oncobeae is characterized by large vessel pits; Hutchinson's Scolopieae and Banareae are characterized by small vessel pits; and tribe Flacourtieae is characterized by both large and small vessel pits. Thus, the secondary xylem indicates need for a change from the phylogenies of Warburg and Gilg. The anatomy suggests the derivation of both the Flacourtieae and Scolopieae from tribe Oncobeae. The Flacourtieae would then occupy a transitional position between the tribes characterized by large vessel pits and the tribe Casearieae, which generally has small vessel pits and exclusively simple perforation plates. The xylem anatomy does not negate this derivation of the Casearieae from tribe Flacourtieae.

Tribal and Generic Anatomy

The generic composition of Hutchinson's (1967) Flacourtiaceae generally agrees with evidence from the secondary xylem. Hutchinson's transfer of *Paropsia* and other genera to the Passifloraceae and the reorganization of the genera in Gilg's Scolopieae to form tribes Scolopieae, Banareae, and Prockieae (Tiliaceae) are supported or at least are not negated by the xylem anatomy. The relationships of the tribes of Flacourtiaceae together with their respective genera and a group of "Anomalous Genera" are discussed in detail below.

Tribe Berberidopsideae. The tribe Berberidopsideae is anatomically and

taxonomically the most primitive tribe of the Flacourtiaceae. The woods of genera in this tribe are homogeneous with the exception of *Ahernia*, *Berberidopsis*, and *Streptothamnus*. Of the eight genera examined, only *Ahernia* has the combination of exclusively simple perforation plates and large vessel pits (group III). *Ahernia* also has many other distinctive features (APPENDIX I). These characteristics indicate affinities to certain genera in Flacourtiaceae; however, morphological characters do not conform these supposed affinities to *Ahernia*.

Berberidopsis and *Streptothamnus* are the two most primitive genera in the Flacourtiaceae. Anatomically both genera have nonseptate tracheids (FIGURE 7), approximately 100 per cent solitary pores, and very high rays (over 1.5 cm.). These three characters, coupled with evidence from the floral morphology (Hutchinson 1967), not only ally these two genera, but also seem to put them somewhere between the Flacourtiaceae and Dilleniaceae. Perhaps a new family could be established to contain them. This Dilleniaceae-Flacourtiaceae relationship will be discussed further under FAMILY RELATIONSHIPS.

Tribe Oncobeae. The genera in the tribe Oncobeae as formulated by Warburg (1894) or Hutchinson (1967) are scarcely distinguishable anatomically (APPENDIX I) and are related to the genera of the Erythrospermeae (Warburg) or Berberidopsideae (Hutchinson). Evidence which supports the close relationship of tribes Erythrospermeae (Berberidopsideae) and Oncobeae is the occasional retention of opposite intervascular pitting and exclusively scalariform perforation plates in some species of *Mayna* and *Carpotroche* (Oncobeae).

After the generic description of *Buchnerodendron*, Hutchinson (1967) stated that it is "an interesting genus providing a definite link with Tiliaceae and resembling a *Sparrmania* [sic]." The wood of *Buchnerodendron* is similar to that in other genera of Oncobeae. An examination of a specimen of *Sparmannia africana* L. f. (SJRw 33838) from South Africa revealed many differences which militate against any close alliance between *Buchnerodendron* and *Sparmannia*.

Tribe Pangieae. Although the wood anatomy of the genera of Pangieae (excluding *Goethalsia*) is somewhat homogeneous, *Hydnocarpus* (*sensu lato*) seems to be distinct. Hutchinson (1967) considers *Hydnocarpus* and *Taraktogenos* to be separate but related genera; however Warburg (1894), Gilg (1925), and Sleumer (1938, 1954) consider these two genera, together with *Asteriastigma*, as one genus — *Hydnocarpus*. In addition, Schaeffer's (1972) study of pollen morphology supports Sleumer and others. All species of *Hydnocarpus* (*sensu lato*) have exclusively scalariform perforation plates and all species, except *H. sumatrana* (Miq.) Koord., contain vitreous silica (FIGURE 6). Since no anatomical feature could be found to support the segregation of *Hydnocarpus* (*sensu lato*), the xylem anatomy favors the submersion of *Taraktogenos* and *Asteriastigma* in *Hydnocarpus*.

Hydnocarpus is distinctive and primitive in that it is the only genus of

the Pangieae with exclusively scalariform perforation plates and opposite or opposite to alternate intervascular pitting. In addition, *Hydnocarpus* has the lowest fiber length to vessel length ratio (1.56) of the Pangieae, some of the longest vessel and fibrous elements of the Flacourtiaceae, and is the only genus of the Flacourtiaceae producing vitreous silica. Thus, *Hydnocarpus* is undoubtedly the most primitive genus in tribe Pangieae. Based on the structure of the wood, a more likely placement of *Hydnocarpus* would be in either the tribe Berberidopsideae or the Oncobeae. The floral morphology, however, does not suggest any such transfer, although the pollen morphology does support the view that *Hydnocarpus* is somewhat isolated. Schaeffer (1972) concluded that only *Chlorocarpa* (no wood available) and *Neoptychocarpus* have pollen that is similar to that of *Hydnocarpus*. Although *Neoptychocarpus* is in a different and more advanced tribe (the Casearieae), the wood of *Neoptychocarpus* is not only primitive but is also similar to the wood of *Lacistema*. *Hydnocarpus*, *Neoptychocarpus*, and *Lacistema* do not appear to be closely related florally, but there do seem to be some common bonds which need further examination.

Evidence from chemotaxonomy suggests a link betwen tribe Oncobeae and *Hydnocarpus*. Of the genera of tribe Pangieae, only species of *Hydnocarpus* produce chaulmoogra oil (i.e. cyclopentene fatty acids). *Pangium* and *Gynocardia* were once thought to contain chaulmoogra oil, but they are now known to contain the cyanogenetic heteroside, gynocardoside (Alston & Turner 1963). Other genera in the plant world known to contain chaulmoogra oil are *Carpotroche*, *Mayna*, *Lindackeria*, *Oncoba*, and *Caloncoba*, all of which belong to the tribe Oncobeae. Supposedly Roig and Rodríguez (1944) isolated chaulmoogra oil from some genera in the tribe Casearieae, but Gibbs (1945) stated that only genera in the tribes Pangieae and Oncobeae contain chaulmoogra oil. With corroborative evidence from chemotaxonomy, pollen morphology, and wood anatomy, it appears that the genus *Hydnocarpus* is somewhat isolated. Also, *Hydnocarpus* has retained some primitive genetic structure of the ancient gene pool from which the tribes Pangieae and Oncobeae and possibly the genera *Neoptychocarpus* and *Lacistema* may have evolved.

Tribe Scolopieae. As formulated by Hutchinson (1967), the tribe Scolopieae consists of *Scolopia*, *Pseudoscolopia*, and *Dioncophyllum* of Gilg's Scolopieae, the genera of Gilg's tribe Phyllobotryeae, and a few genera described since 1925. Of these nine genera only *Scolopia*, *Bartholomaea*, and *Dioncophyllum* (including *Triphyophyllum*) were available for study. Since *Triphyophyllum* is considered by most taxonomists as an aberrant genus in the Flacourtiaceae, it is discussed later under the heading "Anomalous Genera." Of the other two genera, only *Scolopia* is represented in my study by an ample number of wood specimens. From anatomical features summarized in APPENDIX I, the secondary xylem of *Scolopia* and *Bartholomaea* can be compared. Although a few features are inconsistent, there is enough similarity to conclude that *Scolopia* and *Bartholomaea* are allied and belong in the same tribe.

Tribes Banareae and Homalieae. *Banara* and *Pineda* of Gilg's tribe Scolopieae, together with *Trimeria* of Gilg's tribe Homalieae and the anomalous genus *Asteropeia*, form Hutchinson's new tribe Banareae. Since *Asteropeia* is anomalous, it is considered under "Anomalous Genera." In their xylem anatomy, *Banara*, *Pineda*, and *Trimeria* are so similar that they are scarcely separable on this basis.

Of the seven genera of Homalieae only *Homalium* and *Calantica* were available for study. These two genera have very similar secondary xylem, and in some cases species of *Calantica* cannot be distinguished from some species of *Homalium*.

From the summary of anatomical features in APPENDIX I, a comparison can be made of the xylem anatomy in genera of the Scolopieae, Banareae, and Homalieae. It is apparent that the genera in these three tribes are allied and practically indistinguishable on anatomical grounds. Thus, whether the genera of tribes Banareae and Scolopieae constitute one tribe and two subtribes or two separate tribes or whether the genus *Trimeria* is in the Homalieae or Banareae is strictly a matter for taxonomic judgment.

Tribe Prockieae (Tiliaceae). The placement and relationships of the genera of the Prockieae are not fully understood. Within the Prockieae, *Prockia*, *Hasseltia*, *Pleuranthodendron* (= *Hasseltiopsis*), and *Macrohasseltia* (included here by Williams 1961) were examined (APPENDIX I). *Prockia* belongs in the anatomical group VI and the other three genera belong in group II. The secondary xylem of the genera of group II are similar in all aspects except for the size of the intervascular pitting. *Prockia* differs from these genera in that it has long radial multiples and/or radial pore chains, no spiral thickenings in the vessels, no perforated ray cells, exclusively simple perforation plates, and small vessel pitting (group VI). Other features such as ray height and width and crystal type and arrangement tend to unite *Prockia* with the other genera of tribe Prockieae; however, the woods of *Prockia*, *Banara*, *Scolopia*, and *Homalium* are so similar that it is difficult to distinguish among some species of these genera. Although the secondary xylem of *Prockia* suggests a close alliance with the Scolopieae, Banareae, and Homalieae, *Prockia* and the other genera of the Prockieae are united florally by their common possession of axile placentation. Thus, *Prockia* should remain united with the other genera of the Prockieae.

Gilg (1925) placed the genera of the Prockieae in subtribe Prockiinae of tribe Scolopieae (including the Banareae). The wood anatomy can support Gilg's arrangement since all the genera of the Prockieae are grouped together in the subtribe Prockiinae and a relationship to the genera *Scolopia* and *Banara* is implied by the inclusion of all these genera in the tribe Scolopieae.

The xylem anatomy could also support the placement of tribe Prockieae in the family Elaeocarpaceae. On the basis of the axile placentation and valvate calyx, Hutchinson (1967) established the tribe Prockieae in the

Tiliaceae (including the Elaeocarpaceae). For the same reasons, Bentham and Hooker (1862) included the known Prockieae as a separate tribe in their Series B Heteropetalae, a taxon equivalent to the Elaeocarpaceae. A comparison of Kukachka and Rees' (1943) description of the xylem anatomy of Tiliaceae and Elaeocarpaceae with the secondary xylem of tribe Prockieae suggests a close alliance between tribe Prockieae and the Elaeocarpaceae.

Keating (1973) notes that the Scolopieae, Banareae, Homalieae, Flacourtieae, and Prockieae all have similar pollen morphology. He also notes a similarity between the pollen of tribe Homalieae (and presumably the Prockieae) and the family Elaeocarpaceae.

The evidence from pollen morphology and wood anatomy appears then to suggest that tribe Prockieae is closely allied to both the Flacourtiaceae and the Elaeocarpaceae. Thus the correct placement of the Prockieae is still somewhat in doubt.

Evidence from the wood structure also reveals a reduction series in the Prockieae. The intervascular pits are large (10–14 μm.) in *Macrohaseltia*, medium-sized (8–10 μm.) in *Pleuranthodendron*, and small (4–7 μm.) in *Hasseltia*. In addition, the vessel-ray pitting is coarse (over 10 μm.) in these three genera, but *Prockia* has vessel-ray and intervascular pits that are not only the same size but also small (4–7 μm.). Since *Prockia* has exclusively simple perforation plates and the other three genera have both simple and scalariform perforation plates, *Prockia* appears to be the most specialized of these four genera. Thus, a reduction in the size of the vessel pitting from *Macrohasseltia* to *Prockia* seems plausible. Whether there are any evolutionary trends related to this reduction series, however, cannot be determined at this time.

Tribe Flacourtieae. The xylem anatomy in the Flacourtieae (excluding *Aphloia*) is rather diverse. The anatomical groups represented in the tribe are as follows: group II — *Bennettiodendron, Azara* (rarely group I), *Carrierea*, and *Olmediella*; group III — *Poliothyrsis, Itoa*, and *Idesia* (rarely group II); group V — *Dovyalis*; group VI — *Xylosma* and *Flacourtia* (rarely group V). It is apparent that two groups of genera are present in the Flacourtieae. One group has large vessel pitting and the other group has small vessel pitting. These two groups are rather distinct and except for characters present in most genera of the Flacourtiaceae, the only feature which these two groups have in common is the presence of integumented prismatic crystals usually more abundant in the upright ray cells than in the ray cells of the multiseriate portion of the ray.

The seven genera with large vessel pits can be separated into two groups based on the size of the intervascular pits. One group has intervascular pits over 10 μm. in diameter and the other group has some intervascular pits under 10 μm. in diameter. The four genera with intervascular pits over 10 μm. do not have prismatic crystals in chambered ray cells and some of their fibrous elements are nonseptate. Of these genera, *Carrierea* and *Olmediella* have coarse spiral thickenings throughout the

vessels (FIGURES 16, 18). This seems to indicate that these two genera are more closely allied to each other than to *Idesia* and *Itoa*. The three genera with large vessel pitting and some intervascular pits under 10 μm. have septate fibrous elements. Thus, based on the wood structure, *Poliothyrsis*, *Bennettiodendron*, and *Azara* appear to be more closely related to each other than to the other four genera with large vessel pitting.

Of the four genera with small vessel pits, only *Dovyalis* has a slightly different wood structure. *Dovyalis* lacks spiral thickenings in the vessels and also does not have prismatic crystals in chambered upright ray cells.

Recently, Sleumer (1972a) stated that *Ludia* is morphologically very similar to *Scolopia* (tribe Scolopieae). As might be expected, this morphological similarity extends into the secondary xylem. In addition, species of *Ludia*, *Flacourtia*, and *Xylosma* of the Flacourtieae, *Scolopia* and *Bartholomaea* of the Scolopieae, *Homalium* and *Calantica* of the Homalieae, *Banara*, *Pineda*, and *Trimeria* of the Banareae, and *Prockia* of the Prockieae (Tiliaceae), as previously mentioned, are for the most part indistinguishable anatomically (APPENDIX I). Keating (1973) has found that the pollen morphologies of these genera are also scarcely distinguishable from each other.

Tribe Casearieae. For the most part, the wood structure of tribe Casearieae is homogeneous (APPENDIX I). *Tetrathylacium* and *Neoptychocarpus* are exceptions to this homogeneous structure.

Tetrathylacium is the only genus in Casearieae which has exclusively scalariform perforation plates and large vessel pitting (group I). The floral morphology of *Tetrathylacium* is similar to that of other genera in the Casearieae, and its position in the tribe has not been questioned by taxonomists. Although the structure of the wood is primitive, *Tetrathylacium* has a specialized floral structure. Apparently, *Tetrathylacium* has retained some primitive features of the xylem while the floral morphology evolved. Thus, the xylem anatomy of *Tetrathylacium* suggests that the forebears of the genera of Casearieae evolved from some ancient group which had exclusively scalariform perforation plates and large vessel pits (i.e. genera of group I). The data in APPENDIX I suggest that the tribe Berberidopsideae contains the ancestral stock of the Casearieae. This proposed line of evolution also agrees with the phylogenetic sequences of Warburg (1894) and Gilg (1925) (FIGURE 1).

Neoptychocarpus is the only genus in the Flacourtiaceae which has exclusively scalariform perforation plates and small vessel pitting (group IV); otherwise, the secondary xylem is similar to that of other genera of Casearieae (APPENDIX I). On the other hand, the intervascular pitting sometimes tends to be opposite, although it is not clear whether the pits are opposite because of genetic influences or opposite through crowding. Monachino (1948), however, considered that *Neoptychocarpus* was unquestionably correctly placed in the Flacourtiaceae. Whether the presence of exclusively scalariform perforation plates is the retention of a primitive flacourtiaceous feature or whether features of *Neoptychocarpus*

and the other genera of Casearieae are similar because of convergent or parallel evolution is difficult to ascertain.

If *Neoptychocarpus* belongs in the Casearieae, then it probably evolved along the same lines as *Tetrathylacium*. Like *Tetrathylacium*, *Neoptychocarpus* has retained the primitive scalariform perforation plates which are typical of the Berberidopsideae. However, in contrast to *Tetrathylacium*, *Neoptychocarpus* developed small vessel pitting.

Another possible line of evolution is through the genus *Lacistema* (Lacistemaceae). Assuming that opposite intervascular pits in *Neoptychocarpus* are opposite because of genetic influence and not because of some physical or mechanical adjustments, then the secondary xylem of *Lacistema* is similar to that of *Neoptychocarpus*. On the basis of floral morphology, Chirtoiu (1918) suggested that *Lacistema* is more closely related to the Flacourtiaceae than to any other family. Krause (1925) specifically suggested *Prockia* (Flacourtiaceae) as the closest genus to *Lacistema*. Hutchinson (1967) implied some relationship, since he placed the Lacistemaceae and Flacourtiaceae in the order Bixales. Although the floral structure of *Neoptychocarpus* is not closely similar to that of *Lacistema*, the wood anatomy does imply an alliance. However, until more evidence is found to support a closer relationship between *Neoptychocarpus* and *Lacistema*, *Neoptychocarpus* should remain in the Casearieae.

As mentioned before, *Hydnocarpus* and *Neoptychocarpus* have similar pollen, representing a rare type in the Flacourtiaceae (Schaeffer 1972). The similarity in secondary xylem between these two genera is no greater, however, than that between *Neoptychocarpus* and any other genus belonging to group I (APPENDIX I). *Neoptychocarpus* has small vessel pitting and integumented prismatic crystals, whereas *Hydnocarpus* has large vessel pitting and nonintegumented prismatic crystals. Also, *Hydnocarpus* has spiral thickenings in the vessel-element tails of some species and vitreous silica in the vessels of most species. Perhaps *Hydnocarpus*, as well as *Lacistema*, is closely allied to *Neoptychocarpus*; however, these relationships are not clear.

Anomalous Genera

Paropsia, *Barteria*, and *Ancistrothyrsus* (Passifloraceae). Hutchinson (1967), Sleumer (1970), and others consider the tribe Paropsieae of Gilg's Flacourtiaceae as a member of the Passifloraceae. In their study of the systematic anatomy of the Passifloraceae, Ayensu and Stern (1964) concluded that *Paropsia* and related genera are anatomically more similar to Passifloraceae than to Flacourtiaceae. The wood structure of *Paropsia*, *Barteria*, and *Ancistrothyrsus*, differs greatly from that in the Flacourtiaceae. With anatomical evidence and with corroborating observations presented by Ayensu and Stern (1964), Den Berger (1928), Tupper (1934), Sleumer (1970), De Wilde (1971), and Hutchinson (1967), I concur that *Paropsia*, *Barteria*, and *Ancistrothyrsus* are members of the Passifloraceae and not of the Flacourtiaceae.

Soyauxia (Passifloraceae? Medusandraceae?). *Soyauxia* of Gilg's Paropsieae seems out of place in either the Passifloraceae or the Flacourtiaceae. The features of *Soyauxia* (APPENDIX I) suggest a relationship with a primitive group of plants, but probably not the primitive *Berberidopsis* and *Streptothamnus* of the Flacourtiaceae; at least no close relationship is evident. *Soyauxia, Berberidopsis,* and *Streptothamnus* have some features in common, such as solitary pores, long vessel and tracheid elements, and exclusively scalariform perforation plates; however, the structure of the rays and the axial parenchyma differs in each genus. *Soyauxia* has uniseriate rays and an abundance of parenchyma and silica in the ray cells, whereas *Berberidopsis* and *Streptothamnus* have large rays and lack axial parenchyma and silica.

On the basis of a central column in the ovary, Brenan (1953) placed *Soyauxia* in Medusandraceae. Studying the anatomy of *Soyauxia,* Metcalfe (1962) stated, ". . . although there are points of similarity in the structure of these two genera, *Medusandra* differs from *Soyauxia* in possessing a well developed system of secretory canals." Metcalfe argued that this anatomical difference together with morphological differences supports the view that *Soyauxia* and *Medusandra* are not closely related. Using the anatomy of *Peridiscus* (Peridiscaceae) as supporting evidence, Metcalfe also contended that *Soyauxia* is more closely allied to the Flacourtiaceae than to the Passifloraceae. The xylem anatomy does not suggest the placement of *Soyauxia* in the Flacourtiaceae, Passifloraceae, or Peridiscaceae, and until more evidence is available, the placement of *Soyauxia* must remain uncertain.

Peridiscus (Peridiscaceae). Both Warburg (1894) and Gilg (1925) indicated that *Peridiscus* is questionably a member of the Flacourtiaceae. In 1959, Hutchinson accepted the Peridiscaceae and placed it in his Tiliales. Later, in 1967, Hutchinson placed the Peridiscaceae in his Bixales and near the Flacourtiaceae. Sandwith (1962) added the genus *Whittonia* to the Peridiscaceae, and in a sequel to his paper, Metcalfe (1962) discussed the systematic anatomy of the Peridiscaceae. Metcalfe concluded that, "Peridiscaceae may quite well be allied to the Flacourtiaceae." In some respects the wood anatomy of *Peridiscus* is similar to that of some primitive genera of Flacourtiaceae, such as *Erythrospermum.* Both these genera have exclusively scalariform perforation plates, opposite intervascular pitting, and large vessel pitting. In addition, the ray structure, fiber length to vessel length ratio, and vessel and fibrous-element length are similar (APPENDIX I). The major differences between *Peridiscus* and most Flacourtiaceae are the absence of prismatic crystals, the presence of many nonseptate fibrous elements, and the abundance of either diffuse or reticulate (in short tangential lines) apotracheal parenchyma. Therefore, I agree with Metcalfe (1962), who believes that *Peridiscus* is definitely not a member of the Flacourtiaceae; yet the secondary xylem does suggest that *Peridiscus* is allied to the family.

Aphloia (= *Neumannia,* Neumanniaceae). Although the floral morphol-

ogy is somewhat specialized, *Aphloia* shows a primitive xylem anatomy. Hutchinson (1967) placed *Aphloia* in the tribe Flacourtieae. Under the name *Neumannia*, Warburg (1894) and Gilg (1925) also placed *Aphloia* in the Flacourtieae. According to Willis (1966), Van Tieghem proposed *Neumannia* as the basis of the monotypic family Neumanniaceae, which showed uncertain affinities to the Flacourtiaceae. The woods of *Aphloia* and the primitive genera *Berberidopsis* and *Streptothamnus* are similar.

In APPENDIX I the anatomy of these genera can be compared. For the most part, the floral morphology of *Aphloia* seems to resemble the genera of tribe Flacourtieae. However, Willis (1966) notes that there is "perhaps some justification for maintaining the family Neumanniaceae distinct." It is possible that *Aphloia* retained the primitive wood structure of the ancestral stock of tribe Flacourtieae while the floral structure evolved along the same line as the other genera of the Flacourtieae. However, I believe that *Aphloia* evolved from the same forebears as the genera of the Flacourtieae, but deviated sufficiently from the evolutionary line of the Flacourtiaceae to produce a combination of characters which could justify consideration of placement in a separate family.

Asteropeia (Asteropeiaceae). Hutchinson (1967) included *Asteropeia* in his tribe Banareae, but most taxonomists assign this genus elsewhere, generally to the Theaceae. According to Willis (1966), Takhtajan proposed the monotypic family Asteropeiaceae, showing possible affinities with the Linaceae, Tetrameristaceae, or Flacourtiaceae. Based on the wood anatomy (APPENDIX I), *Asteropeia* is not a member of the Flacourtiaceae and there does not seem to be any indication of close affinities with this family. According to Record (1942), the wood of *Asteropeia* is not related to that of the Theaceae. Thus, it seems that Takhtajan's monotypic family Asteropeiaceae is the best position for *Asteropeia*, at least until more information is available to indicate its affinity elsewhere.

Goethalsia (Tiliaceae). The floral and wood structure of *Goethalsia* is not flacourtiaceous. Generally *Goethalsia* is placed in the Tiliaceae, but following the recommendation of Gleason (1934), Hutchinson (1967) placed *Goethalsia* in the tribe Pangieae (Flacourtiaceae). In 1934, Record stated that ". . . the pith, bark and wood of *Goethalsia* all suggest Tiliaceae and not Flacourtiaceae." Burret (1934), a specialist in Tiliaceae, agreed with Record (1934) and noted that Gleason (1934) misinterpreted the flower structure of *Goethalsia*. When Kukachka and Rees (1943) studied the wood anatomy of the Tiliaceae, they found no evidence to support Gleason's transfer of *Goethalsia* to the Flacourtiaceae. Features found in *Goethalsia* and not in genera of the Flacourtiaceae include an abundance of axial parenchyma and nonseptate fibrous elements. Thus, I concur with Record (1934), Burret (1934), and Kukachka and Rees (1943) that *Goethalsia* is tiliaceous, not flacourtiaceous.

Triphyophyllum (Dioncophyllaceae). The xylem anatomy of *Triphyophyllum* (APPENDIX I) is definitely unusual for Flacourtiaceae. Hutchinson

(1967) submerged *Triphyophyllum* in *Dioncophyllum* and placed it in the tribe Scolopieae. Both Warburg (1894) and Gilg (1925) also included *Dioncophyllum* in their Scolopieae. In 1952, Airy Shaw proposed the family Dioncophyllaceae. He stated that "*Dioncophyllum* had nothing whatever to do with the Flacourtiaceae." In an anatomical study, Metcalfe (1952) supported Airy Shaw and suggested that ". . . there may well be affinities between the Dioncophyllaceae and the Nepenthaceae and between the Dioncophyllaceae and Droseraceae." From personal observation, the wood anatomy supports the assertions of both Airy Shaw (1952) and Metcalfe (1952).

Lethedon (Thymelaeaceae or Aquilariaceae). Warburg (1894) placed *Lethedon* (= *Microsemma*) in a questionable group of Flacourtiaceae. Gilg (1925) excluded *Lethedon* from the Flacourtiaceae and placed it in the Thymelaeaceae. Hutchinson (1967) placed *Lethedon* in the Aquilariaceae, a segregate of Gilg's Thymelaeaceae. The secondary xylem of *Lethedon* (APPENDIX I) is definitely not flacourtiaceous, and from the morphology it seems likely that *Lethedon* is related to the Thymelaeaceae or Aquilariaceae.

FAMILY RELATIONSHIPS

Ancestral stock. Judging from the primitive wood structure in some branches of the extant Flacourtiaceae, immediate progenitors of the plants we recognize today as Flacourtiaceae must have been relatively unspecialized. According to Hutchinson (1967), the family Flacourtiaceae is a somewhat indeterminate and intermediate group of plants, somewhere between the Dilleniaceae (Dilleniales) and the order Tiliales. Takhtajan (1969) also suggests a Dillenialean ancestry, but Cronquist (1968) proposes a Thealian one.

Many characters in the Dilleniaceae and in the two primitive genera of Flacourtiaceae are parallel. Features of the wood which occur in the Dilleniaceae but do not appear in *Berberidopsis* and *Streptothamnus* include larger and fewer pores, more axial parenchyma, and raphide crystals. There are free carpels and distinct sepals and petals in the Dilleniaceae but not in *Berberidopsis* and *Streptothamnus*. The secondary xylem of the Dilleniaceae is also similar to that of the Theaceae, and Dickison (1967) suggests that the similarity of wood structure supports the taxonomic alliance between the Dilleniaceae and Theaceae. As might be expected, the woods of *Berberidopsis* and *Streptothamnus* resemble the woods of the Theaceae. Features not found in *Berberidopsis*, *Streptothamnus*, or the Dilleniaceae, but which do occur in the Theaceae, include shorter and narrower rays, a 3–5-locular ovary, scanty endosperm, and axile placentation. Since there appears to be more similarity among *Berberidopsis* and *Streptothamnus* and the Dilleniaceae, the ancestral stock of the Flacourtiaceae would appear to lie in the Dilleniaceae as opposed to the Theaceae.

Cronquist derives the family Flacourtiaceae (Violales) from the Theales and through a different line of evolution also derives the Elaeocarpaceae (Malvales) from the Theales. He notes a similarity between Flacourtiaceae and Elaeocarpaceae, but concludes that their similarity is a product of common ancestry. Because of similar secondary xylem and pollen morphology of the Flacourtiaceae and Elaeocarpaceae, I would expect a more direct line of evolution from the Dilleniales through the Flacourtiaceae to the Tiliales or Malvales, as proposed by Takhtajan (1969) and Hutchinson (1967).

Additional evidence supporting the evolution of the Tiliales or Malvales from the Flacourtiaceae is shown in data from chemotaxonomy. According to Alston and Turner (1963), certain Malvales, especially Sterculiaceae, contain the fatty acid, sterculic acid, which has a three-membered ring. In some Flacourtiaceae, fatty acids with five-membered rings (chaulmoogric and hydnocarpic) are present. Fatty acids with ring structures are not only rare in the plant world, they are also very specific for genera, families, and possibly even for orders. It is easy to imagine then that plants producing cyclic fatty acids with a three-membered ring could have evolved directly from taxa having fatty acids with a five-membered ring.

Intraordinal relationships. The xylem anatomy cannot negate the supposed alliance among the families generally placed in the same order as the Flacourtiaceae. Williams (1962) and Keating (1968) studied the comparative morphology of the Bixaceae and Cochlospermaceae respectively. They found that these two families are more closely related to each other than to any other family. Comparing the Cochlospermaceae and Flacourtiaceae, Keating states, "further, Flacourtiaceae . . . better overlap the range found in Cochlospermaceae than in any other parietalian families named." In a subsequent paper, Keating (1973) noted that the pollen of both the Bixaceae and the Cochlospermaceae lies within the range of the Flacourtiaceae. My work also supports Keating's findings.

Another family similar to the Bixaceae and Cochlospermaceae is the Cistaceae. The anatomy of these small families resembles that of somewhat selected groups of Flacourtiaceae. In addition, the Flacourtiaceae is more primitive than any of these three families. Vestal (1937) proposed a phylogeny of these four families based primarily on wood anatomy. He concluded that the Flacourtiaceae gave rise to the Bixaceae and Cochlospermaceae and that the Bixaceae gave rise to the Cistaceae. This phylogenetic sequence cannot be negated from the evidence gathered from the secondary xylem, but neither can it be strongly substantiated or a close alliance established.

According to Metcalfe and Chalk (1950) and Taylor (1938, 1972), the wood anatomy in the Violaceae is similar to that in the Flacourtiaceae. Taylor (1972) contends that anatomical information ". . . reinforces the suggestion of kinship between the Violaceae and Flacourtiaceae." Takhtajan (1969) states that the family Violaceae is closely allied to the Fla-

courtiaceae through the primitive tribe Rinoreae (Violaceae). Hutchinson (1969) places the Violaceae in its own monotypic order somewhat distant from the Flacourtiaceae and the rest of the Bixales. The anatomical resemblance, coupled with taxonomic evidence, seems to outweigh Hutchinson's arguments for placing the Violaceae in an order by itself.

The relationship of the Peridiscaceae and Lacistemaceae has previously been discussed. The xylem anatomy of *Peridiscus* (Peridiscaceae) indicates a close alliance to the primitive taxa of Flacourtiaceae. *Neoptychocarpus*, of the tribe Casearieae (Flacourtiaceae), and *Lacistema* (Lacistemaceae) have similar wood structure. In addition, the pollen morphology also supports a close alliance (Keating 1973).

Order Passiflorales. According to Hutchinson (1969), ". . . Passiflorales, . . . probably derived from Bixales, show close relationships with Flacourtiaceae." In addition, Takhtajan (1969) states that "it is very difficult to draw a clear taxonomic boundary between the two most primitive families — Passifloraceae and Flacourtiaceae." Species of *Passiflora* (Passifloraceae) and *Hydnocarpus* and *Rawsonia* (Flacourtiaceae) show a positive reaction to antifungal activity tests (Nicolls 1970). The chemical causing antifungal activity is not known, but it is thought to be the same in both the Flacourtiaceae and Passifloraceae, thus supporting a close family relationship. The secondary xylem of each of these families has many distinguishing features and they are easily separated anatomically. Although differences exist, in no way does the wood anatomy negate the possibility that the Passifloraceae is derived from the Flacourtiaceae.

Order Euphorbiales. The secondary xylem of the Euphorbiaceae (Euphorbiales) is diverse, and some selected genera of the Euphorbiaceae are very similar to selected genera of the Flacourtiaceae. Cronquist (1968) places the order Euphorbiales in his subclass V, Rosidae, which is phylogenetically distant from the Flacourtiaceae (subclass IV, Dilleniidae). Takhtajan (1969), Hutchinson (1967), and Sleumer (1954) all suggest somewhat of an alliance between the Euphorbiaceae and Flacourtiaceae. Takhtajan aligns the Euphorbiales close to the Malvales. He states that "one may therefore presume that the Euphorbiales arose from some ancient group intermediate between the Flacourtiaceae and Malvales."

Hutchinson (1967) and Sleumer (1954) point out the resemblance of some Flacourtiaceae, particularly those with unisexual flowers and no petals, to some genera of Euphorbiaceae. Hutchinson proposes that "perhaps a small part of Euphorbiaceae has arisen from the same stock as the Flacourtiaceae"; he also cites *Kiggelaria* (Flacourtiaceae) as a genus possessing characters of a few Euphorbiaceae. According to Metcalfe and Chalk (1950), the wood of *Antidesma*, *Bischoffia*, and *Phyllanthus* of the Euphorbiaceae is very similar to the wood of *Caloncoba*, *Erythrospermum*, and *Kiggelaria* of the Flacourtiaceae. Furthermore, the genera *Acalypha*, *Aporosella*, *Glochidion*, and *Hymenocardia* of the Euphorbiaceae suggest an alliance with the genera of the tribes Casearieae, Homalieae, and Flacourtieae (in part). These morphological and anatomical similarities

may be due to convergent evolution, as envisioned by Cronquist (1968); however, since a moderate number of both morphological and anatomical similarities are noted, it seems probable that some Euphorbiaceae and some Flacourtiaceae are allied, if not directly, then through common ancestry.

Order Salicales. According to Takhtajan (1969) and Cronquist (1968), the Salicales is derived from the Violales (including the Flacourtiaceae). Generally, this order is thought to be isolated and not closely related to any particular group, although it is often associated with taxa of the "Amentiferae." Hutchinson (1969) derived the Salicales from the Hamamelidales; however, Takhtajan and Cronquist claim that the gynoecium of Salicales is anomalous to that found in the subclass Hamamelidae. In an investigation of nectary structure, similarities were noted between the Violales and Salicales. In addition, similarities exist between pollen of some Flacourtiaceae and Salicaceae, although the pollen of Salicaceae is also similar to that of other unrelated families (Cronquist 1968; Keating 1973). However, investigations of the secondary phloem, chemistry, and hair structure suggests that the Flacourtiaceae and Salicaceae are not allied (Metcalfe & Chalk 1950).

According to Takhtajan (1969), who cited an unpublished thesis by Gzyrian (1952) which I did not see, the wood anatomy of Salicaceae is closer to the wood anatomy of Flacourtiaceae than to that of any other family. Takhtajan states that "both in external morphology and in wood anatomy the greatest similarity to the Salicaceae is observed in the subtribe Idesiinae of the Flacourtiaceae." If the wood of *Salix* and *Populus* (Salicaceae) and *Idesia* and *Itoa* (Idesiinae, Flacourtiaceae) are compared, many similarities, such as intervascular and vessel-ray pitting, type of perforation plate, and absence of axial parenchyma, are found to exist among these genera. In the Salicaceae, the more obvious differences include shorter and narrower rays, homocellular or heterocellular rays with only a few rows of upright cells, and no prismatic crystals or septate fibrous elements. Although these differences are distinct, the xylem anatomy does not reveal any features which would negate the evolution of the Salicaceae from Flacourtiaceae.

In addition, it is possible to construct a reduction series from *Idesia* and *Itoa* to *Populus* and *Salix*. The rays of *Idesia* and *Itoa* are 2- to 4-seriate and heterocellular with long uniseriate extensions. A reduction in the width of the rays and in the number of rows of upright ray cells, coupled with the complete loss of septate fibrous elements and prismatic crystals, would produce a wood structure resembling that of *Salix*. With the elimination of upright ray cells in *Salix*, secondary xylem resembling that of *Populus* would be evident. Carlquist's (1961) trends in the evolution of ray types in dicotyledons would support this possibility.

Stern and Brizicky (1958) have pointed out that it is necessary to be aware of the potentially erroneous conclusions inherent in selecting genera from a large heterogeneous family, such as the Flacourtiaceae, for

comparison with homogeneous families of a few genera. However, I believe that enough evidence has been gathered from the floral and wood structure to favor the evolution of the Salicales from Violales (including the Flacourtiaceae). Conclusive evidence supporting or negating this evolutionary trend must come from other independent fields of inquiry.

Orders Tamaricales and Capparales. Since the woods of Tamaricaceae and Capparaceae are relatively specialized and the woods of Flacourtiaceae are more primitive, the xylem anatomy cannot negate the possibility that Tamaricaceae (Tamaricales) and Capparaceae (Capparales) are derived from Flacourtiaceae (Violales or Bixales), but the numerous dissimilarities in the secondary xylem do not support such a derivation.

SUMMARY AND CONCLUSIONS

Anatomically, the Flacourtiaceae is composed of homogeneous tribes loosely united into a family. Based on the types of perforation plates and vessel pits, six anatomical groups are defined. The phylogeny of these groups is determined assuming a monophyletic origin for the Flacourtiaceae. Small vessel pitting in Flacourtiaceae is apparently a more specialized feature than large vessel pitting. In comparing the phylogeny of tribes of Flacourtiaceae, as proposed by Warburg and Gilg, to the phylogeny of the anatomical groups, a strong correlation is suggested. In addition, the wood anatomy supports Hutchinson's definition of the tribes Berberidopsideae and Oncobeae formerly included in Gilg's tribe Oncobeae.

For the most part, the wood anatomy supports the generic and tribal composition of Hutchinson's Flacourtiaceae. The transfer of Gilg's tribe Paropsieae from Flacourtiaceae to Passifloraceae is confirmed. On the basis of axile placentation and valvate calyx, Hutchinson transfers Gilg's subtribe Prockiinae (tribe Scolopieae) from the Flacourtiaceae to the tribe Prockieae in the Tiliaceae (including the Elaeocarpaceae). The secondary xylem in genera of tribe Prockieae is flacourtiaceous; however, the wood anatomy in the Prockieae is similar to that in the Elaeocarpaceae. Consequently, if tribe Prockieae is to be transferred on a morphologic-taxonomic basis, the evidence from the wood anatomy endorses the placement of the Prockieae in the Elaeocarpaceae.

Berberidopsis and *Streptothamnus* have distinctive wood anatomy for Flacourtiaceae. They have very long tracheids, solitary pores, very long vessel elements, and scalariform perforation plates which suggest a very primitive condition. Perhaps a new family should be defined to contain these two aberrant genera.

Hydnocarpus apparently has retained some of the primitive xylem features of the common ancestral stock of the Pangieae and Oncobeae. The long vessel and fibrous elements, opposite intervascular pitting, and scalariform perforation plates suggest the placement of *Hydnocarpus* in the primitive tribe Berberidopsideae, but the floral structure negates such a

suggestion. Chemotaxonomy indicates an alliance with the Oncobeae since only species of *Hydnocarpus* and some genera in Oncobeae contain chaulmoogra oil. In addition, the wood anatomy favors the submersion of *Taraktogenos* and *Asteriastigma* in *Hydnocarpus*.

The secondary xylem in the genera of the Scolopieae, Banareae, and Homalieae and in the genus *Prockia* of the Prockieae (Tiliaceae) is so similar that many genera among these tribes are not easily distinguishable anatomically. Thus, the xylem anatomy can neither support nor negate Hutchinson's formation of the new tribe Banareae and his transfer of *Trimeria* from tribe Homalieae to the Banareae. However, since *Prockia* is distinctive florally, it should remain united with the other genera of the Prockieae. In addition, a reduction series of vessel pitting is proposed for the genera of the Prockieae.

Tribe Flacourtieae has two major groups of genera, one of which has small vessel pitting and the other large vessel pitting. Furthermore, two subgroups exist within the group possessing large vessel pits.

Tetrathylacium and *Neoptychocarpus* of the specialized tribe Casearieae have exclusively scalariform perforation plates. Since *Tetrathylacium* has large vessel pitting (group I) and florally fits well in the Casearieae, it appears to have retained the primitive xylem structure from its ancestral stock, probably among the Berberidopsideae. In contrast, *Neoptychocarpus* has scalariform perforation plates and small vessel pitting; otherwise, it is similar to any other genus of the Casearieae. In many respects the secondary xylem of *Lacistema* (Lacistemaceae) is similar to that of *Neoptychocarpus*; thus, *Lacistema* and *Neoptychocarpus* might have evolved from the same forebears that gave rise to the Flacourtiaceae. However, more evidence is needed to support a close alliance between *Neoptychocarpus* and *Lacistema*.

Hutchinson's placement of the genera *Aphloia, Asteropeia, Dioncophyllum*, and *Goethalsia* in the Flacourtiaceae is negated on the basis of the xylem anatomy. *Aphloia* is anomalous as a member of the tribe Flacourtieae, for it has a primitive and unusual wood structure which to some extent resembles that of *Berberidopsis* and *Streptothamnus*. Therefore, the character of the xylem anatomy supports the proposed monotypic family Neumanniaceae, which has affinities with the Flacourtiaceae. The wood of *Asteropeia* is certainly not flacourtiaceous. Since Record (1942) and others rule out the Theaceae, the proposed monotypic Asteropeiaceae may be justified. Airy Shaw's (1952) statement that "*Dioncophyllum* [has] nothing whatever to do with the Flacourtiaceae" agrees with the evidence from the xylem. The secondary xylem and floral morphology suggest that *Goethalsia* is tiliaceous, not flacourtiaceous. Other genera sometimes associated with the Flacourtiaceae, but having nonflacourtiaceous wood structure, include *Peridiscus* (Peridiscaceae), *Soyauxia* (possibly Medusandraceae or Passifloraceae), and *Lethedon* (= *Microsemma*, Thymelaeaceae or Aquilariaceae).

The stock from which the Flacourtiaceae arose appears to be represented in the forebears of the Dilleniales. According to Cronquist, Fla-

courtiaceae (Violales) is derived from Dilleniales through the Theales. The secondary xylem of *Berberidopsis* and *Streptothamnus* is primitive and seems to indicate affinities with the Dilleniaceae. Thealean ray structure, axile placentae, and scanty endosperm are not suggestive of a flacourtiaceous ancestry.

The other families placed in the same order as Flacourtiaceae are for the most part more specialized than Flacourtiaceae. The wood anatomy does not negate any proposed intraordinal relationships; however, strong support for many of these relationships is also lacking. In some cases the wood structure of families in other orders is more similar to that of the Flacourtiaceae than the wood structure of families within the same order.

The xylem anatomy supports the derivation of order Passiflorales from the Flacourtiaceae through the tribe Paropsieae. Also, based upon anatomical structure, the Malvales or the Tiliales could be derived from the Flacourtiaceae through tribe Prockieae (Tiliaceae). In both cases chemotaxonomic evidence supports such derivations.

Selected genera of Flacourtiaceae and Euphorbiaceae have similar wood structure, lending support to the proposed evolution of order Euphorbiales from the Flacourtiaceae. *Idesia* and *Itoa* of the Flacourtiaceae and *Populus* and *Salix* of the Salicales have similar secondary xylem in some respects, and no features were found which would negate the evolution of order Salicales from the Flacourtiaceae. It has also been suggested that the Tamaricales and Capparales are derived from the Flacourtiaceae. Although the xylem anatomy does not negate the derivation of these orders from the Flacourtiaceae, support for such phylogenies is lacking.

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CENTER FOR WOOD ANATOMY RESEARCH
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THE NEOTROPICAL GENUS TACHIA (GENTIANACEAE)

BASSETT MAGUIRE AND RICHARD E. WEAVER, JR.

THE GENUS *Tachia* Aublet, consisting of nine species as here recognized, is characteristic of the rain forest lowlands and midlands of the Hylaea. It is unusual among the genera of the Gentianaceae in that characters separating it from others are well marked and constant.

All species are semiherbaceous or soft-stemmed perennials that usually develop a single stem. Sometimes they assume small treelike aspects. The essentially sessile flowers, arising in succession from a "cushion" or broad short shoot in the axils of the leaves, and the ovary mounted on a short, persistent, fibrous peg are unique in the family. Some species seem to be imperfectly delineated, possibly because of the scarcity of collected material. Such taxa here recognized may in the future, in the light of more adequate observation, require re-evaluation.

MORPHOLOGY — ANATOMY

Habit. As noted above, all members of the genus are perennial with subligneous, commonly subvirgate and little branched, quite characteristically greenish or bright yellow stems. This yellow coloration, present also in the calyces and often in the corollas, makes the plants conspicuous in their forest habitats.

Leaves. The leaves are entire and petiolate. Species of section TACHIA develop penniveined, coriaceous or chartaceous, seldom membranaceous blades. Those of section SCHOMBURGKIANA are invariably tri- or quintuple-veined and somewhat membranaceous.

Flowers. The calyx provides excellent and consistent criteria for the distinction of species in its degree of division, i.e., in the relative length of tube and lobes. The development or absence of calyx keels is consistent. In *Tachia schomburgkiana* the keel becomes a prominent wing which is extended and oriented beyond and at right angles to the plane of the calyx tube as a prominent lobe.

The corolla is tubular, often somewhat ventricose or expanded, with lobes commonly considerably shorter than the tube. In *Tachia parviflora* the tubes and lobes are essentially equal in length.

The five stamens are commonly exserted; their filiform filaments are adnate to the corolla tube, the point of attachment being a dependable character in the separation of species. Anthers are introrse, oblong, caudate and basifixed, with connective not produced, although the region of transition may sometimes be at an angle with the plane of the anther. Dehiscence is longitudinal and ventral.

The gynoecium is surmounted on a short but obvious glandular-lobed

gynobase, and is 2-carpellary. The ovary is unilocular, but the lateral sutures are deeply intruded, and placentation, therefore, is sometimes subpseudoaxillary. Styles exceed the ovary but are sometimes deciduous. The stigma is bilamellate.

Seeds are small, usually coarsely papillate, subprismatic, and commonly 0.4–0.6 mm. in longest axis.

Pollen. The pollen grains are sphaeroidal or rarely ellipsoidal, tricolporate, and usually 30–40 μm. along the longest axis. The exine is typically reticulate, but the width of the lumina, and therefore the coarseness of the reticulum, vary enormously from species to species. In *Tachia guianensis*, *T. grandifolia*, and *T. schomburgkiana* the lumina are large and the reticulum is relatively fine. In *T. parviflora*, however, the lumina are greatly reduced and the exine appears merely punctate. Finally, in *T. occidentalis* the exine appears completely smooth except for the presence of a few, irregularly spaced globules.

Unfortunately, as Nilsson (1967, 1968, 1970) has found to be the case with many Gentianaceae, the variation in pollen grain morphology is not correlated with gross morphological variation. Therefore, although it does provide specific characters, pollen morphology is of little phyletic significance in this genus.

PHYLOGENY AND GEOGRAPHY

Distribution patterns of the species of *Tachia* show a checkerboard configuration (MAP 1). From the material now available, no two species seem to be sympatric except *T. occidentalis* and *T. parviflora*, and these in only a small part of their assumed overlying ranges. For six species the ranges are, comparatively, "eastern" and local. Three species are "western": the range of *T. occidentalis* is the largest, albeit somewhat disjunct; that of *T. loretensis* is local; and that of *T. parviflora* is limited, but greatly disjunct.

There seems to be no significant geographic or ecologic correlation with presumptive systematic relationships within the genus. Indeed, if the members of section SCHOMBURGKIANA, so delimited largely because of the plinerved leaves, are considered the more primitive group, then its members have achieved the more extended distribution, with the distinctive *Tachia schomburgkiana* occupying a compact range on the eastern periphery of the Roraima sandstone sediments of Guyana and contiguous Venezuela, and the disjunct *T. parviflora* a range of eastern middle altitudes in central Peru and of similar habitat in Amazonian Bolivia. The indefinite locality for the original collection of *T. gracilis*, and the scanty collections from the pediments of Cerro Marahuaca of Roraima sediments in Territorio Amazonas of Venezuela, offer remote intermediate geographic connection.

Distribution of the six members of section TACHIA, characterized by penniveined leaves, similarly does not present any persuasive indication of progressive distribution as related to morphologic modification.

Tachia would fit into the Tachiinae of the Gentianeae as ordered by

MAP 1. Distribution of species of *Tachia*.

Gilg (1895) and thus be aligned in our area with *Macrocarpaea* (Griseb.) Gilg and the later described *Chorisepalum* Gleason & Wodehouse, which is endemic to the Guayana Highland. Palynologically, *Tachia* is similar to these two genera.

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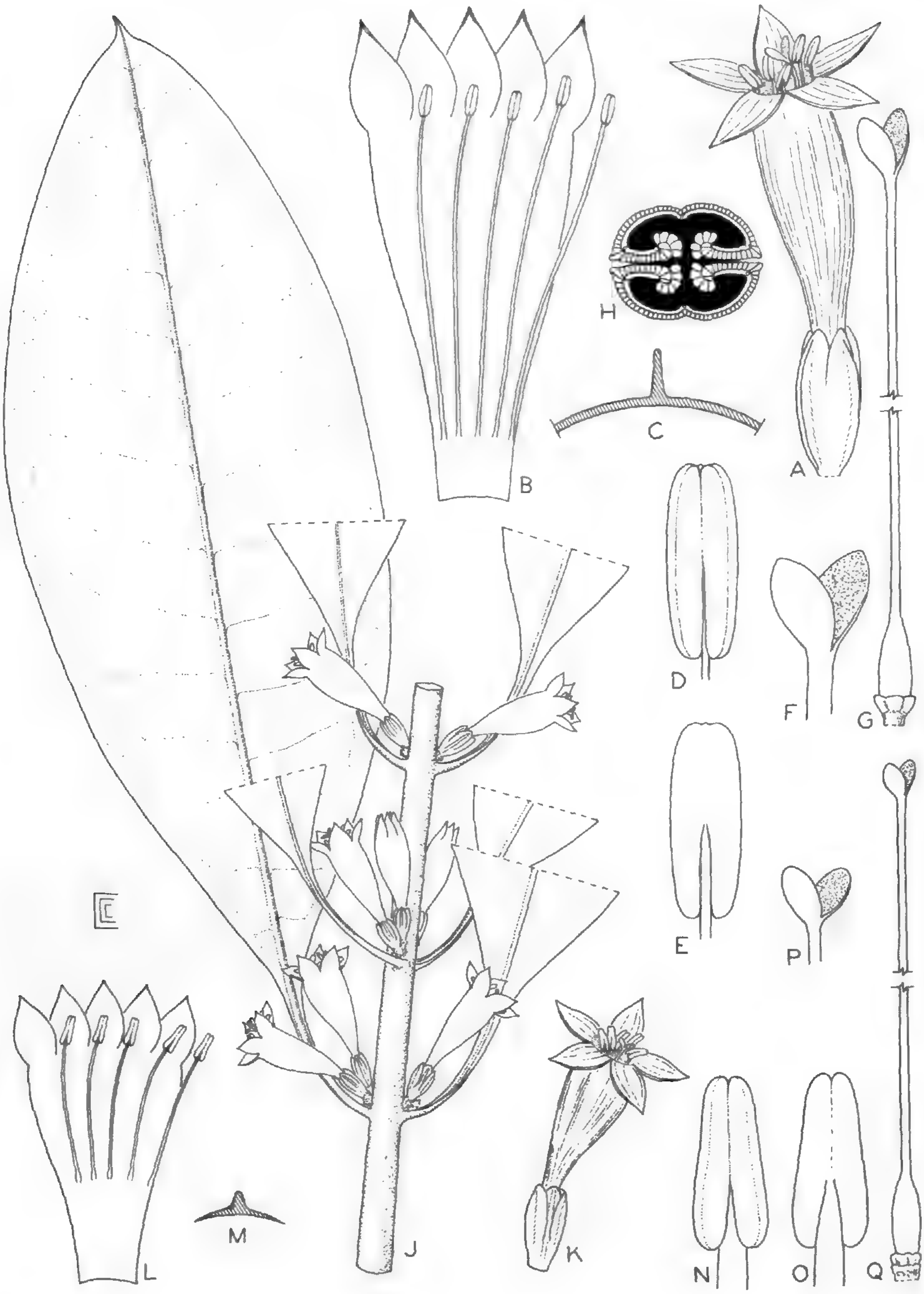

FIGURE 1. A–H, **Tachia occidentalis.** A, flower, × 1; B, opened corolla, × 1; C, sepal, cross-section diagram, × 6; D, anther, ventral view, × 6; E, anther, dorsal view, × 6; F, stigma, *Schunke-Vigo 1047*, × 3; G, pistil, *Schunke-Vigo 1047*, × 2; H, capsule, cross-section diagram, *Wolfe 12229*. J–Q, **Tachia grandifolia,** all from *Silva & Brazão 60842*. J, habit, × 1/2; K, flower, × 1; L, opened flower, × 1; M, sepal, cross-section, × 6; N, anther, ventral view, × 6; O, anther, dorsal view, × 6; P, stigma, × 3; Q, pistil, × 2.

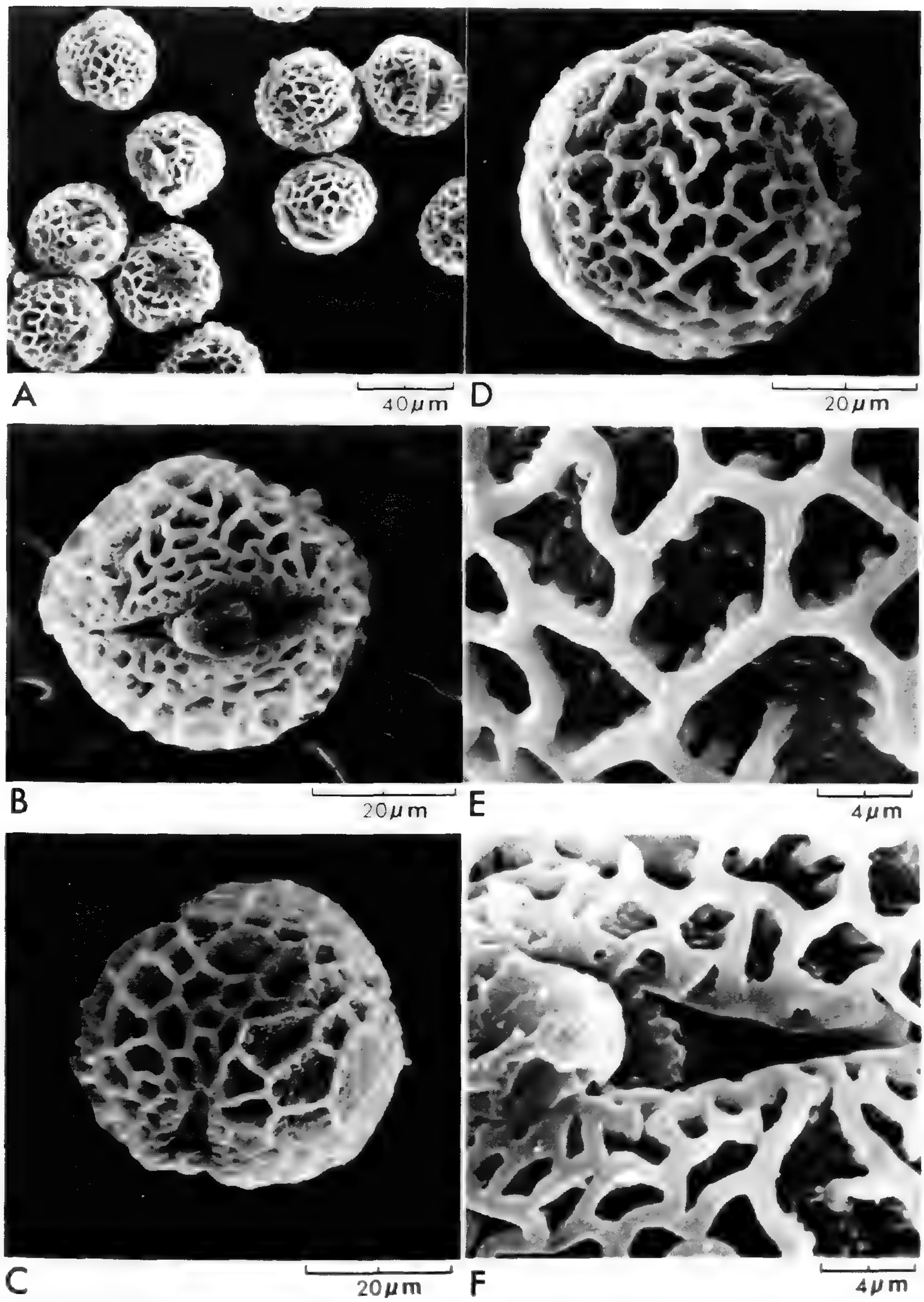

FIGURE 2. **Tachia grandifolia,** *Maguire et al. 37496,* SEM micrographs. Pollen grains sphaeroidal, 3-colporate, exine strongly reticulate. A, general field, × 500; B, sulcus and pore, equatorial view, × 1500; C, polar view, × 1500; D, intersulci, equatorial view, × 1500; E, reticulum, × 5000; F, portion of pore and sulcus, × 5000.

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SYSTEMATIC TREATMENT

Tachia Aublet, Pl. Guiane 1: 75. 1775.

Flowers 5-merous, solitary, rarely binary, sessile or subsessile on an axillary "cushion" or broad short shoot, thereupon often appearing seasonally and successively; calyx tubular, sometimes 5-carinate or alate, the lobes exceeding the tube or subequal, the interior at the base beset with a 5-lobed ring of upwardly directed squamellae; corolla infundibuliform, slightly ventricose, rarely short salverform, the tube much exceeding the apiculate lobes (except in *Tachia parviflora*); stamens 5, exserted, the filaments attached below the middle of the corolla tube or at the juncture of the tube and lobes, the anthers introrse, linear-oblong, caudate, basifixed, 4-celled; pollen grains simple, 3-colporate, sphaeroidal or rarely ellipsoidal, 33–45 μm. in diameter, the polar axis somewhat the longer, the exine clearly and sharply reticulate (psilate and globulate in *T. parviflora*), or punctate; the ovary borne on a short, persistent, glandular gynobase, 1-locular, the placentae deeply intruded, shortly inflexed, the ovules numerous; styles marcescent, exceeding the corolla; the stigmas strongly bilamellate; seeds numerous, small, prismatic, tuberculate.

Subligneous or soft-stemmed shrubby perennials, commonly simple-stemmed, often of small treelike aspect.

TYPE: *Tachia guianensis* Aublet.

This small genus may be divided into two groups, each reflecting close infrarelationships, one with pinnately veined leaves (6 species) and the other with quintuple-veined leaves (3 species). The most sharply distinctive species is *Tachia schomburgkiana*, with thin pli-veined leaves and a prominently winged calyx.

I. Section TACHIA. Blades of the leaves pinnately nerved.
Tachia guianensis (type species), *T. grandifolia*, *T. occidentalis*, *T. smithii*, *T. loretensis*, and *T. grandiflora*.

II. Section **Schomburgkiana** Maguire & Weaver, sect. nov. Laminae foliorum quintuplinervatae.
Tachia schomburgkiana (type species), *T. gracilis*, *T. parviflora*.

KEY TO THE SPECIES OF TACHIA

A. Leaves inconspicuously penninerved (sect. TACHIA).
  B. Calyx divided to below the middle; leaf blades thick and somewhat coriaceous, to 28 cm. long; corolla 4 cm. long or less; pollen grains sphaeroidal, exine reticulate. ..... 1. *Tachia grandifolia*.

B. Calyx divided to the middle or above; leaf blades chartaceous, not more than 20 cm. long; corolla 5 cm. long or longer.
  C. Corolla lobes coiled laterally at anthesis; calyx (2/5–) half as long as the corolla tube; pollen grains ellipsoidal, exine reticulate. ..... 2. *Tachia guianensis.*
  C. Corolla lobes plane at anthesis; calyx a third as long as the corolla tube, rarely nearly half as long.
    D. Calyx narrowly 5-alate, divided 1/3 of its length; pollen grains subsphaeroidal, exine smooth, sparingly beset with globules. ..... 3. *Tachia occidentalis.*
    D. Calyx not alate, at most 5-carinate, divided to ca. the middle.
      E. Corolla narrowly tubular-funnelform, the tube not expanded above; filaments conspicuously recurved or hook-shaped at the apex. ..... 4. *Tachia smithii.*
      E. Corolla funnelform, the tube conspicuously expanded above; filaments straight or upcurved at the very tip.
        F. Corolla less than 6 cm. long; lateral veins of the leaves forming an acute angle (45°–60°) with the midvein and arching toward the tip of the leaf; pollen grains sphaeroidal, exine reticulate. ..... 5. *Tachia loretensis.*
        F. Corolla 7 cm. long or longer; lateral veins of the leaves forming nearly a right angle with the midvein and spreading toward the margins of the leaf. ..... 6. *Tachia grandiflora.*
A. Leaves distinctly 3–5-nerved (sect. SCHOMBURGKIANA).
  G. Corolla more than 5 cm. long, the tube conspicuously surpassing the calyx.
    H. Calyx strongly 5-alate, 2.5–4.0 cm. long, the lobes 1.1–2.8 cm. long; pollen grains sphaeroidal, exine reticulate. ..... 7. *Tachia schomburgkiana.*
    H. Calyx not alate, less than 2 cm. long, the lobes less than 1 cm. long. ..... 8. *Tachia gracilis.*
  G. Corolla less than 2.5 cm. long, the tube barely surpassing the calyx; pollen grains sphaeroidal, non-reticulate, smooth, minutely punctate. ..... 9. *Tachia parviflora.*

1. **Tachia grandifolia** Maguire & Weaver, sp. nov. TYPE: **Brazil.** Amazonas: in catinga forest between Missão Salesiana and Serra Pirapucú [Neblina], Rio Maturacá, Rio Cauaburi-Negro, 400–800 m., *Silva & Brazão 60824* (holotype, NY; isotypes, IAN, RB, US, K). FIGURES 1, J–Q; 2; 3.

Herbae perennes saepe basibus lignosis; caulibus vulgo 2–4 m. altis crassis viridibus ca. 12–15 mm. diametro glabris, internodiis vulgo 12–14 cm. longis; foliis oppositis, petiolis 2–4 cm. longis triangularibus, laminis ovalibus vel oblongo-ovalibus vel aliquando late oblanceolatis 22–28 cm. longis 10–14 cm. latis firme subsucculentis, basibus acutis, apicibus obtusis, abrupte apiculatis vel abrupte brevi-acuminatis, costis prominentibus, inconspicue pinnivenatis; floribus axillaribus vulgo solitariis aliquando pluribus subsessilibus; calyce 10–12 mm. longo cylindrico non-alato valde 5-carinato glabro in sicco valde 5-angulari, tubo crasso intus glabro, lobis 5 oblongis obtusis 5–6 mm. longis cucullatis anguste scariomarginatis;

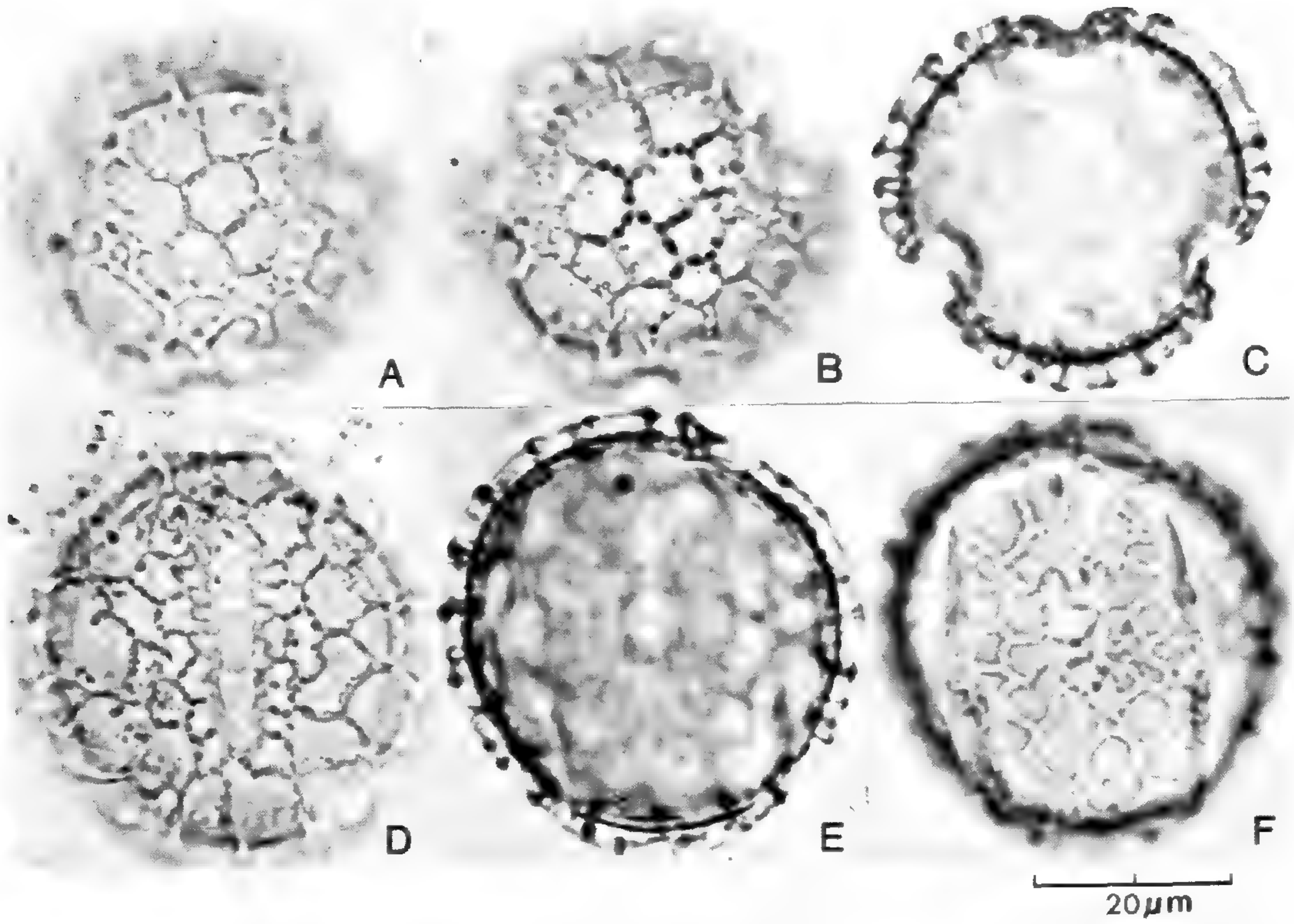

FIGURE 3. **Tachia grandifolia,** *Maguire et al. 37496.* Light microscope micrographs, × 1500. A–C, polar views. A, upper focus level; B, lower focus level; C, median focus level. D–F, equatorial views. D, upper focus level, note sulcus and pore; E, median focus level; F, lower focus level, note laterally placed sulci.

corollis infundibuliformibus ventricosis 4.5–5.0 cm. longis, tubo 1.8–2.0 cm. longo, limbo 2.8–3.0 cm. longo, lobis 8–9 mm. longis acutiusculis; staminibus 5, filamentis 6–8 mm. longis, juncto tubo et limbo affixis, antheris oblongis ca. 3 mm. longis 1 mm. caudatis; pollinibus sphaeroideis 3-colporatis 42–45 μm. diametro sporodermate reticulato muris tenuibus; ovario uniloculari bivalvulo valvulis breviter inflexis, placentationibus valde inflexis subparietalibus, ovulis numerosis, gynobase glandulosa 2–3 mm. alta, stylis 26–28 mm. longis, stigmatibus bilamellatis ovatis obtusis ca. 2 mm. longis; capsulis 15–17 mm. longis; seminibus brunneis prismaticis echinulatis 0.4–0.5 mm. longis.

DISTRIBUTION. Low-altitude catinga or sometimes flooded forests or adjacent terra firma, approaches to Cerro de la Neblina.

SPECIMENS EXAMINED. **Venezuela.** Territorio Amazonas: Río Yatua, Río Pacimoni, occasional at 110 m., Piedra Arauicaua, *Maguire, Wurdack & Bunting 37477* (NY, 2 sheets, VEN, US); Piedra Tururumeri, 110 m., *Maguire, Wurdack, & Bunting 37496* (NY, 2 sheets, VEN, US); woodland at base of Cerro Arauicaua, 125–250 m., *Steyermark & Bunting 102534* (US). **Brazil.** Amazonas: Cucuhy, Rio Negro, 120 m., *Holt & Gehriger 355* (US).

1a. **Tachia grandifolia** Maguire & Weaver var. **orientalis** Maguire & Weaver var. nov. TYPE: **Brazil.** Territorio Roraima: vicinity of

Posto Surucucus Mission, forest on terra firme, Serra dos Surucucus, 2° 42–47′N, 63° 33–36′W, *Prance et al. 10084* (holotype, NY; isotypes, F, GH, US).

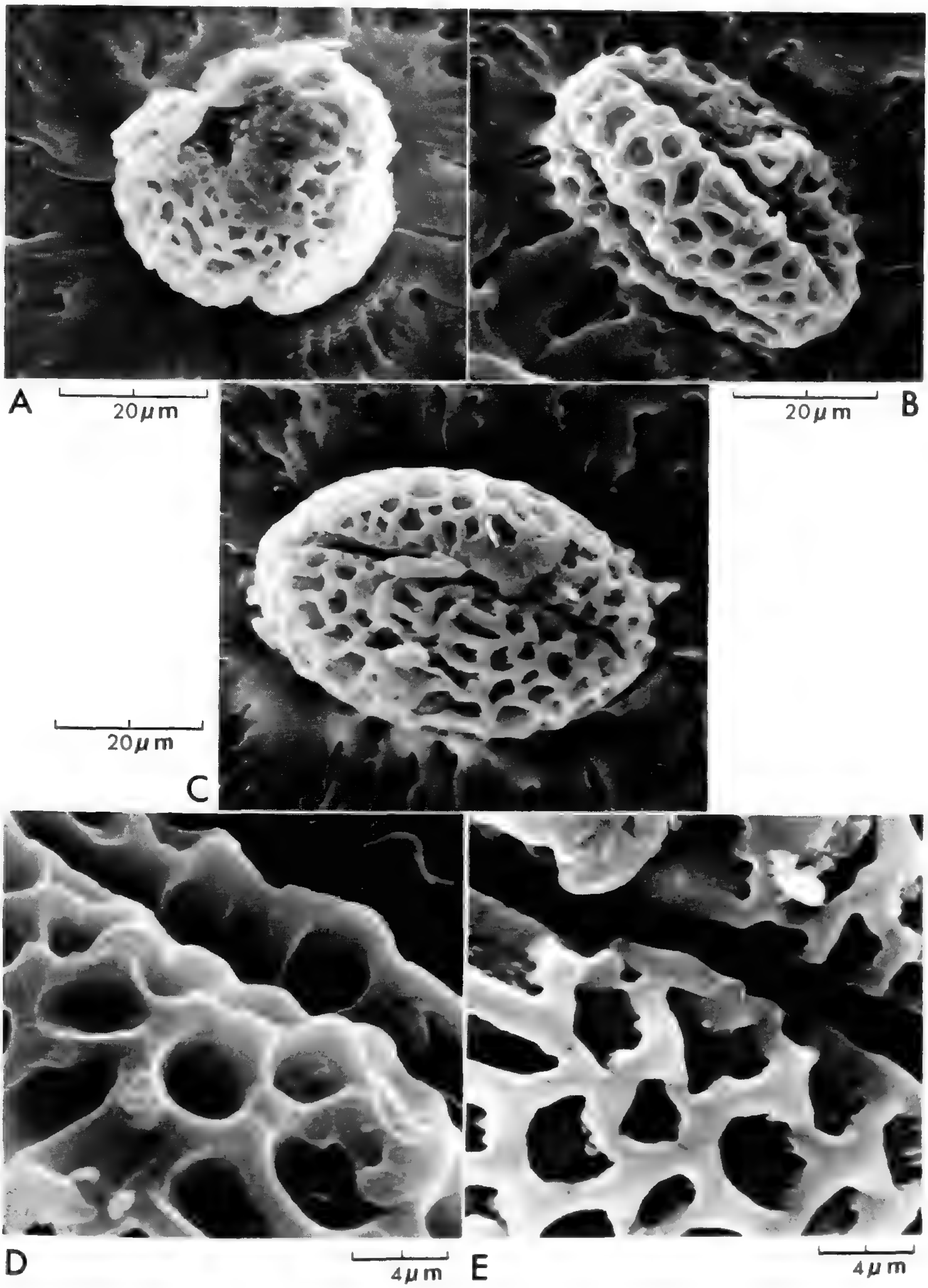

FIGURE 4. **Tachia guianensis,** *Maguire 24611.* Pollen grains ellipsoid, 3-colporate, strongly reticulate. SEM micrographs. A, polar view, × 1500; B, equatorial intersulci view, × 1500; C, equatorial view, sulcus, × 1500; D, reticulum, × 5000; E, reticulum, sulcus, × 5000.

Varietati *grandifoliae* similis sed foliis parvioribus, petiolis tenuibus, 12–26 mm. longis, laminis elliptico-acuminatis, minus coriaceis, vulgo 10–15 cm. longis, frequenter acuminatis.

DISTRIBUTION. Treelet of median altitudes in Roraima Formation forests, drainages of the Uraricoera, Brazil, and the Alto Paragua and Alto Caroní, Venezuela.

SPECIMENS EXAMINED. **Brazil.** Territorio Roraima: 4–6 km. south of Auaris, 800 m. 4°3′N, 64°22′W, *Prance et al. 9823* (F, GH, NY, US); in upland forest

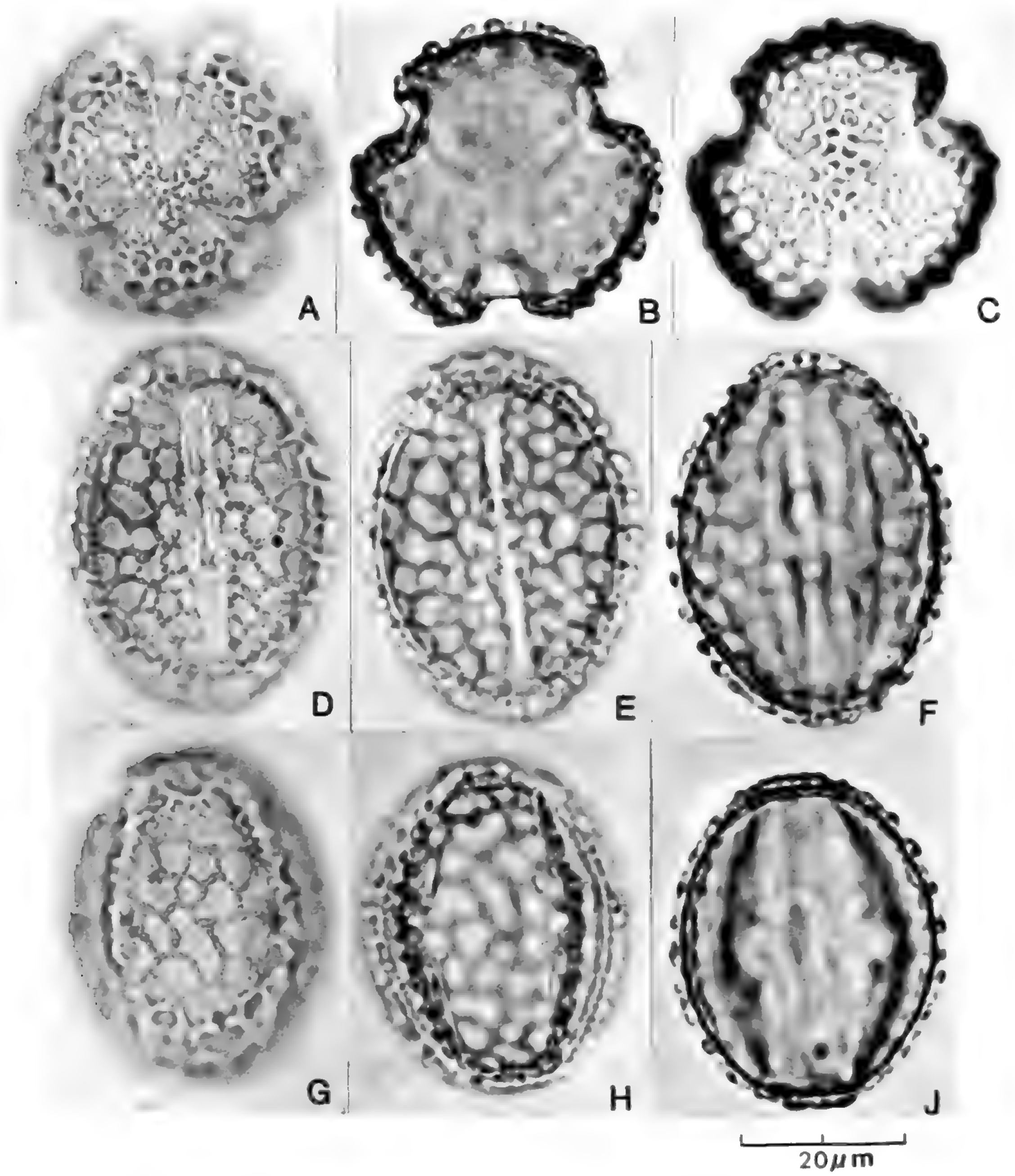

FIGURE 5. **Tachia guianensis,** *Maguire 24611.* Light microscope micrographs, × 1500. A–C, polar views. A, upper focus level; B, median focus level; C, lower focus level. D–F, equatorial views at successive focal levels, grain oriented with sulcus uppermost. G, H, & J, equatorial views at successive focal levels, grain oriented with intersulci area uppermost.

at 1800 m. alt., plateau of Serra dos Surucucus 2°42–47′N, 63°33–36′W, *Prance et al. 9962* (F, INPA, NY, US). **Venezuela.** Bolívar: exposed rocky slopes of quebrada on southwestern-facing portion of Chimantá-tepuí (Torono-tepuí), 1410 m., *Steyermark 75407* (F, NY, 2 sheets); at base of sandstone bluff, Sierra Ichún, tributary of Río Paragua, 500–625 m., *Steyermark 90420* (NY, US).

The variety *orientalis* is obviously a smaller-leaved variant of *Tachia grandifolia*, but, as the name indicates, it is the more eastern segregate. The form and structure of the scanty and ill-preserved flowers and fruit of both varieties obviously demonstrate close consanguinity, but vegetatively var. *orientalis* is readily distinguishable by its smaller, thinner, and acuminate leaves.

Specimens of var. *orientalis* came to our attention after the completion of the main study, and accordingly its description and citations were later inserted into the typescript. The description of *Tachia grandifolia* was drawn wholly from specimens of var. *grandifolia*.

2. **Tachia guianensis** Aublet, Pl. Guiane 1: 75. *t. 29.* 1775. TYPE: an Aublet specimen, presumably of French Guiana (P) (IDC 6213.11: I 7). FIGURES 4, 5.

Shrubs or small trees to 4 m. tall; branches subterete, yellow; leaves thin-membranaceous, elliptic (sometimes broadly so) to oblong-elliptic, caudate, cuneate to somewhat rounded at the base, 8.8–19.0 cm. long, and 3.4–9.0 cm. broad, the petiole 5–21 mm. long; calyx exalate, 2.7–3.5 cm. long, (2/5–)1/2 the length of the corolla tube, 2–3 times as long as the petioles, divided ca. 1/3 of its length (or less) into lanceolate, acute or acuminate, erosulate lobes; corolla yellow, narrowly tubular-funnelform, 6.0–7.7 cm. long, the lobes spreading, coiled laterally at anthesis, oblong-lanceolate, abruptly acuminate, 11–16 mm. long and 4–7 mm. broad, 1/4 as long as the tube; stamens inserted in the lower third of the corolla tube, well below the apex of the calyx; filaments straight or slightly upturned at the apex, 4.0–5.2 cm. long, conspicuously surpassing the corolla tube, the anthers oblong, ca. 3 mm. long; pollen grains sphaeroidal, exine prominently reticulate; style 5.0–5.8 cm. long, finally surpassing the corolla lobes, stigma lobes spathulate to suborbicular, 2–3 mm. long; capsule fusiform, to 4 cm. long, projecting from the persistent calyx.

DISTRIBUTION. Small trees or shrubs with subherbaceous stems, commonly at low or middle altitudes in rain forests of the Guianas.

SPECIMENS EXAMINED. **Guyana.** Kalakoon, Mazaruni River, *Jenman 2406* (NY); dense upland forest, Tumatumari, *Gleason 56* (GH, NY, US); Tacoubea Creek, Kurupung River, *Altson 316* (NY); 400 ft. ca. 83 miles, Bartica-Potaro Road, *Tutin 303* (US); near Makreba Falls, Kurupung River, upper Mazaruni region, *Pinkus 291* (GH, NY, US); wallaba forest near 14th milepost, Bartica-Potaro Road, *Sandwith 1111* (F, NY); Kaieteur Savannas, *Maguire & Fanshawe 23382* (K, NY, US); forest slope, Mount Ayanganna, 1000–1500 m.; *Maguire, Bagshaw, & Maguire 40599* (K, NY); frequent in mixed evergreen forest on laterite, below

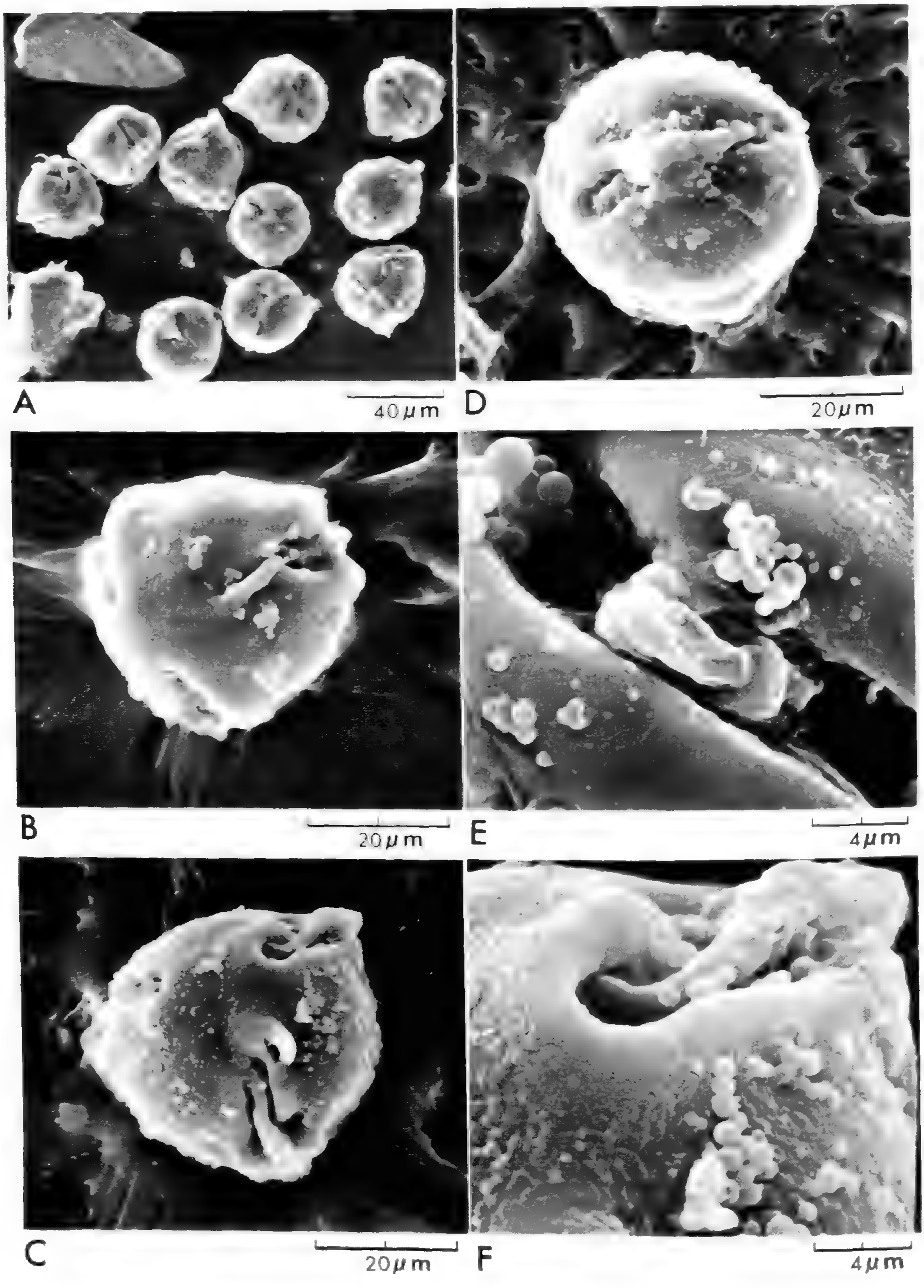

FIGURE 6. **Tachia occidentalis.** SEM micrographs. Pollen grain sphaeroidal-triangular, 3-colporate, exine finely subverrucose, sublaevate. A, general field, *Schultes 12476*, × 500; B, polar view, *Killip & Smith 26163*, × 1500; C, polar view, *Schultes 12476*, × 1500; D, equatorial view, *Schultes 12476*, × 1500; E, pore and sulcus, *Killip & Smith 26163*, × 5000; F, portion of polar view, *Schultes 12476*, × 5000, note heavily bordered sulcus.

talus of cliffs along NE side of Mount Ayanganna, elev. below 762 m., *Tillett, Boyan, & Tillett 45024* (NY, US). **Suriname.** Tafelberg: vicinity Base Camp, Tafelberg Creek, *Maguire 24098* (NY, 2 sheets, U); infrequent in high mixed forest, rocky slopes, Arrowhead Basin, 625 m., *Maguire 24611* (NY, 2 sheets, U); in savanna forest between Tafelberg and source of Saramacca River, on Roraima sand, *Wessels Boer 1540* (A, NY, U).

3. **Tachia occidentalis** Maguire & Weaver, sp. nov. TYPE: **Colombia.** Vaupés: Río Apaporis, Cachivera de Jirijimo y alrededores, ca. 250 m., *Schultes & Cabrera 12476* (holotype, GH). FIGURES 1, A–H; 6.

Frutex vel arbor parva perennis subherbacea saepe basi lignosa; caulibus ad 8 m. altis quadrangularibus vel subteretibus; foliis oppositis laminibus tenuiter membranaceis indistincte pinnivenatis ellipticis vel oblongo-ellipticis abrupte vel graduate ad basim contractis 7–20 cm. longis 2.7–7.7 cm. latis, petiolis 6–17 mm. longis; flore solitario axillari; calyce 14–25 mm. longo petiolis excedentibus anguste 5-alato, lobis ca. 1/3 longitudine tubi; corollis tubulari-infundibuliformibus 6.4–7.7 cm. longis viridibus vel luteo-viridibus aliquantum arcuatis, lobis patentibus vel reflexis oblongo-ovatis abrupte brevi-acuminatis vel apiculatis erosulatis 10–15 mm. longis 5–8 mm. latis; staminibus 5, filamentis circa basin tubi affixis 4.0–4.7 mm. longis tubo vix exserto, antheris anguste oblongis ca. 5 mm. longis; pollinibus subsphaeroideis 3-colporatis ca. 40 μm. diametro sporodermate laevi sparse minute globulifero; stylis aliquantum exsertis, lobis stigmatum ca. 3 mm. longis suborbicularibus; capsulis non vidis.

REPRESENTATIVE SPECIMENS. **Colombia.** Amazonas: trocha entre El Encano y La Chorrera, ca. 180 m., *Schultes 3876* (F, GH, US); Río Popeyacá (tributary of Apaporis between Río Piraparaná and Raudal Yayacopi), near mouth, ca. 700 ft., *Schultes & Cabrera 15571* (US). Vaupés: Raudal de Jirijimo, Río Apaporis, *Schultes & Cabrera 14670* (GH); Río Apaporis, entre los ríos Kananarí y Pacoa, 250 m., *Garcia-Barriga 13932* (NY, US); Río Apaporis, Soratama, *Schultes & Cabrera 16144* (US); Macu-Parana, *Allen 3084* (MO); headwaters of Caño Teemeeña, Lobo Igarapé, *Schultes & Cabrera 17334* (US). **Brazil.** Amazonas: São Paulo de Olivença, *Ducke 1115* (MO, NY, US); Macubeta on Rio Marié, *Fróes* (Krukoff) *12439/183* (A, NY); Rio Negro, Taracuá, *Rodrigues & Pires 141* (US); Rio Negro, Ilha das flores, foz do Rio Uapés, *Pires 394* (NY); Tonantins, *Ducke 22389* (US). Brasiliae borealis: prope San Gabriel da Cachoeira, *R. Spruce 2190* (F). **Peru.** Huanuco: southwest slope of the Río Llullapichis watershed, on the ascent of Cerros del Sira, ca. 860 m., *Wolfe 12229* (F); Agua Blanca (Camino a Monzón), 700–800 m., *Schunke-Vigo 1047* (NY). Junín: Pichis Trail, Santa Rosa, 625–690 m., *Killip & Smith 26163* (F, NY, US). Loreto: Aguaytia, 300 m., *Woytkowski 5348* (F, MO); Santa Ana on the Upper Río Nanay, *Williams 1243* (F); Florída, Río Putumayo, at mouth of Río Zubineta, 180 m., *Klug 2123* (A, F, GH, MO, NY, US).

The most widespread and most frequently collected of the species, *Tachia occidentalis* has for the most part passed as *T. guianensis*. It differs from that species, however, in its shorter, narrowly alate calyx, and its pollen

grains that are characterized by having a smooth rather than a reticulate exine.

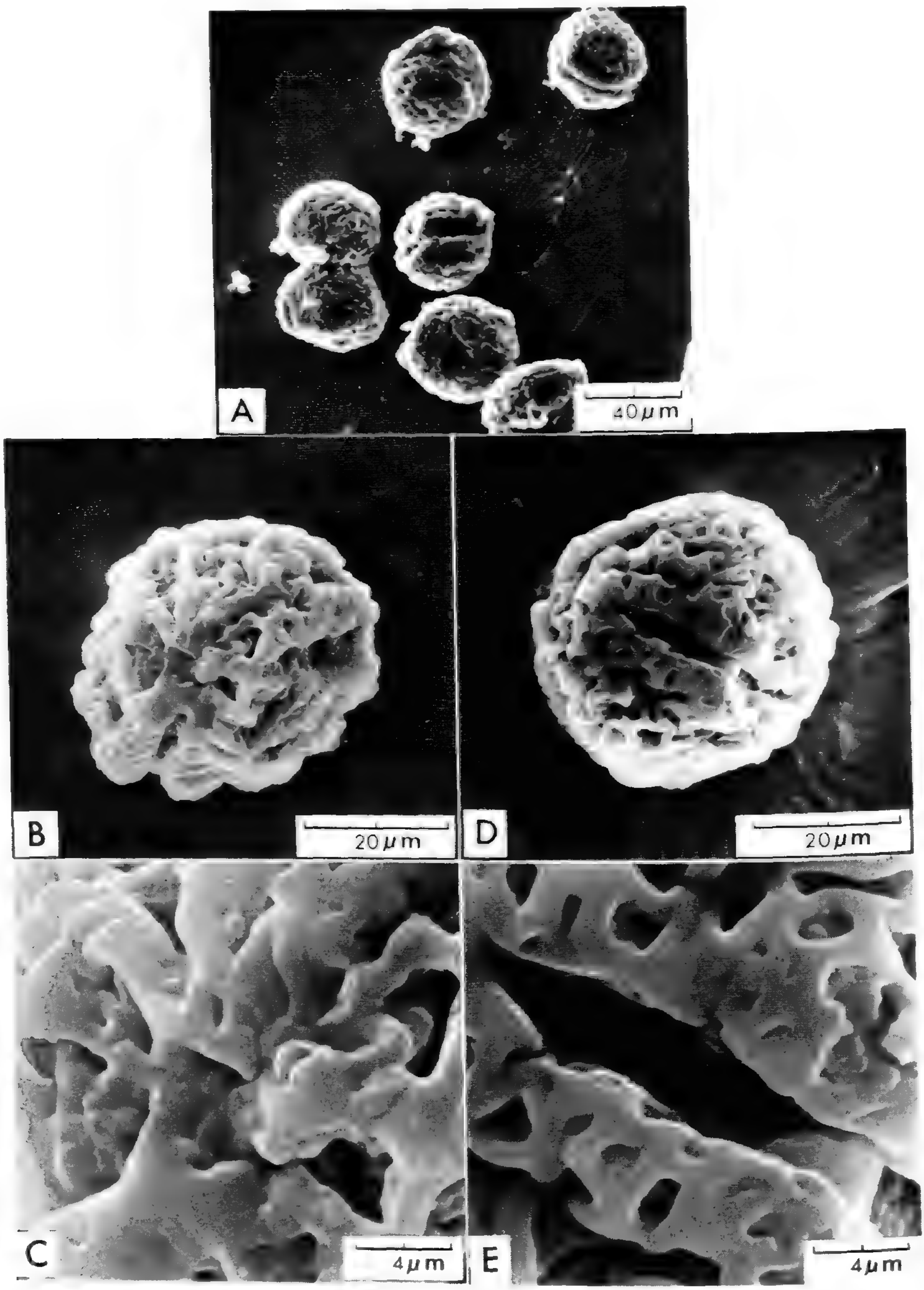

FIGURE 7. **Tachia loretensis,** *Klug 1563.* SEM micrographs. Pollen grains sphaeroidal, 3-colporate, exine reticulate-corrugate. A, general field, × 500; B, polar view, × 1500; C, portion of polar view showing corrugate sculpture, × 5000; D, equatorial view, × 1500; E, portion of pore and sulcus, × 5000.

4. **Tachia smithii** Maguire & Weaver, sp. nov. TYPE: **Brazil.** Pará: in dense forest on southern slopes of the Akarai Mountains, in drainage of Rio Mapuera (Trombetas tributary), 500–700 m., *A. C. Smith 2931* (holotype, NY; isotypes, A, F, MO, US).

Frutex simplex ad 4 m. altus; foliis oppositis, laminibus tenuiter membranaceis ellipticis caudatis cuneato-attenuatis 10.0–17.2 cm. longis 4–8 cm. latis, venis lateralibus inconspicuis cum costa angulo 90° formantibus, petiolo 1–2 cm. longo; flore vulgo solitario axillari; calyce 1.8–2.5 cm. longo ecarinato, lobis oblongis obtusis vel acutiusculis longitudinaliter tubo aequalibus; corollis albis infundibuliformibus 6.5–7.3 cm. longis, lobis recurvatis ovatis abrupte acuminatis erosulatis ca. 15 mm. longis 8–11 mm. latis; staminibus 5, filamentis 3.9–4.5 cm. longis infra medium tubi affixis, filamentis circa apices recurvis, antheris sagittatis ca. 3 mm. longis introrsis; stylo 5.0–5.2 cm. longo, lobis stigmatum ovatis vel ellipticis, 4–6 mm. longis; capsulis non visis.

DISTRIBUTION. Known only from the type locality, this plant is similar to *Tachia guianensis*, with which it may be sympatric. It differs from that species, however, in its generally shorter calyx, its white corolla, its plane corolla lobes, and its conspicuously recurved or hooklike filaments.

5. **Tachia loretensis** Maguire & Weaver, sp. nov. TYPE: **Peru.** Loreto: in dense forest, ca. 100 m. alt., Mishuyacu, near Iquitos, *Killip & Smith 29925* (holotype, US; isotypes, F, NY). FIGURE 7.

Frutex ad 1 m. altus; ramis subteretibus; foliis oppositis, laminis tenuimembranaceis ellipticis brevi-caudatis cuneato-attenuatis 10.0–16.5 cm. longis 3.0–6.5 cm. latis, venis lateralibus inconspicuis pinnatis, formantibus angulo acuto cum costa versus apicem recurvatis, petiolis 1.0–2.5 cm. longis; calyce 1.4–2.0 cm. longis minus 1/2 longitudine corollae lobis et tubo longitudine aequalibus ecarinatis, lobis oblongis, obtusis vel rotundatis erosulatis; corollis albis 5–5.9 cm. longis late tubuliformibus, tubo infra cylindricum supra expansum, lobis late ovatis vel oblongo-ovatis abrupte acuminatis erosulatis 10–13 mm. longis 5–8 mm. latis; staminibus 5 aliquantum exsertis, filamentis 1.6–2.3 cm. longis medio tubi affixis; granis pollinis sphaeroideis ca. 40 μm. diametro sporodermate reticulato; lobis stigmatum spathulatis; capsulis maturis ca. 13 mm. longis.

DISTRIBUTION. Known only from the vicinity of Iquitos, Peru.

SPECIMENS EXAMINED. **Peru.** Loreto: forest, *Klug 1277* (NY, US); forest near Iquitos, 100 m. alt., *Klug 1563* (F, US).

6. **Tachia grandiflora** Maguire & Weaver, sp. nov. TYPE: **Brazil.** Amazonas: Serra da Lua, Río Urubu, between Cachoeira Iracema and Natal, *Prance et al. 5042* (holotype, F; isotypes, GH, INPA, NY, US).

FIGURE 8. A–G, **Tachia parviflora,** *Buchtien 1431.* A, flower, × 2; B, opened corolla, × 2; C, sepal, cross-section diagram, × 3; D, ovary, style, and stigma, × 4; E, ovary, cross-section diagram; F, stigma, × 4; G, capsule, × 2. H–S, **Tachia schomburgkiana.** H, habit, *Maguire, Steyermark, & Maguire 46914* and *Tillett & Tillett 45447*, × 1/2; J, flower, *Pinkus 3*, × 1; K, opened flower, *Pinkus 227*, × 1; L, sepal, cross-section diagram, *Maguire 46794*, × 3; M, anther, ventral view, *Pinkus 3*, × 4; N, anther, dorsal view, *Pinkus 3*, × 4; O, anther, lateral view, *Pinkus 3*, × 4; P, stigma, *Tillett & Tillett 45447*, × 2; Q, ovary, cross-section diagram, *Maguire, Steyermark, & Maguire 46780*; R, capsule, *Pinkus 3*, × 2; S, seed, *Pinkus 3*, × 20.

Frutex cum ramis scandentibus; ramis subteretibus vel angulosis obscuris; foliis oppositis, laminis tenui-membranaceis ellipticis caudatis cuneato-attenuatis 9.5–15.5 cm. longis 4.0–6.6 cm. latis, petiolis 9–14 mm. longis; calyce exalato, 21–22 mm. longo tubo et lobis plus minusve aequalibus, lobis obtusis vel acutiusculis erosulatis; corollis tubuliformibus aliquantum late, tubo infra expansum 7.0–7.7 cm. longo, lobis imbricatis ovatis abrupte acuminatis ca. 16 mm. longis 11–12 mm. latis; stylis et antheris aliquantum exsertis, antheris ca. 4 mm. longis; lobis stigmatum suborbicularibus ca. 3 mm. longis.

DISTRIBUTION. Known only from two collections, the type and the following: **Brazil.** Pará: sousbois de la forêt, Jurupá, *Ducke 16168* (US).

7. **Tachia schomburgkiana** Bentham, Jour. Bot. Kew Misc. 2: 204. 1854. TYPE: **Guyana.** On the mountains covered with thick forest between Roraima and the Cuyuni, at an elevation of 3000–4000 ft., *Richard Schomburgk 1546* (holotype, K, not seen).

FIGURES 8, H–S; 10; 11; 12.

Shrubs to 2 m. tall, branches quadrangular; leaves thin-membranaceous, distinctly 5-nerved, the upper lateral pair closely paralleling the midvein into the apex, elliptic to ovate or ovate-lanceolate, caudate, ± abruptly constricted to the petiole and the base therefore rounded, 8.8–17.0 cm. long and 4.0–8.5 cm. broad, the petiole winged to the base, 1.0–1.5 cm. long; calyx yellowish, 2.6–4.0 cm. long, 1/2 to nearly 3/4 as long as the corolla tube, much exceeding the petioles, the tube strongly 5-alate and the lobes formed by an extension of the 3 mm. broad wings, the lobes long acuminate, 1.1–2.8 cm. long, as long as to nearly half again longer than the tube, auriculate at the base (this probably representing the juncture of the lobes proper with the greatly extended wing), the auricles erosulate; corolla yellow or yellow-green, tubular-funnelform, 6.5–7.4 cm. long, the tube constricted in the lower half, then expanding and cylindric or widening slightly to the apex, the lobes oblong-lanceolate, abruptly short-acuminate, erosulate, apparently recurved, 11–14 mm. long and 5–6 mm. broad, ca. 1/6 the total length of the corolla; stamens 5, the filaments inserted near the base of the corolla tube, below the apex of the calyx tube; filaments well surpassing the corolla tube, 4.2–5.2 cm. long, the anthers oblong, obtuse, 3–4 mm. long; pollen grains sphaeroidal, ca. 40 μm. in diameter, the exine reticulate; style equaling the corolla lobes, 5.0–5.5 cm. long; lobes of the stigma ovate; capsule including the beak 2–2.5 cm. long, the apex barely protruding from the persistent calyx; seeds strongly papillose.

SPECIMENS EXAMINED. **Venezuela.** Bolívar: frequent in montane woodland. 400 m. alt., La Escalera, Río Uiri-yuk, Alto Río Cuyuni, *Maguire, Steyermark, & Maguire 46780* (NY, VEN); occasional in mixed montane forest below La Escalera, 600–800 m., Río Uiri-yuk, Alto Río Cuyuni, *Maguire, Steyermark, & Maguire 46914* (NY, VEN); km. 119 south of El Dorado, 1030 m. alt., *Steyer-*

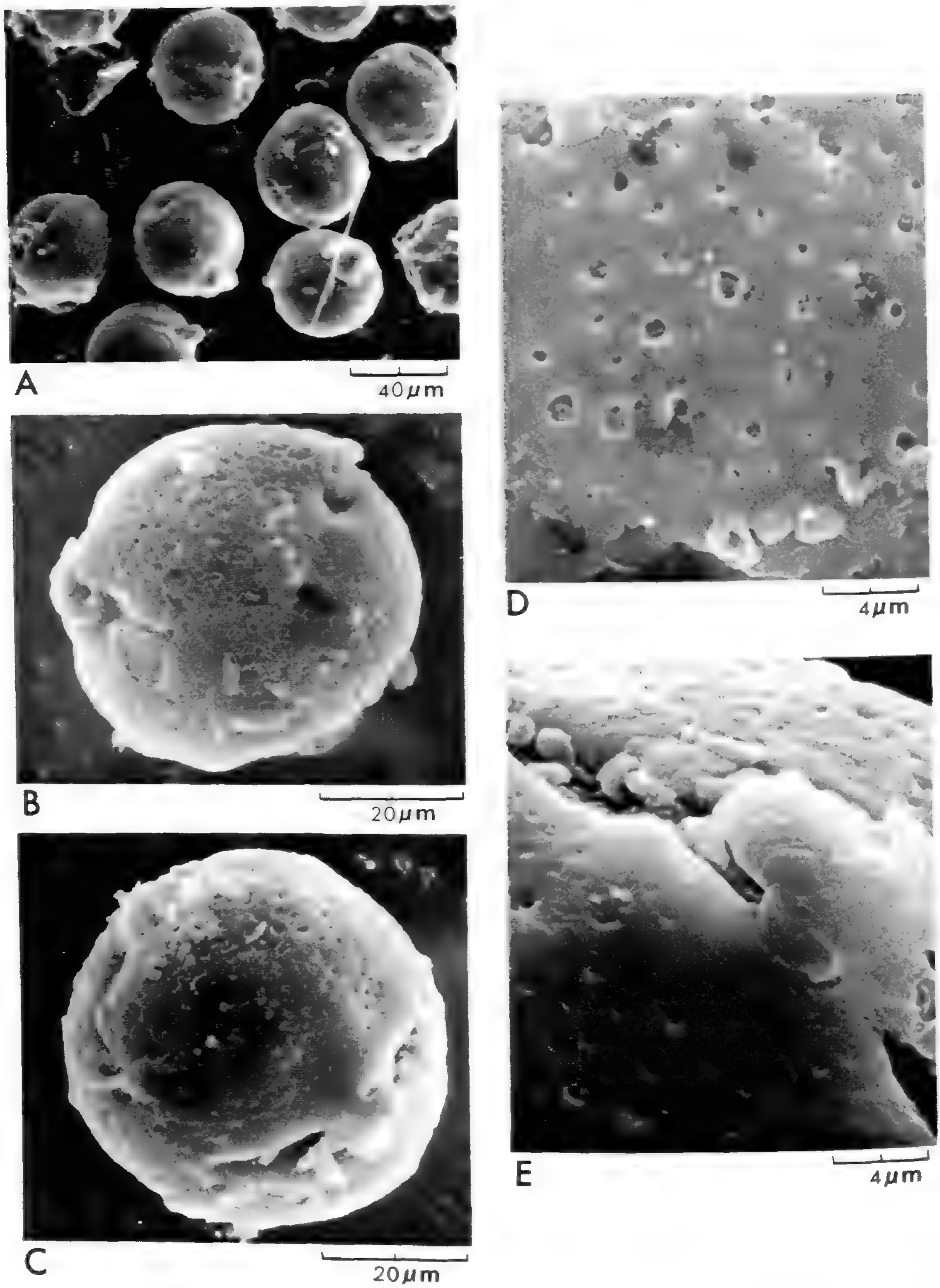

FIGURE 9. **Tachia parviflora,** *Dudley 13072.* SEM micrographs. Pollen grains sphaeroidal, 3-colporate, exine puncti-laevate. A, general field, × 500; B, polar view, × 1500; C, oblique equatorial view, × 1500; D, pitted exine, note irregular puncti or perforations, × 5000; E, portion of spore and sulcus, × 5000.

mark, Dunsterville, & Dunsterville 93044 (NY, US, VEN). **Guyana:** Kamakusa, upper Mazaruni River, *Leng 331* (NY); Makreba Falls, Kurupung River, *Altson 355* (NY, 2 sheets); near Makreba Falls, Kurupung River, rocky soil on hillside,

Pinkus 3 (NY, US); Membaru Creek, upper Mazaruni River, *Pinkus 227* (NY, US); frequent in *Cunuria* forest, 1000 m. elev., *Maguire & Fanshawe 32345* (NY, 2 sheets, US); in mixed evergreen forest, along line to E end of Karowtipu, 500 m. alt., Kako River, *Tillett & Tillett 45447* (NY).

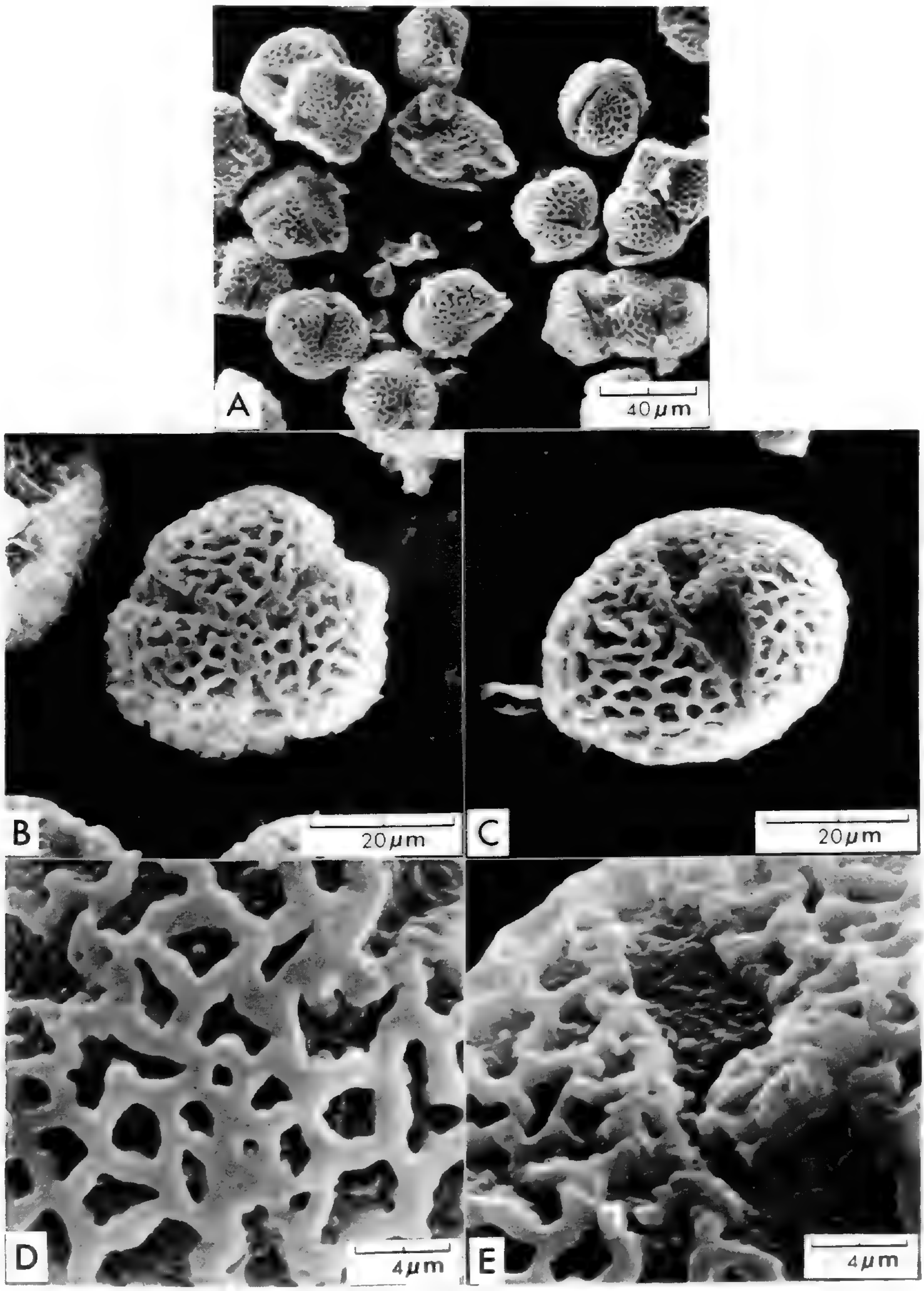

FIGURE 10. **Tachia schomburgkiana,** *Tillett & Tillett 45447*. SEM micrographs. Pollen grains sphaeroidal, 3-colporate, strongly reticulate. A, general field, × 500; B, polar view, × 1500; C, equatorial view, × 1500; D, reticulum, × 5000; E, portion of pore and sulcus, × 5000.

8. **Tachia gracilis** Bentham, Jour. Bot. Kew Misc. 6: 203. 1854. TYPE: **Guyana** (Brazil ?): "Serra Mey." *Schomburgk 145.S* (holotype, K; photograph, NY).

A shrub reputedly to 3 m. tall; leaves thin-membranaceous, distinctly 5-nerved, narrowly ovate to elliptic, caudate, abruptly constricted to the petiole, 5.5–10.5 cm. long and 2–4.3 cm. broad, the petiole 6–17 mm. long; calyx yellow, 14–20 mm. long, longer than the petiole, 2/5–1/2 as long as the corolla tube, weakly carinate, divided halfway to the base into oblong, acutish lobes; corolla tubular or tubular-funnelform, yellow, 5–6 cm. long, the lobes recurved, oblong-lanceolate, abruptly acuminate, 9–11 mm.

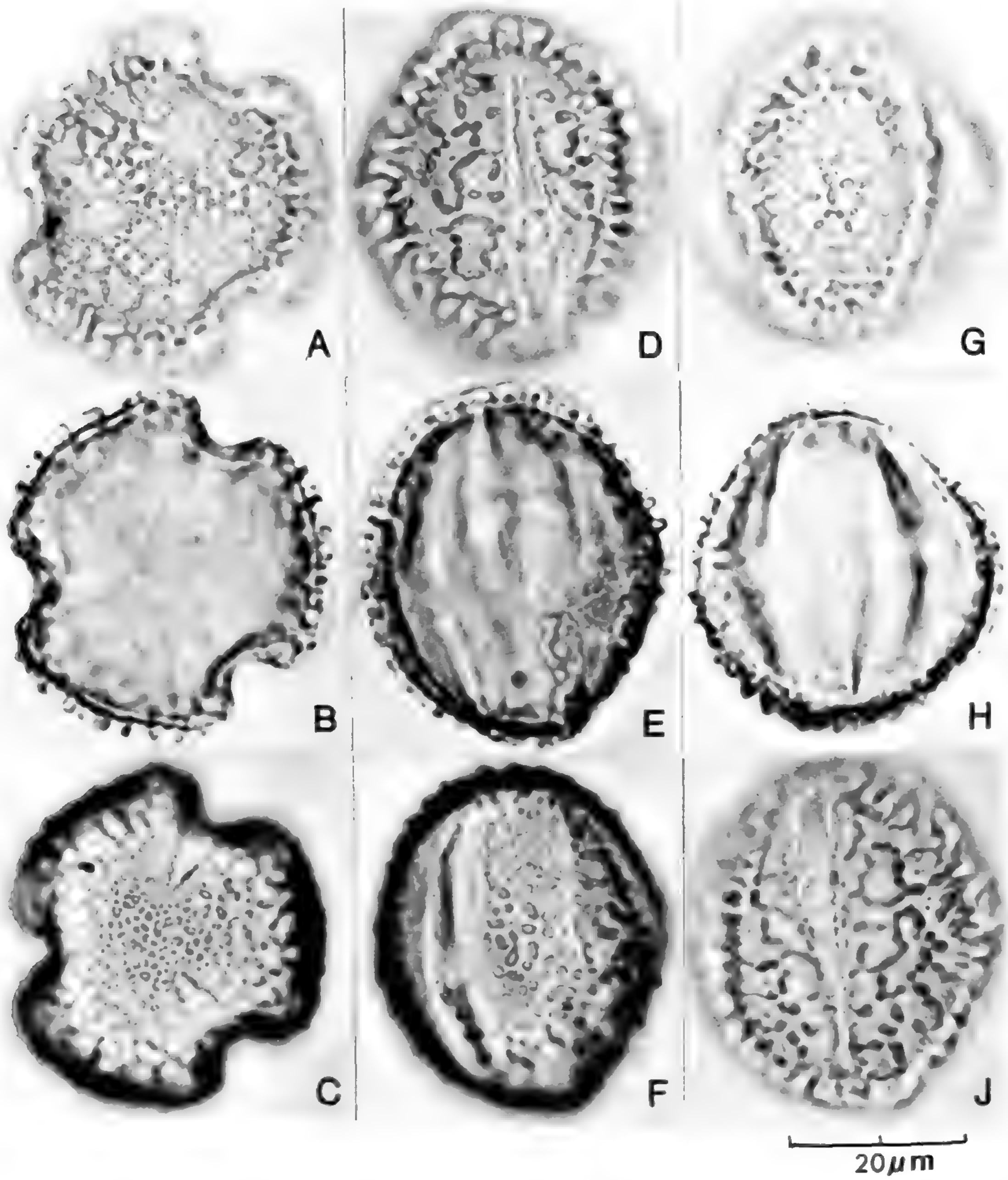

FIGURE 11. **Tachia schomburgkiana**, *Tillett & Tillett 45447*. Light microscope micrographs. × 1500. A–C, polar views at successive focal levels; D–F, equatorial views at successive focal levels, sulcus uppermost; G–J, equatorial views at successive focal levels, intersulci area uppermost.

long and 5–6 mm. broad, ca. 1/5 the total length of the corolla; filaments inserted near the base of the corolla tube, 3.5–4.5 cm. long, well surpassing the corolla tube; anthers oblong, obtuse, ca. 3 mm. long; style 3.7–4.8 cm. long; stigma lobes ovate; capsule ca. 2 cm. long.

SPECIMENS EXAMINED. **Venezuela.** Territorio Amazonas: Cerro Marahuaca, 1000 m., *Maguire & Maguire, Jr. 29207* (NY); Sierra Parima, frontera #8, 1300 m., *Steyermark, Pantchenko, & Dilarmando Mendes 107570-A* (A); Sierra Parima, a lo largo de la frontera Venezolana-Brasilera, a unos 45 km. al Noroeste des las cabeceras del Río Orinoco, 1300 m., *Steyermark 106081* (VEN); Cerro Duida, a lo largo del Orinoco, 1000 m., *Fariñas, Velasquez, & Medina 391* (VEN).

The Schomburgk collection, upon which this name rests, was cited from British Guiana without a collector's number. However, the original ticket bears the number "145.S," the "S" indicating that the collection was represented by a single specimen only. Reference to the lists of Schomburgk collections, deposited at Kew in the Bentham files, shows the number "145.S" to occur in a list of unicate collections without regard to chronology or geography. "Serra Mey," the cited locality, as suggested by the Portuguese geographic name, is probably in Brazil and probably in the Rio Uraricuera (Araricuara), the Alto Río Orinoco or Rio Negro area. A similar disposition has been made for the range designation of *Sipapoa vestita* (Benth.) Maguire of the Malpighiaceae.

9. **Tachia parviflora** Maguire & Weaver, sp. nov. TYPE: **Colombia.** Caquetá: Bosques entre 1000 y 1300 m. alt., vertiente oriental, Sucre, Cordillera Oriental, *Cuatrecasas 9059* (holotype, F; isotype, US).
FIGURES 8, A–G; 9.

?*T. pavonii* Gilg in Engler & Prantl, Nat. Pflanzenfam. **4**(2): 93. 1895 (*nomen nudum*).

Frutex vel arbor parva, ad 6 m. alta, aliquantum scandens; ramis subteretibus; foliis oppositis, laminis tenui-membranaceis 5-nervatis jugo primario interdum indistincto, petiolis 1.0–2.5 cm. longis; floribus frequenter pluribus; calyce 1.0–1.5 cm. longo, tubo brevissimo, lobis ad 1.4 mm. longis ecarinatis lanceolatis obtusis vel acutiusculis scario-marginatis erosulatis; corollis chloritici-albis brevi-hypocrateriformibus 1.4–2.4 cm. longis tubo vix calyce longiore, lobis oblongis abrupte brevi-acuminatis erosulatis ad apicem reflexis 6–9 mm. longis 3–5 mm. latis; staminibus 5, exsertis, filamentis subulatis ad summum tubi affixis ad basim expansis, antheris oblongis ca. 2 mm. longis; granis pollinis sphaeroideis, ca. 40 μm. diametro non reticulatis laevibus minute punctatis; stylis brevibus ca. 8 mm. longis, lobis stigmatum obovatis; capsulis immaturis longioribus calyce rostro prominento.

DISTRIBUTION. Rather widely distributed at median altitudes from Colombia to Bolivia.

SPECIMENS EXAMINED. **Peru.** Huanuco: SW slopes of Rio Llullapichis watershed, on ascent of Cerros del Sira, ca. 1400 m. alt., *Dudley 13072* (F); SW

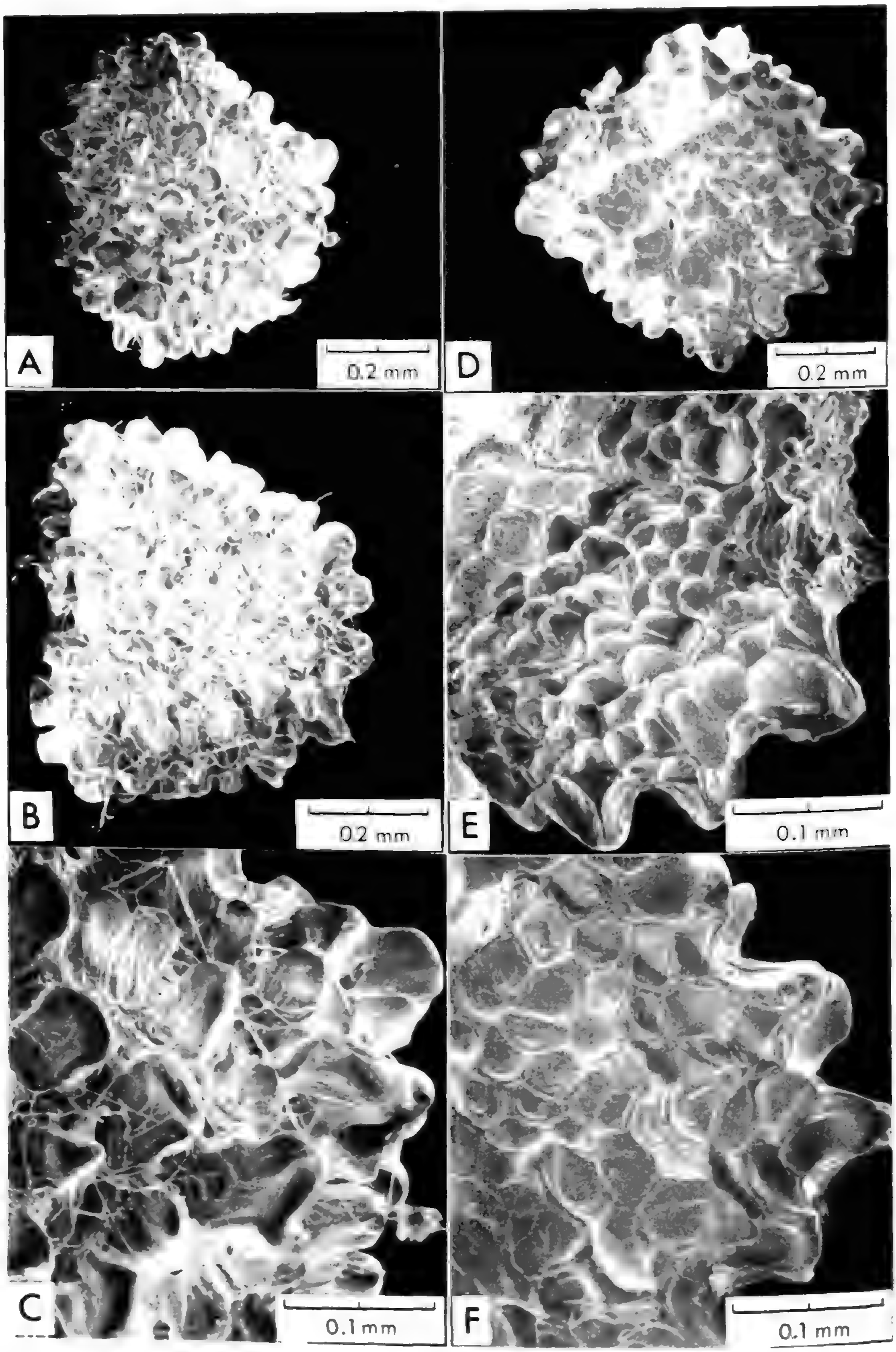

FIGURE 12. **Tachia schomburgkiana.** SEM micrographs. Seed strongly papillose. A–C, *Pinkus 3*. A, × 100; B, × 120; C, × 300. D–F, *Maguire 46794*. D, × 100; E and F, × 300.

slope of Río Llullapichis watershed, on ascent of Cerros del Sira, 860 m., *Wolfe 12228* (F), *12249* (F). **Bolivia.** Larecaja: Mapiri Region, San Carlos, 850 m., *Buchtien 1431* (F, NY, US); Dept. of La Paz, Copacabana (ca. 10 km. south of Mapiri), 850–950 m. alt., *Krukoff 11004, 11091* (A, F, MO, NY, US).

This species is unique in the genus because of its small flowers with salverform corollas. Therefore, it is possibly the species which Gilg (1895) had in mind when he mentioned "*T. Pavonii* Gilg, mit ziemlich kleinen Bl. (üten)." The name "*T. Pavonii*," being a *nomen nudum*, is illegitimate, however.

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SPECIES VERSATILITY IN SHORE HABITATS

HUGH M. RAUP

MATERIALS FOR THE present paper are derived from notes and plant collections made during seven field seasons in the years 1926–30, 1932, and 1935, in the Athabaska-Great Slave Lake region of northwestern Canada. In the course of this work shoreline vegetation was described at approximately 130 places. Seventy-nine of these were on the shores of sloughs, ponds, and small lakes, while the remaining 51 were on the shores of the larger lakes (Athabaska and Great Slave) or on river banks and deltas. The following discussion deals primarily with the vascular flora, though reference is made on occasion to lichens and mosses.

A part of the material was published in the author's "Botanical investigations in Wood Buffalo Park" (1935). Itineraries of the seven expeditions will be found in this paper and in others dealing with the vascular flora and its distribution (Raup, 1930b, 1936, 1941). A brief account of the vegetation of Shelter Point, Lake Athabaska, was published in 1928, and a paper on the shore vegetation at Fort Reliance, Great Slave Lake, in 1930(a). The most complete sets of supporting plant collections are at the National Herbarium of Canada in Ottawa, and at the Harvard University Herbaria in Cambridge, Massachusetts.

Most of the vegetational data for the present study were gathered along transects selected because they showed differences or similarities when compared in the field with other transects. The differences were recorded first in terms of species' *presence* or *absence*, and second in terms of *primary* and *secondary* species. In common ecological parlance the primary species in an assemblage would be termed "dominants." They are the ones that give a specific form, color, or other characteristic to an assemblage of plants by which the latter is readily distinguished visually from those adjoining it. All other species in the assemblage are regarded as secondary. Usually the primary species are those that predominate in numbers of individuals, but in sparse vegetative cover or in tree or shrub vegetations the populations of primary species may be smaller than those of secondary species. The selection of primary species was done by eye.

A general view of the shore floras of the region shows them occupying an extraordinary number of lakes, ponds, and sloughs that dot the landscapes. They are numerous in the great deltas and flood plains of the lower Athabaska, Peace, and Slave rivers, but are especially abundant on the crystalline and metamorphic rocks of the Canadian Shield. Travelers for many years have noted the large numbers of small bodies of water along their routes, but full realization of their extent awaited the advent of aërial photographic mapping. An area of 16 square miles (4 miles square) selected at random in the country north of Lake Athabaska con-

tains over 100 ponds and lakes large enough to appear on a map scaled at 4 miles to one inch. The number of smaller water bodies can only be conjectured, but a conservative estimate would be another 100. The ponds and small lakes throughout this region are infinitely variable in shape, size, and depth. The large lakes also present a wide variety of shorelines, from almost vertical rock cliffs to wide shelving beaches of sand, mud, or shingle. Further variation is found in the morainic and karst topography west of the Slave River, in flood-plain sloughs and deltas, and in the saline flats that border the Salt and Little Buffalo rivers. However these bodies of water were formed and whatever their subsequent history, their abundance and the large proportion of the total flora they harbor force us to consider their marginal plant life as one of the most important elements in the vegetation of the region.

When this study was begun in 1926, major emphasis was placed on the "development of the vegetation." The units of study were to be "communities" or "associations" of plants described in terms of form and floristic content. The "development" was largely confined to the theory of succession among communities, leading to more or less stable climax or climaxes. Time scales for the processes were not clearly defined, but it was assumed that the present state of the vegetation could be rationalized by projection of these processes backward to the disappearance of the last glacial ice.

The vascular flora of the region was not well enough known in 1926 to cover the needs of such a vegetational study. This applied not only to the less common species but also to many abundant ones which, as "dominant" species, gave form and character to "communities." Consequently the collection and identification of the species was the first necessity. Between 1926 and 1935 the known vascular flora of the region was thus increased by about 30%. Most of the new records were range extensions, for the region has very little endemism.

The writer's earliest papers on the region reflect the above frame of reference (1928, 1930a & b, 1935). After the field season of 1935 this frame became almost wholly inadequate.

A determined effort was made to use "communities" or plant "associations" as the basic units of study. This could be effective only if the assemblages of species, or at least of the so-called "dominant" species, were largely repetitive within such habitat complexes as could be defined with the knowledge and facilities at hand. Because the identity of the "communities" rested upon floristic composition, it was thought that they probably had some form of internal organization among mutually compatible species which added validity to their use as study units.

Wide variation in species composition of the shore assemblages began to appear in the early work on Great Slave Lake (1927). Seventeen small bodies of water were studied on Fairchild Point, a peninsula about 10 miles long in this lake. Each of these ponds was unique, either in the arrangement of its vegetation zones or in the "dominant" species composition of the zones. The field seasons in the Wood Buffalo Park (1928–

30) brought out even greater variability, not only among the many ponds and small lakes that were studied, but also within habitats on the shores of individual bodies of water. A lake about 10 miles long on the upland west of the Slave River required eight transects for a fair sampling of its shore vegetation. Twenty-eight different "communities" of vascular plants were described in these transects, involving 20 "dominant" species. Field experience strongly suggested that in the region as a whole the study of more pond and lake shores would yield more different "communities," more zonal variations in the vegetation, and additional "dominant" species.

The use of the "community" or "association" as the basic unit for the study of the shore vegetation became extremely doubtful. Nonetheless, these terms continued to be used (Raup, 1934, 1935), and the complexity was in part avoided by annotated descriptions of assemblages believed to be "typical" of the various habitats. Maximum confusion was reached in the 1935 season when many shores around the whole of Lake Athabaska were examined, particularly those of the intricate lagoon systems on the south shore. Here no two of the hundreds available for study seemed to have the same "community" structures and contents.

The idea of orderly successional development among "communities" had to be greatly restricted in space and time. The last cover of glacial ice did not retreat steadily, but in stages so that land surfaces available for colonization by plants were of varying ages. Owing to the general topography of the region and the geography of its drainage systems, there had been large variations in the levels of its major lakes and in the development of its flood-plain and delta systems (see below; also Raup, 1930b, 1931, 1946, and Cameron, 1922). Lengths of time during which physical habitats could remain relatively stable, and in which long-term biological successions could have occurred began to be notably shortened. A high water level seen at Lake Athabaska in 1935 was maintained throughout the growing season, and effectively drowned all the shore "successions" that were described in prior years. The frequency of such floods has been estimated recently by Stockton and Fritts (1973; see below), and it is not unlikely that time periods during which the shores of this lake can remain physically stable are shorter than the life spans of most of the perennial plants that make up the shore vegetation. If this is the case, successions in this vegetation are reduced to fragments which, if they exist at all, have indeterminate beginnings and ends.

The extent to which analogues of these findings can be seen in the shores of smaller upland lakes and ponds is unknown. Many of these smaller water bodies are held up by morainic dams, are deposited at different times, have varying materials, and erode at different rates. Extreme cases occur in the karst topography west of the Slave River, where fluctuations in pond levels of 10 to 30 feet are not uncommon, giving rise to curious "duplications" of shore zonations at different levels in the same sink hole. Here the fluctuations are due to unpredictable changes in the movement of ground water through the underlying cavernous gypsum.

With the failure of the "community" as a viable, repetitive unit for

study and rationalization of the shore vegetation, and with the greatly restricted use of biological succession for interpreting the development of this vegetation, it became necessary to construct some other frame of reference. The present paper explores the use of the species as the basic study unit. There is abundant precedent for this in the literature of floristic plant geography (cf. Raup, 1942; Wulff, 1943; Cain, 1944; Böcher, 1954). But there is less precedent in ecological plant geography, which has been concerned primarily, during the present century, with the structure, physiology, and "dynamics" of "communities" (cf. Gleason, 1926; Cain, 1947). The use of species as study units has been greatly stimulated since the 1920's by research on ecotypic variation within species and by the realization that taxonomically defined species contain biotypes and ecotypes that behave differently in their relations to environments (Turesson, 1922, 1925, 1927, 1929; Hultén, 1937a; Clausen, Keck, & Hiesey, 1940; Mayr, 1964). The implications of this research for the geography of plants were rather thoroughly reviewed by Cain in his "Foundations of plant geography" (1944).

In the present paper the term "community" is replaced by "assemblage," which carries fewer connotations of relationships among species that are unknown or nonexistent. The terms "primary" and "secondary," though not common in ecological literature, are not new in the sense in which they are used here. They were so used by Hultén in his "Flora of the Aleutian Islands" (1937b).

THE VASCULAR FLORA AND ITS SHORE HABITATS

The total known vascular flora of the Athabaska-Great Slave Lake region numbers approximately 750 species. The shore flora contains 424 of these, or about 57% of the total. Seven species are excluded from the following studies. Three appear to be endemic or so localized that their ranges and local behavior are not well known. The other four, though they have wide ranges southward in the continent, are apparently sporadic in the southern part of our region. Thus the number for the total shore flora in the following analyses will be 417.

Species units used here are those in the author's catalogue of the flora of the region (1936) except for a few additions and changes made by more recent students. Sixty-three families are represented in the shore flora, and 177 genera. Twelve of the families are represented by 10 or more species each and supply two thirds of the flora (262 spp., 63%). The same families supply a similar proportion of all the primary species (93 spp., 64%). The 12 families are as follows (numbers in parentheses indicate first the total number of species and second the number of primary species): Cyperaceae (59–23), Compositae (38–5), Gramineae (37–22), Salicaceae (23–14), Rosaceae (18–7), Ranunculaceae (16–1), Zosteraceae (15–7), Juncaceae (13–3), Ericaceae (12–10), Caryophyllaceae (11–0), Scrophulariaceae (10–0), Saxifragaceae (10–1). Half of these families

produce five or less of the primary species so that nearly half of all the primary species in the flora come from only six of the families. These families are among those that have been most poorly collected in boreal America, because their numerous species are not commonly recognized in the field and usually have been lumped together as "willows," "grasses," "sedges," "rushes," or the last three simply as "gramineous" plants. The genus *Carex* alone has 40 species in this flora, 14 of which were noted as primary in one or more assemblages. The Gramineae are represented by 10 genera and 37 species, among which 22 were primary. *Salix* has 21 species, of which 13 were primary. Of the 14 species of *Potamogeton*, six were found to be primary. The preceding four groups, which probably are the most frequently "generalized" by students of vegetation, contain more than one fourth of the shore flora of this region, and about 38% of all the primary species that give the shore scape its characteristic features.

A common arrangement of shore vegetation in the region has four major "form types." First there is a zone of aquatics, both submerged and emergent. Inshore from this is usually a zone of some kind of wet meadow made up principally of grasses, sedges, and rushes. The third landward zone is mainly of upright or decumbent shrubs. Finally there is a marginal zone of upright shrubs and trees which merges with the surrounding forest. For purposes of study and analysis this is an oversimplification. It gives no indication of the wide variation that occurs from one body of water to the next, or even on different shores of the same lake or pond. For purposes of analysis, therefore, 10 types are recognized, although it is probable that with further field work more would be found. Because the 10 types all occupy sites that differ in moisture regime, substrate or topographic position, they are considered as habitat-vegetation complexes, and the term "habitat" will be used for them in most cases. In the following list the numbers in parentheses are the approximate numbers of different assemblages seen in each type.

The term "muskeg" refers to vegetations that develop in undrained depressions with beds of hygrophytic mosses.

1. Aquatic habitats, with submerged and/or emergent plants (29).
2. Saline or brackish sloughs or wet meadows (15).
3. Muskeg grass-sedge meadows, with moss substrata (35).
4. Open (treeless) shrub muskegs (37).
5. Shrub-tree borders of muskegs (32).
6. Damp to wet sand and/or gravel on shores of rivers and ponds or on the lower beaches of large lakes (12).
7. Vegetation of upright shrubs and trees on upper beaches of large lakes (41).
8. Grass-sedge meadows on river flood plains or local river deposits, with silt or silt and thin moss substrata (49).
9. Shrub-tree borders of meadows on flood plains or local river deposits (25).
10. Vegetation of herbs and low or trailing shrubs on middle beaches of large lakes (22).

Data are not available from which to describe with any degree of precision the physical and nutritional properties of these habitats. The arrangement (from 1 to 10) of the preceding list approximates, from greatest to least, a scale of moisture availability. Factors of physical disturbance are obvious in such places as the lower and middle beaches of large lakes and in local river deposits. Currents and waves are active in summer, and at the spring break-up of ice there is much scouring of shores along the large rivers. Ice-push on the shores of the large lakes displaces large quantities of material. Further, the levels of the large lakes are known to change by several feet owing either to flooding from the main rivers or to gale winds. The middle beaches are commonly of sand, which is moved by dry westerly winds. Though frost heaving and thrusting no doubt occur in many of the soils, their distribution and the variations in their intensity are not known. Water supply to upland ponds and muskegs varies greatly with precipitation, and in dry summers fire is known to run through some muskegs and grass-sedge meadows. It may be that such sites, apparently rather stable, are more susceptible to disturbance than is yet known.

TOPOGRAPHY OF THE REGION

The topography, geological structure, soils, and general climatic features of the Athabaska-Great Slave Lake region were reviewed at some length in an earlier paper (Raup, 1946). This material will not be repeated except in a broad outline intended to clarify discussions of the geographic ranges of species.

The region is divided into two major subregions by a boundary running generally from S–SE to N–NW. Geologically this boundary is between Precambrian rocks to the east and Paleozoic or younger rocks to the west. The western area is underlaid by Silurian, Devonian, and Cretaceous sedimentary rocks, its surfaces mantled with wide expanses of morainic deposits, sand plains, ancient lake beds of clayey silt, and river alluvium. Outcrops of limestone, shale or gypsum are few. Topographically this area has representatives of two physiographic provinces. There are extensive alluvial lowlands in the broad valleys of the main rivers (the Peace, Athabaska, Slave, Buffalo, Little Buffalo, and Hay rivers) which make up the Mackenzie Lowland Province, with altitudes ranging from about 500 to about 700 feet above sea level in our area. This includes the wide deltas of these rivers at Athabaska and Great Slave lakes. Above it to the west of the Slave River, margined in places by well-defined limestone escarpments about 400 feet high, is a broad plain that gradually slopes upward to the southwest and is part of the Alberta Plateau Province. Much of this area is underlaid by gypsiferous rocks, on which an extensive karst topography is developed. At the west and southwest margins of our area are outliers of the Cretaceous portion of the Alberta Plateau, rising to altitudes of 2500 to 3000 feet above sea level.

The dividing boundary runs northward along the eastern margin of the

lower Athabaska River valley, crosses the western end of Lake Athabaska, and then follows the eastern margin of the Slave River lowland to Great Slave Lake. It appears again on the eastern shore of the north arm of this lake.

East of this boundary is the Laurentian Plateau Province, or "Canadian Shield." In our area its highest altitudes reach to about 1700 feet above the sea. It is characterized by abundant outcrops of Precambrian rocks, and by thin and scattered deposits mainly of morainic materials and beach or glacio-fluvial sands and gravels. South of Lake Athabaska, with occasional representatives on the north shore, is a large area of sandstones and quartzites, the weathering of which has produced the extensive beaches, dunes, and sand plains that border the lake on the south. Between the Athabaska and Great Slave lakes, and around the east arm and east shore of the north arm of the latter, are many areas of ancient Precambrian, highly metamorphosed sedimentary rocks. Finally there are the granitic and gneissic rocks that are so wide-spread in the Canadian Shield that the ancient metamorphic rocks appear as "islands" interspersed among them.

Drainage systems on both sides of the boundary are poorly developed, giving rise to a multitude of undrained or poorly drained depressions, which in this region contain shallow ponds and lakes and a great variety of sloughs, muskegs, and grass-sedge meadows. The muskegs are most extensive on the uplands, while sloughs and meadows are most abundant on the flood plains and deltas of the large rivers, where meandering streams have produced a plethora of abandoned channels containing lakes and ponds. Small bodies of water are most abundant on the Canadian Shield east of the boundary, where basins in the resistant rocks have for the most part remained intact since the glacial ice receded.

Major features of the region are the two large lakes, Athabaska and Great Slave. The first is approximately 190 miles long, about 35 miles wide, and as presently mapped lies almost entirely in the Precambrian area. Formerly it had a large western extension over Paleozoic rocks and a southward extension up the Athabaska River valley, but these have been largely filled by alluvial deposits from the Athabaska and Peace rivers, leaving some shallow bodies of water, the largest of which are now mapped as Lakes Mamawi and Claire. Great Slave Lake is about 350 miles long from southwest to northeast. Its basin crosses the major boundary noted above, with a broad western portion on Paleozoic rocks. In an earlier period the western part was wider and had a long extension up the present valley of the lower Slave River. This has been filled with alluvium carried also from the Peace and Athabaska. The great alluvial deposits of these rivers are well known for the immense amounts of driftwood they contain.

The present level of Lake Athabaska is about 690 feet above the sea, and Great Slave Lake is at about 495 feet. Earlier levels in post-glacial time have been placed at about 800, 1100, and 1600 feet above the sea (Cameron, 1922; see also Raup, 1946). The higher levels are believed to have been formed at stages in the retreat of the glacier during which the water from the Peace and Athabaska rivers was impounded by glacial ice

before the latter had released the normal flow through the upper Mackenzie River valley.

That major changes have occurred in the levels of the large lakes is evident in the abandoned gravel or sand beaches found high in the neighboring hills. These were measured to at least 240 feet above the current lake level on the north shore of Lake Athabaska, and they have been reported up to about 600 feet around the eastern arm of Great Slave Lake. They run in an apparently continuous series down to the present shores. It was assumed in our early studies of vegetation on the northwest shore of Lake Athabaska that the lowering of the lake was still going on, although very slowly and probably not rapidly enough to have much effect upon the development of shore vegetation. Evidence that the water level fluctuated to some extent was seen in September, 1932, when a southwest gale temporarily lowered it about four feet near the western end of the lake. Other evidence was in heavy driftwood found on broad sand beaches several feet above the existing lake level, but this was thought to be due to storm waves or ice-push. Raised barrier beaches, on the other hand, were believed to be the result of the long-term, though gradual, lowering of the general level of the lake.

Measurements that later pertained to lake levels were made in 1926 of the plant zonation on shore rocks at Lake Athabaska (L. C. Raup, 1930). Four well-defined zones were seen, the lowest of which is a dark-colored crust of *Verrucaria nigrescens* (vertical width ca. 9 inches). The second zone, also a dark crust, consists of the same *Verrucaria* plus *Dermatocarpon miniatum* (vertical width ca. 5 feet). The third is gray in color, the primary species being *Rhizocarpon geminatum*, *Physcia caesia*, and *Lecanora cinerea* (vertical width ca. 2 feet). The fourth and uppermost zone forms a transition to the neighboring upland. On rocky headlands the primary species here are *Parmelia saxatilis* and *Gyrophora Muhlenbergii*. Where there is much sand on the upper beaches *Stereocaulon tomentosum* appears. Measurements of these zones and their heights above the lake level were made at 14 stations along the shore at Shelter Point, ranging from vertical cliffs to gently sloping shores of boulders, gravel, or sand. Heights of the zones above the lake were essentially the same, suggesting that they were related to the general water level rather than to wave or ice action, which would vary with the exposure of the shore. But lichens grow very slowly, and it was impossible to say whether they marked a general, though gradual, fall in the level of the lake.

There were major floods in the Athabaska and Peace rivers during the Spring of 1935. In normal flow the Athabaska empties into the western part of Lake Athabaska and its water is carried through the western end to the Slave River. Most of the normal flow from the Peace River goes directly into the Slave, but there are reversible channels in its delta by which some flood water gets into Lake Athabaska and thence into the Slave. The floods in these main rivers in 1935 were so great that the level of Lake Athabaska was raised 6.5 feet above that seen by our field parties in 1926 and 1932. This took it above the two lowermost lichen zones and

about a foot into the third zone, as shown by examination of the stations measured in 1926. Similar lichen zones were seen on the shores of Great Slave Lake, but here they were much narrower, suggesting similar high water episodes that have a smaller magnitude.

A recent study of water levels in Lake Athabaska (Stockton & Fritts, 1973), based on analyses of the growth rings of trees, shows that relatively large fluctuations of level have occurred in the past. Some gauge measurements of flow in the Peace and Athabaska rivers for the years 1935 to 1967 were available, with a few from the lake itself, and from the data the authors estimated the levels of the lake for these years. A peak level of about 693.2 feet above sea level is their estimate for 1935. They then projected their analysis backward in time to 1810. Their estimate for 1926, the year in which our field party made its first measurements, was about 687 feet. If this is approximately correct, the difference in 1935 would have been about 6 feet, while our actual measurements showed 6.5 feet. The frequency of these high water levels is not known with precision. The projected estimates of Stockton and Fritts show a similar peak in 1921 and somewhat higher ones in 1908 and 1900. From this time back to the mid-1830's, large fluctuations apparently occurred, but at levels for the most part below 690 feet. From about 1821 to the mid-1830's, several peaks were again high (ca. 692 to ca. 693.5 feet).

THE PRIMARY SPECIES

Of the 417 species considered in the shore flora, 145 were noted in one place or another as primary in their assemblages; that is, they were sufficiently abundant or prominent to give the assemblages their distinctive form and appearance. Some of them were found as single primary species, but more were members of combinations, with others having approximately equal rank in their respective assemblages. The disposition of the primary species in this respect is as follows:

74 spp.	Found only in combinations of 2–4 spp. each	134 spp. Found in combinations
60 spp.	Found in combinations or as single primary spp.	
11 spp.	Found only as single primary spp.	71 spp. Found as single primary spp.

The 134 primary species found in combinations represented 180 different assemblages. Another 71 assemblages were characterized by single primary species, making the total number of different assemblages seen in the shore vegetation 251. The total number of assemblages described was 550. An estimate of the number of times a given assemblage was repeated in the course of the field observations was thus about 2.2. This, of course, is an average. Some of the assemblages were unique, while others were seen

several times. Owing in part to varying areas among the 10 habitat complexes, and in part to the varying extent of field studies among them, the numbers of different assemblages seen in them is far from uniform, ranging from about 12 on wet sand or gravel shores to as many as 49 in flood-plain meadows. Further, they add up to 297, which is 46 more than the total of 251 previously mentioned. The discrepancy is due to the 46 having been seen in more than one of the habitats.

The following 10 primary species were found in 95 of the 180 combinations recognized (numbers of combinations in parentheses). In making these combinations they were associated with 59 other primary species.

Alnus incana subsp. *tenuifolia* (19)	*Betula papyrifera* subsp. *humilis* (13)
Salix planifolia (18)	*Ledum groenlandicum* (12)
Chamaedaphne calyculata (16)	*Myrica Gale* (11)
Carex aquatilis (15)	*Populus balsamifera* (11)
Equisetum fluviatile (13)	*Juncus balticus* var. *littoralis* (10)

The second 10 species, in order of decreasing numbers of combinations, were found in 33 and added 16 to the number of associated species.

Picea mariana (9)	*Nuphar variegatum* (8)
Carex rostrata (9)	*Calamagrostis canadensis* (8)
Salix Bebbiana (9)	*Equisetum pratense* (7)
Empetrum nigrum (9)	*Arctostaphylos Uva-ursi* (7)
Equisetum arvense (8)	*Salix glauca* var. *acutifolia* (7)

Thus the 20 primary species found in the largest numbers of combinations ranging from 7 to 19, inclusive, appeared in 128 of the 180 combinations observed. In these assemblages they were associated with 75 of the 134 primary species that were seen in combinations. All of the second 10 species noted above were included among those associated with the first 10. Thus the total number of primary species involved in the 128 assemblages was 85, or 63.4% of all species found in combinations.

These observations raise some questions about the relations of primary species to their habitats. If 145 of them were to be distributed evenly throughout the 10 habitats described above, they would average about 14 in each. If it is assumed that there is a close and restrictive relationship of these species to their habitats, then either there are many undetected microhabitats within each of the 10, or there are possibly 14 primary species that have the same environmental requirements and have been randomly distributed throughout each of the 10 habitats.

With present or foreseeable knowledge of these habitats, it would be possible to make a small number of subdivisions in some of them, such as on the beaches of large lakes or in some of the muskegs; however, definition of the theoretical 14, adding up to 145 in all, seems impracticable, even with the most modern techniques of analysis. The problem is further complicated by the fact that the number 14 is far from realistic. When the numbers of primary species noted in each of the habitats are

added together, the total is 251 (See FIGURE 13), indicating that nearly three fourths of them (106) were growing in more than one of the habitats, and about one fourth in as many as 5 to 7 different habitats (see below). Nearly half of them (66) had reached primary status in more than one habitat. In a relatively uniform site, such as the flood-plain grass-sedge meadow, 30 primary species were seen, and in the muskeg grass-sedge meadow there were 40.

The tendency of the primary species to spread widely throughout the habitats suggests that the possibility of finding appreciable numbers of them having similar restrictive environmental requirements is remote. It also suggests a third alternative: that the habitat relations of a great many of the species are not narrowly restrictive and that the species have wider latitude in their selection of habitats than is commonly assumed for them.

Another question arises with respect to compatibility among species growing together as "co-primaries" in their respective assemblages. If the compatibility is assumed to be to any extent restrictive, it becomes difficult to rationalize when 134 of the primary species are found in 180 different combinations of 2 to 4 each, and when individual primary species are seen in combination with as many as 19 different ones.

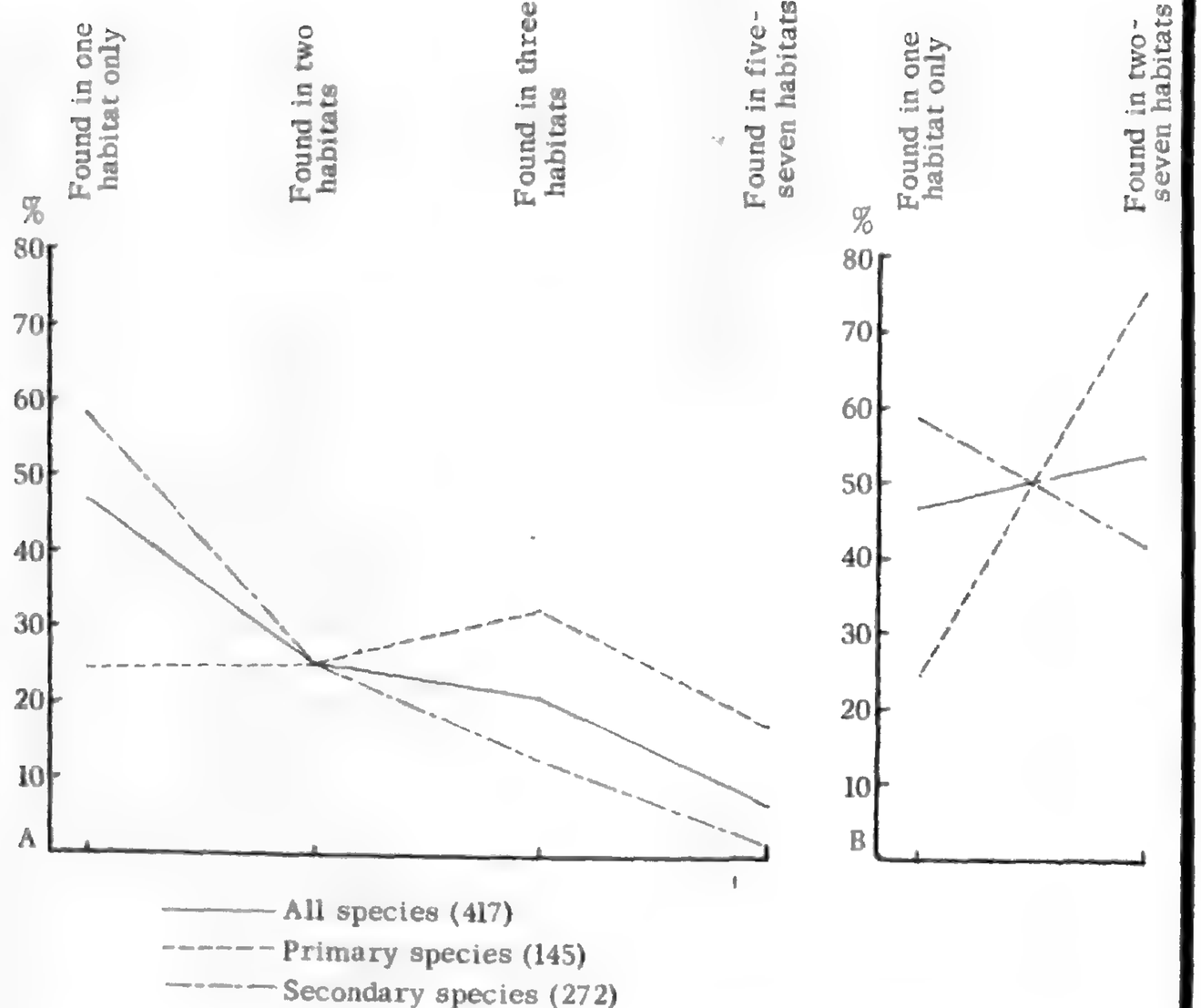
HABITAT TOLERANCES OF THE SPECIES

The term "tolerance" is used here in the sense of "versatility" or "flexibility" on the part of species with respect to the differing kinds of habitats in which they were found. These terms are equivalent to "ecological amplitude," which has been used commonly in ecological literature. Interpretations of species versatility with respect to habitat have been primarily physiological in the literature of ecology, and they have been based largely on the idea that limiting factors in the environment may be recombined in such a way that species can live in differing habitats. Varying competition among species is thought to play a major role. A clear statement of this idea has been published by Küchler (1967).

In the total shore flora (417 spp.), 165 species were found in one habitat only. Thus more than half the flora (60.5%) showed capacity to live in two or more kinds of habitat. FIGURE 1 shows the general distribution of species in terms of this capacity. FIGURE 1A contains the distribution in four groups: species found in 1, 2, 3 to 4, and 5 to 7 habitats. The last three of these are added together in FIGURE 1B to show the contrast between those found in only one habitat and those in 2 to 7.

Methods of analysis used for the text figures and tables in the present paper aim only at relative comparisons of the behavior of species with respect to their occupance of habitats. They are meant merely to illustrate a group of ideas thought to be useful for a rationalization of the shore vegetation.

The method of computing percentages, unless otherwise stated, will be uniform throughout the following analyses. The base numbers for the



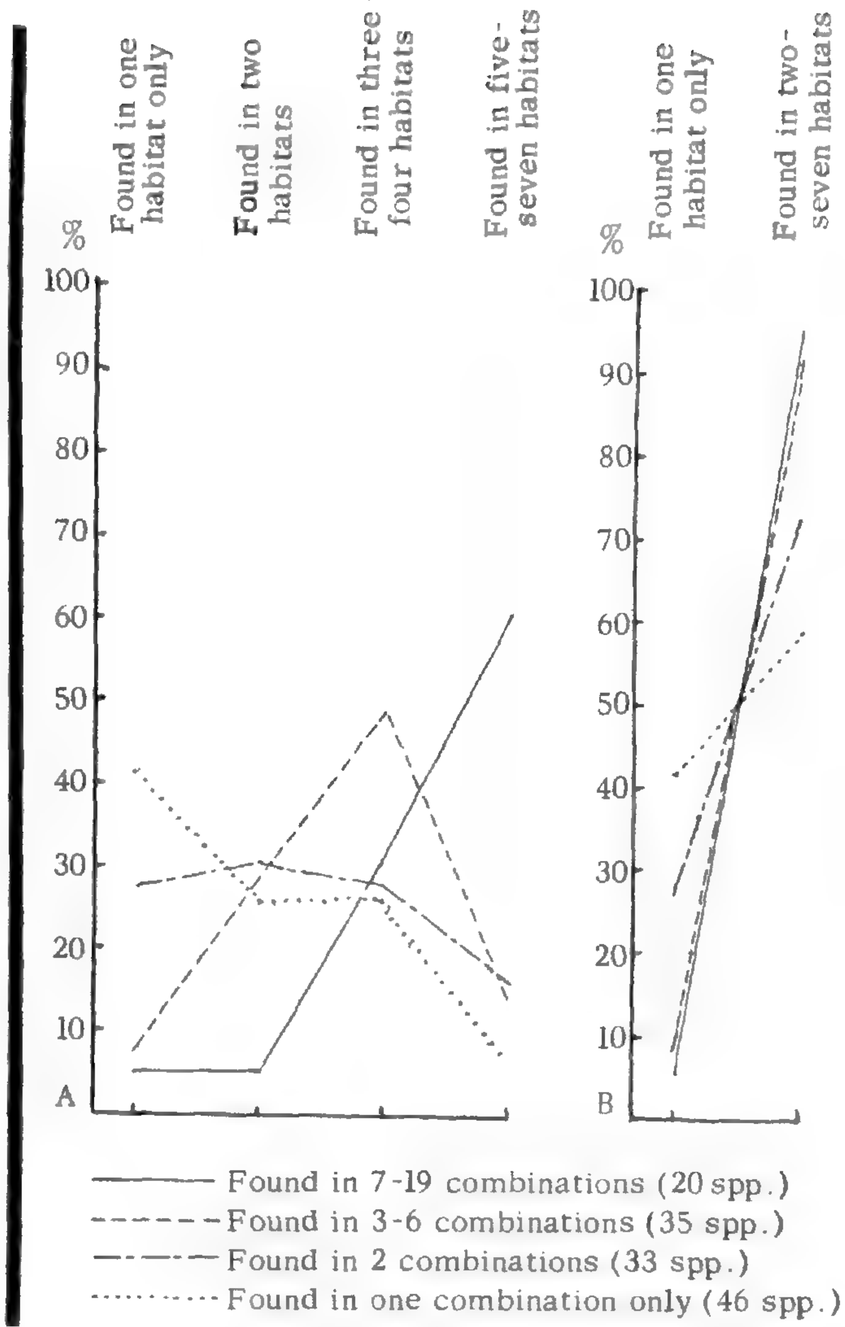


FIGURE 1 (left). Distribution of shore species with respect to the number of habitats in which they were found. Percentages based on the total numbers of all species, primary species, and secondary species. FIGURE 2 (right). Distribution of 134 primary species, found in varying numbers of combinations with other primary species, with respect to the number of habitats in which they were found. Base numbers for percentages are the total numbers of primary species found in 7 to 19, 3 to 6, 2, and 1 combinations.

percentages will be the total numbers of species within the groups being analyzed. In FIGURE 1, for example, there are three base numbers. Where the whole shore flora is concerned and it is desirable to know how all the species in this flora are apportioned in a range of the numbers of habitats occupied, the base number is 417. Similarly, for the primary and secondary species the numbers are 145 and 272 respectively.

The primary species are relatively almost as abundant among those found in 5 to 7 habitats as among those found in only one (FIGURE 1A). The secondary species, on the other hand, though with more than twice the percentage of the primary species confined to one habitat, are represented among those found in 5 to 7 habitats by only about 1/8 the percentage of the primary species. Thus, in the shore flora as a whole, the primary species show far more tolerance of habitat variation than do the species that have secondary roles in the assemblages. They are more versatile in finding shore habitats in which they can grow. In some of these differing habitats they retain their primary position, while in others they join the secondary species.

The capacity of 134 of the primary species to form combinations may be analyzed in the same way. To do this the numbers of combinations in which the species were found were grouped as follows: 7 to 19, 3 to 6, 2, 1. These groups were then analyzed in terms of their appearance in 1, 2, 3 to 4, 5 to 7, and 2 to 7 habitats (FIGURE 2). The group for 7 to 19 combinations are the 20 species noted above in the discussion of the primary species.

Of the 20 species forming the largest numbers of combinations, nearly all were also found in more than one habitat. Only 5% of them were seen in only one (FIGURE 2B). In contrast, the group of 46 species that were seen in only one combination showed about 44% in a single habitat. The 35 species forming 3 to 6 combinations appear to be almost as versatile in habitat selection as the 20 that were found in 7 to 19 combinations, while the 33 seen in 2 combinations are about midway between the two preceding groups. Thus there appears to be general coincidence between species' tolerance of habitat variation and their capacity to form combinations with other primary species.

It is proposed that the above differences in behavior of the species are, at least in part, inherent, are probably biotypic or ecotypic, and were probably already in being during the invasion of the habitats following the retreat of the glacial ice and the drainage of the postglacial lakes. Evidence for such historical conditioning of the species has been reviewed by Hultén (1937a), Anderson (1936), Cain (1944), Raup (1947a & b), and others. It is related to the varying biotype depauperation in species populations during the glacial period. If this proposal is realistic, it is probable that a large element of randomness should be inserted into any rationalization of the present vegetation. It is further proposed to use the apparent gradients of species versatility as criteria in comparative studies of geographic range patterns, the behavior of the life-forms of the plants, and the floras of the various habitats.

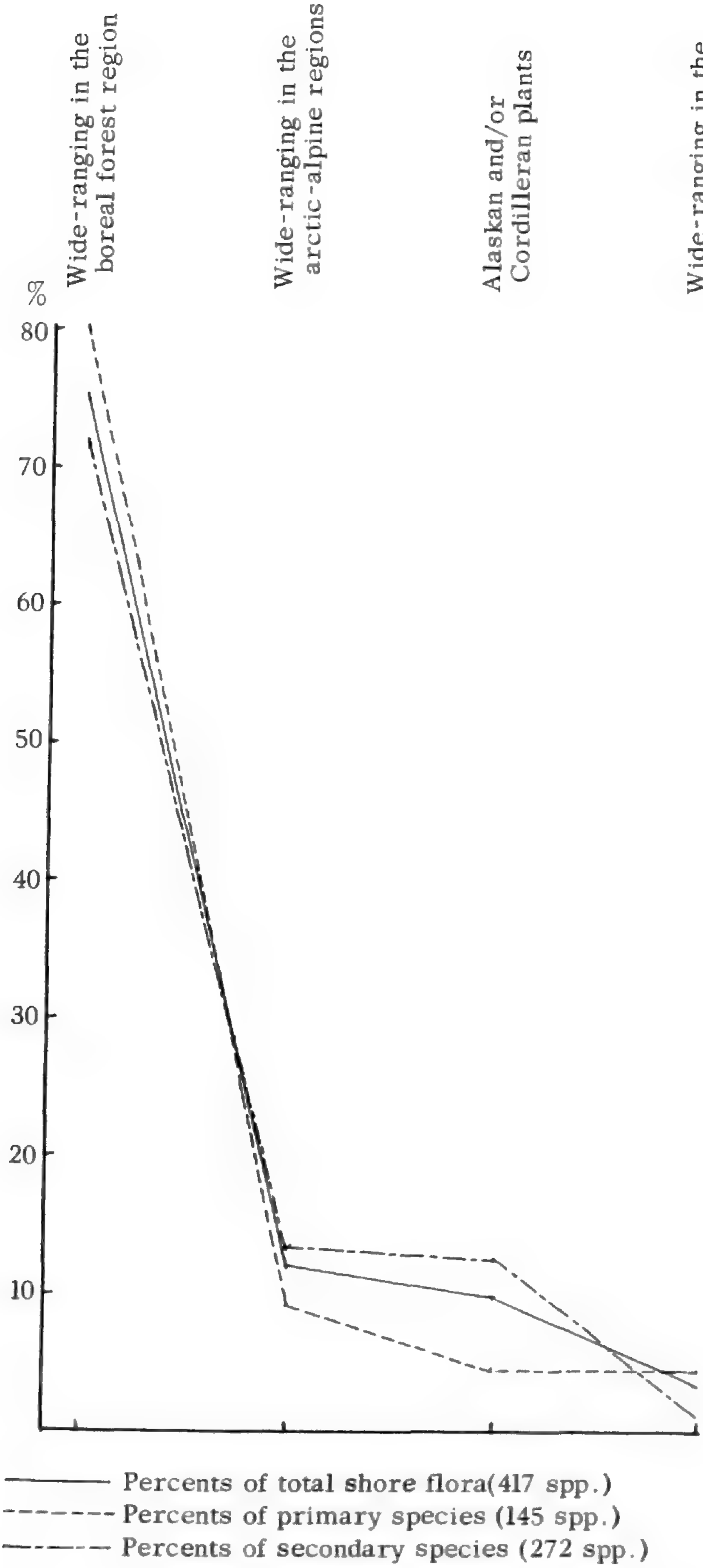


FIGURE 3. Proportional representation in the shore flora of the four major geographic elements in the vascular flora of boreal America.

THE GEOGRAPHIC RANGES OF THE SHORE SPECIES

RANGES OF THE SHORE SPECIES IN NORTH AMERICA

The first of the geographic organizations follows one used by the present writer in studies of the Mackenzie Mountain flora (1947a). It contains four general range patterns into which the shore flora considered here can be placed. These patterns are as follows:

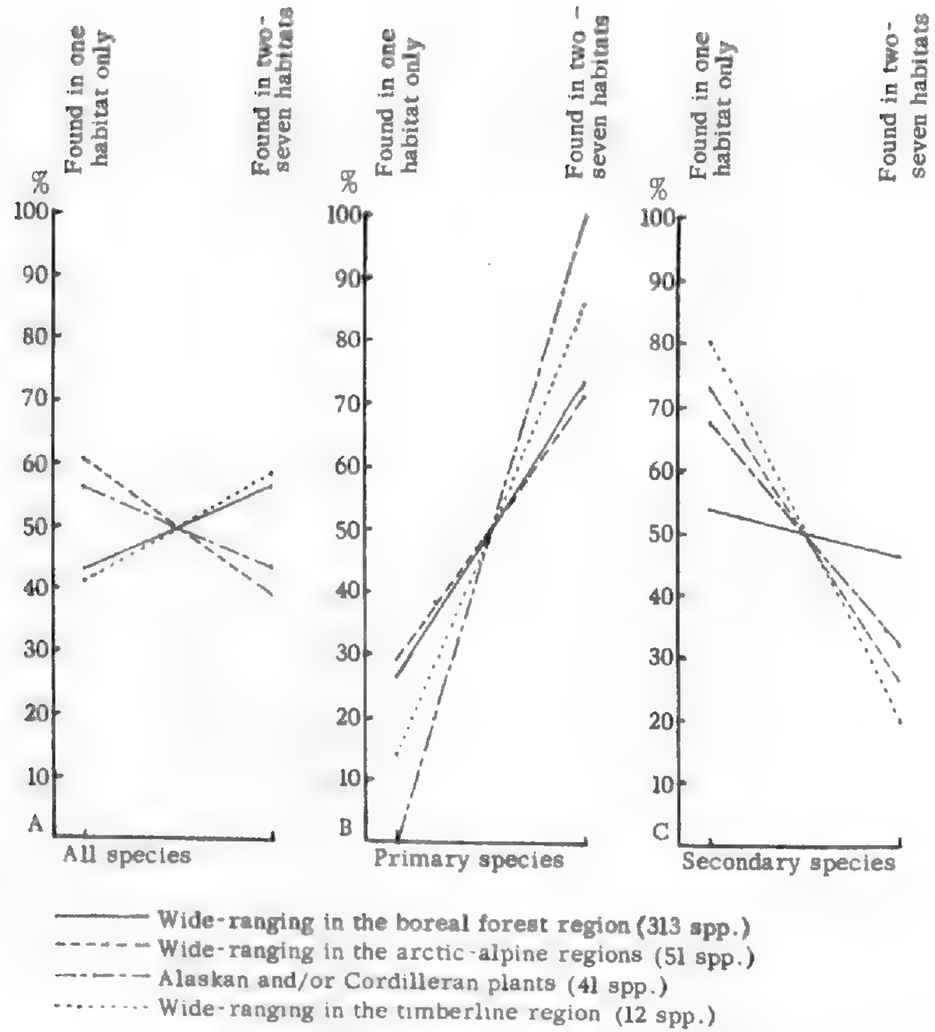
1. Species wide-ranging in the boreal forest.
2. Species wide-ranging in arctic and alpine areas.
3. Species wide-ranging in the arctic timberline region, extending in a band across all or most of the continent on both sides of the timberline.
4. Species more or less restricted to the Alaskan and/or Cordilleran regions or to their adjacent plains.

The number of shore species in the four geographic elements, and their percentages of the total flora are shown in FIGURE 3. It is obvious that this flora is composed primarily of species that range widely in the boreal conifer forest region of the continent, extending from Newfoundland to Alaska. A large number of these species (131) are not restricted to the boreal forest, but extend far southward in the mountains and interior plains and plateaus of Canada and the United States.

The boreal forest group have their northern limits at or near the arctic timberline. The wide-ranging arctic and alpine plants, on the other hand, have their southern or lower limits at or near the timberlines. Most of them appear in this region only around the eastern or northern parts of Great Slave Lake, within a few miles of the arctic timberline. The "timberline" range pattern is made by a small number of species that have wide east-west ranges which extend across the arctic timberline but do not reach far into the forest or the tundra. More limited ranges are in a floristic element derived from the northern Cordillera and Alaska. Some of these species extend eastward as far as the Hudson or James bays, but most reach only to our region or eastward on the arctic coast or islands.

The boreal forest element outnumbers all the other affinities taken together by a factor of about three. Differences among the three less well represented elements are within a range of about 12%.

FIGURE 4(A, B, & C) analyzes the behavior of all the species and of the primary and secondary species in the four geographic affinities in terms of their tolerance to habitat variation. In the shore flora as a whole (all species) those species showing the widest tolerance are clearly those from the boreal forest group and from the small timberline group, the latter showing a little more flexibility than the former. In both the other affinities there are fewer species found in 2 to 7 habitats than in one, with the Alaskan-Cordilleran group a little more versatile than the arctic-alpine. The primary species all show high tolerance ratings but are also in two groups. The most versatile are the Alaskan-Cordilleran and timberline



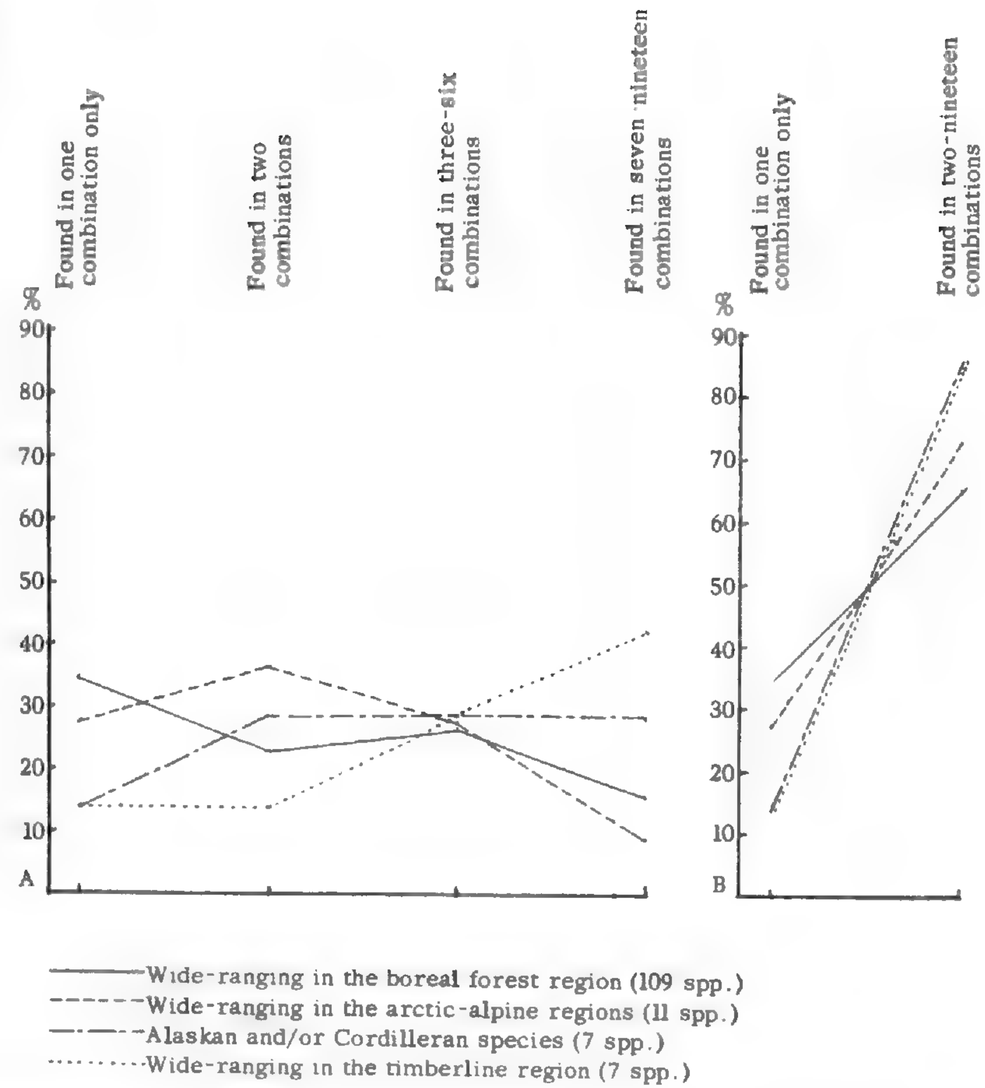


FIGURE 4 (left). Analyses of the four major geographic elements in the shore flora with respect to the numbers of habitats in which their species were found. Percentages based on the total numbers of all species, primary species, and secondary species derived from each geographic element. FIGURE 5 (right). Analyses of the four major geographic elements in the shore flora with respect to the numbers of combinations seen among the 134 primary species that were found in combinations. Percentages based on the total numbers of combination-forming primary species in each geographic element.

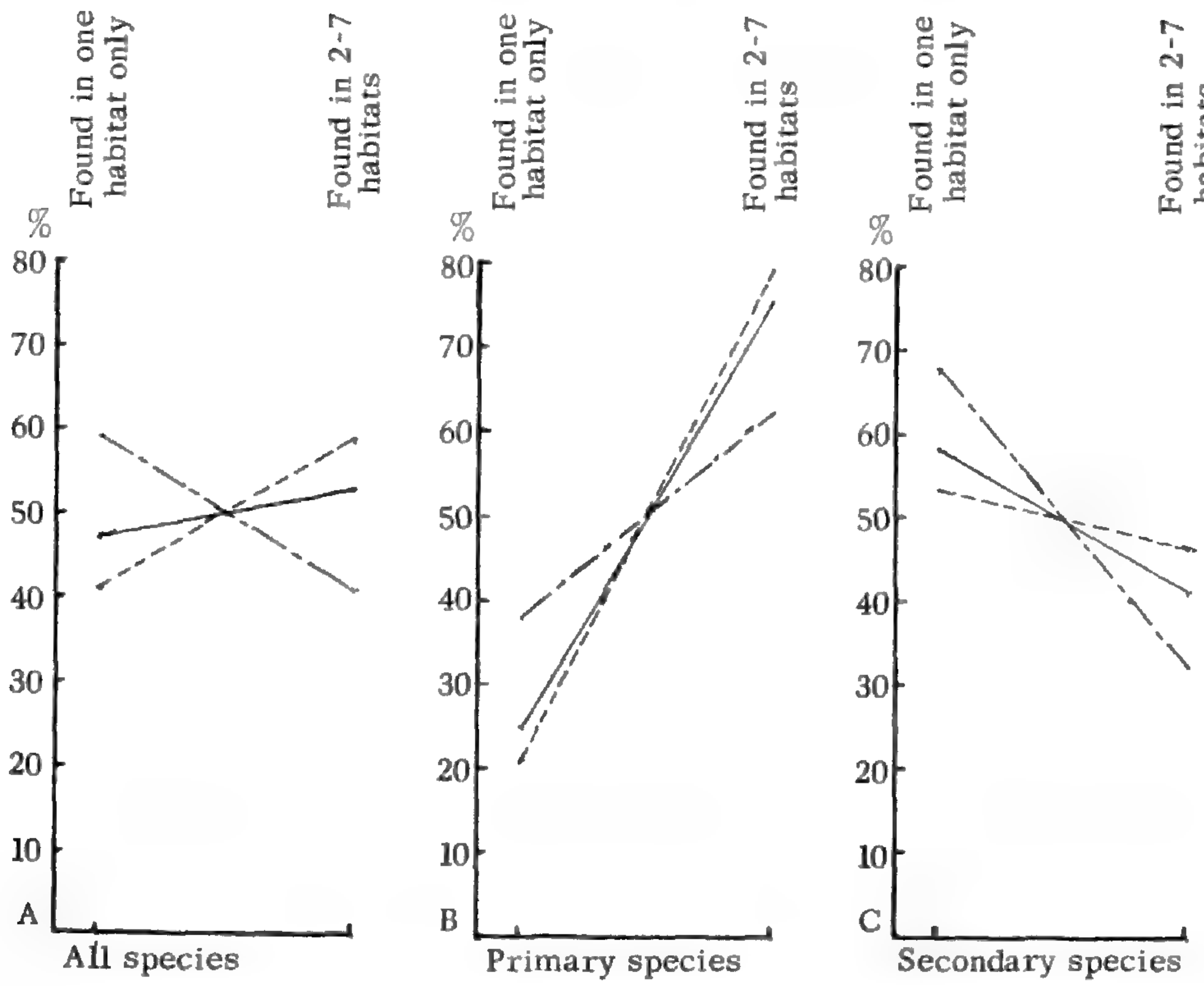
groups, with many more found in 2 to 7 habitats than in only one. The other two affinities form the other group, nearly equaling each other and showing about two and a half times as many of the more flexible species as were found in only one habitat. Among the secondary species all of the three lesser affinities show relatively low versatility, ranging within about 10% of each other and showing many more species found in only one habitat than in more than one. In the boreal forest affinity, on the other hand, nearly half of the secondary species were found in 2 to 7 habitats.

FIGURE 5 shows the distribution among the four geographic affinities of the 134 primary species found in combinations. The latter are grouped, as before, in terms of the numbers of combinations in which they were found (7 to 19, 3 to 6, 2, 1). Most of these species (ca. 81%) are derived from the boreal forest affinity. However, in spite of their large numbers, these species are the least versatile among the four geographic elements at forming combinations. The most versatile are the primary species in the Alaskan-Cordilleran and timberline elements, which is consistent with their versatility in habitat tolerance.

FIGURES 4 and 5 suggest that the boreal forest element in the shore flora, though it contributes about 75% of all the species and is relatively high in habitat versatility when the whole flora is considered, shows relatively low versatility among its primary species, in both habitat selection and the formation of combinations. The widest tolerance in both cases is shown by the two smallest geographic elements, the timberline and the Alaskan-Cordilleran groups. In the timberline group, with its wide transcontinental range, this is understandable, but why all of the seven primary species in the Alaskan-Cordilleran group should have wide habitat versatility is unknown.

Another approach can be made to the relation of range size to species versatility by using the remarkable series of range maps published in recent years by Dr. Eric Hultén (1958, 1962, 1968, 1971). Of the 417 species treated in the present paper, 369 were mapped in Hultén's papers. These species were arranged in two groups, the first of which (283 spp.) show wide continental ranges, spanning all or most of the tundra or boreal forest regions, or having wide ranges in the northern Cordillera, Alaska, and the neighboring interior plains. The second group (86 spp.) have much smaller ranges: in the western American Arctic, in Alaska, or in the northern Cordillera but extending eastward to the Athabaska-Great Slave Lake region. Maps were found elsewhere (Raup, 1947a, 1959) for four of the species not treated by Hultén, all of which are wide-ranging. Nearly all of the 44 remaining proved to be species of southern affinity in the boreal forest region, limited in our area to small, more or less isolated populations, most of them in the southern part. These were added to the 86 small or discontinuous ranges mapped by Hultén to make 130 species of limited or distinctly marginal range. These are contrasted with 287 wide-ranging species and with the whole flora (417 spp.) in FIGURE 6.

The relative versatility shown by the whole flora in FIGURE 6 (solid line) is equivalent to that shown in FIGURE 1B. In the whole flora, as well



——— Total shore flora (417 spp.)
– – – – – Species with wide continuous ranges in tundra or boreal forest regions of North America (287 spp.)
—·—·— Species with relatively small range areas in northwestern America, or with much disrupted ranges, or with main ranges farther south and represented here by more or less isolated marginal populations (130 spp.)

FIGURE 6. Analysis of habitat versatility in two groups of species, one with large continuous range areas and the other with much smaller or discontinuous ranges. Data mainly from Hultén (1958, 1962, 1968, 1971). Base numbers for percentages are the total numbers for all, primary, and secondary species in each of the geographic groups.

as among the primary and secondary species, the plants with small or discontinuous ranges are considerably lower in versatility, as reflected by their populations in our region, than species with wide continuous ranges. Because there appears to be a relationship between "primaryness" in species and their wider versatility, it could be expected that a segment of the flora showing low versatility would provide proportionally fewer primary species than one with wider tolerance. This proves to be the case here, for the more restricted group is about 29% primary while the wide-ranging group is about 38%.

SPECIES RANGES WITHIN THE ATHABASKA-GREAT SLAVE LAKE REGION

Although the bulk of the shore flora is of species that range widely in northern America, there are many that have more or less limited ranges within our region. There are 170 species that are ubiquitous, their popu-

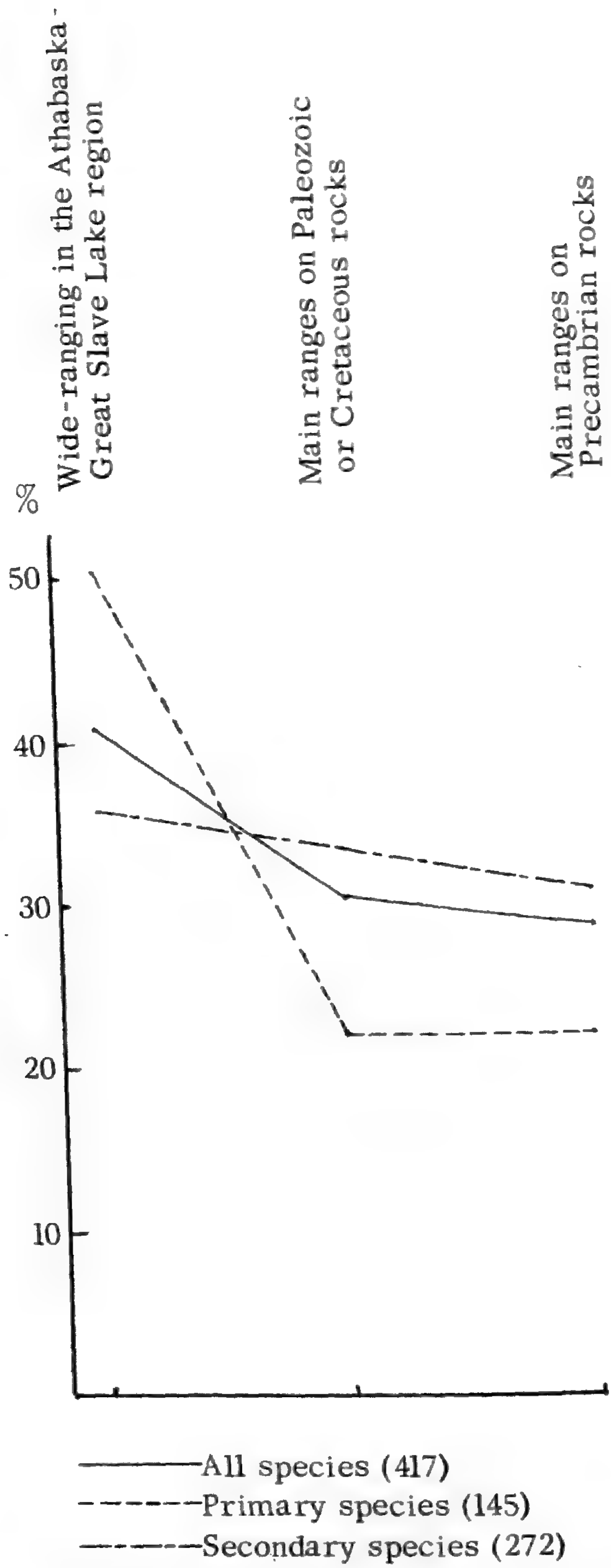


FIGURE 7. Analysis of the shore flora with respect to its local distribution within the Athabaska-Great Slave Lake region. Percentages based on total numbers of all species, primary species, and secondary species.

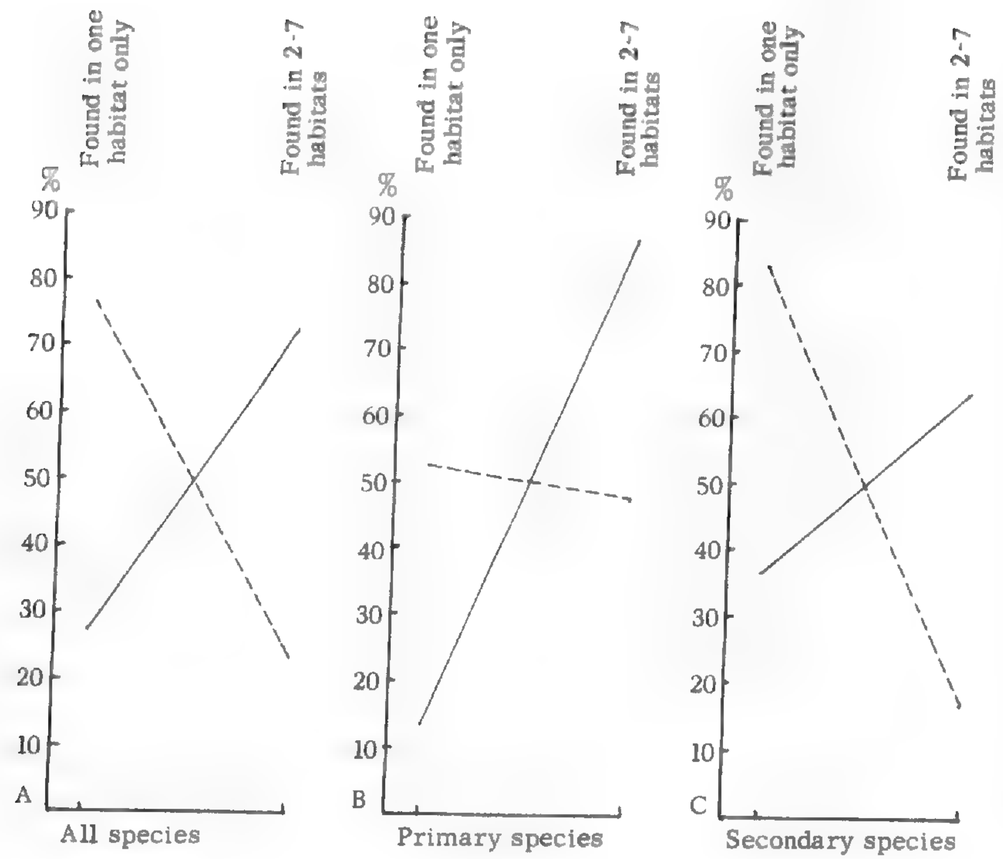
lations being essentially continuous throughout our whole region. Second is a group of 127 species whose main ranges are west of the major N–S boundary noted in the discussion of topography. Third are 120 species whose main ranges are east of this boundary. Thus for 247 species (59% of the flora) the boundary appears to be more or less restrictive. Of the 127 species mainly west of the boundary, 90 were found *only* in this area, while of the 120 species mainly in the eastern area, 94 are apparently confined to it. About one fourth of the nonubiquitous flora (63 spp.), therefore, shows some overlap of the boundary, usually not more than 10 to 20 miles.

FIGURE 7 shows the percentage representations of shore species in the two geographic subdivisions of the region, and compares them to the proportions of wide-ranging (ubiquitous) species. It appears that (1) the wides are most abundant in the region as a whole and their proportions in the two subregions are about the same; (2) the primary species are most heavily represented (about 50%) among the wides, while in the subregions the other half of them are about equally divided; (3) the secondary species are within about 5% of being equally represented among the three elements of the flora.

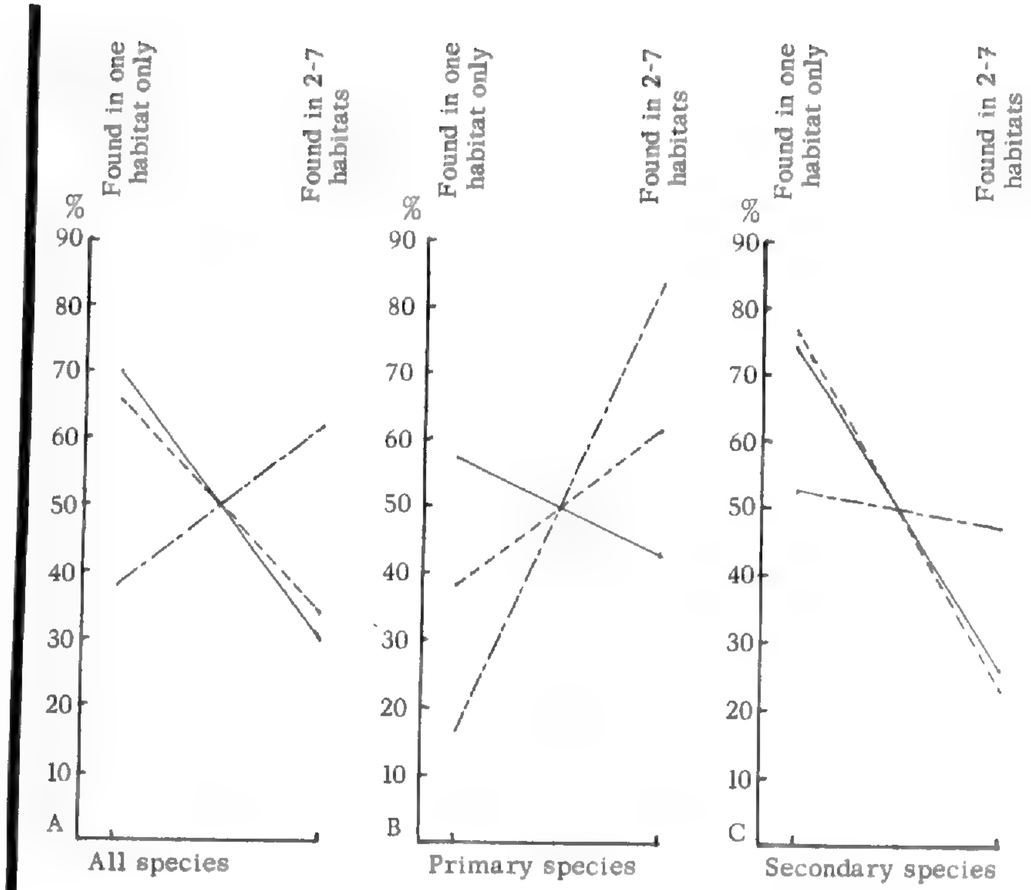
Analyses of the nonwide elements in the shore flora in terms of their versatility in habitat selection were made in order to see whether there were correlations between versatility and range size.

First an effort was made to define the smallest geographic range patterns that would be commensurate with the volumes and variations in the distribution of field data. Four of these smaller range areas were defined, two on each side of the major boundary described above. West of this boundary are the uplands with 13 species not found elsewhere in the region and the lowlands with 38 species not seen elsewhere. East of the boundary are the granitic and metamorphic rock areas north of Lake Athabaska and around the eastern parts of Great Slave Lake, with 48 restricted species, and the sandstone and quartzite areas south of Lake Athabaska with 15 species. Thus there are, in all, 114 species that appear to be restricted to one or another of these lesser geographic areas.

FIGURE 8 compares the behavior, with respect to species versatility in habitat tolerance, of the ubiquitous species and those of the smallest geographic extent. FIGURE 8A shows that the ubiquitous species found in more than one habitat greatly outnumber those found in only one, whereas less than half of the geographically restricted species seem able to live in more than one. As noted earlier the primary species in the shore flora as a whole show greater tolerance of habitat variation than do the secondary species. This is reflected in FIGURE 8(B & C). The wide-ranging primary species found in more than one habitat are about six times as numerous as those found in only one. In the geographically restricted group the versatility of the primary species, though much less than among the wides, is still much greater than that of the secondary species. The secondary species show a contrast approaching that of the wides, though with generally less versatility in evidence.



———Wide-ranging species in the Athabaska-Great Slave Lake region (170)
------Species having greatly restricted ranges, i.e. missing in all but one or another of the minor subregions (114)



———Species found only in areas underlain by Paleozoic or Cretaceous rocks, or by alluvium derived from these rocks (90)
------Species found only in areas underlain by Precambrian rocks (94)
-·-·-·-Species with main ranges over Paleozoic and/or Cretaceous, or over Precambrian rocks, but with some overlap of these ranges (63)

FIGURE 8 (left). Analyses, with respect to habitat versatility, of 170 species of wide continuous range within the Athabaska-Great Slave Lake region and of 114 species apparently restricted to much smaller areas within the region. Percentages based on numbers for all species, primary species, and secondary species found in each geographic group. FIGURE 9 (right). Analyses, with respect to habitat versatility, of species found only on one side or the other of the Paleozoic-Precambrian boundary and of species with main ranges on one side or the other, but with some overlap of the boundary. Percentages based on numbers of all species, primary species, and secondary species in each geographic group.

Analogous results appear when the ubiquitous species are eliminated and only those species whose main ranges lie on one side of the major boundary or the other are considered. In FIGURE 9 the two wholly restricted groups and the group with some boundary overlap are analyzed and compared in terms of relative tolerance of habitat variation. About half of the overlapping species have their main ranges to the east, and the other half to the west of the boundary. The species with overlapping ranges appear to have much higher tolerance ratings than do those in the more restricted areas. Consistent with the preceding analysis (FIGURE 8), the least differences are among the primary species. It is notable that only three of the overlapping primary species are primary on both sides of the boundary, and it is suggestive that primary species found only east of the boundary have considerably wider habitat tolerance than those confined to the area west of the boundary.

It was shown earlier that the number of combinations formed among primary species appeared to reflect their relative versatility in habitat selection. The nonubiquitous species noted as primary only west or east of the major N–S boundary are analyzed in FIGURE 10 for their combination-forming proclivities and are compared to those of the overlapping primary species. FIGURE 10 is analogous to FIGURE 9B. The overlapping species show proportionately many more combinations than do those found only in one or the other of the two major subregions.

The data from analysis of the species' geographic patterns indicates a positive correlation between size of range and versatility in the occupance of habitats. In the flora as a whole species derived from the largest ranges show the largest proportions of the more versatile species (FIGURES 4A & 6). Relations to size of range are more striking when the behavior of plants ubiquitous in our region is compared to that of species greatly restricted in range (FIGURE 8). In the latter the primary species show even fewer growing in more than one habitat than in one.

The relation of habitat versatility to a prominent vegetative boundary is shown in FIGURE 9, where the nonubiquitous species that do not cross the boundary are compared with those that do cross it for relatively short distances. The latter show notably greater habitat versatility than the former.

LIFE-FORMS IN THE SHORE FLORA

The shore flora of the region is here classified in six rather generalized life-form groups:

1. Trees: all single-stemmed woody plants.
2. Shrubs: all multiple-stemmed woody plants, whether upright, decumbent, or trailing.
3. Perennial herbs with only fibrous roots as underground organs: mostly caespitose plants; term usually shortened in the following text to "perennials with fibrous roots" or "fibrous-rooted perennials."

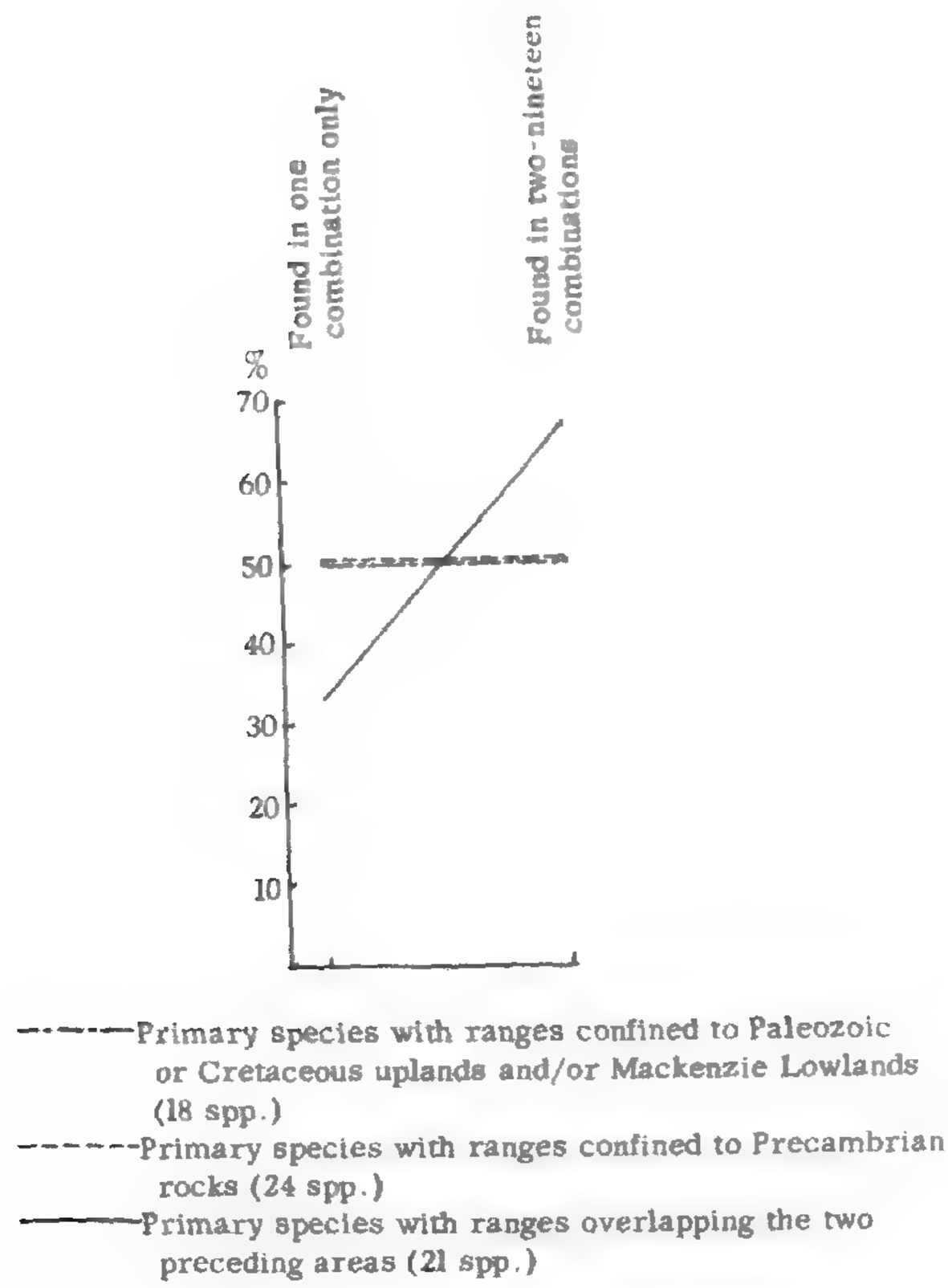
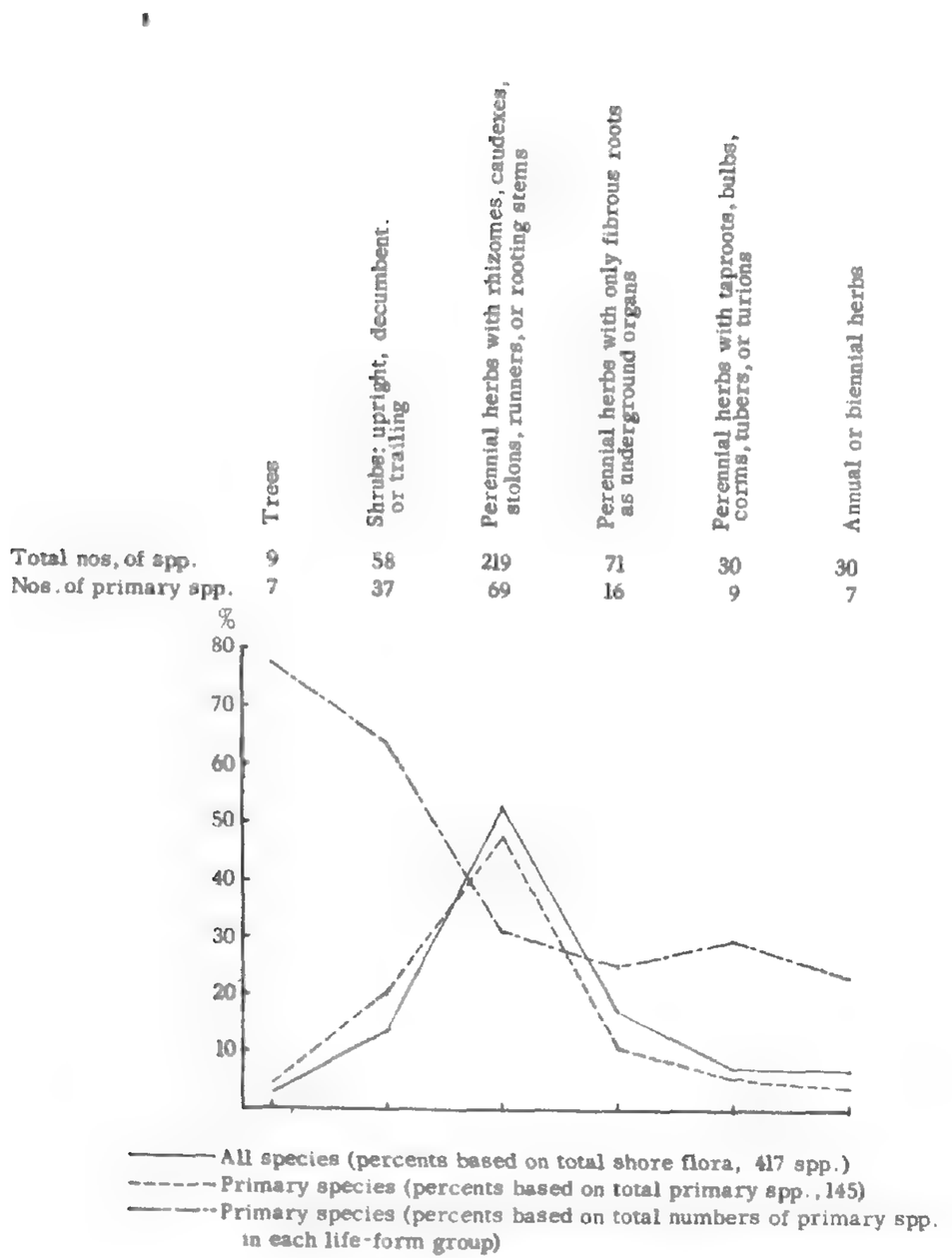


FIGURE 10. Analysis of the primary species in FIGURE 9 with respect to the numbers of combinations in which they were found. Percentages based on the total numbers of primary species found in combinations and restricted to or overlapping the two subregions.

4. Perennial herbs with caudexes, rhizomes, runners, stolons, or with stems that root at the nodes: this group brings together most of the plants that have means of vegetative propagation by underground or aboveground organs; term usually shortened in the following text to "perennials with rhizomes" or "rhizomatous perennials."
5. Perennial herbs with taproots, bulbs, corms, tubers, or turions: these plants have storage organs, but no means of vegetative traveling; term commonly shortened to "taprooted perennials" in the following text.
6. Annual or biennial herbs.

FIGURE 11 (solid line) shows the numbers of species in the above life-form categories and their percentage representation in the whole shore flora. Perennial herbs with rhizomes, caudexes, etc. are predominant, comprising a little over half of the total flora, with about three times as many species as fibrous-rooted perennials and nearly four times as many



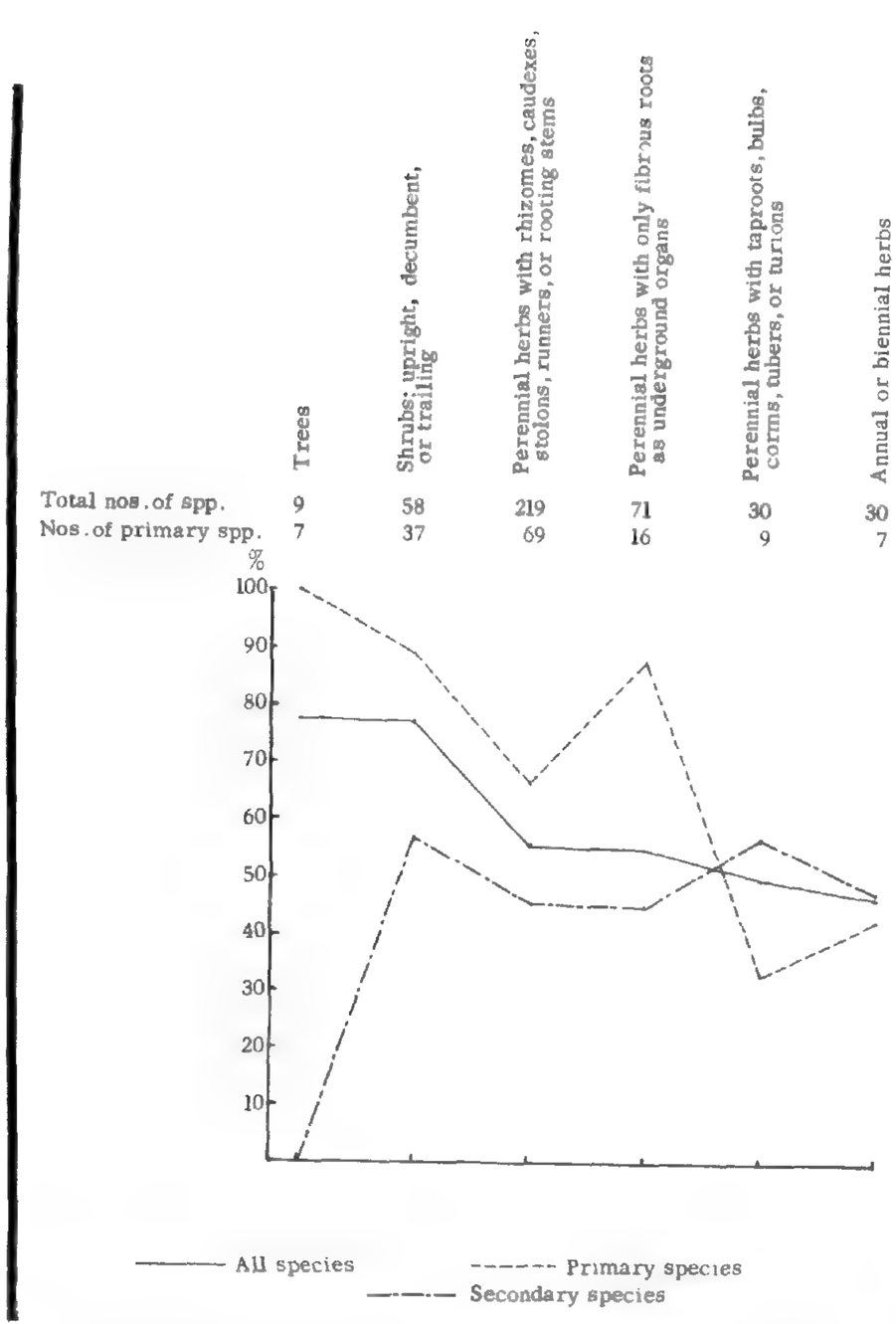


FIGURE 11 (left). Proportional representation of life-forms among all species and all primary species in the shore flora; also the proportions of primary species in each life-form group. FIGURE 12 (right). Analysis of life-forms for relative versatility in the occupation of more than one habitat. Percentages based on the numbers of all species, primary species, and secondary species in each life-form found growing in more than one habitat (2 to 7).

as the shrubs. Tree species are least numerous, while taprooted plants and the annual-biennial group come between the trees and the shrubs.

The primary species in FIGURE 11 are plotted in two ways. The dashed line shows the percentages of the life-forms based on the total number of primary species in the whole flora (145). The trend of this curve resembles closely that for the whole flora except in the trees and shrubs, where the proportions of primary species exceed those in the flora as a whole. In the second method of plotting, the life-form groups are considered as separate elements of the flora and the fraction of primary species in each is shown by the dot-dashed line. Here the trees and shrubs show much larger proportions of their species as primary than any of the other forms. The most numerous group in the flora, the rhizomatous perennials, has only about 30% of its species primary, while the shrubs are nearly 65% primary. All of the nonwoody forms vary from about 24% to about 32% primary.

In FIGURE 12 the six life-form groups are analyzed for the contributions they make to high tolerance of habitat variation. The curves show variations in the proportions, within each group, of species found in more than one habitat. For example, among all the rhizomatous perennial herbs in the flora (cf. solid line) about 55% were found in more than one habitat. About 67% of the primary species in this group were in more than one habitat (dashed line), and about 45% of the secondary species (dot-dashed line). Curves for species found in only one habitat would, of course, be mirror images of these.

In the shore flora as a whole (solid line) the trees and shrubs are by far the most versatile, while all the herbaceous forms vary within a range of about 9% (47–56%) near the median point, where about half are versatile and half were seen in only one habitat.

Among the primary species (dashed line) the shrubs and trees were 9 to 10 times more likely to be found in 2 to 7 habitats than in only one. Fibrous-rooted perennials proved to be almost as tolerant as the shrubs, and considerably more so than the far more numerous rhizomatous perennials. Least versatile of all the life-forms appear to be perennials with taproots, etc., with only about a third of their primary species showing wide tolerance, even less than that of the primary annual-biennial group or of their own secondary species. The secondary species (dot-dashed line), excepting the trees, all vary within a range of about 12% around the median point of about 50% versatility. The percentages for trees probably are exaggerated, for only two secondary species are involved, both of them found in more than one habitat.

Comparison of FIGURES 11 (dot-dashed line) and 12 shows that the high percentages of primary species among the trees and shrubs are consistent with the wide habitat versatility in these forms. But in the herbaceous forms the coincidence does not occur. Although the primary species among these forms show only small differences around 25–30%, they differ widely in versatility, from about 35% among taprooted species to about 87% among fibrous-rooted perennials.

Analyses of the life-forms of the primary species in the four geographic affinities of the shore flora were also made to show the incidence of varying habitat versatility among them. In the predominant boreal forest element, the tolerance ratings are not much different from those seen in FIGURE 12, though rhizomatous perennials show somewhat less versatility. The timberline element, though small, also reflects the ratings in FIGURE 12. The most striking departure from this pattern was found in the arctic-alpine affinity, which deserves particular attention.

In the 14 primary species of the arctic-alpine element of the shore flora, the taprooted and fibrous-rooted perennials have the greatest flexibility in habitat selection, with all of them found to be living in more than one habitat. The shrubs, with three times as many in more than one habitat as in one. are second in the scale of tolerance. If those in the arctic-alpine element are considered as taprooted perennials, the most tolerant group here would be further accentuated (see below). The rhizome perennials have an intermediate rating with about 63% found in more than one habitat. There are, of course, no trees from this affinity, and no primary annual or biennial plants.

It may be useful to contrast the findings on life-forms here with those in the high Arctic. For comparison, a study made in the Mesters Vig district of Northeast Greenland will be used (Raup, 1969). The classification used there was based on the writer's own observations supplemented by those of Gelting (1934) and Böcher (1938).

In the part of Greenland covered by the above studies there are no trees, and woody plants are limited to low or trailing shrubs. Following the practice of Gelting, all of the shrubs (11 spp.) were classified as taprooted perennials. It may be that many of the shrubs in the Athabaska-Great Slave Lake region could be so treated, but not enough is known of their root systems to justify such a classification. Also absent in the Mesters Vig district, as in most of Northeast Greenland, are nearly all annual and biennial herbs. Thus comparison of the two floras must be limited to the perennial herbs. In the Mesters Vig area the classification was as follows:

Species with fibrous roots predominant	64 (41.6%)
Species with taproots or short, oblique rhizomes	65 (42.2%)
Species with well-developed underground rhizomes	25 (16.2%)

Approximate equivalents of these groups in the Athabaska-Great Slave Lake region are:

Perennial herbs with rhizomes, caudexes, etc.	219 (68.4%)
Perennial herbs with fibrous roots	71 (22.2%)
Perennial herbs with taproots, bulbs, etc.	30 (9.4%)

The species with taproots and fibrous roots are the predominant forms in the arctic flora at Mesters Vig, while rhizomatous species so numerous in the region studied here are reduced to about 16% of the flora. It is possible that the high versatility shown by the fibrous and taprooted species

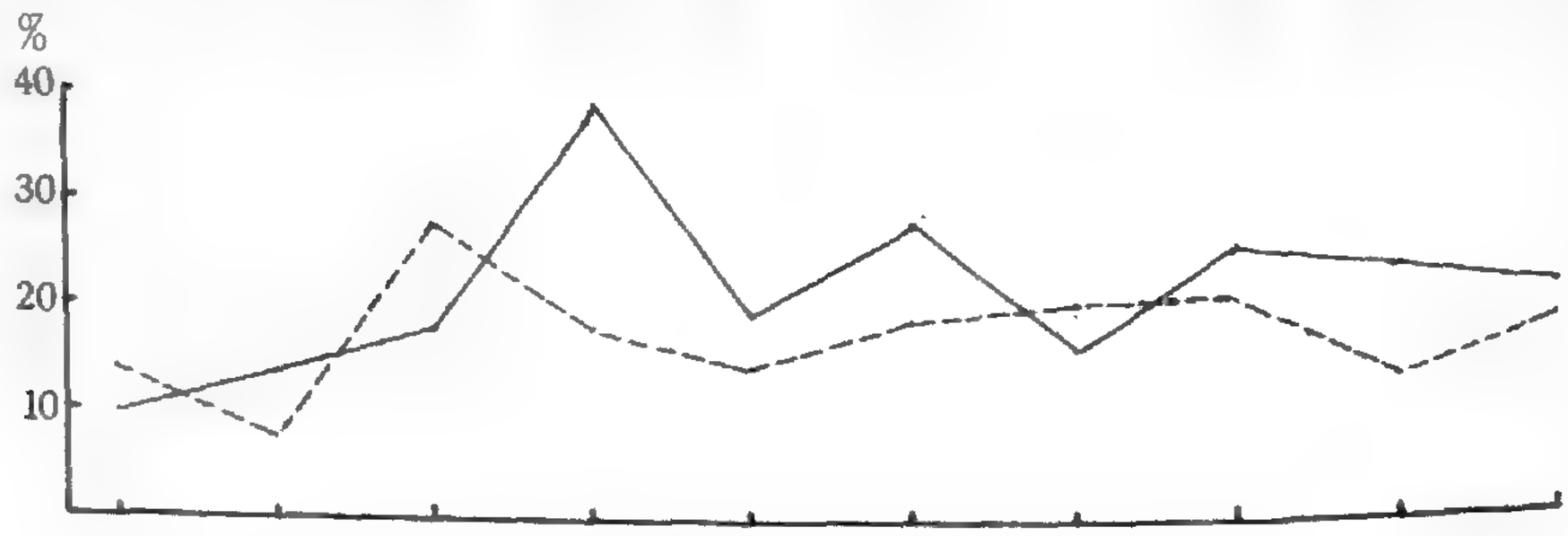
in the arctic-alpine element of our flora reflects the predominance of these forms in the arctic tundra. A large proportion of this element was found in the areas nearest the arctic timberline.

In the Alaskan-Cordilleran element there are only seven primary species, but it is notable that the taprooted plants have a high rating for versatility, as in the tundra, and that the rhizomatous perennials are even lower in the scale than in the arctic-alpine element.

ANALYSES OF VEGETATION TYPES IN THE SHORE FLORA

FIGURE 13 shows the number of species found in each of the 10 habitat-vegetation complexes defined earlier, and the percentage of the total shore flora found in each (solid line). The numbers of primary species in each habitat are also shown, with the percentage of total primary species (145) in each (dashed line).

	Aquatic habitats, with both submerged and emergent species	Saline or brackish sloughs and wet meadows	Muskeg grass-sedge meadows with moss substrata	Open (treeless) shrub muskegs	Shrub-tree borders of muskegs	Damp to wet sand and/or gravel on shores of rivers and ponds or on lower beaches of large lakes	Upper beaches of large lakes; vegetation of upright shrubs and trees	Grass-sedge meadows on river floodplains or on local river deposits, with silt or silt and thin moss substrata	Shrub-tree borders of meadows on floodplains or local river deposits	Middle beaches of large lakes; vegetation of herbs and low or trailing shrubs
Total nos. of spp.	42	57	78	161	81	114	66	108	100	89
Nos. of primary spp.	20	11	40	26	21	27	30	30	19	27



——— Percents of total shore flora (417 spp.) found in each habitat.
- - - - - Percents of total primary species (145) found in each habitat.

FIGURE 13. Proportional representation of all species and of all primary species among ten shore habitats.

Reasons for the variation in numbers of species found in the 10 habitats are not clear. The variations might be due to sampling differences, but if this were true the habitats in which the largest numbers of different assemblages were described should show the largest numbers of species. This

correlation, however, does not occur. The treeless shrub muskeg, for example, had the largest number of species (161), seen in 37 different assemblages, while the flood-plain meadows, with the largest number of different assemblages (49), had only 108 species listed. The next largest number of species was in the damp to wet sandy shores of lakes and rivers (114) and was noted in the smallest number of different assemblages (12).

A somewhat better coincidence is with the probable areas occupied by the habitats. No accurate figures are available for this, but it is probable that shrub muskegs occupy more area in the shore vegetation than any other type. A tentative scale of areas, based on the writer's field observations, is given below. The habitats are listed from largest to smallest, with the numbers of species, from greatest to least, listed on the right as they occur in the areas.

1.	Treeless shrub muskegs	1
2.	Flood-plain meadows	3
3.	Shrub-tree borders of flood-plain meadows	4
4.	Damp to wet sand or gravel lake and river shores	2
5.	Shrub-tree borders of muskegs	5
6.	Muskeg meadows	8
7.	Shrubs and trees on upper lake beaches	7
8.	Aquatic habitats	10
9.	Middle beaches of large lakes	6
10.	Saline or brackish habitats	9

The correlation here is far from complete, but it suggests that size of area may have some significance.

Addition of the numbers of species in the 10 habitats gives a total of 896, which is a little over twice the number in the shore flora and indicates the extent to which in general, the species showed their habitat versatility.

FIGURE 14 gives the proportional representation, in each of the 10 habitats, of the primary and secondary species that were found in more than one habitat (2 to 7). The base numbers for percentages in both are the total floras of the habitats. Curves for species found in only one habitat would be mirror images of those in FIGURE 14.

Reasons for variations in the proportions of more versatile species from one habitat to another, ranging from about 20% to 100%, can only be suggested with present knowledge of the habitats and without more information on the gradient of versatility that seems to exist among the plants. It is probable that there is an inverse relationship between gradients of structural and physiological specialization on one hand, and of habitat versatility on the other. The most highly specialized species in the shore flora probably are the aquatics and the halophytes, and FIGURE 14 shows them to be at the bottom of the scale of versatility.

A certain amount of specialization for resistance to desiccation is to be expected, if the above reasoning is tenable, toward the dry end of the moisture gradient. If the halophytes were considered specialized for physiological dryness, they could be placed at the opposite side of the graph in FIGURE 14 and would accentuate the drop in versatility that is suggested

	Aquatic habitats, with both submerged and emergent species	Saline or brackish sloughs and wet meadows	Muskeg grass-sedge meadows with moss substrata	Open (treeless) shrub muskegs	Shrub-tree borders of muskegs	Damp to wet sand and/or gravel on shores of rivers and ponds or on lower beaches of large lakes	Upper beaches of large lakes: vegetation of upright shrubs and trees	Grass-sedge meadows on river floodplains or on local river deposits, with silt or silt and thin moss substrata	Shrub-tree borders of meadows on floodplains or local river deposits	Middle beaches of large lakes: vegetation of herbs and low or trailing shrubs
Nos. of primary spp.	20	11	40	26	21	27	30	30	19	27
Nos. of secondary spp.	22	46	38	135	60	87	36	78	81	62

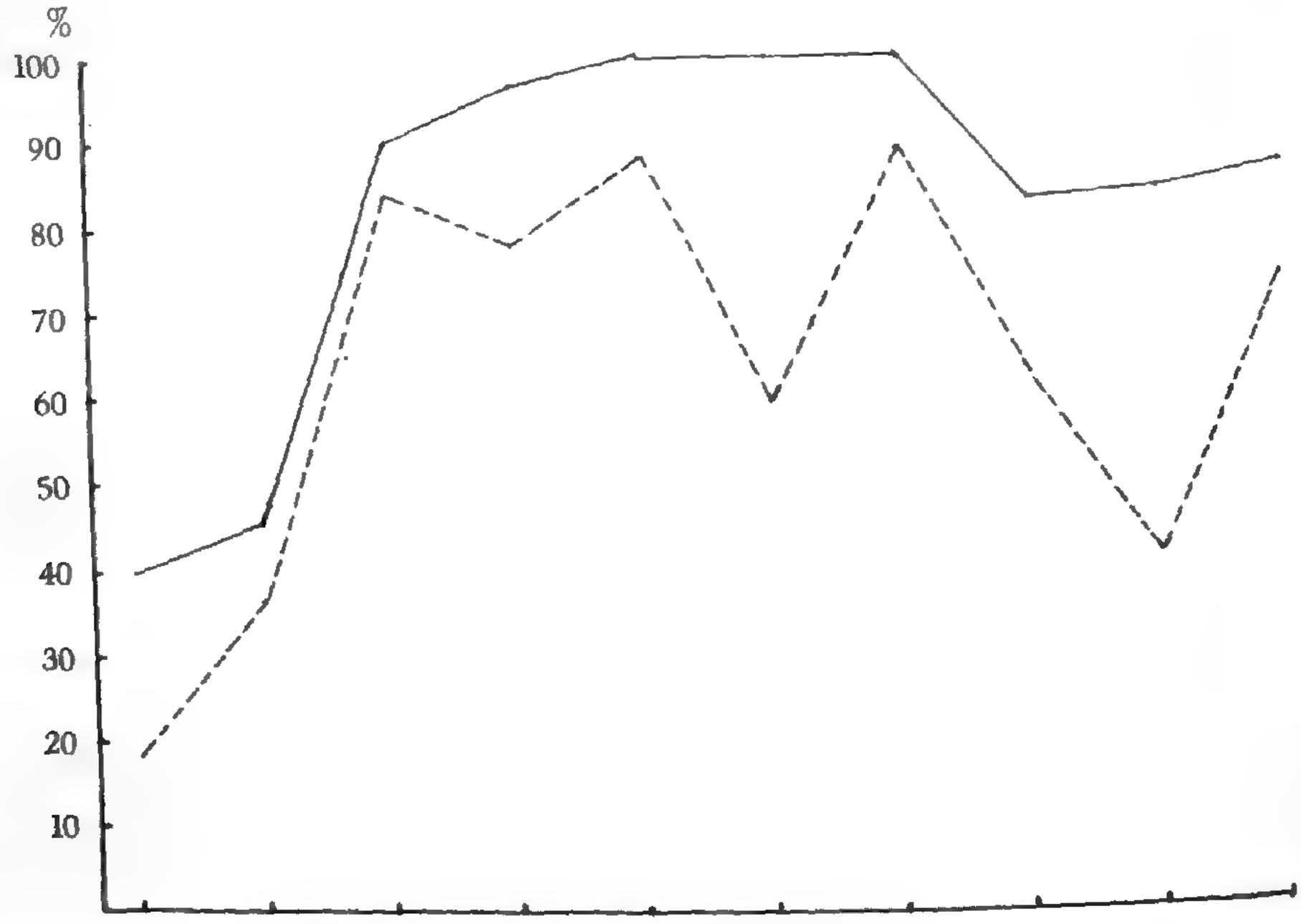


FIGURE 14. Analyses of shore habitat floras with respect to the habitat versatility of the primary and secondary species found in them. Base numbers for percentages are the numbers of primary and secondary species in each habitat.

by the three vegetations at the drier end of the gradient. The high versatility shown by the muskeg floras, the vegetation of the upper beaches, and wet sand or gravel shores would be expected, as would lowered flexibility in the flood-plain meadows and their shrub-tree borders. The latter sites are subject to flooding in spring or early summer, but become relatively dry in mid- or late summer. Their silty alluvial soils are fairly well drained after the floods recede, and most of them do not have thick moss mats to hold water and retard evaporation. Their shrub-tree borders usually are on low levees where drainage is better than in the meadows.

The middle beaches of the large lakes are the driest sites on the shores owing to their topographic position, their exposure to winds, and their coarse-textured soils.

Most of the high versatility in FIGURE 14 is in vegetations containing large percentages of the upright shrubs and trees of the flora. FIGURE 12 and TABLE 1 (below) indicate that these forms, wherever they occur, show high versatility. It is probable that their presence has influenced the trends of the curves in FIGURE 14.

Seventy-nine of the 145 primary species in the shore flora (54.5%) were found to be primary in only one or another of the 10 habitats. Thus nearly half of the primary species noted in any one habitat were likely to appear as primary in at least one other and possibly in six others. Of the 66 species found to be primary in more than one habitat, most were seen in 2 (46), 15 in 3 to 4, and 5 in 5 to 7. All but one of the 20 primary species found in the largest numbers of combinations (7 to 19) are among the more versatile of the primary species. The exception is *Nuphar variegatum*, a highly specialized aquatic.

TABLE 1. **Analysis of habitat floras for their percentage representations of life-forms. Numbers in parentheses are for primary species.**

	Aquatic habitats, with both submerged and emergent species	Saline or brackish sloughs and wet meadows	Muskeg grass-sedge meadows with moss substrata	Open (treeless) shrub muskegs	Shrub-tree borders of muskegs	Damp to wet sand and/or gravel on shores of rivers and ponds or on lower beaches of large lakes	Upper beaches of large lakes: vegetation of upright shrubs and trees	Grass-sedge meadows on river floodplains or on local river deposits, with silt or silt and thin moss substrata	Shrub-tree borders of meadows on floodplains or local river deposits	Middle beaches of large lakes: vegetation of herbs and low or trailing shrubs
Nos. of species	42 (20)	57 (11)	78 (40)	161 (26)	81 (21)	114 (27)	66 (30)	108 (30)	100 (19)	89 (27)
Trees	0 (0)	1.8 (0)	0 (0)	3.1 (0)	7.4 (4.9)	6.1 (2.6)	13.6 (9.1)	0.9 (0)	6.0 (1.0)	6.7 (0)
Shrubs	0 (0)	10.5 (0)	5.1 (3.8)	21.7 (9.9)	37.0 (17.3)	16.7 (7.0)	39.4 (25.8)	9.3 (0)	35.0 (12.0)	29.2 (9.0)
Perennial herbs with fibrous roots	9.5 (0)	12.3 (3.5)	19.2 (6.4)	17.4 (0.6)	7.4 (0)	20.2 (4.4)	12.1 (1.5)	14.8 (1.9)	8.0 (0)	14.6 (4.5)
Perennial herbs with rhizomes	71.4 (31.0)	52.6 (12.3)	67.9 (37.2)	48.4 (5.0)	39.5 (3.7)	41.2 (8.8)	27.3 (7.6)	62.0 (23.1)	48.0 (6.0)	34.8 (13.5)
Perennial herbs with taproots	16.7 (14.3)	3.5 (1.8)	3.8 (3.8)	6.8 (0.6)	7.4 (0)	7.9 (0)	6.1 (1.5)	3.7 (0)	3.0 (0)	10.1 (2.2)
Annual and biennial plants	2.4 (2.4)	19.3 (3.5)	3.8 (0)	2.5 (0)	1.2 (0)	7.9 (0.9)	1.5 (0)	9.3 (2.8)	(0) (0)	4.5 (1.1)

The predominance of perennial herbs with rhizomes, caudexes, etc., noted earlier, appears again in TABLE 1, where the 10 habitat floras are analyzed in terms of life-forms. They show the highest percentages in all but one of these floras. The exception is among the trees and upright shrubs on the upper beaches of large lakes, where they are least represented. They are most abundant in the grass-sedge meadows and in aquatic habitats, in which they range between 62 and 71% of the floras. Except on the upper beaches noted above, they do not fall below about 35% in any of the habitats.

Next in descending order of abundance are the shrubs, which of course reach their largest percentages in the shrub muskegs and in the shrub-tree borders of meadows and lake beaches. In these habitats they range between 21 and about 40% of the species. In the meadows they range from 5 to about 10%. The middle beaches of large lakes have a larger proportion of shrubs than the shrub muskegs, but most of them are decumbent or trailing, while in the muskegs most are upright.

Third are fibrous-rooted perennial herbs, ranging from about 8% to about 20% of the habitat floras. They have their lowest percentages in aquatic and shrub-tree border habitats, and their highest in muskeg grass-sedge meadows and in the damp to wet sand and gravel shores of lakes and rivers. They have a relatively large percentage (14.6) on the middle beaches of large lakes, where they represent a tundra element of the flora in which their life-form is much more common than in our region.

Perennial herbs with taproots, bulbs, corms, tubers or turions range, with two exceptions, from 3% to about 8% of the floras. The exceptions are in aquatic and middle beach habitats, at the two ends of the moisture gradient. They are relatively prominent among the aquatics because some of these plants perennate by detached winter buds (turions). On the middle beaches, with 10.1%, they are mainly taprooted plants which, like the fibrous-rooted species, represent the tundra flora in which plants with taproots are abundant.

Many of the most characteristic plants of saline or brackish habitats in this region are annuals, and the category of annual or biennial herbs has its highest percentage in these sites (19.3). In all the others they range from 1.2 to 9.3%, in most of them below about 5%. All of the habitats in which their percentages are above about 5% are located mainly in the lowlands along the main rivers, which have been the major travel routes since the early fur trading days. Many of the annuals in the shore flora are introduced weeds, so that it is not surprising to find relatively large proportions of this form in the flood-plain meadows and on river banks. Since the field work was done for this paper there has been much more travel away from the old routes, notably eastward into the Canadian Shield. It is probable that annual and biennial weed species have increased in numbers and distribution during the last 40 years.

The trees have minor roles in most of the habitats, although they have some prominence in the shrub-tree borders of muskegs and meadows, and particularly on the upper beaches of large lakes. They were found in small

numbers, as seedlings or very small trees, in all the other habitats except in open water and in muskeg meadows.

TABLE 1 gives the percentages of primary species produced by each of the life-forms in the various habitats. The only life-form that had primary species in all of the habitats is that of rhizomatous perennial herbs. In general, the forms that showed very low representations in one or more of the habitats produced no primary species or very few. On the other hand, rhizomatous perennials which showed consistently high percentages of all species produced some very low numbers of primary species. As might be expected, these were in the shrub muskegs, the shrub-tree borders, and in the saline or brackish habitats.

It was noted earlier that by far the largest geographic element in the shore flora is a group of 313 species that range widely in the boreal forest region, nearly all of them reaching across the northern part of the continent from Newfoundland to Alaska (FIGURE 3). The predominance of this affinity appears again in TABLE 2, where the representations of the

TABLE 2. **Analysis of habitat floras for their percentage representations of the four major geographic elements of the shore flora. Numbers in parentheses are for primary species.**

	Aquatic habitats, with both submerged and emergent species	Saline or brackish sloughs and wet meadows	Muskeg grass-sedge meadows with moss substrata	Open (treeless) shrub muskegs	Shrub-tree borders of muskegs	Damp to wet sand and/or gravel on shores of rivers and ponds or on lower beaches of large lakes	Upper beaches of large lakes: vegetation of upright shrubs and trees	Grass-sedge meadows on river floodplains or on local river deposits, with silt or silt and thin moss substrata	Shrub-tree borders of meadows on fooodplains or local river deposits	Middle beaches of large lakes: vegetation of herbs and low or trailing shrubs
Nos. of species	42 (20)	57 (11)	78 (40)	161 (26)	81 (21)	114 (27)	66 (30)	108 (30)	100 (19)	89 (27)
Boreal forest	95.2 (47.6)	80.7 (19.3)	78.2 (42.3)	75.2 (12.4)	81.5 (19.8)	71.9 (21.1)	77.3 (34.8)	88.9 (26.9)	85.0 (17.0)	62.9 (15.7)
Arctic-alpine	2.4 (0)	1.8 (0)	12.8 (2.6)	13.7 (0.6)	7.4 (1.2)	15.8 (0.9)	9.1 (4.5)	0.9 (0)	3.0 (0)	18.0 (11.2)
Alaskan-Cordilleran	2.4 (0)	15.8 (0)	3.8 (2.6)	6.8 (0.6)	4.9 (2.5)	8.8 (0.9)	10.6 (4.5)	10.2 (0.9)	10.0 (2.0)	12.4 (1.3)
Timberline	0 (0)	1.8 (0)	5.1 (3.8)	4.3 (2.5)	6.2 (2.5)	3.5 (0.9)	3.0 (1.5)	0 (0)	2.0 (0)	6.7 (2.6)

four major geographic elements of the flora are noted as they appear in the ten habitats used in the present study. There is wide variation in their distribution among the habitats.

The boreal forest group shows a range of representation of about 33%. It is highest in aquatic habitats and lowest in the shrub muskegs and on the middle beaches of the large lakes. Other relatively high points are reached in the lowland meadows and in the shrub borders of these meadows. Another relatively low point is on the wet to damp sand or gravel beaches and river shores. All the other habitats have median percentages, ranging from about 77 to 81. The primary species produced by the boreal forest group vary from this pattern, although the highest percentage is also reached in the aquatic habitats. Their lowest point is in the shrub muskegs. Relatively high percentages appear in the grass-sedge muskeg meadows and in the shrub-tree borders of the upper beaches of large lakes. Though this element makes one of its largest contributions in the lowland meadows and their borders, its primary species in these sites are median. The reverse proportions appear on the upper beaches and in muskeg meadows, where the element has produced relatively large percentages of primary species.

The second major element of the shore flora, derived from wide-ranging arctic-alpine plants, contains 51 species. It makes very small contributions to the saline and aquatic habitats, none at all to lowland meadows, and only minor ones to the shrub-tree borders of these meadows. In the last two of these, the boreal forest plants are heavily represented. On the other hand, the element shows the highest percentage on the middle beaches of the large lakes, where the boreal forest group was near its lowest point. It is relatively high in damp to wet sand or gravel beaches and in muskegs, and in both of these habitats the boreal forest group is median. Thus the arctic-alpine species, in general, complement the boreal forest group in their distribution, suggesting that in general the wet sand and gravel beaches, the middle beaches of the large lakes, and possibly some of the muskegs most closely resemble the arctic habitats, while the lowland meadows and the shrub-tree borders more closely resemble habitats in the boreal forest region.

Primary species in the arctic-alpine element show very low percentages except in the middle and upper beaches of the large lakes, particularly in the former. This further suggests the general predominance of the boreal forest element, which is represented not only by the largest number of species, but also by a large proportion of the primary species. The unique position of the middle beaches is shown by the fact that the arctic-alpine group supplies almost as many primary species there (within about 5%) as the much more numerous boreal forest group.

The last two geographic affinities to be considered are the Alaskan-Cordilleran group, with 41 species, and the timberline group, with only 12 species. Both make only small contributions to the flora, but they differ considerably. The Alaskan-Cordilleran plants are most numerous on the middle beaches and in the saline or brackish habitats, and are relatively common on the sand and gravel shores and in the lowland meadows or their borders. Their lowest proportions are in the aquatic habitats, the muskegs and muskeg borders. Judged by distributions in the preceding

two elements, this proportion is indicative of the mixed boreal forest and arctic-alpine character of the Alaskan-Cordilleran element. It will be seen that the Alaskan-Cordilleran group contributes very small numbers of primary species to the vegetation (less than 5%) and none at all to the saline and aquatic habitats. The timberline group is by definition also a mixed one, bridging the arctic timberline. Compared to the Alaskan-Cordilleran element, it contributes, relatively, many more primary species.

SUMMARY AND DISCUSSION

This study deals with the shore vegetation of lakes and rivers in the Athabaska-Great Slave Lake region of northwestern Canada. It is based on about 130 transects that extended from open water to the shrub-tree borders. Ten habitat-vegetation complexes are defined to embrace the principal variations that were found. Definitions of the habitats are based mainly on differences in local topography, substrata, and moisture regimes. Vegetative components are defined physiognomically as grass-sedge meadows, treeless shrub muskegs, shrub-tree borders, etc. Within the habitats the vegetation is described in terms of assemblages of vascular plant species which are visibly different from one another owing to the abundance and/or prominence of one or more "primary" species. All other species in the assemblages are considered "secondary."

In the course of the field work 424 species of vascular plants were noted, seven of which were eliminated from the analyses because they were endemic or marginal and their behavior was not sufficiently known. Assemblages described numbered 550. Of these, 251 were found to differ from one another in their primary species composition. Thus the average number of times a given assemblage was repeated was 2.2.

One hundred and forty-five of the shore species were noted as primary in one or more of the different assemblages in which they occurred. All but 11 of them (134 spp.) were found in varying combinations of two to four species each, and 60 of these were also found as single primary species in their assemblages. The 134 primary species formed 180 different combinations. Twenty of these species were found in 7 to 19 combinations each, involving 75 other primary species and accounting for 128 of the 180 combinations observed.

With so little repetition among the assemblages, the feasibility of generalizing or rationalizing the vegetation in terms of these assemblages becomes remote. The large number of different combinations among the primary species suggests that most of the latter have very wide latitude in their "choice" of associates. It suggests a greatly reduced probability that species compatibility, or some kind of obligate relationship among species, has much effect upon the primary composition of the assemblages.

Coefficients of species' group relations to habitat, or of "preferred" associations among species, could be derived statistically, but the scale of refinement thus achieved would be far from commensurate with the scale of our present or foreseeable knowledge of the habitats; nor would it be

commensurate with our limited understanding of differences in behavior known to occur among the species.

About 60% (252) of all the shore species were found growing in more than one of the 10 habitats, some of them in as many as 5 to 7 (FIGURE 1). The "most successful" species — those that were found to be primary in the assemblages — were drawn mainly from those species growing in more than one habitat. It is proposed that the number of different habitats used by a given species is a rough index of its inherent tolerance or versatility ("ecological amplitude") in adjusting to habitat variation. It is suggested that the primary species have attained this rank at least in part because they are inherently more versatile than the secondary species. Their versatility appears to apply to both physical and biological habitats, for the primary species growing in the greater number of different habitats also formed the greater number of combinations with other primary species (FIGURE 2).

Size of geographic range appears to be correlated with differing tolerances of habitat variation. In general, the larger the continuous range, the greater the incidence of wide tolerance among the species. This is suggested by analysis of the major geographic elements of the flora (FIGURES 4, 5, & 6), but is shown more clearly by species that have more or less limited ranges within the Athabaska-Great Slave Lake region (FIGURES 7 & 8). A major floristic boundary shows much greater tolerance among the species that cross it even for short distances than among those that do not (FIGURES 8 & 9).

Wide versatility in habitat occupance is not evenly distributed among life-forms of the plants. In the shore flora as a whole the trees and shrubs are the most versatile, while the herbaceous plants form a second group that do not differ greatly among themselves (FIGURE 12). The primary species in this group, however, show notable differences. Perennials that have fibrous roots as underground organs show considerably more versatility than the much more numerous perennials with caudexes, stolons, runners, or rooting stems. They are nearly as versatile as the primary shrubs. Least versatile are the perennials with taproots, bulbs, corms, tubers, or turions. Primary annual and biennial species are also very low in the scale of tolerance.

The life-forms of species in different geographic affinities show some notable variations from the above. Plants whose general ranges are arctic-alpine have appreciably greater versatility in their fibrous-rooted and taprooted perennials than is shown by these forms in the boreal forest or timberline affinities. This difference is shared in part by the Alaskan-Cordilleran affinity, which has in it an arctic-alpine element. It is probable that the wider tolerance in these forms reflects their predominance in the arctic tundra.

Variations in the incidence of wide versatility in the floras of the 10 habitats is shown in FIGURE 14. An explanation of the variation can only be suggested. It may be assumed that the most highly specialized species

in the flora, morphologically and physiologically, are the aquatics and the halophytes. If this is the case, they are the least likely to be found in other habitats and should show the least versatility, as they do in FIGURE 14. By the same reasoning, there should be some effects of specialization for partial desiccation toward the drier end of the moisture gradient. This is suggested among the last three of the habitats on the right side of the figure, where percentages of widely tolerant species are appreciably lower than in the preceding five habitats.

In view of the findings in this paper, it appears that the shore species of the Athabaska-Great Slave Lake region are behaving not so much as members of "communities" in which there are necessary relationships to specific habitats or to other species, but as populations of individual species that have found, perhaps in part by chance, sites that are satisfactory to them. Their adaptation to site seems to have considerable flexibility, which varies from one species to another. The flexibility is most pronounced among the primary species — those that give form and color to supposed "communities" and make the shore vegetation look the way it does. The present paper, therefore, has dealt primarily with the behavior and distribution of species rather than of "communities." The term "community" is replaced by "assemblage," which carries fewer implications of relationships that are nonexistent or unknown.

Only the effects of differences in versatility among the species are apparent, in local or regional behavior and distribution. It is presumed that the differences are due to biotypic or ecotypic variations within the populations which, in turn, have been conditioned historically. Such variations are known to occur in species that have been studied cytotaxonomically and experimentally (Turesson, 1922, 1925; Anderson, 1936; Clausen, Keck, & Hiesey, 1940; Mayr, 1964; Johnson & Packer, 1965). Their probable significance in the study of "dominance," and in the concept of "niche" in ecological systems, has been stated by McNaughton and Wolf (1970). The genetic differentiation of plant populations within small areas has been discussed by Bradshaw (1972), who concludes that "the ecological amplitude of most species . . . . has a strong genetical component." Further understanding of the ecological and geographic behavior of the vegetation discussed here will depend in large measure upon investigations of its history and the processes of its inheritance. The starting point for this is at the species level.

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THE TAXONOMIC STATUS OF THE GENUS BAUERELLA (RUTACEAE) *

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IN THE COURSE OF a recent study of the genus *Acronychia* (Jour. Arnold Arb. **55**: 469–567. 1974), it became apparent to me that its generic limits were never very clearly established and that as a result an unusually diverse assemblage of plants have been included in it — some having bisexual flowers, others having unisexual flowers; some with eight stamens, others with four; and some having drupaceous fruits, others having capsular fruits. Such diversity may not necessarily be excessive in tropical genera (see, for example, Gillett's discussion of the generic limits of *Cyrtandra*, 1970), but in this instance I believe it is.

I have found that *Acronychia*, when rather narrowly interpreted around the type species, *A. laevis* J. R. & G. Forst., comprises a clearly monophyletic genus of 42 species distributed from India south and east to New Caledonia and Australia. The majority of the species are endemic to either Australia or New Guinea and a number of them, having narrow distributions and, in some cases, being geographically disjunct vicarious species, appear to be relicts. The major unifying characteristics of these plants are opposite leaves, bisexual flowers, and drupaceous fruits. As far as I have been able to determine, this combination of characters serves to distinguish the species from all of the other genera of the Rutaceae in the Indo-Pacific region.

If broader generic limits are accepted for *Acronychia*, such as those presented by Engler (1931: 309, *figs. 140* and *141*), in the standard major work for the Rutaceae of the Indo-Pacific region, then the mutually close relationships of the species, and their apparent phylogeny, would be obscured. Also, the genus would then be indistinguishable, taxonomically, from several other genera, including *Melicope*, *Euodia*, and *Evodiella*.

Among the plants which I have excluded from *Acronychia* is *A. baueri* Schott, the type species of the genus *Bauerella* Borzi. In carrying out his work on the floras of Norfolk and Lord Howe Islands, Peter Green (1970) made a thorough study of this species, the type of which may have come from Norfolk Island. He determined that it is conspecific with *A. simplicifolia* (Endl.) McGillivray & Green and recognized therein three geographical subspecies: one from eastern Australia (from northeastern Queensland south, quite continuously, to southeastern New South Wales)

* This is the sixth in a series of papers on the Rutaceae. The series was initially restricted in its coverage to genera of the Malesian region, but, as I am finding it increasingly evident that Australian genera often hold the key to the understanding of Malesian genera, I would now like to expand its coverage to include the Australasian region (Australia, New Zealand, New Caledonia, and Papuasia).

and Lord Howe and Norfolk Islands; one from New Caledonia and the New Hebrides; and one from Fiji. He also described an additional, closely related species from New Caledonia, *A. leiocarpa* P. S. Green. I agree with Green's delimitations of the species and subspecies of these plants, but I am of the opinion that they are more correctly placed in *Bauerella* than in *Acronychia*.

Bauerella has been recognized as being distinct from *Acronychia* by Engler (1900: 35 and 1931: 310) — on the basis, however, of characters that are hardly diagnostic, considering the broad range of plants he included in the latter — and, in recent years, by students of the New Caledonian flora, including Däniker (1932) and Guillaumin (1948). Australian botanists, on the other hand, have preferred to include the genus in *Acronychia*, one reason being, perhaps, that Bentham (1863) accepted *A. baueri* without giving any indication that it might be generically distinct from *A. laevis* and *A. imperforata* F. Muell., both of which belong to *Acronychia sensu stricto*.

With the exception of *Acronychia* and *Phellodendron*, the drupaceous fruits and opposite leaves of *Bauerella* serve to distinguish it from all of the recognized genera of the Rutaceae in the Indo-Pacific region. The three species from northwestern Malesia and adjacent mainland Asia which I have excluded from *Acronychia*, but have not yet placed generically (*A. obovata* Merr., *A. oligophlebia* Merr., and *A. porteri* Hook. f.), are similar to *Bauerella* in having unisexual flowers and drupaceous fruits, but differ in having petals that are deciduous in fruit and stamens with narrow, geniculate filaments. *Phellodendron*, a genus of possibly a dozen species distributed in subtropical and temperate eastern Asia, also has opposite leaves and drupaceous fruits, but differs from *Bauerella* in several floral characters and in its pinnately compound, as opposed to simple, leaves.

The taxonomic differences between *Acronychia* and *Bauerella* are summarized in the following table, and the comparative floral morphology is illustrated in FIGURE 1.

Acronychia	**Bauerella**
Plants with bisexual flowers	Plants apparently always dioecious, with functionally unisexual flowers
Flower buds longer than wide	Flower buds globose or subglobose
Sepals usually imbricate	Sepals usually valvate
Petals valvate	Petals narrowly imbricate in bud
Petals deciduous or rarely semipersistent in fruit	Petals persistent in fruit
Stigma scarcely differentiated from the style	Stigma (in functionally carpellate flowers) broadly 4-lobed, peltate

An amplified generic description of *Bauerella* and an enumeration of the known species and subspecies are included in this paper.

A large number of herbarium specimens were examined in this study, but only a few are cited, since the majority were previously cited by Green. The contributing herbaria are listed below, however, with abbreviations

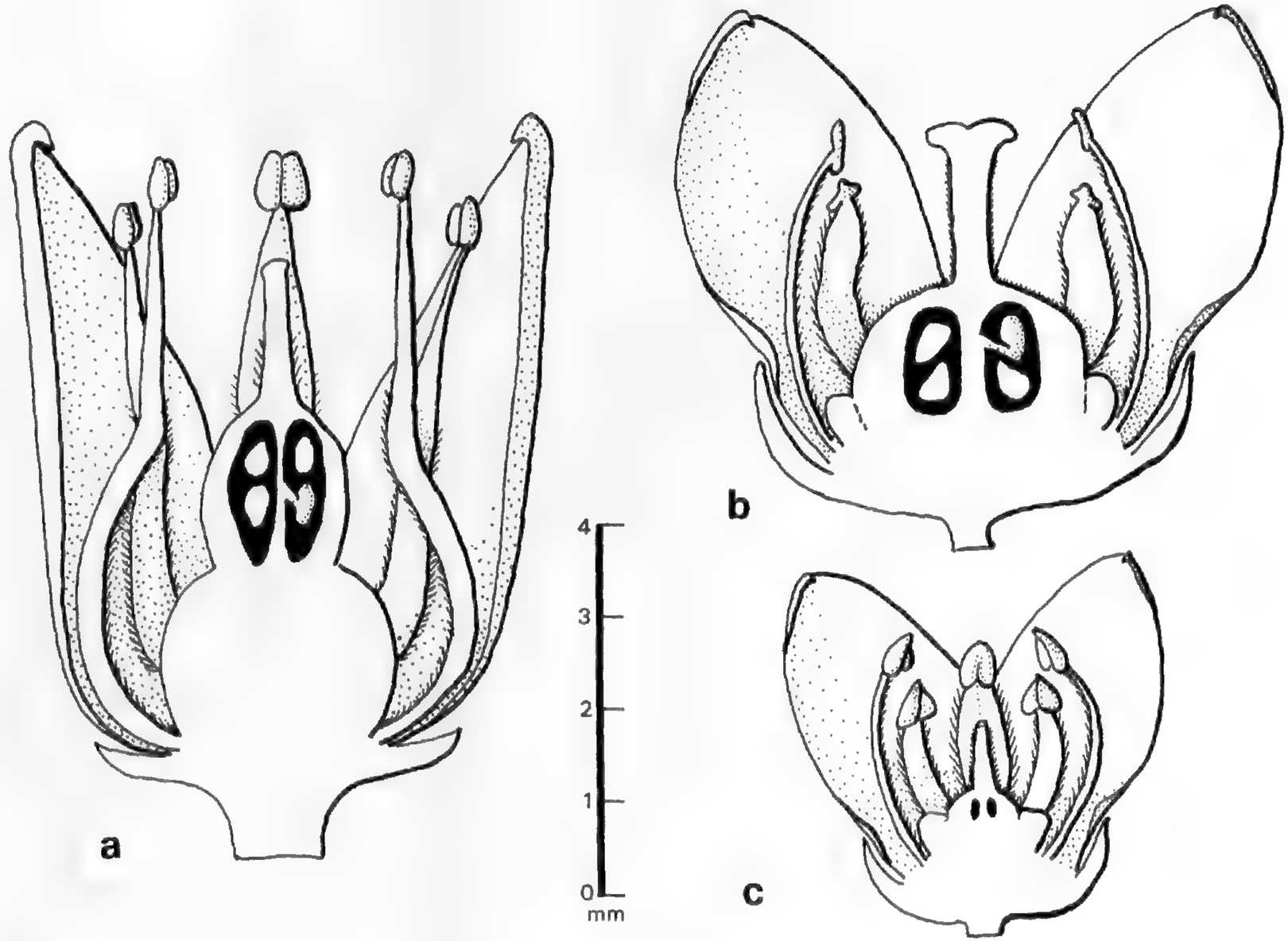

FIGURE 1. Comparative floral morphology of *Acronychia* and *Bauerella*, all drawn to the same scale from preserved flowers: a, bisexual flower of *Acronychia murina* (*Pullen 5290*) — the enlarged disc is characteristic of this species, but in some other species of *Acronychia* it is similar to that of *Bauerella simplicifolia*; b, functionally carpellate flower of *Bauerella simplicifolia* (*Moriarty 1510*) — note the poorly developed anthers and peltate stigma; c, functionally staminate flower of *Bauerella simplicifolia* (*Moriarty 1511*) — note the reduced ovary, lacking ovules, and the undifferentiated stigma.

from Lanjouw and Stafleu's *Index Herbariorum*, Part I. ed. 5 (Regnum Vegetabile 31. 1964).

A	Arnold Arboretum of Harvard University, Cambridge
AD	State Herbarium of South Australia, Adelaide
BISH	Bernice P. Bishop Museum, Honolulu
BM	British Museum (Natural History), London
BRI	Queensland Herbarium, Brisbane
CANB	Herbarium Australiense, C.S.I.R.O., Canberra
GH	Gray Herbarium of Harvard University, Cambridge
K	Royal Botanic Gardens, Kew
MEL	National Herbarium of Victoria, Melbourne
MICH	University Herbarium, University of Michigan, Ann Arbor
NSW	National Herbarium of New South Wales, Sydney
NY	New York Botanical Garden, New York
P	Muséum National d'Histoire Naturelle, Paris
PR	Botanical Department, National Museum, Prague
UC	Herbarium of the University of California, Berkeley
US	National Museum of Natural History (Department of Botany), Smithsonian Institution, Washington, D.C.
W	Naturhistorisches Museum, Wien

I wish to thank the directors and curators of these herbaria for making specimens in their care available to me. Thanks are also extended to L. A. Craven, of the C.S.I.R.O. Division of Plant Industry, and V. K. Moriarty, of the C.S.I.R.O. Division of Applied Chemistry, for their special efforts in making field observations and collections for me.

Bauerella Borzi, Bol. Orto Bot. Palermo 1: 155. 1897. TYPE SPECIES: *Bauerella australiana* Borzi, *nomen illegit.* (≡ *Bauerella baueri* (Schott) Däniker, ≡ *Acronychia baueri* Schott).

Shrubs or small to medium trees; apparently always dioecious; indumentum of minute, simple trichomes. Leaves opposite or rarely in whorls of three, simple, petiolate; leaf blades pellucid-dotted, entire, pinnately veined. Inflorescences axillary, pedunculate, narrowly paniculate to subracemose. Flowers functionally unisexual, small and inconspicuous, globose or subglobose in bud; sepals 4, distinct or basally connate, valvate or rarely basally imbricate, persistent in fruit; petals 4, distinct, narrowly imbricate in bud, persistent in fruit; stamens 8, distinct, shorter than the petals, the antesepalous slightly longer than the antepetalous, filaments flat, elliptic-oblong, ciliate, anthers 2-celled, obtuse or obtusely apiculate, dorsifixed, without pollen in functionally carpellate flowers; disc intrastaminal, pulvinate; gynoecium a single, 4-carpellate, 4-loculate pistil, rudimentary (reduced in size and without fully differentiated stigma or functional ovules; the latter usually not visible with 10 × magnification) in functionally staminate flowers, ovules 2 per locule, subcollateral or superposed, style short, stigma peltate, broadly 4-lobed. Fruit a 4-loculate drupe; mesocarp drying spongy-crustaceous to subwoody, endocarp car-

tilaginous. Seeds carunculate, 2 or (by abortion) 1 per locule; testa longitudinally roughened, with a thin, crustaceous outer layer (often not completely covering the seed) and a thick, bony inner layer; endosperm fleshy; embryo straight, cotyledons flattened, hypocotyl terminal.

The leaves range in length from about 3 to 20 cm. The leaf blades vary from chartaceous to subcoriaceous and range in shape from narrowly elliptic to obovate. The petioles are usually about one-third the length of the leaf blades. Inflorescences range in size from one-half to one and one-half times the length of the subtending petiole and tend to be narrowly paniculate, with a relatively large number of sessile or subsessile flowers, when functionally staminate, or subracemose, with relatively fewer pedicellate flowers, when functionally carpellate. Also, as is shown in FIGURE 1, there is a considerable size difference between the sexes of the flowers. Variations in size and shape of the drupes are shown by Green (1970: 212, *fig. 1*).

Collections and field observations made of *Bauerella simplicifolia* subsp. *simplicifolia* in Brisbane (*Moriarty 1510* and *1511*, both CANB) and on Mt. Dromedary, in southeastern New South Wales (*Craven 2583* and *2588*, both CANB), have shown that the plants are dioecious. This is almost certainly the condition throughout the genus, because, in over 250 different collections examined, I have not found any single specimen bearing flowers of both sexes or both fruits and male flowers.

In its distribution, *Bauerella* demonstrates, as do a significant number of other eastern Australian rain forest genera, a strong phytogeographic link between Australia and New Caledonia. Its further eastward presence in the New Hebrides and Fiji, however, coupled with its absence in New Guinea, is quite unusual. Interestingly, this distribution closely parallels that of the curious amentiferous genus *Balanops* (Balanopaceae).

ENUMERATION OF THE SPECIES AND SUBSPECIES

1. **Bauerella simplicifolia** (Endl.) Hartley, comb. nov.

Vepris simplicifolia Endl. Prodr. Fl. Norfolk 89. 1833. TYPE: *Bauer*, December 5, 1804, Norfolk Island [W (sterile specimen and original Bauer pencil sketch of a flowering and fruiting specimen), holotype].

Acronychia simplicifolia (Endl.) McGillivray & Green, Jour. Arnold Arb. **51**: 209. 1970.

1a. **Bauerella simplicifolia** (Endl.) Hartley subsp. **simplicifolia**.

Acronychia simplicifolia (Endl.) McGillivray & Green subsp. *simplicifolia*, Jour. Arnold Arb. **51**: 209, *fig. 1a*. 1970.

Acronychia endlicheri Schott, Rutaceae. Frag. Bot. 3, *t. 2*. 1834, *nomen illegit.*, based on *Vepris simplicifolia* Endl.

Acronychia baueri Schott, Rutaceae. Frag. Bot. 5, *t. 3*. 1834. TYPE: *Bauer*, locality unknown, possibly Norfolk Island (not seen).

Acronychia hillii F. Muell. Frag. Phytogr. Austral. **1**: 26. 1858. SYNTYPES:

Hill, Queensland, Brisbane River (MEL); *Mueller*, July, 1855, Queensland, Brisbane River (BM, GH, K, MEL, P).

Bauerella australiana Borzi, Bol. Orto Bot. Palermo **1**: 155. 1897, *nomen illegit.*, based on *Acronychia baueri* Schott.

Bauerella baueri (Schott) Däniker, Viert. Naturf. Ges. Zürich **77** (Beibl. 19): 202. 1932.

1b. **Bauerella simplicifolia** (Endl.) Hartley subsp. **neo-scotica** (P. S. Green) Hartley, comb. nov.

Acronychia simplicifolia (Endl.) McGillivray & Green subsp. *neo-scotica* P. S. Green, Jour. Arnold Arb. **51**: 211, *fig. 1b*. 1970. TYPE: *Deplanche 511*, New Caledonia, Port-Boisé (K, holotype).

1c. **Bauerella simplicifolia** (Endl.) Hartley subsp. **petiolaris** (A. Gray) Hartley, comb. nov.

Acronychia petiolaris A. Gray, U. S. Expl. Exped. (Wilkes Exped.) **14** (Bot. 1): 335. 1854 & Atlas, *t. 33A*. 1857. TYPE: *U. S. Expl. Exped.*, Fiji, Mathuata (GH, holotype; US, isotype).

Acronychia simplicifolia (Endl.) McGillivray & Green subsp. *petiolaris* (A. Gray) P. S. Green, Jour. Arnold Arb. **51**: 212, *fig. 1c*. 1970.

2. **Bauerella leiocarpa** (P. S. Green) Hartley, comb. nov.

Acronychia leiocarpa P. S. Green, Jour. Arnold Arb. **51**: 213, *fig. 1d*. 1970. TYPE: *Green 1211*, New Caledonia, NE slope of Ouen Toro, Nouméa (K, holotype).

Although it probably never will be settled, there is some question as to whether or not it is correct to treat *Bauerella baueri* as a synonym of *B. simplicifolia*. Schott described *Acronychia baueri* as being distinct from *Vepris simplicifolia* (as *Acronychia endlicheri*) mainly on the basis of its having staminal filaments that were eglandular, those of *V. simplicifolia* having been described as glandular. Unfortunately, I have not been able to check the accuracy of the descriptions of these species, because the only authentic (and probably the only extant) plant material at hand is a single, sterile sheet of *V. simplicifolia*. However, all of the flowering specimens I have seen, including several from Norfolk Island, the type locality of *V. simplicifolia*, agree with the description of *A. baueri* in having eglandular filaments. I suspect that the condition described for *V. simplicifolia* may have been the result of a misinterpretation of the material by Bauer and subsequently by Endlicher; the glands shown on the filaments in Bauer's sketch (W) are sessile and possibly are "blisters" caused by boiling the flowers. I do not think it is at all likely that two distinct species are involved.

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WHAT AND WHENCE WAS MILLER'S CARYOPHYLLUS COTINIFOLIUS?

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PHILIP MILLER, in the 8th edition of his *Gardeners Dictionary* (1768), took up the genus *Caryophyllus* Linnaeus for a group of myrtaceous plants including the clove, *Caryophyllus aromaticus* L., the type of the generic name. *Caryophyllus* in Miller's sense was a heterogeneous taxon, including *C. aromaticus* (now usually treated as a species of *Syzygium*), *C. pimento* (a species of *Pimenta*), *C. racemosus* (also assigned to *Pimenta*), and two other species, *C. fruticosus* and *C. cotinifolia* [sic]. Neither *C. fruticosus* nor *C. cotinifolia* (correctly *cotinifolius*) has been satisfactorily accounted for since Miller's time.

Since 1828 (DC. Prodr. 3: 276) *C. fruticosus* has been considered to be a synonym of *Eugenia biflora* (L.) DC. This verdict was accepted by Urban in his account of West Indian Myrtaceae (Bot. Jahrb. 19: 630. 1895). Miller's specimen at BM, however, represents another species of *Eugenia*, namely the same as that represented by Miller's specimen of *Caryophyllus cotinifolius*, discussed below. Miller's description of *C. fruticosus*, in which the leaves are said to be "shorter and rounder at their points than those of the last species [*C. pimento*]," would seem to apply to the plant in the herbarium, not to any of the known forms of *Eugenia biflora*. There is of course the possibility that Miller's specimen at BM has become mislabelled at some time during the last two centuries. In any event the question is academic, because the name *Eugenia fruticosa* is preoccupied.

The name *Caryophyllus cotinifolius* has been treated even more cursorily. Miller evidently derived the specific epithet from "Myrtus cotini folio Plum. Cat. 19," which he cited in synonymy. His description, however, was based entirely on a plant which he said he received from "the late Mr. Robert Millar, surgeon, from Carthagena in New Spain." Miller's plant at BM, which I take to be the type of his name, is a species of *Eugenia*, whereas the basis for *Myrtus cotini folio* is a species of *Myrcia*, *M. citrifolia* (Aubl.) Urb. Plumier's drawing corresponding to "Plum. Cat. 19" formed the basis for Burman's *plate 208, fig. 2*, representing *Myrtus cotini folio* (in Plumier, Pl. Amer., 1759). De Candolle (1828, p. 243), in describing *Myrcia coriacea*, cited "Plum. ed. Burm. t. 208. f. 2" in synonymy, wherefore Buek, in the index to De Candolle's *Prodromus*, presumably reasoning back from this to "Plum. Cat. 19," referred *Caryophyllus cotinifolius* Mill. to the synonymy of *Myrcia coriacea*. Taking the same view, the authors of the *Index Kewensis* equated *Caryophyllus co-*

tinifolius with *Myrcia coriacea,* and Urban (Bot. Jahrb. 19: 577. 1895), although with expression of considerable doubt ["??"], concurred. Urban later (loc. cit., p. 672), after studying a fruit taken from Miller's specimen at BM, stated that the plant must be a species of *Eugenia.* Except for these scanty references, *Caryophyllus cotinifolius* seems to have been

FIGURE 1. *Eugenia cotinifolia,* from Jacquin, Obs. Bot. 3: *pl. 53.* 1768. Approximately 7/8 original size.

overlooked. Berg apparently did not mention it in his treatment of American Myrtaceae (1855–1861).

Miller's specimen at BM represents a *Eugenia* with coriaceous, obtuse, obovate, essentially glabrous leaves, and small globose or somewhat elongate fruits on essentially glabrous peduncles a centimeter long or a little more. As Miller says, "the flowers are produced from the side of the branches, sometimes four, five, or six foot-stalks arise from the same point; at other times, they come out single, or perhaps by pairs." The leaves resemble those of *Myrcia citrifolia* in size and shape, in having short petioles, and in having the midvein somewhat elevated on the upper surface. Because Miller's name was published in 1768 it seems highly likely that it is the valid name for the species to which it pertains. The problem is that, up to the present time, nothing like this plant seems to have been found in northern South America (the supposed type-region), or indeed anywhere else in tropical America.

To complicate the situation, Jacquin published in the same year (Obs. Bot. 3: 3. *pl. 53.* 1768) the name *Eugenia cotinifolia*, based on a specimen of unknown origin, in the herbarium of Gronovius. I have not been able to locate Gronovius's specimen that Jacquin saw, but Jacquin published a plate (presumably drawn from the same specimen) showing a *Eugenia* with broad, coriaceous, obtuse leaves like those of *Myrcia citrifolia*, and long-pedicellate solitary flowers. As far as one can tell from the plate, it seems to represent the same species as *Caryophyllus cotinifolius*. Linnaeus (Mant. 243. 1771) accepted *E. cotinifolia* Jacq. as a valid species, stating that it came from "Cayenna."

Thus there seem to have been at least two contemporary 18th-century collections (perhaps three, if Miller's specimen of *C. fruticosus* is not merely a mislabelled duplicate of *C. cotinifolius*), of a tropical American species that has not been found since. Miller says his collection came from Cartagena, in the northern lowlands of Colombia; his specimen of *C. fruticosus*, if correctly labelled, came from Jamaica; we do not know the source of the Gronovius-Jacquin specimen, but Linnaeus said it came from the Guianas. It is entirely possible that the Gronovian specimen came from Miller. Miller was in no doubt that his specimens came from "Carthagena," where the surgeon Robert Millar collected, but it is certainly conceivable that the latter stopped somewhere in the West Indies and gathered some seeds, while en route from Europe to the Spanish Main, or on his return voyage.

Accordingly it is of particular interest that what seems to be a slightly newer specimen of the same species has come to light. In 1895 Urban described a species called *Eugenia dussii*, based in part on a fruiting specimen from Guadeloupe (*Duss 2200*), and in part on a flowering specimen from St. Lucia (*Anderson*, in herb. Kew). *Duss 2200* seems to have been a mixture; at least an isosyntype, at NY, consists of a vigorously grown but quite sterile, glabrous, leafy branch of *Eugenia pseudopsidium* or possibly *E. lambertiana*, and detached fruits and pedicels of what is presumably *Eugenia monticola*. Urban referred in the protologue to the "pedicellis . . .

brevissime patenti-pilosis," and the "baccae . . . minute pilosulae v. glabrescentes," suggesting that the material he studied was similar or

FIGURE 2. *Caryophyllus cotinifolius*; Philip Miller's specimen at BM, photographed in 1964. Approximately 7/8 natural size.

identical to that on the sheet at NY. The Anderson specimen at K, which I have seen through the courtesy of the Director, is a flowering specimen of quite another species. The leaves are elliptic-obovate, rounded at apex and prolonged into somewhat flattened petioles at base, exactly as in Miller's *Caryophyllus cotinifolius*. They are also very copiously glandular-punctate beneath, unlike *E. lambertiana* and *E. pseudopsidium*. In the disposition and number of flowers in the inflorescence, in length of pedicels, and in other observable details, the two specimens agree well. The pedicels and hypanthium are minutely hispidulous in the Anderson plant, whereas these parts in Miller's fruiting specimen are essentially glabrous, as might be expected through erosion of the pubescence in age. In short, were these not the only specimens representing their respective species, I should not hesitate to call them conspecific.

If they do represent the same species, what is the correct name of that species? Miller's *Dictionary* was published, according to Stafleu (Tax. Lit. 314. 1967), on 16 April 1768. Apparently the precise date of publication of the 3rd volume of Jacquin's *Observationum Botanicarum* is unknown, but the year was 1768. If page 3 and plate 53 were published before 16 April, and if Jacquin's *Eugenia cotinifolia* is indeed the same as Miller's *Caryophyllus cotinifolius*, then the correct name is *Eugenia cotinifolia* Jacq., and *E. dussii* falls into synonymy. If on the other hand the third volume of *Obs. Bot.* was published after 16 April 1768, the name *Caryophyllus cotinifolius* has priority but cannot be transferred to *Eugenia* because of the existing *E. cotinifolia* Jacq., based on a different type. Under these circumstances the name *Eugenia dussii* Urb., with the lectotype the flowering specimen collected by Anderson and now at K, would seem to be the correct one for the species.

Although *Eugenia dussii* was described in 1895, the lectotype and only known specimen must have been collected before 1811, the date of death of Alexander Anderson. Anderson was superintendent of the botanical garden on St. Vincent for many years, and introduced to the garden a large number of species from the West Indies and from other parts of the world (cf. Guilding, L., *An account of the botanical garden in the island of St. Vincent, from its first establishment to the present time.* 47 pp., Glasgow, 1825). It is interesting to speculate upon the source of Anderson's collection of *E. dussii* and of the 18th-century collections that appear to belong to the same species. Perhaps the species is extinct; on the other hand a new generation of explorers may discover it anew on St. Lucia, or even as far around the Caribbean as Cartagena.

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KADSURA HETEROCLITA — MICROSPORANGIUM AND POLLEN

M. R. VIJAYARAGHAVAN AND USHA DHAR

THE SCHISANDRACEAE, among the Ranales, reveal many interesting features of morphology, anatomy, and palynology (see Wodehouse, 1935; Bailey & Nast, 1948; Erdtman, 1952). *Kadsura* Juss., a genus of woody, evergreen, climbing shrubs, is distributed in temperate and subtropical Asia. In India it is found in Assam. Perusal of literature suggests that embryological studies in this genus are meager (see Hayashi, 1960). The ontogeny of the anther wall has never been investigated. The present work deals with the vasculature of the stamen, development of wall layers, and the morphology of the pollen in *K. heteroclita* Craib.

MATERIAL AND METHODS

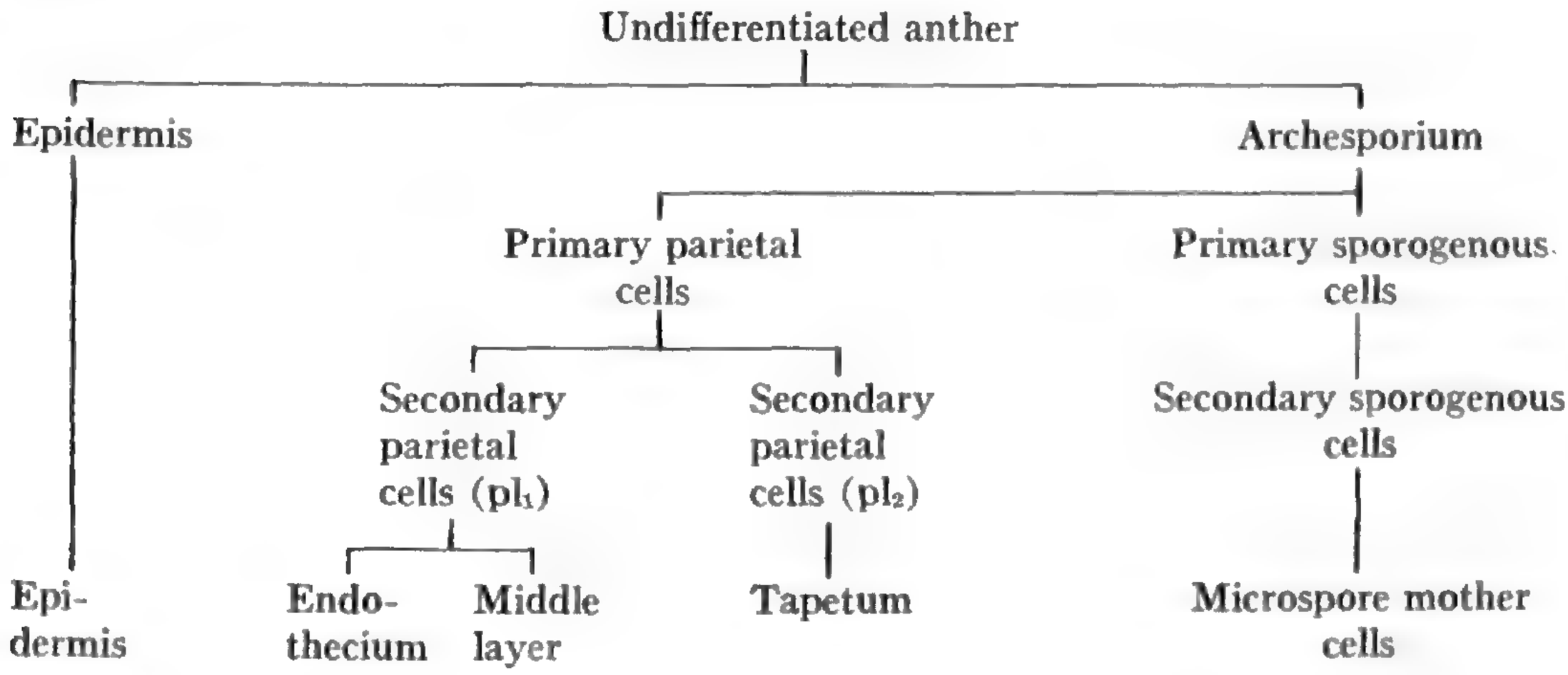
The male flowers of *Kadsura heteroclita* were obtained through the courtesy of D. B. Deb, Botanical Survey of India, Assam, India, in August, 1963. Formalin-acetic-alcohol was used as a fixative and the material was subsequently preserved in 70 per cent ethanol. Dehydration, infiltration, and embedding were done in the conventional way (Sass, 1958). The sections were cut between 7 and 10 μm. and stained with a safranin-fast green combination. The pollen grains were acetolysed following the revised technique of Erdtman (1960). A few mature stamens were cleared in a 2.5 per cent aqueous solution of sodium hydroxide for study of the vasculature. They were dehydrated through ascending grades of alcohol; stained in a 1 per cent solution of safranin (prepared in a 1:1 mixture of absolute alcohol and xylene); and finally transferred to xylene and mounted in canada balsam.

OBSERVATIONS

Microsporangium. The anthers are tetrasporangiate (FIGURE 1A). Two sporangia of one anther lie close to the two sporangia of the adjacent anther (FIGURE 2A). Anther lobes are widely separated by a massive connective. Each stamen is vascularized by a single trace which bifurcates in the region of the connective (FIGURE 2F).

The youngest anther available revealed the epidermis and the two secondary parietal layers pl_1 and pl_2. The inner of the two parietal layers, pl_2, matures directly into the tapetum, whereas the outer parietal layer, pl_1, segments periclinally to form two layers (FIGURE 1B). Of these, the outer layer develops into the endothecium and the inner into the middle layer. The anther wall thus consists of four layers, namely, epidermis,

endothecium, middle layer, and tapetum (FIGURE 1C). A few cells of the endothecium and middle layer are occasionally two-layered (FIGURE 1D). The following chart summarizes the development of the anther wall:



The development of the anther wall conforms to the dicotyledonous type (Davis, 1966).

The epidermis consists of isodiametric cells, and as the anther matures, in the region of the connective, a few of its cells become papillate (FIGURES 1F, 2C). The cells of the endothecium, prior to dehiscence, develop fibrous thickenings (FIGURE 1F). A few cells of the connective, interestingly, show such thickenings. At about the tetrad stage the middle layer becomes flattened and the tapetum degenerates (FIGURE 1E). The cells of the tapetum are uninucleate and rarely become binucleate. At the time of dehiscence, only the epidermis and the fibrous endothecium persist (FIGURE 2D). The septum between the adjacent loculi breaks down and the two loculi become confluent (FIGURE 1F).

Tannin-containing cells and ethereal oil cells are present in the connective (FIGURES 1F, 2B). Crystals are also seen in some cells (FIGURE 2E).

Microsporogenesis and male gametophyte. Cytokinesis is of the simultaneous type. Both tetrahedral and decussate tetrads are formed, the former being more frequent (FIGURE 1E). The deposition of callose is conspicuous at the microspore tetrad stage (FIGURE 1I). Young microspores are uninucleate with dense cytoplasm (FIGURE 1J). Pollen grains are shed at the 2-celled stage (FIGURE 1K).

Each pollen grain is hexacolpate and possesses three long and three short meridionally arranged furrows. The longer furrows meet and fuse at one of the poles to form the triradiate mark (FIGURE 1G). All six furrows end evenly around the area at the blank pole (FIGURE 1H). The short furrows extend about as far toward the convergent pole as toward the blank pole. Both kinds of furrows are linear, each with a median thickening of the furrow membrane. The exine is reticulately sculptured.

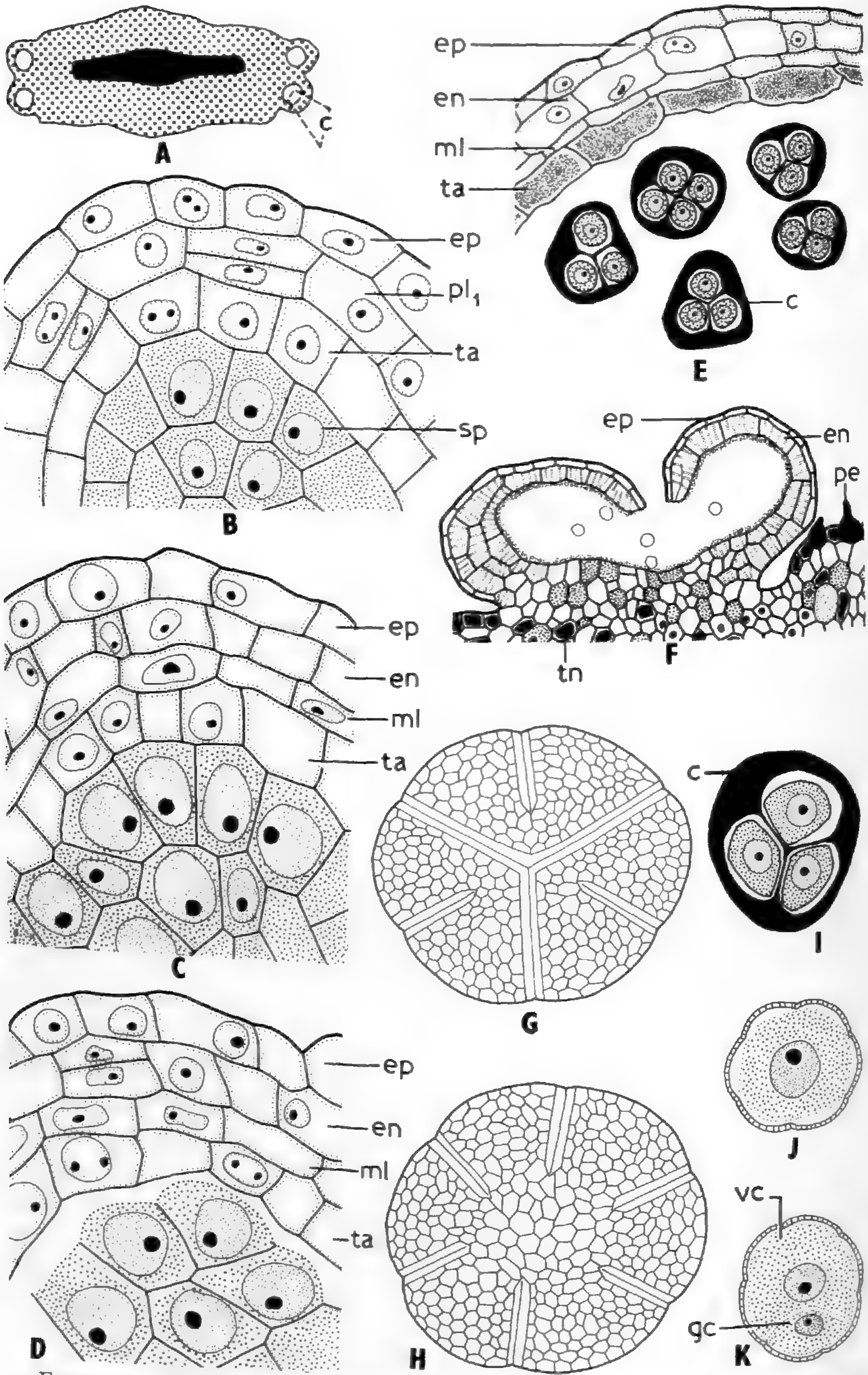


FIGURE 1. **Kadsura heteroclita,** microsporangium, microsporogenesis and male gametophyte. A, transection of an anther at the microspore mother cell stage (diagrammatic), × 37. B, transverse section of a portion of an anther lobe showing periclinal divisions of the outer secondary parietal layer (pl_1) to form

DISCUSSION

Position of anther sacs. The stamen in *Kadsura heteroclita* is differentiated into a filament, a connective, and an anther with four protuberant, lateral sporangia. This is in contrast to the broad, leaflike stamens with more or less embedded sporangia, either on the adaxial side as in the Magnoliaceae (Canright, 1952) and Austrobaileyaceae (Bailey & Swamy, 1949) or on the abaxial side as in the Degeneriaceae (Swamy, 1949) and Himantandraceae (Bailey *et al.*, 1943).

The connective is massive with cells containing tannin, ethereal oil, and crystals. Accumulation of tannin is reported in the epidermal cells in *Schisandra grandiflora* Hook. f. & Thomson (Kapil & Jalan, 1964). Crystals are observed in *S. neglecta* A. C. Smith but are absent in *S. grandiflora* (Kapil & Jalan, 1964). Raphides are common in the connective of stamens in all genera of the Tetraceroideae (Dickison, 1970).

Vascular supply of the stamen. Each stamen in *Kadsura heteroclita* is traversed by a single vascular trace which bifurcates in the connective, the branches being directed toward the sporangia. Ozenda (1952) in *Schisandra henryi* C. B. Clark and Jalan (1962) in *S. neglecta* also reported bifurcation of the vascular trace. In *S. grandiflora,* however, the trace usually terminates blindly near the apex or rarely branches. In *Pseudowintera colorata* (Raoul) Dandy (Winteraceae) generally a single strand enters and bifurcates, but rarely, two independent traces enter the stamen (Bhandari, 1963). According to Eames (1961), branching in the connective is rare in stamens with one trace. The stamen of *K. heteroclita* can be regarded as advanced in possessing a single vascular trace, but its branching in the connective, with each pair of sporangia receiving a separate trace, is a primitive feature.

Microsporangium wall. Little is known about the ontogeny of the anther wall in the Schisandraceae. In *Kadsura heteroclita* it has been observed to be of the dicotyledonous type (Davis, 1966). The anther wall

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the endothecium and the middle layer, the inner layer (pl_2) directly forming the tapetum, × 615. C, magnified view of the portion marked c in A to show four wall layers, namely, epidermis, endothecium, middle layer, and tapetum, × 615. D, part of cross section of an anther lobe showing periclinal division in a cell of the endothecium, × 615. E, transverse section of a portion of an anther lobe at the microspore tetrad stage, showing tetrahedral and decussate tetrads. The middle layer is flattened and tapetal cells are degenerating, × 306. F, a part of a dehisced anther showing fibrous thickenings in the endothecium and a few cells of the connective. The connective shows many papillate epidermal cells, × 73. G, hexacolpate pollen grain in dorsal view with triradiate mark. The exine is reticulate, × 1261. H, ventral view of the pollen grain, × 1261. I, tetrahedral tetrad. Thick callose surrounds the microspores, × 615. J, K, 1- and 2-celled pollen grains, × 615. (c = callose; en = endothecium; ep = epidermis; gc = generative cell; ml = middle layer; pe = papillate epidermis; pl = outer secondary parietal layer; sp = sporogenous cells; ta = tapetum; tn = tannin; vc = vegetative cell.)

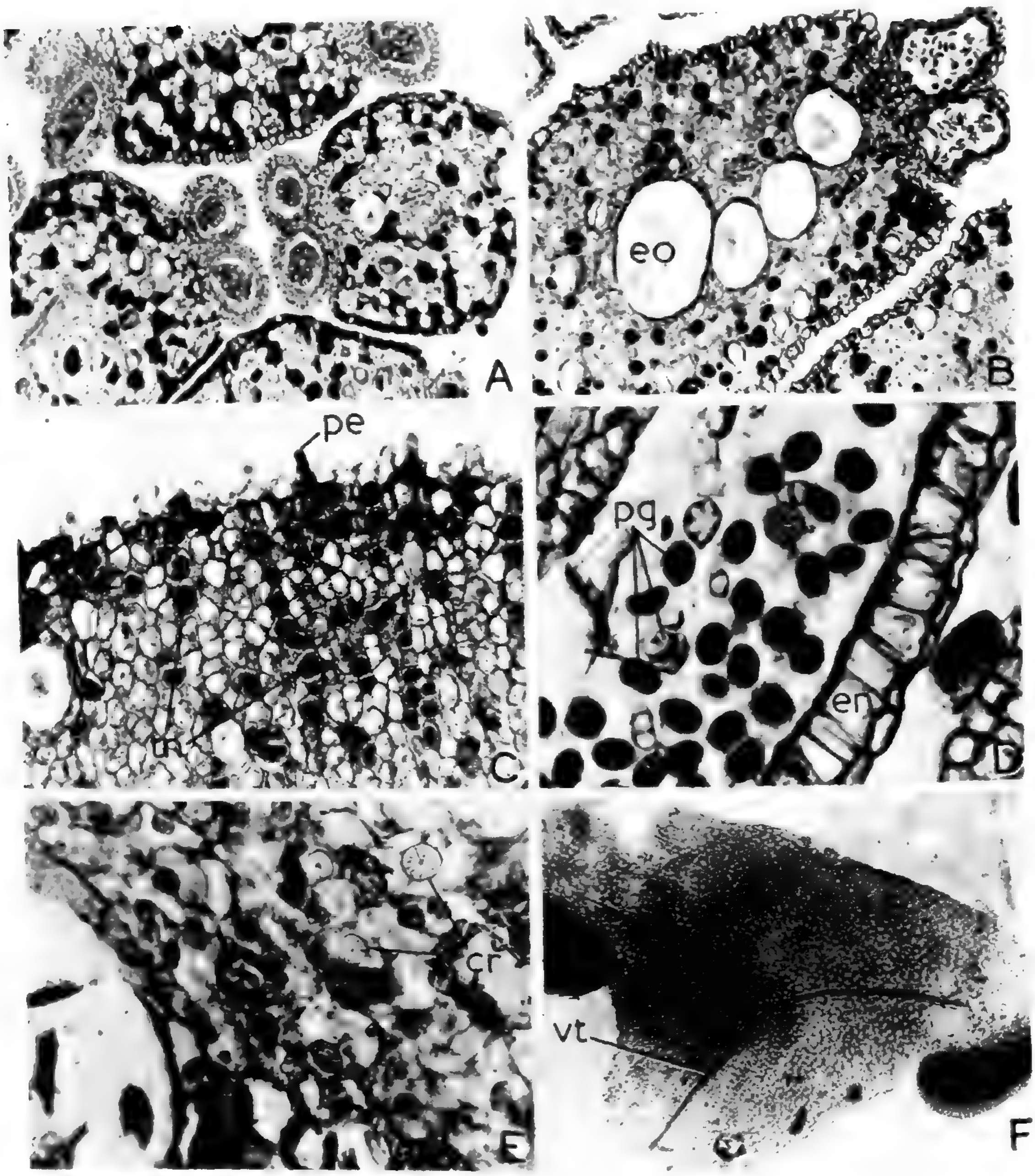

FIGURE 2. **Kadsura heteroclita,** microsporangium. A, transverse section of stamens showing the two sporangia of one anther juxtaposed with two sporangia of adjacent anther, × 56. B, cross section through stamen to show massive connective with cells containing tannin and ethereal oil, × 56. C, a part of the connective magnified to show the papillate epidermis, × 56. D, portion of anther showing fibrous thickenings in the endothecium and hexacolpate pollen grains, × 195. E, crystals in connective, × 210. F, a cleared stamen with dichotomously branched vascular trace, × 29. (cr = crystal; en = endothecium; eo = ethereal oil cell; pe = papillate epidermis; pg = pollen grain; tn = tannin; vt = vascular trace.)

comprises the epidermis, endothecium, middle layer, and tapetum. The epidermal cells of the anther wall are smooth in *K. heteroclita* but papillate in *Schisandra grandiflora* (Kapil & Jalan, 1964) and *Calycanthus fertilis* Walt. (Calycanthaceae; Mathur, 1968). However, a few epidermal cells of the connective in *K. heteroclita* become papillate. Prior to

dehiscence, endothecial cells and a few cells of the connective develop fibrous thickenings such as in *S. grandiflora*. The tapetal cells are uninucleate and rarely become binucleate. In both *Schisandra nigra* Maxim. and *Kadsura japonica* Dunal the tapetal cells are initially uninucleate but later become binucleate (Hayashi, 1960). Kapil and Jalan (1969) reported multinucleate tapetal cells in *S. grandiflora*. Binucleate tapetal cells were also observed in *Austrobaileya* C. T. White (Austrobaileyaceae; Bailey & Swamy, 1949), *Pseudowintera colorata* (Winteraceae; Bhandari, 1963), and *Sarcandra irvingbaileyi* Swamy (Chloranthaceae; Vijayaraghavan, 1964).

Microsporogenesis and microspores. Divisions of the microspore mother cells are simultaneous in *Kadsura heteroclita*, and both tetrahedral and decussate types of tetrads are formed, as observed in *Schisandra grandiflora* (Kapil & Jalan, 1964). Only tetrahedral tetrads, however, occur in *S. nigra* and *Kadsura japonica* (Hayashi, 1960). In *K. heteroclita* there is a deposition of thick callose around the microspore tetrads. Such callose deposition has not been reported earlier in this family.

The pollen grains in *Kadsura heteroclita* are unique in being heteropolar with 6 colpi, three long and three short, the longer ones meeting at one of the poles to form a triradiate mark as observed in *K. roxburghiana* Arn. (unpublished work) and other taxa of the Schisandraceae. There are variations in the size of the furrows. In *K. peltigera* Rehder & Wilson, *K. japonica* Juss., *Schisandra chinensis* K. Koch (Wodehouse, 1935), *K. roxburghiana* (unpublished work), and *K. heteroclita*, the short furrows are rather long, extending as far toward the convergent pole as toward the blank pole. On the other hand, in *K. paucidenticulata* Merr. and *S. coccinea* Michx. (Wodehouse, 1935), the short furrows extend farther toward the blank pole than toward the convergent pole. Parasyncolpate and synrugoidate types of pollen grains have been reported in *S. chinensis* (Erdtman, 1952), and in *S. grandiflora* and *S. neglecta* (Jalan & Kapil, 1964). In *K. heteroclita* and *K. roxburghiana*, however, they are absent. Wodehouse (1936) remarked, "Thus we find combined in this remarkable grain the main features of the pteridosperms, of the higher gymnosperms and of the higher dicotyledons . . ." and stated that the triradiate mark is homologous to the triradiate crest found in fern spores. Pollen grains are shed at the 2-celled stage in *K. heteroclita* as in *S. nigra* (Hayashi, 1960) and in *S. grandiflora* (Kapil & Jalan, 1964).

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REPRODUCTIVE ADAPTATIONS IN PROSOPIS (LEGUMINOSAE, MIMOSOIDEAE)[1]

OTTO T. SOLBRIG AND PHILIP D. CANTINO

THE GENUS *Prosopis* L. comprises about 40 species of shrubs and trees, which are distributed over the drier, warmer areas of the Americas, Africa, and western Asia (Burkart, 1940; Johnston, 1962). In this paper we will present quantitative data concerning the phenology, the production of flowers, fruits, and seeds, the destruction of seeds by bruchid beetles, and the percentage of seed germination in three related arborescent species of *Prosopis*. On the basis of this data, together with some additional qualitative observations, we will discuss some aspects of the adaptive "strategy" of reproduction in these species, a "strategy" that is probably shared by other arborescent phreatophytes of semidesert regions, particularly those belonging to the Mimosoideae. This study is part of a comprehensive investigation of convergent adaptation in desert regions with similar climates (Solbrig, 1972a).

MATERIALS AND METHODS

Although some data will be presented for other species, we are primarily concerned with the South American species *Prosopis chilensis* (Mol.) Stuntz and *P. flexuosa* DC. and the North American species *P. velutina* Wooton.[2] More precisely, *P. chilensis* occurs in southern Peru, central Chile, and west-central Argentina (Burkart, 1940); *P. flexuosa* is endemic to west-central Argentina (Burkart, 1952); *P. velutina* occurs in Arizona and the Mexican state of Sonora (Benson, 1941; Johnston, 1962). All three species are trees of medium height (rarely exceeding 18 meters) which, owing to their extremely deep root systems, are able to survive as phreatophytes in semiarid shrublands where few other trees can grow. Although there are no precise studies of the underground water resources at the particular study sites of this investigation, anecdotal information from wells in the areas where the three species occur indicates

[1] Contribution of the Structure of Ecosystems Program of the US/IBP.

[2] Nomenclature follows Burkart (1952) for South American species and Johnston (1962) for North American species.

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that at depths of from 30 to 100 meters there are permanent sources of water. Observations by Vervoorst (1954) indicate that roots of *P. flexuosa* may reach 80 meters in depth, making the tree capable of tapping a deep supply of water that is unavailable to most other plants. We feel it to be a reasonable assumption that the other two related species, of similar height and occurring under much the same environmental conditions, have the same mode of survival.

The bulk of the observations were made in two areas. In South America the study sites were located in the Bolsón de Pipanaco, near the town of Andalgalá, Catamarca Province, Argentina. The Bolsón is a basin of about 3000 square miles, nearly surrounded by mountains, with an annual rainfall ranging from 75 mm. at the southern end to 300 mm. at the northern end. Nearly all of the rain comes during the summer months, December through March (FIGURE 1). In North America our observations were made in the area surrounding Tucson, Arizona, principally on the Silver Bell Bajada. The climate here (FIGURE 2) is generally similar to that of the Argentine study site, with a comparable total annual rainfall; one notable difference, however, is that in Arizona the rain is divided between two rainy seasons, one in the winter and one in the summer. The vegetation of the two areas is similar in structure and biomass, but not in floristic composition. There are, however, several dominant genera (*Prosopis, Larrea, Acacia, Cercidium*) that are represented in the two areas by the same or closely related species (Solbrig, 1972a, b).

Phenology. Over a two-year period, an investigation was conducted on the phenology of *Prosopis chilensis* and *P. velutina*.[3] Six populations of the former and three of the latter were studied, with ten trees in each population randomly selected and marked for observation. At regular intervals (weekly for some sites, monthly for others) the populations were visited, and the stages of flowering, fruiting, leaf-production, and leaf-fall were observed. The stages were recorded as positive or negative; no attempt was made to quantify the intensity of the stage. Thus quantitative estimates can be made regarding, for instance, the proportion of the population that had at least one fresh flower bud or one incipient fruit at a given time, but no such estimate can be made of the proportion of plants that had numerous fresh buds. We have, however, complemented the quantitative data with qualitative observations on the relative intensity of flower and fruit production through time.

Flower and fruit production. An investigation of flower and fruit production was carried out with two objectives: the determination of the relationship between the number of flowers produced and the number of mature fruits, and the estimation of the annual seed yield of an average tree. In order to obtain the necessary data, we adopted the following pro-

[3] The observations in Argentina were made by J. LeClaire, P. Reppun, G. Brown, and P. Cantino; the Arizona observations by T. W. Yang and Y. Abe.

cedure. Ten trees of each of the three species were chosen at random, with no more than five trees in the same population. (Five populations of *Prosopis flexuosa* were sampled, seven of *P. chilensis*, and two of *P. velutina*.) On each tree one or two large branches were chosen for accurate flower-counts; the choice of branches was not random in that only branches within reach of the ground were considered, but within the subset of conveniently located branches the choice was made randomly. On each branch an accurate count was made of the number of inflorescences and the lengths of 25 of them, the number of incipient fruits produced, and the number of mature fruits. The counts and measurements were done without removal of inflorescences or fruits. From other branches on the same trees inflorescences were removed, their lengths measured, and the number of flowers counted, from which data a calculation was made of the average number of flowers per centimeter of inflorescence. By multiplying the average number of flowers per cm. times the average inflorescence length (calculated from the 25 inflorescences measured on the marked branch) times the number of inflorescences on the branch, we arrived at an estimate of the number of flowers on the branch. Using this estimate and the counts of incipient and mature fruits on the branch, we calculated the number of fruits initiated and fully developed per thousand flowers.

Seed destruction by bruchid beetles. Using the same ten trees of each species chosen for the study of flower and fruit production, we conducted an investigation to determine the extent of seed destruction by developing bruchid beetles, the timing of the damage, and the variation in the amount of damage from tree to tree. In the case of *Prosopis chilensis*, eight of the trees were located in a district that was heavily grazed by herds of domesticated goats. After only a few weeks the goats had removed all the fruits from the ground, necessitating the selection of four new trees in another area to continue the study. Unfortunately there was a time lapse of several weeks between the last sampling of the original trees and the first sampling of the newly chosen trees.

In Argentina a weekly sample of ten fruits was taken from each tree and a second sample of ten fruits from the ground beneath the tree. The sampling was initiated when the fruits appeared nearly ripe and was continued for three and one-half months. Each of the collected fruits was inspected and the number of seeds with and without bruchid emergence holes was recorded. The weekly samples of eight of the trees (four of *Prosopis flexuosa* and four of *P. chilensis*) were sent to Ing. Agr. Arturo Terán, who recorded further bruchid emergence in the succeeding weeks and identified the bruchids. In Arizona fruit samples from *P. velutina* were collected only once, at maturity. The bruchids that emerged were sent to Dr. John Kingsolver for identification.

In an additional study of seed damage by bruchids, samples of mature fruits were collected over a three-year period from 290 *Prosopis* trees and shrubs, representing 83 populations and 15 species, in Argentina, Mexico,

and the United States. Up to 10 fruits from each tree were shelled, the tough endocarps broken, and the number of fully developed, underdeveloped, and bruchid-damaged seeds recorded. In all, close to 30,000 seeds from about 2600 fruits were inspected. Because of the time-consuming nature of the seed-inspection process, it extended over a six-month period after collection of the fruits, allowing for some secondary infection of the fruits resulting from oviposition by emerging adult bruchids. As a result, the data may indicate a greater amount of seed damage, in some cases, than actually existed at fruit maturity. Nevertheless, the data serve to give a rough idea of the amount of damage that occurs in different populations and species of *Prosopis*.

Germination and seedling development. Many of the seeds collected in the previous study were germinated for subsequent use in genetic studies using isozymes (Solbrig & Bawa, in preparation). The seeds were removed from the endocarps, scarified, and planted in a sandy-loam mixture in plastic trays. The trays were placed in an incubator with artificial light, watered copiously, and maintained at a constant temperature of 68° F. After approximately six weeks, the seedlings were transplanted into three-inch pots and kept in a greenhouse; after a year, they were transplanted into six-inch pots. Measurements of the seedlings were made at regular intervals.

An additional experiment was conducted with the seeds of *Prosopis chilensis* to investigate the effect on the germination rate of previous passage through the intestinal tract of livestock. In two trials, seeds were removed from the excrement of goats and horses and planted in trays of soil collected at the edge of a wash where *P. chilensis* occurs naturally. The soil was strained before use to remove any seeds already present. Two other sets of seeds were planted as a control, one consisting of seeds removed by hand from their endocarps without intentional scarification of the seed coat and the other consisting of seeds with endocarps intact. The soil was kept moist for a two-week period, after which time the number of seedlings in each category was recorded. No attempt was made to maintain a constant temperature during the experiment; the trays were kept side by side on a window sill, where they received full sunlight during part of the day. Room temperature ranged from a minimum of 69° to a maximum of 97° F.

RESULTS

Phenology. The timing of leaf production in *Prosopis chilensis*, which has a winter-deciduous habit in the region of our study, was highly regular, varying little from site to site or between the two years of the study. Leaf initiation commenced in September, well before the onset of the summer rains, proceeded at a high rate for about two months, and then continued at a much reduced and rather irregular pace throughout the summer. In April and May the production of new foliage ceased and

leaf-fall began, leading once again to the nearly bare trees of midwinter (FIGURE 1).

Flowering of *Prosopis chilensis* occurred in a single burst of bloom in October and November. The timing varied by as much as two weeks from site to site, but within any given population the onset of flowering was highly synchronized. The regularity of the event, coupled with the fact that it occurred before the end of the winter drought, leads us to believe that flowering must be triggered by an environmental factor other than water supply, most likely photoperiod. The fruits reached maturity in mid-to-late December and dropped soon afterwards, the vast majority falling to the ground by the end of January (FIGURE 1).

Although we have no quantitative data on the phenology of *Prosopis flexuosa*, we observed that the entire pattern of foliage, flower, and fruit production was very similar to that of *P. chilensis*.

The Arizona data, generously given to us by T. W. Yang, plus previous work on the phenology of *Prosopis velutina* (Glendening & Paulsen, 1955; Turner, 1963), indicate a pattern of phenology for that species (FIGURE 2) that is basically similar to that of *P. chilensis*, but the data and resulting charts are a bit difficult to interpret for two reasons. First of all, the timing of the rainfall in 1972 at the Arizona site (FIGURE 2) was highly unusual. February and March, months during which rains can be expected in that region, were exceptionally dry, whereas October and November, normally dry months, experienced heavy rains. The timing of the rainfall in 1973 was more typical of the region. Secondly, data collection began in June, 1972, after that season's leaf production and blooming were already in progress.

In 1973, leaf initiation in *Prosopis velutina* began in March, proceeded at a high rate on all trees until mid-May, and declined to zero by the end of July. In 1972, leaf initiation may also have begun in March, but there were additional periods of peak leaf production in July and August, and again in October, the latter presumably in response to the exceptional October rainfall.

The initiation of blooming in *Prosopis velutina*, as in *P. chilensis*, is synchronized within populations and very likely under photoperiodic control. In 1972, blooming probably began at the Arizona site in May, as it did in 1973; we lack data earlier than June, 1972, but the production of fruits in June and July of 1972 is proof that blooming must have occurred before the study was initiated. The fact that only 40 per cent of the trees produced fruits during that period is evidence that this was a poorer bloom than that of May, 1973, probably because of the scarcity of rainfall in February and March of 1972. Additional periods of bloom occurred in July and in late August, 1972, in response to summer rainfall. In the more "normal" year, 1973, on the other hand, there was a single period of bloom, peaking in May and June.

In summary, it appears that blooming in both *Prosopis chilensis* and *P. velutina*, and perhaps leaf production as well, are initially triggered by an environmental stimulus other than water availability, probably photo-

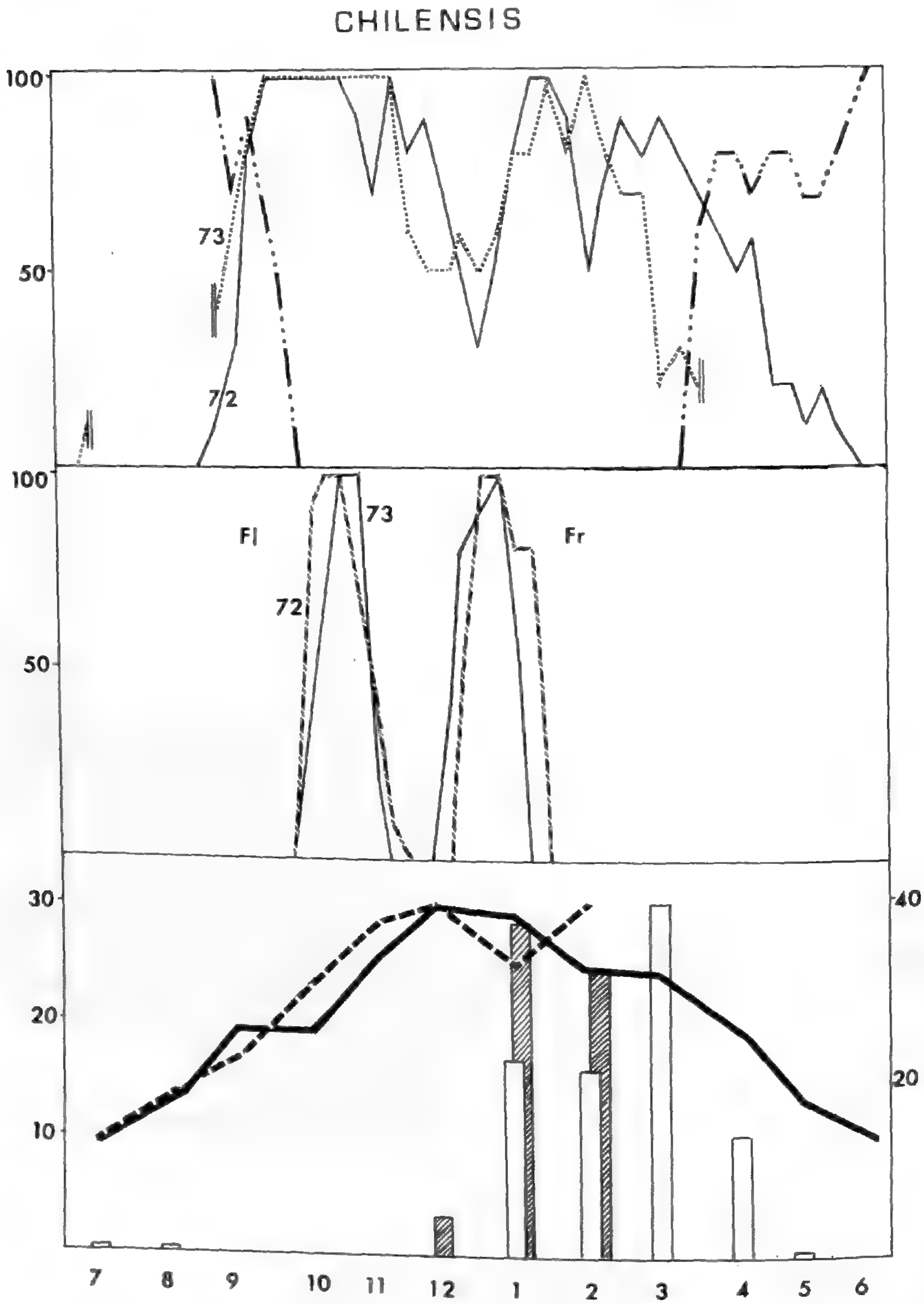

FIGURE 1. Phenology of **Prosopis chilensis** in Andalgalá. UPPER GRAPH: leaf growth and leaf fall as a percentage of plants in the population (solid line, leaf growth in 1972–73; dotted line, leaf growth in 1973–74; dashed dots, leaf fall in 1973). MIDDLE GRAPH: flowering and fruiting as a percentage of plants in the population (solid line, 1972–73; broken line, 1973–74). LOWER GRAPH: temperature in degrees centigrade (solid line, 1972–73; broken line, 1973–74) and rainfall (white bars, 1972–73; dashed bars, 1973–74). Abscissa represents months of the year; ordinate represents percentage (upper two graphs) or degrees (lower graph, left) and millimeters (lower graph, right).

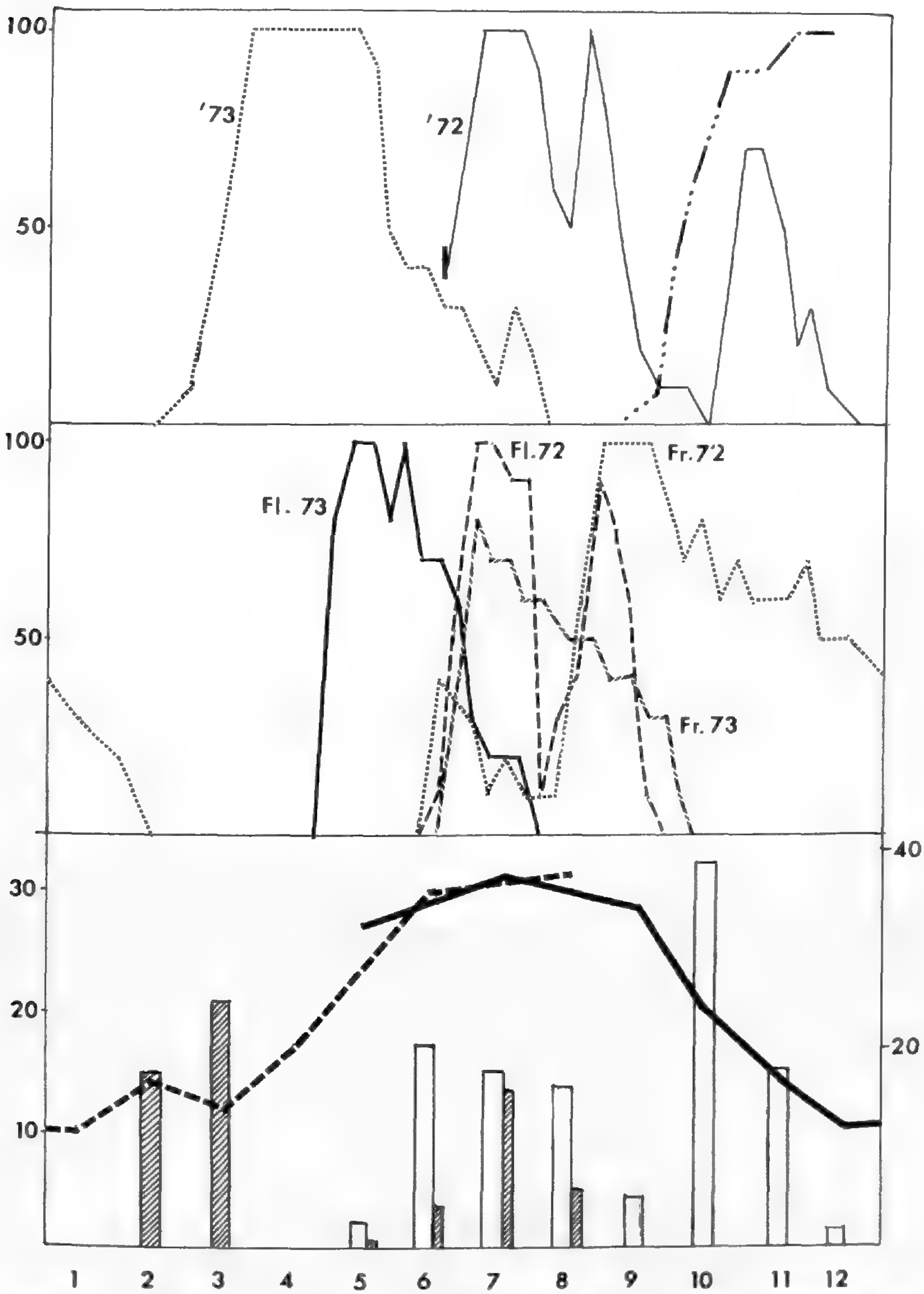

FIGURE 2. Phenology of **Prosopis velutina** in the Tucson area. UPPER GRAPH: leaf growth and leaf fall as a percentage of plants in the population (solid line, leaf growth in 1972; dotted line, leaf growth in 1973; dashed dots, leaf fall in 1972). MIDDLE GRAPH: flowering and fruiting as a percentage of plants in the population (dashed line, flowering in 1972; solid line, flowering in 1973; dotted line, fruiting in 1972; broken line, fruiting in 1973). LOWER GRAPH: temperature in degrees centigrade (solid line, 1972; dashed line, 1973) and rainfall in millimeters (white bars, 1972; hatched bars, 1973). Abscissa represents months of the year; ordinate represents percentage (upper two graphs) or degrees (lower graph, left) and millimeters (lower graph, right).

TABLE 1. Number of flowers, incipient fruits, and mature fruits.

TREE NO.	NO. FLOWERS	INCIPIENT FRUITS		MATURE FRUITS	
		NO.	‰	NO.	‰
		Prosopis flexuosa			
1	184,000	689	3.74	222	1.21
2	76,000	50	0.66	25	0.33
3	86,000	427	4.97	56	0.65
4	38,000	40	1.05	1	0.03
5	18,000	21	1.17	0	—
6	20,000	55	2.75	25	1.25
7	45,000	2	0.09	0	—
8	28,000	75	2.68	32	1.14
9	37,000	51	1.38	28	0.76
10	28,000	40	1.43	15	0.54
$\bar{x}$	56,000	145	2.59	40.4	0.72
		Prosopis chilensis			
1	45,000	92	2.04	3	0.07
2	47,000	13	0.28	0	—
3	43,000	148	3.44	0	—
4	28,000	31	1.11	1	0.04
5	20,000	14	0.70	0	—
6	16,000	15	0.94	2	0.13
7	40,000	73	1.83	4	0.10
9	60,000	100	1.67	11	0.18
10	115,000	145	1.26	15	0.13
$\bar{x}$	46,000	70.1	1.52	4	0.09
		Prosopis velutina			
1	263,905	—	—	116	0.44
2	89,300	—	—	52	0.58
3	19,975	—	—	7	0.35
4	62,980	—	—	130	2.06
5	119,850	—	—	211	1.76
6	90,005	—	—	13	0.14
7	18,095	—	—	6	0.33
8	39,245	—	—	98	2.50
9	287,405	—	—	89	0.31
10	123,845	—	—	9	0.07
$\bar{x}$	111,461	—	—	73	0.65

period; but the existence of later blooms and the continuation of leaf production are dependent on sufficient rainfall.

Flower and fruit production. Each of the three species studied produced an average of between 220 and 240 flowers per inflorescence, of which

usually no more than two developed into mature fruits; many inflorescences produced no fruit at all. In *Prosopis flexuosa* only 26 flowers in 10,000 initiated development into fruits, and about 7 reached maturity (TABLE 1). In *P. chilensis* only about one in 10,000 flowers developed into a mature fruit. The fruit/flower ratio of *P. velutina* was similar to that of *P. flexuosa*. The possible causes of this extremely low ratio will be discussed later.

Seed destruction by bruchids and percentage of underdeveloped seeds. The bruchid beetles found emerging from the seeds of *Prosopis chilensis* have been identified as *Rhipibruchus picturatus*, *Scutobruchus ceratioborus*, and *Scutobruchus* spp. (two undescribed species); those from *P. flexuosa* as *Rhipibruchus picturatus*, *Scutobruchus ceratioborus*, and *Scutobruchus* sp. (undescribed); and those from *P. velutina* as *Neltumius arizonensis*, *Algarobius prosopis*, and *Mimosestes amicus*.

In the 15 species of *Prosopis* surveyed (TABLE 2), averages of from 1 to 25 per cent of the seeds had been damaged by bruchids by the time of collection (shortly after fruit maturity). The variation within species was great, however, with several populations having more than 60 per cent damage. Species belonging to section STROMBOCARPA (*P. reptans*, *P. strombulifera*, and *P. torquata*) exhibited less damage than most of those in section ALGAROBIA (all other species in TABLE 2). The percentage of the seeds that were underdeveloped ranged from about 2 per cent to 53 per cent in the 83 populations surveyed, with averages for the 15 species ranging from about 7 per cent to 25 per cent.

The results obtained in the study of bruchid damage to the seeds of *Prosopis flexuosa* as a function of time are shown in TABLE 3 and FIGURE 3. By the end of the first month after fruit maturity, all the fruits had fallen to the ground, and only 2.7 per cent of the seeds had bruchid emergence holes. When the study was terminated at the end of 15 weeks, fruits could still be found beneath seven of the original nine trees, and 26.1 per cent of the seeds had bruchid emergence holes. During the first five weeks of the study, the percentage of seeds with bruchid holes remained relatively constant, but starting in the sixth week, the percentage of seeds damaged climbed at an approximately linear rate (FIGURE 3). The equation $Y = 2.13\ T - 9.56$, obtained through linear regression analysis ($r = 0.94$), estimates the amount of seed damage at any time between the fifth and fifteenth week following fruit maturity (with Y equal to the percentage of seeds with bruchid holes and T equal to the number of weeks since the first fruits reached maturity). Extreme variation is evident among the nine trees studied (FIGURE 3). Trees no. 3 and no. 4 form a striking example, growing less than 50 meters apart and suffering 0.7 per cent and 53.5 per cent seed damage respectively at the end of 15 weeks. Because the seeds of tree no. 3 were a bit smaller than average, we considered the possibility that they might not have been viable, but a test yielded 56 per cent germination, a rate that is consistent with the results of other germination tests with *P. flexuosa* (see TABLE 4 and the next section).

TABLE 2. **Number of seeds per fruit, bruchid-damaged seeds, and underdeveloped seeds in species of Prosopis.**

SPECIES	NO. OF POPUL.	NO. OF TREES	NO. OF FRUITS	NO. OF SEEDS/ FRUIT	% GOOD SEEDS	% BRUCHID-DAMAGED SEEDS	% UNDERDEVELOPED SEEDS
Section ALGAROBIA (South America)							
P. alba	17	22	213	17.9±1.5	70.3±5.6	16.9±4.7	13.6±2.7
P. caldenia	4	47	377	19.2±0.9	62.3±5.7	15.9±3.1	22.7±3.9
P. chilensis	6	29	340	18.9±2.3	72.7±4.5	13.4±3.7	14.0±4.3
P. flexuosa	4	12	146	11.5±1.5	73.9±7.4	10.2±6.0	15.0±5.4
P. kuntzei	8	9	85	9.4±1.7	61.2±8.2	24.2±7.1	14.6±2.0
P. nigra	10	10	126				
P. pugionata	1	3	24	12.2±0.6	91.6±0.8	1.5±0.1	7.1±0.7
P. ruscifolia	11	62	600	13.5±1.1	71.6±5.7	11.3±2.0	12.8±4.2
P. sericantha	3	15	196	8.0±0.7	76.8±4.5	2.8±1.5	20.4±5.2
Section ALGAROBIA (North America)							
P. glandulosa	3	7	57				
P. laevigata	5	16	55	14.8±0.7	63.0±4.5	18.9±3.8	17.7±2.4
P. velutina	6	6	60				
Section STROMBOCARPA (South America)							
P. reptans	1	6	35	3.2±0.3	73.5±4.1	1.7±0.7	24.8±4.2
P. strombulifera	1	17	124	6.3±0.4	66.8±1.8	8.5±1.0	24.9±1.6
P. torquata	3	12	144	9.3±0.4	80.2±6.1	1.2±0.4	18.6±5.7

TABLE 3. **Bruchid damage to seeds of P. flexuosa.**

Tree # / Date	1 no.*	1 %	2 no.	2 %	3 no.	3 %	4 no.	4 %	5 no.	5 %	6 no.	6 %	7 no.	7 %	8 no.	8 %	9 no.	9 %	Total no.	Total %
									On ground											
Jan. 1	0	0	13	7.9	0	0	8	5.7	0	0	0	0	0	0	2	1.8	2	1.6	25	2.1
8	0	0	8	5.6	1	0.7	6	3.4	8	5.7	3	2.0	1	0.7	13	10.7	6	4.4	46	3.1
18	2	1.6	1	0.7	0	0	4	2.3	4	3.3	3	1.9	4	2.5	10	7.11	8	4.7	36	2.7
25	0	0	3	2.3	0	0	4	2.3	3	2.5	8	4.8	3	2.2	6	3.3	4	2.5	31	2.3
Feb. 1	1	0.8	4	3.3	1	0.7	7	3.9	6	5.6	6	3.8	0	0	7	5.0	3	1.7	35	2.7
8	1	0.8	5	3.4	0	0	18	11.0	2	1.7	3	1.9	8	6.5	2	1.5	10	7.6	49	3.9
18	2	1.6	8	6.3	0	0	30	20.4	17	11.3	9	5.2	4	2.9	19	13.9	31	19.7	120	9.1
25	3	2.8	19	12.8	0	0	12	9.4	—	—	10	6.1	7	4.5	6	6.0	15	10.9	72	6.6
Mar. 1	0	0	33	25.6	0	0	34	29.1	—	—	10	6.5	10	6.6	6	4.9	11	8.9	104	9.7
15	3	2.9	40	31.0	0	0	49	39.6	—	—	5	3.3	2	1.6	—	—	19	12.8	128	13.1
22	1	0.8	17	12.0	0	0	50	37.3	—	—	8	5.1	1	0.8	—	—	22	18.3	99	10.4
Apr. 2	3	2.9	35	30.4	2	1.4	68	46.6	—	—	37	21.6	20	14.2	—	—	66	46.5	231	24.0
6	0	0	17	12.7	1	0.7	88	57.1	—	—	11	6.7	58	43.0	—	—	61	36.3	236	23.5
15	0	0	53	39.6	1	0.7	83	53.5	—	—	38	18.8	27	21.1	—	—	61	39.6	263	26.1
									In trees											
Jan. 1	0	0	1	0.7	0	0	2	1.0	2	1.4	0	0	0	0	6	3.1	1	0.6	12	0.8
8	0	0	0	0	0	0	1	0.6	0	0	0	0	0	0	0	0	0	0	1	0.1
18	0	0	3	2.4	1	0.8	—	—	1	0.8	3	1.8	0	0	7	3.9	5	2.8	20	1.7
25	4	2.6	0	0	0	0	—	—	6	4.8	6	3.7	5	3.0	9	4.6	1	0.6	31	2.6
Feb. 1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	3.0	5	3.0

* Number of seeds with bruchid emergence holes.

It is conceivable that the seeds were too small to support the full development of a bruchid; however, tree no. 1, with average-sized seeds, also suffered virtually no bruchid damage.

All of the above data concerning seed damage (including TABLE 3 and FIGURE 3) are based on the observation of bruchid emergence holes on the outer surface of the pods. It should be noted that the actual damage at a given time is always greater than that implied by the number of emergence holes. There is no way to determine by simple observation the number of seeds that contain partially developed bruchids. FIGURE 4 presents graphically the relationship between apparent seed damage (i.e. the percentage of seeds with emergence holes) and actual seed damage (i.e. the percentage of seeds with emergence holes plus the percentage of seeds containing developing bruchids). The graph is based on data supplied to us by Ing. Agr. Arturo Terán, who tabulated the bruchid emergences subsequent to the collection date from the weekly samples of pods collected beneath eight of our study trees of *Prosopis flexuosa* and *P. chilensis*. (However, only the data from the four trees of *P. flexuosa* were used in the preparation of FIGURE 4, involving approximately 500 pods and 7000 seeds.)

Because of several unexpected problems in the field, we do not have sufficient data to describe seed damage as a function of time for *Prosopis chilensis* and *P. velutina*. In the case of *P. chilensis*, the fruits rapidly disappeared from beneath the trees, mostly having been eaten by goats; at the end of 13 weeks, we found fruits under only two of the 13 trees involved in the study, and 90 per cent of the seeds in these remaining fruits had bruchid holes. Thus from the limited data that we have, it appears that seed destruction proceeds at a much faster rate in *P. chilensis* than in *P. flexuosa*. *Prosopis velutina* was sampled only once, about one month after maturation of the first fruits in the population, and 11.5 per cent of the seeds were found to have bruchid holes. Glendening and Paulsen (1955) studied the bruchid damage to seeds of *P. velutina* over a 400-day period following fruit maturity. Their data indicate a linear increase in bruchid damage between the fifth and tenth weeks, during which time the percentage of seeds showing bruchid emergence holes climbed from about 10 per cent to about 50 per cent. After the tenth week, there was a gradual decrease in the rate of appearance of new emergence holes, so that the overall curve of damage versus time is sigmoid. Thus *P. velutina* appears to suffer a more rapid rate of damage than *P. flexuosa*, but a slower rate than *P. chilensis*.

Germination. The seeds of section ALGAROBIA of the genus *Prosopis*, to which the species under study belong, weigh 20–40 mg. and have the approximate dimensions 5.5 × 3.5 × 2.0 mm. (Palacios & Bravo, 1974). The leathery endocarp that surrounds each seed is impermeable to water and must be broken for the seed to germinate; repeated attempts to germinate seeds with intact endocarps yielded less than one per cent germination.

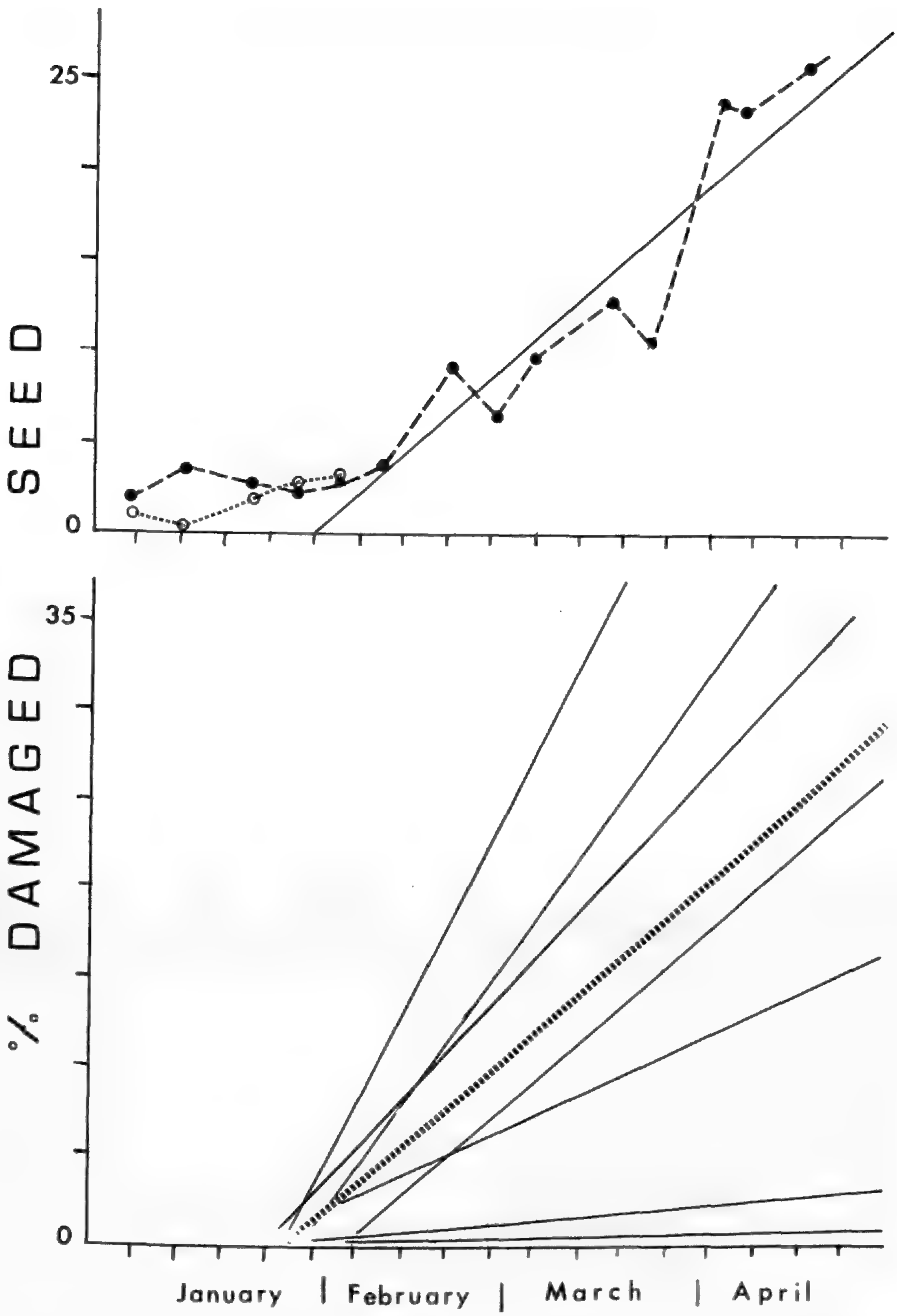

FIGURE 3. Percentage of damaged seeds in relation to time in **Prosopis flexuosa.** UPPER GRAPH: all trees together (dotted line, samples from the tree; dashed line, samples from the ground; solid line indicates regression of damage in time after 5th week (r=0.95)). LOWER GRAPH: regressions for the logarithmic phase of seed damage for individual trees (r varies from 0.96 to 0.50); note the great variation between individual trees. Broken line represents average for all trees.

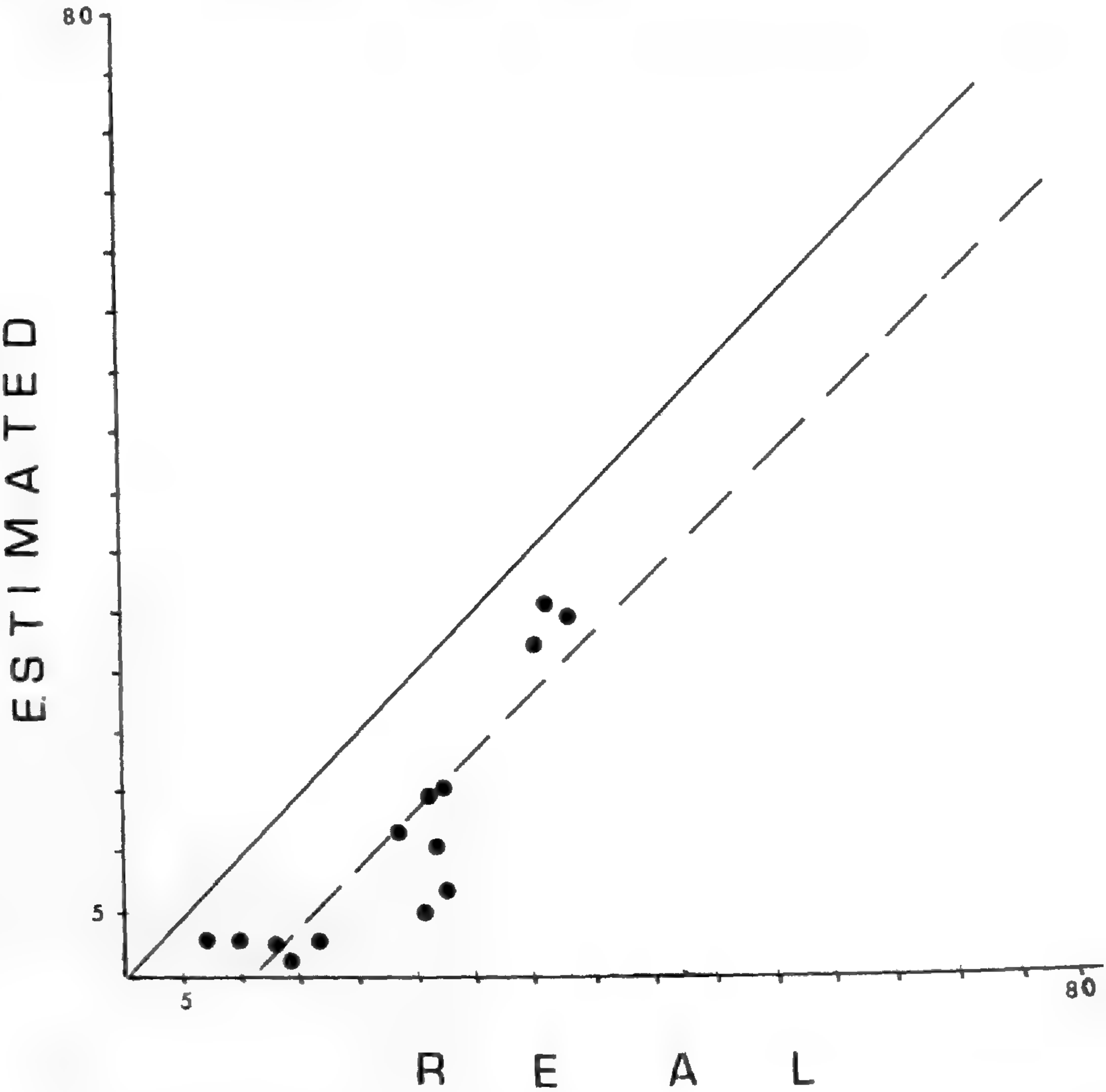

FIGURE 4. Relationship between estimated bruchid damage as shown by percentage of seeds with exit holes and real damage as indicated by percentage of seeds actually destroyed. Solid line indicates ideal 1:1 relationship; dashed line shows actual regression (r=0.89).

The germination percentages of scarified seeds, removed from the endocarps, varied greatly between populations, to such an extent that differences between species were obscured (TABLE 4). Although values obtained for different populations ranged from 87 per cent down to only 2.5 per cent, the averages for all but four of the species fell between 25 per cent and 55 per cent. The explanation for this rather poor germination lies not in any inherent quality of the seed, but apparently in the maintenance of too low a soil temperature during the experiment. Scifres and Brock (1970a), working with *Prosopis glandulosa*, obtained up to 96 per cent germination on wet filter paper and 90 per cent in wet sand. They found the temperature of the germination medium to be a critical factor; in moist sand at 85° F., 90 per cent of the seeds had germinated after 72 hours, but in the same time period only 30 per cent germinated

TABLE 4. **Germination percentages for seeds of Prosopis species.**

SPECIES	NO. OF POPUL.	NO. OF SEEDS	GERMINATION MAXIMUM	GERMINATION MINIMUM	GERMINATION AVERAGE
Section ALGAROBIA (South America)					
P. alba	2	160	48.8	10.0	29.4±19.4
P. caldenia	2	1120	36.2	16.5	26.4± 9.8
P. chilensis	9	2301	87.5	2.5	41.3± 6.3
P. flexuosa	3	263	74.3	45.0	54.6± 7.9
P. nigra	3	344	80.2	34.6	50.9±14.7
P. ruscifolia	1	160	—	—	10.7
P. sericantha	2	696	81.3	21.4	53.7± 7.4
Section ALGAROBIA (North America)					
P. glandulosa	3	250	82.2	26.3	49.3±16.0
P. laevigata	1	78	—	—	29.5
P. velutina	1	90	—	—	82.2
Section STROMBOCARPA (South America)					
P. strombulifera	11	118	—	—	31.0
P. torquata	3	817	54.0	14.6	32.4±11.5
Section STROMBOCARPA (North America)					
P. pubescens	2	160	8.8	2.5	5.7± 3.2
Section CAVENICARPA					
P. ferox	1	96	—	—	29.2
P. tamarugo	6	480	17.5	2.5	7.3± 2.2

at 70° F. and 42 per cent at 100° F. Similarly, Eilberg (1973) obtained 96 per cent germination with scarified seeds of *P. ruscifolia* at a temperature of 79° F. On the other hand, Glendening and Paulsen (1955), under field conditions, obtained values similar to ours.

In two trials, 20 per cent and 52 per cent germination were obtained with seeds of *Prosopis chilensis* taken from goat excrement; the corresponding trials yielded 24 per cent and 28 per cent success with seeds taken from horse excrement, 40 per cent and 12 per cent success with seeds removed by hand from the endocarps, and 2 per cent and 6 per cent success with seeds retaining the endocarps. Although the variation is great, germination percentages obtained with seeds from goat and horse excrement are comparable to values for seeds removed by hand from the endocarps, and significantly greater than values for seeds with endocarps intact.

It is worth mentioning that some of the seeds taken from excrement of goats and horses contained developing bruchids, as evidenced by the emergence of a number of adult bruchids from seeds stored inside closed containers several weeks after removal from the excrement. This contrasts with Janzen's observations concerning *Acacia cornigera*, another legumi-

nous tree which suffers seed damage from bruchid beetles; Janzen has observed that dispersal of the seeds by birds and mammals probably does not lead to bruchid dispersal because bruchid-occupied seeds are broken up as they pass through the animal (Janzen, 1969).

Seedling development. The seedlings of all species of *Prosopis* studied are similar in morphology, but they vary in size. They possess two fleshy, oval cotyledons averaging 2 cm. in length. The shoot shows strong apical dominance, no branching having been observed on any seedling during the two-year duration of the experiment (except in cases of damage to the apical meristem). In all species the first two to five leaves produced by the seedlings are pinnatifid, with six to ten pairs of oval leaflets, while all later leaves are bipinnatifid. Spines were often present on the first and succeeding nodes, but there was considerable variation within species, with some individuals developing no spines at all. The root is a taproot, with no obvious lateral branching. Under the favorable conditions of the greenhouse, shoot and taproot growth was rapid (TABLE 5).

DISCUSSION

In order that the descriptive and quantitative data presented above may be of more general use, we will discuss it in the context of a theoretical model of plant population dynamics. In the process we hope to elucidate certain aspects of the reproductive "strategy" of arborescent *Prosopis* and of desert phreatophytes in general.

In a model developed by Harper and White (1971), biomass and number of individuals in plant populations are regulated by the dynamics of four successive stages of the plant's life cycle: (1) the size of the "seed bank" of viable seeds in and on the soil, (2) the "environmental sieve" that determines whether or not a seed is recruited into a population of seedlings, (3) the correlated changes in plant number and size as a seedling population becomes thinned and individuals increase in size, and (4) the phase of seed production which contributes to a new seed-rain. In our discussion we will start, for convenience, with Stage 4.

Seed production. The size of the seed-rain of any plant is dependent on the number of functional flowers produced, the number of ovules per flower, the efficiency of pollination (both in terms of percentage of flowers pollinated and percentage of ovules fertilized within each flower), and the mortality rate of fruits during the process of maturation due to predation and stress from the physical environment.

In *Prosopis* a huge crop of flowers is produced (in the order of several million flowers on an average tree during a single season), but only two or three flowers in a thousand initiate development into fruits. Is it reasonable to attribute this extremely low fruit/flower ratio to inefficient pollination? To attempt to answer this question, we must know something about the breeding system of the plant and the pollination agents. The

TABLE 5. **Shoot growth rate in Prosopis (in cm.).**

SPECIES	PLANTING DATE	1ST MEASUREMENT AGE †	N	$\bar{x}$	MAX.	MIN.	2ND MEASUREMENT AGE †	N	$\bar{x}$	MAX.	MIN.
P. FLEXUOSA											
Solbrig 4217 (Catamarca, Andalgalá)	3–25	1	10	9.5	12.2	7.5	7	3	70.1	76	61
Solbrig 4219 (Catamarca, Andalgalá)	3–25	1	20	11.9	14.2	10.3	7	6	70.0	96	55
P. CHILENSIS											
Vuilleumier 1022 (La Rioja, Aimogasta)	3–13	1	76	13.6	21.5	4.0	11	10	92.2	117	62
Vuilleumier 1020 (La Rioja, Bazan)	10–22	2	42	8.5	16.8	2.3	—	—	—	—	—

* Growth rates of two species were studied under greenhouse conditions.
† Age in months.

flowers of *Prosopis* are protogynous. The stigma has a central depression into which the pollen must fall for fertilization to occur. Tests with *Prosopis torquata* indicate that the plants are self-incompatible (B. Simpson, personal communication). Although all three of these factors tend to reduce the efficiency of pollination (that is, the number of fertilizations per insect visitor), the following evidence indicates to us that inefficient pollination cannot be the sole explanation for the low fruit/flower ratio. The flowers are visited by many species of insects, and in such large quantities that visitors to a tree in full bloom can be heard for some distance. Furthermore, *Prosopis* trees usually grow sufficiently close together to permit cross-pollination on a large scale. Pollination efficiency is quite high within the few flowers that do produce fruit, with 50 to 100 per cent of the ovules developing into seeds. With a density of 30 to 50 flowers per cm. of inflorescence, it is highly unlikely that a bee, or other insect, would consistently pollinate a single flower only without dropping some pollen on its neighbors. By means of artificial pollination, Dr. Beryl Simpson has increased fruit production of *P. torquata* by a factor of two to four (personal communication), indicating that poor pollination is a factor contributing to a reduced fruit yield in that species. Yet even under a regime of artificially increased pollination, the fruit/flower ratio is still extremely low.

In our opinion, the production of a large number of flowers in *Prosopis* is an adaptation that serves to attract insects to the individually small (3–6 mm.) and inconspicuous flowers. In other words, the vast majority of the flowers serve as the functional equivalents of petals, although any one of them is apparently potentially capable of developing into a fruit.

The production of a great many flowers for each mature fruit is characteristic of many genera of the subfamily Mimosoideae and may well be an adaptation for insect attraction in these cases as well. A further elaboration of this theme can be found in a few Mimosoid genera, such as *Dichrostachys* and *Neptunia*, that produce dense, spicate inflorescences in which there is a floral dimorphism; showy sterile flowers are located below the less conspicuous fertile flowers, presumably attracting insects to the latter. The analogy between the sterile flowers of these genera and petals is even more apt than in the case of *Prosopis*.

Although there is no floral dimorphism in *Prosopis*, it is possible that some, or even most of the flowers are indeed sterile. Detailed anatomical studies of *Albizia lebbeck*, another member of the Mimosoideae with a high flower/fruit ratio, have revealed that the embryo sacs and pollen of most of the flowers degenerate before fertilization can occur (Maheshwari, 1931). There is no obvious superficial difference between the sterile and fertile flowers in *A. lebbeck*, nor is there any regularity in their relative locations on the inflorescence. Although we do not have direct evidence that degeneration of this sort occurs in *Prosopis*, it is one possible explanation for the puzzling low fruit/flower ratio. A second explanation might be the production of a chemical inhibitor in conjunction with fertilization, which in some way prevents fertilization of neighboring flowers.

In the case of either mechanism, the result would be the same; a great quantity of flowers could be produced, attracting insects and ensuring pollination, while limiting the fruit initiations to the small number that the plant could support.

As can be seen in TABLES 1 and 2, there is considerable variation between individuals and populations in the number of fruits produced per thousand flowers and the number of fully developed seeds per fruit. Many factors, both genetic and environmental, may be contributing to this variation, but we do not have sufficient data to determine its cause with any certainty. In spite of the variation, however, we can make a rough estimate of the quantity of seeds produced by an average tree in one reproductive season. We have already stated that an average tree of *Prosopis chilensis* produces several million flowers (we will use 10 million as a very rough estimate) and that one mature fruit is produced for every 10,000 flowers. An average fruit contains 19 seeds (see TABLE 2). Multiplying the three factors yields a result of 19,000 seeds/tree/reproductive season. By the same method, we have calculated that an average tree of *P. flexuosa* produces about 80,000 seeds. An actual count of the total seed crop of a tree of *P. velutina* by Glendening and Paulsen (1955) yielded 142,000 seeds. Combining these estimates and taking into account a large margin of error for our gross approximation of the number of flowers on a tree, we can state that on the order of 10^4 to 10^5 seeds are produced by a *Prosopis* tree in a single reproductive season.

The seed-bank. Shortly after a fruit reaches maturity, an abscission layer forms at the base of the pedicel and the fruit falls to the ground; there its complement of seeds become components of the "seed-bank," subject to the action of the "environmental sieve." Little is known about the size of the seed-bank of arborescent *Prosopis*. Seeds of *P. velutina* have been found to be viable after 50 years storage in a herbarium (Glendening & Paulsen, 1955), and it has been shown that they may remain viable in the soil for at least 10 years (Tschirley & Martin, 1960). However, Glendening and Paulsen found that seeds of *P. velutina* deteriorated considerably during two years of storage in soil and that none germinated under field conditions after three years. How many viable seeds actually exist in the soil in any given area is unknown.

The environmental sieve. The "environmental sieve," as defined by Harper and White (1971), is the sum of environmental factors which determine whether or not a particular seed will be recruited into the seedling population. The sieve can be viewed as comprising three components: the physical environment, the biological environment, and dispersal. Two of the components, the physical environment of the soil and the biological environment (attack by herbivores and microorganisms), act upon the seed once it has come to rest. The third component, dispersal, determines where the seed will come to rest and thus influences which set of physical and biological factors will act upon the seed. The biological component of

the sieve, being the first to exert a strong effect on the population of newly produced *Prosopis* seeds, will be discussed first.

As far as we have been able to determine, the only herbivores that effect a significant reduction in the population of freshly produced seeds are the bruchid beetles. The adult bruchid lays its eggs on the outside of the developing fruit. When the eggs hatch, the larvae burrow into the fruit, a single larva settling inside each attacked seed. After a number of weeks (the exact development time of the species that attack *Prosopis* is not known), the adults emerge from the seeds, having destroyed them in the process. In many species of bruchids, including some and possibly all of those that attack *Prosopis*, the adults may oviposit shortly after emergence from the seed, allowing a rapid succession of attacking bruchid generations.

D. H. Janzen (1969) has developed a body of theory concerning the evolutionary "strategies" by which the seeds of tropical leguminous trees escape destruction by bruchids. The underlying premise, upon which Janzen bases the existence of a selection pressure sufficiently strong to drive the evolution of seed-escape mechanisms, is that virtually all seeds of a bruchid-attacked species that remain on or beneath the tree will be destroyed by succeeding generations of bruchids. Dispersal, as Janzen points out, is therefore of great importance as a means of escape from the inevitable destruction that will occur if the seed remains near the tree.

Our data lend support to the premise of eventual destruction of virtually all nondispersed seeds, but the data are ambiguous concerning the importance of bruchid attack relative to other factors that might prevent germination beneath the parent tree. The fruits of *Prosopis chilensis* are rapidly dispersed by livestock and water, but the few fruits that remained beneath the tagged trees 13 weeks after maturity had already suffered 90 per cent seed destruction by bruchids. Several seedlings were found growing out of decaying pods beneath one tree of *P. chilensis*, indicating that at least a few seeds escape destruction by bruchids without dispersal. No second-year plants or saplings have been observed beneath tagged trees, nor have we ever seen young *Prosopis* plants directly beneath the crown of any tree. However we have, on rare occasions, observed young plants one to two meters in height within three meters of the edge of the area shaded by the crown of a tree of *P. chilensis*. There is, of course, no way of knowing whether these young plants developed from undispersed seeds of the nearby tree that escaped destruction by bruchids, or from seeds of a different tree that were carried to their present position by animals or flood waters.

The fruits of *Prosopis flexuosa* are attacked at a much slower rate, but dispersal is also slower. At the termination of the study, 15 weeks after fruit maturity, only 26 per cent of the seeds had bruchid emergence holes, but there were still large quantities of fruits lying beneath a number of the tagged trees. Assuming a continuation of the linear rate of seed destruction that occurred between the fifth and fifteenth week (FIGURE 3), all the seeds would theoretically be destroyed by the 51st week after fruit

maturity. However, in actuality, the fruits disappear from beneath the trees well before the 51 weeks have passed. (We found no fruits beneath the trees in November, approximately 40 weeks after the maturation of the previous year's crop.) We can make no estimate concerning the final percentage of nondispersed seeds of *P. flexuosa* that are actually destroyed by bruchids; however, we observed no seedlings or saplings beneath or near any tree of that species. We can conclude, then, from our data on both species, that owing to bruchid attack and possibly other factors (e.g., insufficient sunlight beneath the parent tree), dispersal is almost a prerequisite for seedling establishment.

The slower rate of attack on *Prosopis flexuosa* fruits and the apparent immunity of certain trees of that species to attack by bruchids raises the possibility that *P. flexuosa* may have evolved a chemical defense against bruchids. We lack direct evidence, but it is known (Carman, 1973) that the foliage of *Prosopis* contains toxic nonproteinaceous amino acids. Therefore, it is quite conceivable that a compound toxic to bruchids might be present in the seeds. There are, however, other possible explanations for the low rate of seed destruction in *P. flexuosa*, and we are not presently in a position to judge which is correct.

The importance of dispersal as a means of escape from the parent tree has been pointed out. It should also be noted that the earlier the dispersal occurs, the less likely will be the destruction of any given seed by bruchids. As Janzen (1969) has observed, the strong selection pressure created by bruchid attack has led to the evolution in the Leguminosae of mechanisms that facilitate rapid seed dispersal; the fruit of *Prosopis* is apparently such an adaptation. The mature fruit consists of a single-layered exocarp, a multilayered mesocarp, and a tough, leathery endocarp that surrounds each seed individually. The mesocarp is fleshy, sweet, and nutritious; Catlin (1925) found it to have a protein content of 13.91 per cent. Many kinds of mammals eat the fruits and eject the seeds, undamaged, in their feces. The present dispersal agents are predominantly domesticated ungulates (goats and horses in Argentina; cattle and horses in Arizona), which are extremely efficient in fruit removal. In the parts of the Argentine study site where goats were present, they removed all fruits from beneath tagged *P. chilensis* trees within two weeks after fruit-drop. Similarly, cattle removed all fruits from beneath tagged *P. velutina* trees within two weeks after fruit-drop. The marked trees of *P. flexuosa*, on the other hand, were located in an area where no livestock ranged, a fact that is largely responsible for the much slower dispersal of the fruits of that species. Among wild native mammals, foxes, armadillos, skunks, jack rabbits, cottontail rabbits, coyotes, wolves, and assorted small rodents, particularly kangaroo rats and woodrats, are known to eat the fruits (Graham, 1941; Martin, *et al.*, 1951; D. Greegor, personal communication), but their combined effect on dispersal is today probably of relatively little consequence in comparison to the magnitude and rapidity of dispersal by livestock.

It is well known that the seeds of a number of species of *Prosopis* are

able to germinate after passage through the digestive tract of mammalian dispersal agents, as demonstrated by the presence of seedlings growing out of the excrement of horses and cattle. This has been documented by the work of Glendening and Paulsen (1955) on *P. velutina*, the work of Eilberg (1973) on *P. ruscifolia*, and our germination tests with seeds of *P. chilensis* taken from the excrement of goats and horses. While the endocarps are usually removed from the seeds during passage through the digestive tract of goats and cattle, it was observed that many of the seeds found in the feces of horses and foxes retained their endocarps. The endocarps in horse excrement were generally cracked and thus no longer able to impede germination, but the endocarps usually emerged unbroken in the feces of foxes. Thus the seeds dispersed by foxes must await the additional process of breakage of the endocarp before germination can occur, whereas the seeds dispersed by goats, cattle, and horses can germinate soon after excretion, if the environmental conditions permit.

Although mammals are the most important dispersal agents, water clearly contributes to the process, and birds and ants may play a part as well. The fruits of *Prosopis chilensis* and *P. velutina*, species that grow along washes, are subject to dispersal by water during summer flash floods. Fruits that have dropped to the river bed from overhanging branches are swept away and probably broken up by the crushing action of boulders in the churning waters. Although some seeds may be destroyed in the process, it is likely that many survive to be deposited in the river bed or on its banks when the waters subside. In the austral summer of 1973, a particularly wet season, floods were an important source of fruit dispersal for *P. chilensis* trees growing in areas where there were no goats. *Prosopis flexuosa* can occur along washes, but most of the trees of this species in the Argentine study area grow on the interfluvial flats where water-dispersal of this kind cannot occur. (We did observe one case in which the fruits of a *P. flexuosa* tree on the flats were swept away by overland sheet flow after a particularly heavy rainstorm, but this was unusual.) The lack of water-dispersal and the absence of livestock in the *P. flexuosa* study sites are, together, quite sufficient to explain the slow rate of dispersal of this species in comparison with that of *P. chilensis*.

Birds probably play little part in the dispersal of *Prosopis* seeds at the Argentine site but may be more important in Arizona. The only birds that we have observed eating *Prosopis* fruits in Argentina are parrots, which generally attack the fruits while they are still on the tree, eating the fleshy mesocarp and letting the seeds fall to the ground still enclosed in the tough endocarps. The seeds dropped by the parrots may escape attack by bruchids (it is not known whether the adult beetles will lay eggs on a naked endocarp removed from the fruit), but, as we pointed out earlier, it is highly unlikely that any seedling would survive and become established beneath the crown of the parent tree. A number of other birds that occur in the Argentine study area (*Eudromia elegans*, *Columba maculosa*, *Zenaida auriculata*, and possibly *Rhea americana*) are likely to feed on *Prosopis* fruits, but we have not actually observed any doing so.

According to Martin, *et al.* (1951), *Prosopis* seeds are eaten extensively in the southwestern United States by the gambel's quail (*Lophortyx gambelii*), and occasionally by white-winged doves, ravens, and two other species of quail. We have no observations of this occurrence ourselves and can make no comment on its significance in terms of dispersal or predation.

Ants have been observed in Argentina carrying individual *Prosopis* seeds, still enclosed in the endocarps, and even whole sections of fruits. According to Dr. Jim Hunt (personal communication), the ants involved, *Acromyrmex lobicornis* and *A. striatus*, are "gardening ants" that carry vegetable matter of all kinds into their subterranean nests, where it serves as a substrate for the specialized fungi that the ants culture and use for food. The seed, which may be carried as much as 50 meters from the tree, is not eaten by the ants, but it is uncertain whether it would remain viable after serving as a fungal substrate. At any rate, the frequency of seed-removal by ants does not appear to be great enough to be considered significant in terms of either predation or dispersal.

At the beginning of our discussion of the "environmental sieve," we stated that the importance of dispersal as a component of the sieve lies in its function as a determinant of the location where the seed will come to rest and, consequently, the set of physical and biological stresses that will be brought to bear on the seed. The various modes of dispersal should be considered, then, in terms of the precision with which they place *Prosopis* seeds in a position that is favorable for germination. Water-dispersal has the advantage that the seeds are necessarily deposited along the wash, the habitat where the mature trees grow and therefore presumably the most favorable environment for germination or subsequent survival or both. Animals and birds, on the other hand, undoubtedly excrete many seeds in places, such as exposed flats, where they have no chance of germination, although loss of seeds in this manner is somewhat reduced by the tendency on the part of many animals to stay in the washes because that is where the food is. Balanced against this advantage of flood-dispersal is the irregularity of its breaking effect on the fruits; it is probable that many seeds are crushed by rocks, while others are not freed from the endocarp or remain inside an intact portion of the fruit. In the passage through the mammalian digestive tract, on the other hand, seed survivorship is high and, in some animal species, the endocarps are broken with factory precision, preparing the seeds for quick germination. If we are correct in our premise that the fruit of *Prosopis* is specialized for dispersal by animals, not water, this in itself indicates that in the long run animal-dispersal produces more germinations in locations favorable for maturation than does water-dispersal (or, more accurately, that it did in the region where the genus evolved). It is worth mentioning, however, that at least one related species of tree (*Acacia caven*), growing in the same general habitat as *Prosopis* at the Argentine site, has fruits that are apparently adapted for water-dispersal.

Two components of the "environmental sieve" have now been discussed.

The remaining component, the suitability of the physical environment at the location where the seed comes to rest, will ultimately determine which of the relatively few surviving seeds will germinate and become established. Assuming that the endocarp has been removed or broken in the process of dispersal and the seed scarified, germination and subsequent survival of the seedling are dependent upon the depth at which the seed is located, the soil temperature, and the soil moisture.

Scifres and Brock (1970b), working with *Prosopis glandulosa*, found depth of planting to be a critical factor in seedling emergence. Under favorable temperature and moisture conditions in the laboratory, seedlings emerged from 80 per cent of the seeds planted at 0.5 to 1.0 cm., as compared to less than 20 per cent emergence from seeds planted below 2.0 cm. Interestingly, 100 per cent of the seeds placed on top of the soil germinated, but in no case did seedling establishment occur. The low probability of germination of deeply placed seeds is a factor that would probably work against seeds dispersed in a flash flood.

The importance of soil temperature has already been pointed out, 80° to 85° F. being the most favorable temperature for the species for which data are available (*Prosopis ruscifolia, P. velutina, P. glandulosa*).

For plants of the desert environment, the amount of moisture present in the upper levels of the soil and the timing of its availability are the most critical factors influencing germination and seedling survival. We suspect that the seedlings of phreatophytes are particularly vulnerable to drought, as a consequence of the survival strategy of the mature plant. Owing to their ability to tap a constant water supply, phreatophytes have not been forced to evolve the extensive physiological and morphological adaptations that allow such drought-resistant shrubs as *Larrea cuneifolia* and *Tricomaria usillo* to survive. As a result, the phreatophyte seedling is in a particularly vulnerable position, lacking both the deep root system of the parent tree and the high degree of morphological adaptation of the seedlings of desert shrubs. Indeed, it seems amazing to us that *Prosopis* seedlings ever become established at all in the region of the Argentine study area, where the dry season usually lasts nine months or more. Judging from the scarcity of both seedlings and saplings in that area, germination is a rare event, and establishment must occur only in those very unusual years when heavy summer rains are combined with occasional light rains at intervals during the winter drought, allowing the young plant to survive the first critical year. Seedling establishment is probably considerably easier for *P. velutina* in Arizona, where there are summer and winter rainy seasons.

It would be interesting to survey the age structure of a population of *Prosopis chilensis* or *P. flexuosa*; we suspect that the result would show that most of the trees germinated during a very few years. Furthermore, if we are correct in our premise that phreatophyte seedlings are more vulnerable than the seedlings of desert-adapted shrubs, a study comparing the age structures of populations of *P. chilensis* and of a dominant shrub of the same region, such as *Larrea cuneifolia*, should show that the

shrubs became established during a greater number of years than the *Prosopis*.

For an "opportunistic" desert species that can become established only in rare wet years, the seed-longevity of 50 years that has been documented for *Prosopis velutina* is clearly an advantage; whether seeds can survive that long under field conditions is, however, doubtful (Glendening & Paulsen, 1955). Also advantageous are the rapid growth of the taproot in *Prosopis* seedlings and the timing of fruit-drop at the beginning of the summer rainy season; both factors help maximize the depth reached by the root during the brief period of optimum growth conditions, which in turn maximizes the probability of survival until the next rain. The advantageous timing of fruit-drop in *Prosopis* is made possible by its phreatophytic habit. For most desert perennials, blooming is tied to the timing of rainfall, but the availability of a constant water supply gives the phreatophyte the flexibility to bloom at whatever time is most favorable for subsequent germination of the seeds produced.

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CYTOTAXONOMIC NOTES ON SOME GENTIANACEAE

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CHROMOSOME NUMBERS HAVE PROVED to be of considerable value in generic delimitation in the Gentianaceae, particularly with regard to *Gentiana* L., *Gentianella* Moench, and their relatives. But of the approximately 65 variously recognized genera, chromosome counts have been previously available for only 33, and of these 11 are monotypic or are known cytologically from only a single count. Chromosome numbers are reported here for 21 species in 11 genera, including 4 genera for which counts have previously been unavailable; one of the counts is tentative, however.

The standard squash technique has been used. Flower buds were fixed in 3:1 ethanol-acetic acid, stored in 70% ethanol, and the pollen-mother-cells were subsequently squashed in acetocarmine. Permanent slides were made using the quick-freeze method of Conger and Fairchild (1953). Voucher specimens are deposited in the herbaria of the Arnold Arboretum (A and AAH), except for that for *Bartonia verna*, which is at DUKE. A summary of the results is presented in TABLE 1; for the sake of comparison, all previously reported counts for the genera investigated are listed in the APPENDIX. Photographs of chromosomes of representatives of each of the genera are shown in FIGURE 1. All photographs were made from temporary slides.

Bartonia Muhl. ex Willd.

The three to four species of *Bartonia*, a genus of semisaprophytes or semiparasites, are distributed in the eastern and central United States and the maritime provinces of Canada. Previously, chromosome numbers were reported for *B. paniculata* (Michx.) Muhl. and *B. virginica* (L.) BSP., both $n = 26$. The chromosome number of *B. verna* (Michx.) Muhl., $n = 22$, is reported here for the first time. Only *B. texana* Correll remains to be investigated cytologically. However, this plant, known from a single locality in Texas, may not be distinct from the variable *B. paniculata*.

Two basic chromosome numbers ($x = 11$ and $x = 13$), which correspond to two morphological groups, are found in this small genus. *Bartonia verna*, restricted to the Coastal Plain of the southeastern United States, is spring-flowering and has relatively long, single-veined corolla lobes. The more widely distributed *B. paniculata* and *B. virginica* are summer-flowering and have short, 3-veined corolla lobes.

Calolisianthus (Griseb.) Gilg

A genus of perhaps ten species, primarily Brazilian in distribution, *Calolisianthus* is unknown cytologically except for the single species reported

FIGURE 1. Chromosomes of Gentianaceae, × 750: A, *Bartonia verna*, Metaphase II, $n = 22$; B, *Calolisianthus frigidus*, Diakinesis, $n = 40$; C, *Chelonanthus bifidus*, Diakinesis, $n = 20$; D, *Chironia baccifera*, Diakinesis, $n = 34$; E, *Coutoubea spicata*, Diakinesis, $n = 15$; F, *Gentiana sedifolia*, Diakinesis, $n = 20$; G, *Gentianella dacrydioides*, Metaphase II, $n = 18$; H, *Halenia inaequalis*, Metaphase II, $n = 11$; J, *Macrocarpaea glabra*, Diakinesis, $n = 21$; K, *Symbolanthus tricolor*, Diakinesis, $n = 40$.

here. Although *C. frigidus* (Sw.) Gilg does not deviate strikingly from other species in the genus in terms of its floral and vegetative features, Nilsson (1970) found that its pollen more closely resembles that of species of *Symbolanthus* than that of its supposed congeners. The chromosome number of *C. frigidus*, $n = 40$, is the same as that of the two *Symbolanthus* species investigated so far. However, until more is known of the chromosome numbers in both genera, we prefer not to draw any conclusions concerning the relationship of *C. frigidus* to *Symbolanthus*. It certainly would not appear to fit morphologically into that genus.

Chelonanthus (Griseb.) Gilg

The 15 to 20 species of *Chelonanthus* are distributed through much of mainland tropical America. Previously, a chromosome number, $n = 20$, was reported only for *C. alatus* (Aubl.) Pulle (Weaver, 1969). The two

species investigated in this study also have this same number of chromosomes. Although these three species comprise one-fifth or less of the total number of species in the genus, they represent the primary morphological groups: *C. alatus*, with a gibbous-campanulate corolla, a dichasium with long, secund, racemelike side branches, and pollen in tetrads; *C. bifidus* (HBK.) Gilg, with a funnelform corolla, a normal compound dichasium, and pollen in tetrads; and *C. uliginosus* (Griseb.) Gilg, with pollen in polyads. Therefore it is to be expected that $n = 20$ is general in the genus.

Chironia L.

Most of the species of *Chironia*, of which there are around 35, are South African in distribution, but several range northward into tropical Africa and Madagascar. This genus and the very closely related monotypic *Orphium* E. Mey. comprise Gilg's Gentianeae-Chironiinae, delimited primarily on the basis of the large pollen grains of the plants. The chromosome number of *C. baccifera* L. ($n = 34$), reported here for the first time, is the only published one for the genus. Chromosome numbers based on $x = 17$ are rare in the family, having been found elsewhere up to now in only three species of *Sabatia* Adans. (Perry, 1971) and one of *Canscora* Lam. (Mukherjee, 1968).

Chironia baccifera, restricted to South Africa, is the only species in the genus with a berrylike fruit, and it has been considered to constitute a monotypic subgenus.

Coutoubea Aubl.

The three to five species of *Coutoubea* are restricted in distribution to northern South America, with the exception of *C. spicata* Aubl., which ranges north in Central America to British Honduras. The chromosome number $n = 15$, reported here for *C. spicata*, represents the first published count for the genus.

Gentiana L.

A large genus, primarily of the Northern Hemisphere, *Gentiana* in the strict sense has been subdivided into ten sections of greatly varying size. The only species investigated in this study, *G. sedifolia* HBK., belongs to the section CHONDROPHYLLAE Bunge, a group of species low in stature with ± hyaline-margined leaves, usually solitary flowers, symmetrical corolla plaits which are often nearly as large as the corolla lobes, distinct anthers and stigmas, often long-stipitate capsules, and wingless seeds. Most of the species are high-elevation plants, and they are particularly diverse in the Himalayas and the mountains of China. Members of this section are the only species of *Gentiana* found in the Southern Hemisphere. Previously, chromosome numbers have been reported for eleven species in this section, the base numbers being $x = 5$ (seven species), $x = 9$ (one species), and $x = 13$ (three species). All of these base numbers are

present in other sections of *Gentiana*, $x = 13$ being perhaps the commonest and most widespread one in the genus. However, $x = 5$ is common only in sect. GENTIANA and $x = 9$ in sect. MEGALANTHE Gaudin (= sect. THYLACITES Griseb.).

The section CHONDROPHYLLAE contains both annual (or monocarpic) and perennial species, and several authors have subdivided the section into series along these lines. All of the perennial species for which chromosome numbers are available are $n = 13$, while all of the annuals are $n = 10$ or $n = 20$ except for *G. douglasiana* Bong. ($n = 13$) and *G. prostrata* Haenke ($n = 16$–18, 18). *Gentiana douglasiana* probably does not belong in sect. CHONDROPHYLLAE. It is unique among *Gentiana* species in its lack of an intracalycine membrane and in its pollen grains, which according to Nilsson (1967) have three colpoid apertures without ora in addition to the three oriferous colpi typical in the family.

The taxonomy of the New World CHONDROPHYLLAE is somewhat confused. The common alpine and arctic species of western North America is usually considered to be conspecific with *Gentiana prostrata* Haenke of the eastern Alps. Kusnezow (1894) referred the annual Andean *Gentiana* (as subg. EUGENTIANA) to this same species, but he also recognized *G. sedifolia*, which he considered to be a biennial, as the only other representative of the genus in South America. Gilg (1906) referred all of the Andean *Gentiana* to *G. prostrata*, but later (1916) changed his mind. Pringle (*in litt.*) considers at least three taxa of *Gentiana* to be present in the Andes: *G. sedifolia* in Venezuela, Colombia, Ecuador, and northern Peru; an unnamed taxon in the central Andes of Peru; and a plant which may be conspecific with *G. prostrata*, from central Chile south to Tierra del Fuego.

One of the two reported chromosome counts for "*Gentiana prostrata*" was made from material collected in Peru ($n = 18$, Diers, 1961). The report here of a different number for *G. sedifolia* ($n = 20$) lends support to the contention that there are at least two species of *Gentiana* in the Andes.

Gentianella Moench

The genus *Gentianella*, comprising perhaps 250 to 300 species, is nearly cosmopolitan in its distribution, but the center of diversity is in the Andes, a region from which Gilg (1916) recognized 182 species. The genus has never been monographed in its entirety, and the existing sectional classification is a residual one from Kusnezow's treatment (in Gilg, 1895) of what he called *Gentiana* subg. GENTIANELLA, several of his sections having since been elevated to generic status. Including those in this paper, chromosome numbers have now been reported for about 30 species in three sections: sect. GENTIANELLA, sect. ANDICOLA (Griseb.) Holub, and sect. ARCTOPHILA (Griseb.) Holub. All species have $n = 18$ chromosomes, with the exception of the following three: *G. moorcroftiana* (Wall. ex Griseb.) Airy Shaw, with $n = 9$ (Mehra & Vasudevan, 1972) and $2n = 26$ (Wada, 1966); *G. auriculata* (Pall.) Gillett, with $n = 24$ (Soko-

lovskaya, 1968); and *G. uliginosa* (Willd.) Börner, with n = ca. 27 (Holmen, in Löve & Löve, 1961).

Therefore, *Gentianella* in the strict sense appears to be quite homogeneous in regard to chromosome number, apparently with a base number of $x = 9$ (except for *G. auriculata* and, if the study material for Wada's report was correctly identified, for *G. moorcroftiana*), strengthening the argument for the separation of *Comastoma* (Wettst.) Toyokuni ($x = 5$) and *Gentianopsis* Ma ($x = 11, 13$) as distinct.

Although *Gentianella* and *Gentiana* L. are widely recognized as generically distinct, many specific transferals remain to be made. We propose the following new combinations relevant to this study:

Gentianella corymbosa (HBK.) Weaver & Rüdenberg, comb. nov. BASIONYM: *Gentiana corymbosa* HBK. Nov. Gen. & Sp. 3: 133 (*folio ed.*); 171 (*quarto ed.*). 1818.

Gentianella dacrydioides (Gilg) Weaver & Rüdenberg, comb. nov. BASIONYM: *Gentiana dacrydioides* Gilg, Engl. Bot. Jahrb. 22: 311. 1896.

Gentianella nevadensis (Gilg) Weaver & Rüdenberg, comb. nov. BASIONYM: *Gentiana nevadensis* Gilg, *loc. cit.* 313.

Halenia Borkh.

Most of the 70 to 80 species of *Halenia* are high-elevation plants of Central and South America. Two species are native to the Old World. Previously, chromosome numbers have been reported for eight species, representing both Old World and New World plants, and all are $n = 11$. The six species reported here all have that same number. In addition, a Costa Rican collection (*Weaver 2734*) tentatively identified as *H. rhyacophila* Allen, also $n = 11$, may represent an undescribed species.

Our observations of one bud of *Halenia inaequalis* (*Weaver 2624*) showed inversion bridges with or without fragments at Anaphase I. However, buds from another plant had cells based on $n = 11$ without irregularities. In addition, 11 bivalents plus two single, small chromosomes were observed at Metaphase II in a bud of *H. brevicornis* (*Weaver 2600*). The two single chromosomes did not pair, one of them lying free in the cytoplasm and the other located in close proximity to the end of one bivalent. Unfortunately, the material was so scarce that this collection contained only one bud with pollen-mother-cells at a countable stage. Another collection of this species (*Weaver 2625*) lacked these small chromosomes.

Lagenanthus Gilg

The sole species of this genus, the magnificent *Lagenanthus princeps* (Lindl.) Gilg, is restricted in distribution to the mountains of a small area in southwestern Venezuela and adjacent Colombia. Ewan (1952) de-

scribed a second species, *L. parviflorus*, from Panama. The type (and only specimen) (*Allen 3601*, MO), which has been examined, consists merely of a vegetative scrap and a detached flower lacking the gynoecium. Nevertheless, it is clear that this plant is not a member of the Gentianaceae.

Our collection of *Lagenanthus princeps* produced only a few cells at all suitable for study, and none of these were sufficiently clear to make an absolutely certain chromosome count. However, the haploid number appears to be $n = 40$. This number would coincide well with the results obtained from the only other supposed close relatives of *Lagenanthus* investigated to date, all of which have chromosome numbers based on $x = 10$: *Calolisianthus frigidus* ($n = 40$), *Symbolanthus* (2 species, $n = 40$), and *Chelonanthus* (3 species, $n = 20$).

Macrocarpaea (Griseb.) Gilg

A genus of perhaps 50 species, many of which are represented in collections but not yet described, *Macrocarpaea* is distributed primarily in the higher elevations of tropical South America, with outliers in Costa Rica, Panama, and the Greater Antilles. Chromosome numbers have now been reported for four species: the Jamaican *M. thamnoides* (Griseb.) Gilg (Weaver, 1969), the Costa Rican *M. valerii* Standl. (Weaver, 1972), and the two Colombian species reported here. All have $n = 21$. In addition, two collections representing undescribed Colombian species (*Weaver 2634, 2050*) have this same number of chromosomes. However, considering the large number of species and their diversity, it would be premature to expect that $n = 21$ is general in the genus.

TABLE 1. **Chromosome numbers of Gentianaceae determined during this study.**

TAXON	HAPLOID NUMBER	LOCALITY
Bartonia verna (Michx.) Muhl.	$n = 22$	UNITED STATES. North Carolina: Brunswick Co., 10 mi. NNE of Supply, *Weaver 1961* (DUKE).
Calolisianthus frigidus (Sw.) Gilg	$n = 40$	ST. VINCENT: Soufrière, *Howard, Cooley, & Weaver 17712* (A).
Chelonanthus bifidus (HBK.) Gilg	$n = 20$	COLOMBIA. Meta: ca. 5 km. N of Villavicencio, *Weaver 2640* (A).
Chelonanthus uliginosus (Griseb.) Gilg	$n = 20$	COLOMBIA. Cundinamarca: between Bogotá & Villavicencio, *Weaver 2639* (A).
Chironia baccifera L.	$n = 34$	CULTIVATED: greenhouses of the Arnold Arboretum, Jamaica Plain, Mass., U.S.A.; seeds received from the National Botanical Garden,

		Kirstenbosch, South Africa, *Weaver 2737* (AAH).
Coutoubea spicata Aubl.	$n = 15$	BRITISH HONDURAS: just W of Hattieville on the Western Highway, *Weaver 2735* (A).
Gentiana sedifolia HBK.	$n = 20$	VENEZUELA. Mérida: Laguna Mucubají, *Weaver 2620* (A).
Gentianella corymbosa (HBK.) Weaver & Rüdenberg	$n = 18$	COLOMBIA. Cundinamarca: Monserrate, *Weaver 2631* (A).
Gentianella crassulifolia (Griseb.) Fabris	$n = 18$	COLOMBIA. Nariño: Vólcan de Galeras, *Weaver 2656* (A).
Gentianella dacrydioides (Gilg) Weaver & Rüdenberg	$n = 18$	COLOMBIA. Putumayo: between El Encano & Santiago, *Weaver 2655* (A).
Gentianella nevadensis (Gilg) Weaver & Rüdenberg	$n = 18$	VENEZUELA. Mérida: Laguna Mucubají, *Weaver 2606* (A).
Halenia brevicornis (HBK.) G. Don	$n = 11 + 2$	VENEZUELA. Mérida: Cuenca Santo Domingo, *Weaver 2600* (A).
	$n = 11$	VENEZUELA. Mérida: Teleferico de Mérida, between La Aguada & La Montaña, *Weaver 2625* (A).
Halenia cuatrecasasii Allen	$n = 11$	COLOMBIA. Cundinamarca: Monserrate, *Weaver 2630* (A).
Halenia phyllophora Allen	$n = 11$	COLOMBIA. Putumayo: between El Encano & Santiago, *Weaver 2654* (A).
Halenia rhyacophila Allen	$n = 11$	COSTA RICA. Cartago: Cerro Buenavista, *Weaver 2733* (A).
Halenia viridis (Griseb.) Gilg	$n = 11$	VENEZUELA. Mérida: Laguna Mucubají, *Weaver 2605* (A).
Halenia inaequalis Wedd.	$n = 11$	VENEZUELA. Mérida: Teleferico de Mérida, between La Aguada & La Montaña, *Weaver 2624* (A).
Lagenanthus princeps (Lindl.) Gilg	$n =$ ca. 40	VENEZUELA. Tachira: base of Paramo de Tamá, *Weaver 2612* (A).
Macrocarpaea densiflora (Benth.) Ewan	$n = 21$	COLOMBIA. Tolima: between Fresno & Manizales, *Weaver 2644* (A).
Macrocarpaea glabra (L. f.) Gilg	$n = 21$	COLOMBIA. Cundinamarca: above Bogotá on road to Villavicencio, *Weaver 2636* (A).
Symbolanthus tricolor Gilg	$n = 40$	COLOMBIA. Cundinamarca: near San Miguel, *Weaver 2635* (A).

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APPENDIX. **Previously reported chromosome numbers in the genera of Gentianaceae investigated during this study.**

TAXON	HAPLOID NUMBER	REFERENCE
Bartonia Muhl.		
Bartonia paniculata (Michx.) Muhl.	26	Rork, 1949
Bartonia virginica (L.) BSP.	26	Rork, 1949
	ca. 26	Moore, in Gillett, 1959
Chelonanthus (Griseb.) Gilg		
Chelonanthus alatus (Aubl.) Pulle	20	Weaver, 1969
Gentiana L.		
Sect. CHONDROPHYLLAE Bunge		
Gentiana altaica Laxm.	13	Sokolovskaya & Strelkova, 1938
Gentiana argentea Royle	10	Mehra & Vasudevan, 1972
Gentiana carinata Griseb.	10	Mehra & Gill, 1968
Gentiana capitata Ham.	10	Mehra & Vasudevan, 1972
Gentiana crutwellii H. Sm.	10	Borgmann, 1964
Gentiana douglasiana Bong.	13	Taylor & Mulligan, 1968
Gentiana ettinghausenii F. Muell.	10	Borgmann, 1964
Gentiana piundensis Van Royen	10	Borgmann, 1964
Gentiana prostrata Haenke	18	Diers, 1961
	16–18	Johnson & Packer, 1968
Gentiana pyrenaica L.	13	Küpfer & Favarger, 1967
	13	Favarger & Küpfer, 1968
Gentiana zollingeri Fawcett	10	Wada, 1956
	10	Wada, 1966
Gentianella Moench		
Sect. GENTIANELLA		
Gentianella acuta (Michx.) Hiit.	18	A. Löve, 1954
Gentianella amarella (L.) Börner	18	D. Löve, 1953
subsp. *lingulata* (Ag.) Löve & Löve	18	A. & D. Löve, 1956
Gentianella anisodonta (Borbás) Löve & Löve	18	Favarger, 1965
Gentianella aspera (Hegetschw. & Heer) Dorstál ex Skalický, Chrtek, & Gill	18	Favarger, 1965
Gentianella auriculata (Pall.) J. M. Gillett	24	Sokolovskaya, 1968
Gentianella austriaca (A. & J. Kern.) Holub	18	Favarger, 1952
Gentianella campestris (L.) Börner		
subsp. *campestris*	18	Favarger, 1949

subsp. *islandica* (Murb.) Dörfler	18	A. & D. Löve, 1956
Gentianella engadinensis (Wettst.) Holub	18	Favarger, 1965
Gentianella germanica (Willd.) Warburg	18	Reese, in A. & D. Löve, 1961
Gentianella hypericifolia (Murb.) Pritchard	18	Küpfer & Favarger, 1967
	18	Favarger & Küpfer, 1968
Gentianella insubrica (H. Kunz) Holub	18	Favarger, 1952
Gentianella moorcroftiana (Wall. ex Griseb.) Airy Shaw	9	Mehra & Vasudevan, 1972
	13	Wada, 1966
Gentianella rhaetica (A. & J. Kern) A. & D. Löve	18	Favarger, 1965
Gentianella uliginosa (Willd.) Börner	ca. 27	Holmen, in A. & D. Löve, 1961
Sect. ANDICOLA (Griseb.) Holub		
Gentiana aff. *briquetiana* Gilg *	18	Diers, 1961
Gentiana aff. *brunneo-tincta* Gilg *	18	Huynh, 1965
Gentiana aff. *dolichopoda* Gilg *	18	Diers, 1961
Gentiana inaequicalyx Gilg *	18	Diers, 1961
Gentiana aff. *kuntzei* Gilg *	18	Diers, 1961
Gentianella peruviana (Griseb.) Fabris	18	Diers, 1961
Gentiana primuloides Gilg *	18	Diers, 1961
Gentiana pulla Fabris *	18	Diers, 1961
Gentianella punicea (Wedd.) Holub	18	Diers, 1961
Gentianella saxosa (G. Forst.) Holub	18	Favarger, 1952
Gentianella umbellata (R. & P.) Favarger	18	Huynh, 1965
Sect. ARCTOPHILA (Griseb.) Holub		
Gentianella aurea (L.) H. Sm.	18	D. Löve, 1953
Gentianella quinquefolia (L.) Small	18	Rork, 1949
Halenia Borkh.		
Halenia crassiuscula Robins. & Seat.	11	Beaman, *et al.*, 1962
Halenia corniculata (L.) Cornaz	11	Sokolovskaya, 1963
	11	Wada, 1966
Halenia decumbens Benth.	11	Niehaus & Wong, Jr., 1971

Halenia deflexa (Sm.) Griseb.	11	Mulligan, 1967
Halenia elliptica D. Don	11	Favarger, 1952
Halenia multiflora Benth.	11	Niehaus & Wong, Jr., 1971
Halenia shannonii Briq.	11	Beaman, *et al.*, 1962
Halenia umbellata (R. & P.) Gilg	11	Favarger & Huynh, 1965
	11	Huynh, 1965
Macrocarpaea (Griseb.) Gilg		
Macrocarpaea thamnoides (Griseb.) Gilg	21	Weaver, 1969
Macrocarpaea valerii Standl.	21	Weaver, 1972
Symbolanthus G. Don		
Symbolanthus pulcherrimus Gilg	40	Weaver, 1969

* Combination in *Gentianella* not yet made.

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THE OXALIDACEAE IN THE SOUTHEASTERN UNITED STATES [1]

KENNETH R. ROBERTSON

OXALIDACEAE R. Brown in Tuckey, Narr. Exped. Congo 433. 1818, "Oxalideae," nom. cons.
(OXALIS FAMILY)

Perennial or annual herbs [or shrubs (often dendroid), lianas, or trees]. Leaves alternate, palmately compound [or even- or odd-pinnately compound or unifoliolate], frequently in basal rosettes or apical clusters, petioled [or sessile], the petiole with a basal joint; leaflets pinnately nerved, often showing "sleep" movements, the petiolules with a basal pulvinus; stipules (or stipulelike appendages) present or absent. Inflorescences axillary or seemingly terminal [sometimes cauliflorous], bracteate, few- to many-flowered cymes, pseudoumbels [panicles or racemes] or the flowers solitary; pedicels articulated. Flowers perfect [very rarely some imperfect, the plants then androdioecious or dioecious], regular, 5-merous, often heterostylous, sometimes cleistogamous; disc absent. Sepals 5, free or basally connate, persistent in fruit, imbricate in aestivation. Petals 5, free or coherent above the base, often clawed, contorted [quincuncial or cochlear] in aestivation, inserted at the base of the staminal tube. Androecium of 10 [or 15] stamens; filaments of 2 lengths, the epipetalous ones shorter than the episepalous ones, all connate below into a ring or tube, persistent in fruit; anthers dorsifixed, versatile, 2-locular at anthesis, dehiscing extrorsely by longitudinal slits. Gynoecium of 5 [rarely 3] united, superior, epipetalous carpels; styles free [or united], terminal, persistent; stigmas terminal, capitate, punctate, or penicillate, often 2-lobed; each locule with one or more anatropous, superposed, or collateral, bitegmic, tenuinucellar [or crassinucellar] ovules pendulous from an axile placenta, the micropyle apical and abaxial. Fruit a loculicidal capsule (sometimes appearing septicidal due to deep septal folds)

[1] Prepared for a generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of the National Science Foundation (Grant GB–6459X, principal investigator, Carroll E. Wood, Jr.). This treatment follows the format established in the first paper in the series (Jour. Arnold Arb. **39**: 296–346. 1958). The area covered includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on plants in this area, with additional information from extraterritorial taxa in brackets. References that I have not seen are marked by an asterisk.

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[or a berry or rarely dry and indehiscent]. Seeds usually arillate; endosperm abundant [rarely absent]; embryo straight [or oblique], the radicle superior. Embryo sac development of the Polygonum type, embryo development of the Asterad type. TYPE GENUS: *Oxalis* L.

Perhaps 800 or more species in seven genera. The vast majority of species belong to *Oxalis*, the only genus in our area. *Biophytum* DC., the next largest genus (with about 70 species), is pantropical in distribution; evidently no species are common to both hemispheres. The other genera are *Dapania* Korth. (one species in Madagascar, two in western Malesia), *Sarcotheca* Blume (11 species in western Malesia), *Averrhoa* L. (two species, cultivated pantropically), *Lepidobotrys Staudtii* Engler, of tropical West Africa, and *Hypseocharis* Remy (nine described species of Peru, Bolivia, and Argentina).

Within the family, it is clear that *Oxalis* and *Biophytum* form a natural group, while *Averrhoa*, *Sarcotheca*, and *Dapania* constitute another (sometimes separated as Averrhoaceae). Both *Hypseocharis* and *Lepidobotrys* are poorly known, and their affinities are less certain; they have been segregated as Hypseocharitaceae and Lepidobotryaceae. Veldkamp (1971) speculated that *Hypseocharis* seems to link Oxalidaceae and Geraniaceae. Hutchinson allied Averrhoaceae with the Rutales and Lepidobotryaceae (including *Dapania* and *Sarcotheca*) with the Malpighiales. There is rather general agreement (Cronquist, Hutchinson, Scholz, Takhtajan, and Thorne) that Oxalidaceae *sensu stricto*, Geraniaceae, Tropaeolaceae, and Balsaminaceae are related families.

Averrhoa is one of the few genera of flowering plants with more than a single species that is known only in, or as an escape from, cultivation. The geographical origin of *A. Carambola* L., $2n = 22, 24$, and *A. Bilimbi* L., $2n = 22, 24$, is uncertain. It is commonly said that both are of Indo-Malesian origin, since in pre-Linnaean literature they are always attributed to that region and their closest relatives are plants of Malesia and Madagascar (see Veldkamp). An American origin for the species has also been postulated, and Webster presents an example of convergent evolution in support of this hypothesis. In overall appearance *Phyllanthus acidus* (L.) Skeels, of the Euphorbiaceae, is remarkably similar to the two species of *Averrhoa*, particularly *A. Bilimbi*. (Linnaeus, in fact, described *Phyllanthus acidus* as a species of *Averrhoa*.) All three of these species are cultivated throughout the tropics and are of uncertain provenance. According to Webster, *Phyllanthus acidus* is of New World origin, since its closest congeners are from that region and since a collection from the Pará River delta in northeastern Brazil is evidently the only known specimen of this species from its native habitat. "By analogy with the documented evidence for *P. acidus*, it appears most likely that both species of *Averrhoa* are also originally American plants which have had a similar history. The great superficial resemblance between these three species may not be entirely coincidence, for it is possible that all three are members of the sub-littoral forests of the South American coastline; and their similarity in life form

may have a selective basis. Probably, as suggested by Merrill and Trimen, these plants were first encountered by the Portuguese on the Brazilian coast and from there carried to India and other parts of the Old World" (Webster).

Heterostyly is common in the family. Many species of *Oxalis*, a few of *Biophytum*, and *Averrhoa Bilimbi* are tristylous. Distyly occurs in *Averrhoa Carambola* and in species of *Oxalis*, *Biophytum*, *Sarcotheca*, and *Dapania* (with two species androdioecious). Some species of *Oxalis* and *Biophytum* are homostylous. The species of *Hypseocharis* evidently are homostylous, although the styles elongate after anthesis. *Lepidobotrys Staudtii* is described as dioecious. Cleistogamous, as well as chasmogamous, flowers occur in certain species of *Oxalis*.

It has been postulated that the breeding system of ancestral Oxalidaceae combined morphological heterotristyly and physiological self-incompatibility (see Ornduff; Eiten argues, however, that homostyly is the original condition). In the idealized oxalidaceous tristylous system, there are three positions or levels for the one set of stigmas and the two sets of anthers. Long-styled flowers have the stigmas at the highest position, with the two sets of anthers at the middle and lowest positions. In midstyled flowers, one set of anthers is in the highest position, the stigmas are in the center position, and the other set of anthers is in the lowest position. The anthers occupy the upper and center positions in the short-styled flowers, with the stigmas in the lowest position (see FIGURE 1, o–q). In addition to differing in the lengths of the styles and filaments, the three types of flowers can differ in the size of the pollen grains (which are largest in anthers of the upper level and smallest in anthers of the lowest position), in the shape of the stigmas, in the pubescence of the filaments and styles, and in the curvature of the styles. In this idealized situation, pollen from anthers of the uppermost position of midstyled and short-styled flowers will be compatible only with stigmas of long-styled flowers; pollen from anthers of the middle level of long- and short-styled flowers will germinate only on stigmas of midstyled flowers; and pollen of the lowest position of long-styled and midstyled flowers will be compatible only with stigmas of short-styled flowers.

Some species, among them *Oxalis valdiviensis* Barnéoud (Chile), *O. Regnellii* Miq. (South America), and *O. purpurea* L. (including *O. speciosa* Ecklon & Zeyher; South Africa), have retained this type of breeding system of tristyly and self-incompatibility. However, it seems that many or most species of the family have shifted away from a system that requires cross-pollination toward ones that allow autogamy. In many cases, there is a partial to complete loss of self-incompatibility, which may or may not be accompanied by morphological changes. Thus, some populations of *O. Dillenii* subsp. *filipes* are strongly tristylous and wholly self-compatible. According to Denton (p. 482), the reverse occurs in *Oxalis* sect. IONOXALIS, and even the homostylous species are self-incompatible.

One or two of the possible flower forms may be lost within a species, resulting in distyly or homostyly. Only long- and short-styled flowers

seem to occur in *Oxalis violacea*, *O. Priceae* subsp. *Priceae*, *Biophytum Petersianum* Klotzsch., *Dapania pentandra*, and the species of *Sarcotheca*. Long-styled and midstyled flowers are found in *O. albicans* and *Averrhoa Carambola*. Evidently, only long-styled flowers occur in *O. thelyoxys* (Cuba), *O. magellanica* (Southern Hemisphere), and *O. Acetosella* subsp. *Griffithii* (Asia). It is sometimes said that this is the situation in *O. Acetosella* subsp. *Acetosella* and subsp. *montana*, but an examination of herbarium specimens shows that the level of insertion of the stigmas is mostly either considerably above the upper whorl of anthers or slightly below them; it needs to be determined whether this is a variable character or a case of distyly with long-styled and midstyled flowers. Darwin thought that European populations were variable in this respect.

The distance between the stigmas and anthers is small enough in some species, or in populations of some species, to ensure self-pollination, even though the flowers are heterostylous. Ornduff (1972) called such flowers "quasi-homostylous" and noted their occurrence in *Oxalis Dillenii* subsp. *filipes* and subsp. *Dillenii*. Another mechanism that promotes self-pollination is a change in the relative lengths of the filaments and styles so that the stigmas are inserted at the same level as either the upper or lower whorl of anthers. This condition, termed "semihomostyly," has been observed in *O. Dillenii* subsp. *filipes* and subsp. *Dillenii*, and in a species of *Biophytum* (Mayura Devi, 1966).[2]

According to Veldkamp (1971), the pollen is shed in the buds of some species of *Biophytum*. Evidently, some seemingly normal flower buds of certain *Oxalis* species do not open, but are autogamous and set fruit; this seems to occur mostly late in the growing season, at least in Massachusetts. Much reduced, truly cleistogamous flowers are produced in *O. Acetosella* and some other species (see FIGURE 1, c).

Several different genetic systems have been proposed to explain the inheritance of style length in the few species of *Oxalis* that have been studied in this respect (see discussion and table in Mulcahy). Two species that occur in our area, *O. Priceae* and *O. Dillenii* subsp. *filipes* (see Mulcahy and Ornduff, respectively), seem to have a system with two loci and two alleles at each locus. "Short" is dominant and has the generalized genotype of S__mm or S__M__. "Medium" is recessive to "Short" and its genotypes are ssMm or ssMM. "Long" is a double recessive, ssmm. Although much has been written about breeding systems of *Oxalis*, very few species have been examined in detail, and it may very well be that generalizations accepted now will have to be changed.

The family is of only slight economic importance. Several species of *Oxalis* are cultivated as ornamentals; some are especially well suited to the rock garden and alpine house. *Averrhoa Carambola* is cultivated commercially to some extent and in dooryards in southern Florida. The yellow to orange, deeply angled fruits, star-shaped in cross section and up

[2] Mayura Devi identifies the plants as *Biophytum sensitivum* DC., but Veldkamp (1971) says they certainly do not belong to this species.

to five inches long, vary greatly in degree of acidity from tree to tree. The fruits are eaten fresh, used in drinks, or made into jelly and jam. The flavor and odor are sometimes likened to quince, *Cydonia oblonga*. *Averrhoa Bilimbi*, the cucumber or pickle tree, which has rather cylindrical, extremely acid fruits that are used in drinks, jellies, pickles, and curries, is seldom grown in Florida. Leaves of *Oxalis* species are used in salads, but excess use should be avoided because of the presence of oxalic acid. *Oxalis Pes-caprae* and *O. corniculata* are known to accumulate lethal concentrations of soluble oxalates under certain conditions. *Oxalis tuberosa* Molina, oca, $2n = 14, 60, 63–64, 68–70$, is a major food crop in Andean South America, particularly in the area around Lake Titicaca. The tubers contain large amounts of oxalates and are treated in various ways, such as by submerging them in water for several weeks and then placing them in open areas, where they are exposed to freezing by night and drying by day. Several species of *Oxalis* sect. CORNICULATAE act as aecial hosts for the maize, sorghum, and andropogon rusts (see discussion in Eiten, 1963).

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1. **Oxalis** Linnaeus, Sp. Pl. 1: 433. 1753; Gen. Pl. ed. 5. 198. 1754.

Perennial or annual, caulescent or acaulescent herbs [rarely undershrubs], sometimes with bulbs (often with contractile roots below) or rhizomes [or tubers]. Indumentum of septate and/or nonseptate trichomes that vary in length, shape, density, and distribution. White or sometimes orange, red, or black calcium oxalate deposits frequent on sepal apices, bracts, bulb scales, and leaves, infrequent on petal tips and gynoecia. Leaves basal and/or cauline (often in apical clusters), trifoliolate [to many-foliolate or rarely unifoliolate], often heteroblastic, long petiolate [to nearly sessile], the petiole with a persistent, basal articulation; leaflets often with reddish or purple markings, mostly obcordate or emarginate [or entire or deeply divided], nearly sessile, with a basal pulvinus, folding and drooping at night; stipules absent or small, paired, and adnate to the basal articulation of the petiole. Inflorescences from basal rosettes or axillary, the flowers solitary or in few- to many-flowered cymes or modified cymes, such as pseudoumbels. Flowers tristylous, distylous, homostylous, semihomostylous, or quasihomostylous. Petals shortly clawed below, yellow, orange, white, or violet [to red], the base of the blade often with nectar guides, withering after expansion, sometimes forming a calyptra on the fruit. Filaments monadelphous below, alternate ones longer and sometimes with an abaxial appendage. Carpels 5, connate adaxially, free laterally; styles free, erect in long- and midstyled flowers, abaxially curved and projecting between the filaments in short-styled flowers; stigmas punctate, capitate, or penicillate, faintly to prominently 2-lobed. Capsules globose, oblate, or broadly to narrowly cylindric, often 5-angled or star-shaped in cross section, dehiscing by loculicidal slits (often appearing septicidal), the valves persistent. Seeds in the capsule each enclosed by a turgid, translucent aril that turns inside out explosively; seed flattened, elliptic with pointed ends, often with transverse and/or longitudinal ridges; endosperm present [or absent]. (Including *Acetosella* Kuntze, 1891, not Fourreau, 1869; *Bolboxalis* Small; *Ionoxalis* Small; and *Xanthoxalis* Small.) TYPE SPECIES: *O. Acetosella* L.;

see J. K. Small, N. Am. Fl. **25**(1): 25. 1907. (Name from Greek, *oxys*, acid, in reference to the supposed medicinal use of these plants; see Linnaeus, Phil. Bot. ed. 1. 184. 1751. This name was used by the ancient Greeks for *Rumex Acetosella* and was first applied to this genus by Linnaeus.) — WOOD-SORREL.

Estimates of the number of species range from 300 to more than 800, the latter probably being closer to the actual number. The genus is cosmopolitan but is most diverse in South Africa and South America, and, to a lesser degree, in Central America and Mexico; relatively few species are indigenous to North America and Eurasia. In the world-wide treatment of the family for *Das Pflanzenreich*, Knuth recognized 791 species of *Oxalis*, grouping them primarily on variations in stem structure into 37 mostly unnatural sections and numerous subsections and series. Since that time, important taxonomic treatments include Salter's study of the genus in South Africa, Eiten's synopsis of sect. CORNICULATAE, and Denton's monograph of the North American species of sect. IONOXALIS. Currently, Dr. Alicia Lourteig is in the midst of a major world-wide revision of the genus (exclusive of the South African species) with particular emphasis on the poorly understood South American species.

Small (Fl. Southeast. U. S. 1903; N. Am. Fl. 1907) placed the North American species of *Oxalis* in eight genera. His scheme has not been adopted generally, and, in view of the variation that occurs within *Oxalis* on a world-wide basis, it seems best to recognize only one inclusive genus.

Section OXALIS (sect. *Acetosellae* Knuth) (flowers solitary from elongated, underground rhizomes) is represented in our area by *Oxalis Acetosella* subsp. *montana* (Raf.) Hultén ex D. Löve (*O. montana* Raf.), $2n = 22$, which occurs in rich, moist woods from Newfoundland and eastern Quebec to Manitoba and Saskatchewan, south to Pennsylvania, eastern Ohio, Kentucky, Michigan, Wisconsin, and Minnesota, and in the mountains of the Virginias, North Carolina, and Georgia. The attractive flowers of this plant have white or light pink petals marked with darker pink veins and basal yellow spots. Individuals with solid dark pink or purplish flowers can be referred to f. *rhodantha* Fern. In the chasmogamous flowers of this subspecies, the stigmas are either considerably above the upper whorl of anthers or slightly below them (see family discussion). Reduced, cleistogamous flowers are also produced, particularly late in the growing season. Young (1968) notes that the cleistogamous flowers of the European populations are apetalous, but at least some of the cleistogamous flowers on North American plants have small petals (see FIGURE 1, c).

Oxalis Acetosella has a very broad distribution (see maps in Veldkamp, 1971, and Hultén). Subspecies *Acetosella* is Eurasian, occurring from Iceland, the British Isles, and Scandinavia, south to Spain, Italy, and Anatolia, and west to the Caucasus Mountains, China, Korea, Kamchatka, and Japan. Subspecies *Griffithii* (Edgew. & Hooker f.) Hara, $2n = 22$, is mostly of southern and western Asia, from northwestern India through China to Japan, Formosa, and the Philippine Islands. Related plants are

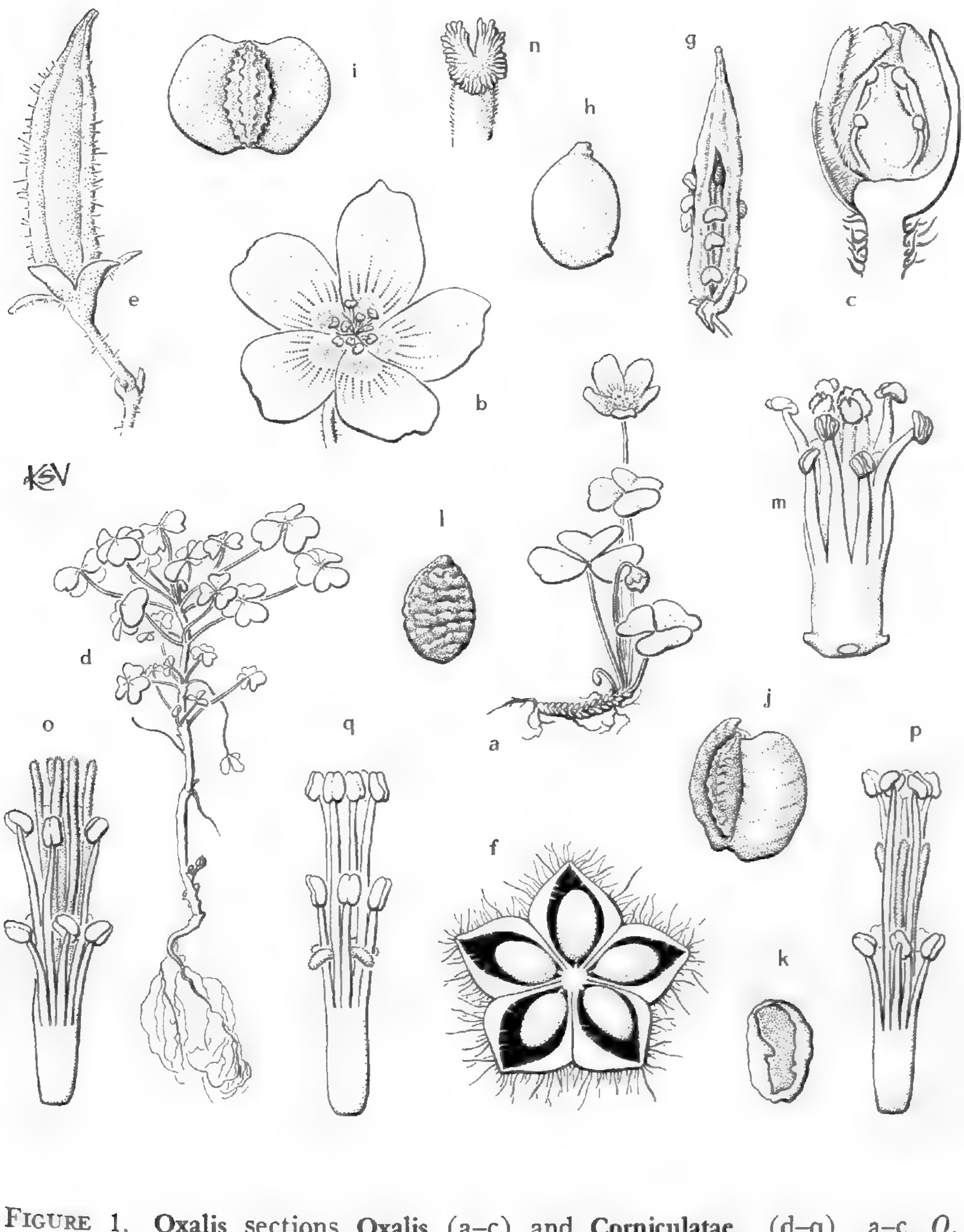

FIGURE 1. **Oxalis** sections **Oxalis** (a–c) and **Corniculatae** (d–q). a–c, *O. Acetosella* subsp. *montana*: a, plant with chasmogamous flower and immature fruit from cleistogamous flower — note persistent swollen leaf bases on rhizome, × ½; b, chasmogamous flower, veins of petals deep pink, basal spot yellow, × 2; c, cleistogamous flower in off-center vertical section, upper set of anthers touching stigmas, lower set of anthers sterile, × 12. d–l, *O. stricta*: d, habit, × ½; e, mature fruit before dehiscence, × 3; f, same in cross section, carpels free laterally, seeds enclosed by aril, dehiscence through loculicidal slits, × 12; g, capsule during dehiscence — note seeds and arils, × 3; h, seed enclosed by aril, × 12; i, j, two views of aril splitting away from seed, × 12; k, aril after eversion, × 12; l, seed, × 12. m, n, *O. Dillenii* subsp. *filipes*: m, androecium and gynoecium from quasi-homostylous flower, × 10; n, penicillate, 2-lobed stigma, × 25. o–q, *O. grandis*: androecium and gynoecium from long-styled, midstyled, and short-styled flowers, respectively, semidiagrammatic, × 6.

found in the United States from the Olympic Mountains of Washington to Monterey County, California; these are treated as either subsp. *oregana* (Nutt. ex Torrey & Gray) D. Löve or as a distinct species, *O. oregana* Nutt. ex Torrey & Gray. *Oxalis magellanica* Forster f., $2n = 10$, is a closely allied, Southern Hemisphere counterpart of *O. Acetosella* that is known from Andean South America (southern Peru to Patagonia), New Zealand, Tasmania, the Victorian Alps of southwestern Australia, and New Guinea. Veldkamp indicates that only long-styled flowers are found in both *O. Acetosella* subsp. *Griffithii* and *O. magellanica*.

Section IONOXALIS (Small) Knuth (acaulescent, the flowering peduncles arising from scaly bulbs, the petals violet, purple, pink, or white) is composed of about 50 species of the New World, with the greatest diversity in Mexico and South America. Only *Oxalis violacea* L. (*Ionoxalis violacea* (L.) Small), $2n = 28$, is indigenous in eastern North America, where it occurs in a variety of habitats, including woods, pinelands, and prairies, from southern New England to Minnesota and South Dakota, south to Georgia, upper Florida, Louisiana, and Texas. It occurs disjunctly in Arizona and New Mexico. The plant is easily recognized by its dark pink, violet, or purple (white in f. *albida* Fassett) flowers in several-flowered, simple umbels on unbranched peduncles that overtop the leaves, by the oblate capsules, and by the moderate-sized leaflets (8–15 mm. long and 10–23 mm. broad) with reddish markings above or a solid reddish cast below and with calcium oxalate deposits only at the apical notch. The leaflets are partly folded most of the time, seldom expanding fully. The plants are usually glabrous, but in the region from Arkansas, Missouri, Mississippi, and Alabama, north to Ohio, New York, and Vermont, some individuals have multicellular, often glandular, trichomes on the petioles; these may be called var. *trichophora* Fassett. *Oxalis violacea* flowers in the spring and often again in late fall following autumnal rains. The flowers are distylous with long- and short-styled forms.

Several other species of this section are cultivated in the southeastern United States, and a few have become established. *Oxalis corymbosa* DC. (including *O. martiana* Zucc., *Ionoxalis martiana* (Zucc.) Small), $2n = 24, 28, 30$, has flowers in irregularly branched cymes, nonseptate trichomes on the petioles and peduncles, large leaflets (27 to 46 mm. long and 34 to 63 mm. wide) that are mostly fully expanded during the day, randomly distributed calcium oxalate deposits in the leaflets, and usually abundant bulblets. A native of South America, it is found in scattered localities from South Carolina to Florida and Texas; it is also widespread in the West Indies. According to Denton, this species does not set seed in North America (although Small describes capsules and seeds), and Veldkamp (1971) reports the same situation in Malesia. Small recorded *O. intermedia* A. Rich. (as *Ionoxalis intermedia* (A. Rich.) Small) from hammocks in southern peninsular Florida, and Denton noted a variant allied to this species from Sarasota, Florida. *Oxalis intermedia* is readily recognized by its obdeltoid leaflets.

Evidently escaped from cultivation in the Carolinas and perhaps else-

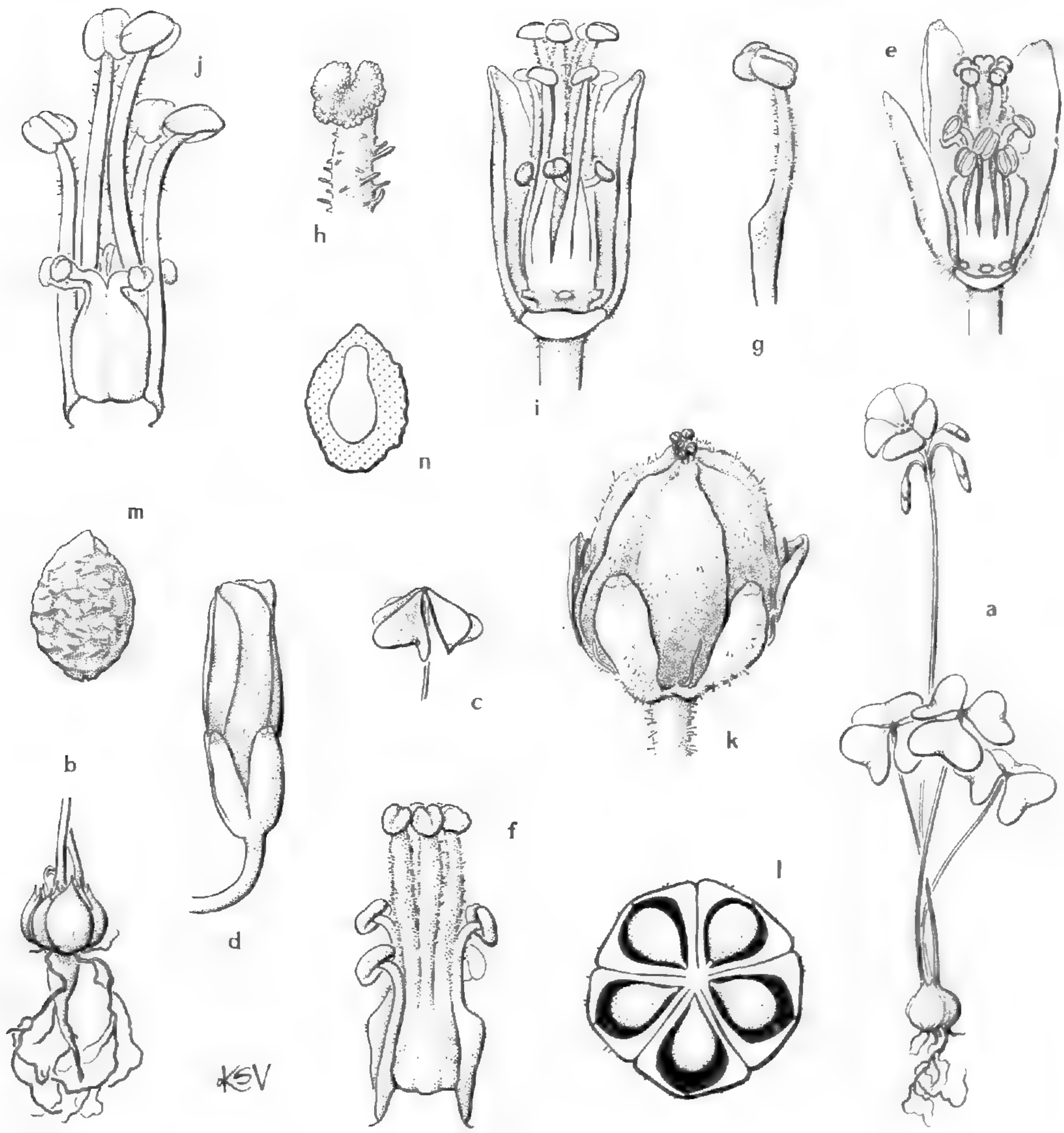

FIGURE 2. **Oxalis** section **Ionoxalis.** a–n, *O. violacea*: a, flowering plant, × ½; b, scaly bulb with contractile taproot below, × 1; c, leaflets in folded position — note oxalate deposits at apex of notch, × ½; d, flower bud, petals contorted, × 3; e, long-styled flower, petals (scars indicated by open circles) and 2 sepals removed — note abaxial appendages on longer filaments, × 6; f, androecium (4 stamens removed) and gynoecium from long-styled flower, × 10; g, longer stamen from long-styled flower, × 12; h, tip of style and stigma from long-styled flower, × 25; i, short-styled flower, petals and 2 sepals removed, × 6; j, androecium and gynoecium from short-styled flower, × 10; k, nearly mature capsule from short-styled flower, × 5; l, same in cross section, placentation axile, dehiscence through loculicidal slit, carpels connate only adaxially, seeds enclosed by aril, × 6; m, seed with aril removed, × 12; n, seed in vertical section, endosperm even-stippled, embryo unshaded, × 12.

where are plants superficially rather similar to *O. corymbosa*, but which have fleshy, more or less cylindrical rootstocks (not scaly bulbs) and densely pubescent pedicels, calyx lobes, and petals. These plants are known in the horticultural trade as *O. rubra* St.-Hil., $2n = 42$, a native of South America, but their identity is suspect. Knuth placed *O. rubra* in his sect. ARTICULATAE.

Oxalis Pes-caprae L. (*O. cernua* Thunb., *Bolboxalis cernua* (Thunb.) Small), $2n = 28$, indigenous to South Africa, is cultivated in our area and, according to Small, has perhaps escaped at least in northern Florida. This species has showy yellow flowers in several-flowered, leafless cymes that exceed the rosette of basal leaves and has a caudex at the apex of a long contractile taproot. It reproduces mostly by bulbils.

Section CORNICULATAE DC. (flowers yellow, stems creeping to erect, bulbs absent) is mostly of temperate North America. The nomenclature of some of the species is particularly confusing, since several specific names have been applied differently. Small placed the North American species of this section in his segregate genus *Xanthoxalis*. The section was revised by Eiten (published in an abbreviated form), and his nomenclature and classification, which differ substantially from previous accounts, are used here, since both have been widely adopted. Dr. Lourteig's studies may change the number of taxa, the ranks at which they are recognized, and some of their names. Eiten recognized 14 species and eight subspecies; five species are restricted to South America, three mostly to eastern North America, two to the Greater Antilles, two to western North America, one to eastern North America and eastern Asia (introduced elsewhere), and one is a cosmopolitan weed.

Eiten divided this section into two subsections, the first of which is subsect. CORNICULATAE. (According to Article 22 of the 1972 edition of the International Code of Botanical Nomenclature, this becomes subsect. BOREALES Knuth.) In species of this group, the stems are usually several from the crown of a taproot (any horizontal stems are above ground); septate trichomes are absent from stems, petioles, and pedicels (but sometimes present on capsules); the inflorescences are umbellate; and the pedicels are usually strongly reflexed in fruit with the capsules erect. *Oxalis corniculata* L. (*Xanthoxalis corniculata* (L.) Small, *O. repens* Thunb., *X. Langloisii* Small), $2n = 24, 36$ (38?), 42, ca. 46, 48, is a pantropical weed with creeping stems rooting at the nodes, broadly auriculate stipules, and small, mostly homostylous flowers. This species, evidently native to the Old World and extremely variable in Australasia, is a troublesome lawn weed in warm regions and is frequently encountered as a weed in greenhouses farther north. Several varieties have been described, but Eiten recognized only one polymorphic species.

Another group of plants of this subsection, with erect flowering stems that do not root at the nodes, is taxonomically and nomenclaturally difficult. Eiten grouped them into two species and five subspecies. Plants with small, mostly homostylous flowers (petals less than 13 mm. long)

belong to *Oxalis Dillenii* Jacquin, while those with larger strongly tristylous flowers (petals mostly longer than 15 mm.) belong to *O. Priceae* Small. Two subspecies of *O. Dillenii* based on differences in the indumentum of the capsules were recognized by Eiten: subsp. *Dillenii* (*O. stricta* auct., not L. [following Eiten's lectotypification], *O. florida* Salisb., *O. Lyonii* Pursh, *O. Navieri* Jordan, *O. recurva* var. *floridana* Wiegand, *O. Dillenii* var. *radicans* Shinners), $2n = 18, 20, 22, 20–24$, which is common nearly throughout eastern North America (locally naturalized in Europe) and subsp. *filipes* (Small) Eiten (*O. filipes* Small, *O. Brittoniae* Small, *O. florida* var. *strigosifolia* Wiegand), $2n = 16$, which occurs from Florida to Louisiana, north to Connecticut, Tennessee, and Missouri. *Oxalis Priceae* (*O. recurva* Elliott, nom. dub. according to Eiten) is confined to the southeastern United States; Eiten recognized three subspecies that differ in the pubescence of the stems and pedicels. Subspecies *Priceae* (*O. cespitosa* Raf., not *O. caespitosa* St.-Hil., *O. hirsuticaulis* Small) occurs in Kentucky, Tennessee, Mississippi, Alabama, and Georgia; subsp. *colorea* (Small) Eiten (*Xanthoxalis colorea* Small) occurs along the coast from North Carolina to Florida and Louisiana; and subsp. *texana* (Small) Eiten (*X. texana* Small, *O. recurva* var. *texana* (Small) Wiegand) occurs in eastern Texas and Louisiana and in scattered localities on the Coastal Plain to northern Florida and Georgia.

Subsection STRICTAE Eiten of sect. CORNICULATAE is characterized by the stems arising singly from underground rhizomes; the presence of septate trichomes on stems, petioles, and pedicels; cymose inflorescences; and pedicels that are not reflexed in fruit. It includes *Oxalis stricta* L., $2n = 18, 24, 18–24$, *O. grandis* Small, and *O. Suksdorfii* Trelease, the last mostly confined to western Oregon and adjacent Washington and California. Plants from eastern North America (Newfoundland to North Dakota and British Columbia, south to Florida, Arkansas, Oklahoma, New Mexico, and Arizona) and from eastern Asia (extensively naturalized in Europe) with small, mostly homostylous flowers (the petals usually less than 1 cm. long) and with leaves lacking colored margins were called *O. stricta* L. by Eiten. These plants have had a tortuous nomenclatural history, having been called *O. corniculata* by Gray, *Xanthoxalis cymosa*, *X. Bushii*, and *X. rufa* by Small, and *O. europaea* by authors of numerous twentieth-century manuals and floras; the eastern Asiatic plants are usually known as *O. fontana* Bunge.

The name "*Oxalis stricta* L." was first lectotypified by Robinson and was applied by him to those plants Eiten called *O. Dillenii*. Eiten rejected Robinson's typification and used the name for the plants native to eastern North America and eastern Asia. Dr. Lourteig has indicated in conversation that she thinks Robinson's typification is correct, that the name *O. stricta* should be applied to those plants Eiten called *O. Dillenii*, and that *O. fontana* is the correct name for the plants Eiten called *O. stricta*.

Oxalis grandis Small is a very attractive species with large, red- or purple-margined leaflets and showy, strongly tristylous flowers. These

plants occur in rich woods, usually in the mountains, rarely on the Upper Piedmont, from Pennsylvania to southern Illinois, south to Georgia, Alabama, Tennessee, and Kentucky.

The carpels of many species of *Oxalis* are connate only toward the floral axis, with most of the lateral walls being free and merely closely juxtapositioned (see FIGURES 1, f, and 2, l). To the casual observer, it appears that the capsules are septicidal because of the folds (the "episeptal rimae" of Veldkamp) between the carpels. However, dehiscence takes place through a loculicidal slit on the abaxial side of each carpel. At maturity, the slits open slightly, and the abaxial carpel walls are thin and flaplike. The seeds are enclosed by a smooth, turgid aril, which splits suddenly along an abaxial suture and turns inside out. This motion ejects the seed, and often the aril, through the slit to a considerable distance from the parent plant. The ejection of one seed sets off a chain reaction that results in the dispersal of most seeds in one capsule in a very short time. The seeds of some species, such as *O. corniculata*, are sticky and adhere to objects on which they land.

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GAULTHERIA SWARTZII, NOM. NOV. AND THE COMBINATIONS IN RAEUSCHEL'S NOMENCLATOR

RICHARD A. HOWARD

TWO NAMES have been used over the years for a plant of the mountains of Guadeloupe. Swartz described the species briefly but validly as *Epigaea cordifolia* (Prodr. 73. 1788), citing its locality as Guadeloupe. Four years later Richard (Actes Soc. Hist. Nat. Paris **1**: 109. 1792) described a plant as *Gaultheria sphagnicola.* When published, however, this name was illegitimate, being superfluous, for Richard also cited *E. cordifolia* Sw. In 1797 Raeuschel published the binomial *Gaultheria cordifolia* (Nomencl. ed. 3. 124. 1797), which Urban (Symb. Ant. **3**: 330. 1902) and Airy-Shaw (Kew Bull. **1940**: 310. 1940) apparently regarded as a new combination. Assuming the basionym to be *Epigaea cordifolia* Sw., Small (N. Am. Fl. **29**: 75. 1914) considered the Raeuschel name to be a *nomen nudum* and used the binomial *Gaultheria sphagnicola* Rich., as did Camp (Bull. Torrey Bot. Club **66**: 19. 1939). Thus for *Gaultheria* two invalid names occur in recent literature and a new name is needed for this species. I propose **Gaultheria swartzii** nom. nov.

Raeuschel's binomial *Gaultheria cordifolia* is accompanied only by the name Cayenne and the classic symbol for a woody plant. There is no reference to Swartz's publication in the introduction. The binomial is not a combination and is a *nomen nudum.* However, the treatment of names in Raeuschel's *Nomenclator botanicus* has been inconsistent even in recent years. Steyermark's massive treatment of the Rubiaceae in Maguire *et al.*, *Botany of the Guayana Highlands*, Pt. *IX* (Mem. N. Y. Bot. Gard. **23**: 227–832. 1972) illustrates this. In treating a comparable problem in *Psychotria guianensis* Raeuschel (*loc. cit.* 457), Steyermark concluded that most botanists consulted agreed that the binomial was a *nomen nudum* without either direct or indirect reference to any previously published name, and therefore it was illegitimate. However, for *Psychotria officinalis* (*loc. cit.* 614) Steyermark noted W. T. Stearn's suggestion that a combination be attributed not to Raeuschel (1797) but to Sandwith (1931), although Sandwith did not discuss the problem (Kew Bull. **1931**: 473. 1931). Elsewhere in his publication Steyermark accepted Raeuschel's combinations for *Psychotria paniculata* (Aubl.) Raeusch. (*loc. cit.* 500) and *Psychotria racemosa* (Aubl.) Raeusch. (*loc. cit.* 542), even though these names carried no direct or indirect reference to the Aublet binomial. For these as well as for many other combinations attributed to Raeuschel a search must be made for a later valid combination or an alternative name.

Gaultheria swartzii Howard, nom. nov.

Brossaea coccinea L. Sp. Pl. 1190. 1753; not *Gaultheria coccinea* H.B.K. (1819) or *Gaultheria coccinea* (L.) Urb. 1902.
Epigaea cordifolia Sw. Prodr. 73. 1788; not *Gaultheria cordifolia* H.B.K.
Gaultheria sphagnicola Rich. Actes Soc. Hist. Nat. Paris **1**: 109. 1792; *nomen illegit.*
Brossaea anastomosans Griseb. Fl. Brit. W. Ind. 142. 1859; *nomen illegit.* and also not *Gaultheria anastomosans* (L.) H.B.K. (1819).

Brossaea coccinea L. is based on Plumier, Gen. 5, *t. 17*. Urban proposed the combination *Gaultheria coccinea* (L.) Urb. (Symb. Ant. 3: 330. 1902), at which time he added the reference Plumier, Plantarum Americanarum ed. Burm. *t. 64, f. 2*. Small (N. Am. Fl. **29**: 75. 1902) lists *Brossaea coccinea* L. in the synonymy of *Gaultheria sphagnicola* with a question and the Urban name *Gaultheria coccinea* "in part." Airy-Shaw (Kew Bull. **1940**: 310. 1940) assigned *Gaultheria coccinea* (L.) Urb. to the synonymy of *Gaultheria cordifolia* (Sw.) Raeusch. No Plumier material has been seen, and it is possible the plant in question may have been seen in Guadeloupe and not in Hispaniola. In any case, *Gaultheria coccinea* H.B.K. (Nov. Gen. Sp. 3: 284. 1819) from Venezuela precludes any use of the Linnaean basionym.

Brossaea anastomosans Griseb. (Fl. Brit. W. Ind. 142. 1859) is a combination for *Andromeda anastomosans* L., although Grisebach also cited in synonymy *Epigaea cordifolia* Sw. *Gaultheria anastomosans* (L.) H.B.K. (Nov. Gen. Sp. 3: 283. 1819) has the same basionym. Grisebach's general description does not permit typification by any of the synonyms cited.

To select a lectotype of *Gaultheria swartzii* is not an easy matter. In the original publication, Swartz (Prodr. 73. 1788) indicated the species to be from Guadeloupe. In the subsequent treatment, Swartz (Fl. Ind. Occ. 2: 842. 1800) cited a Du Ponthieu collection from Guadeloupe and one by Le Blond from Cayenne. I have seen neither collection. Richard (Actes Soc. Hist. Nat. Paris 1: 109. 1792) did not cite a specimen, but in the Richard herbarium (P) there is a specimen labeled "type" and named *Gaultheria sphagnicola* from the Soufrière of Guadeloupe. The label notes, however, that the plant also occurs in Martinique on Monte Calvo. If the Du Ponthieu specimen were located, this logically would be the lectotype.

Small (N. Am. Fl. **29**: 75. 1914) indicated the range of this species to be Guadeloupe, Trinidad, and northern South America. A. De Candolle (DC. Prodr. 7: 592. 1838), under *Epigaea cordifolia,* cited a collection (*Sieber 346*) from Trinidad. Sieber's collections often have unreliable data, and this specimen, which I have not seen, may be from Guadeloupe or Martinique. The species has not been collected in Trinidad according to Hill & Burtt (Fl. Trin. & Tobago 2(2): 114. 1940). The Le Blond collection, also cited by De Candolle from "Cayennae seu Guianae Gallicae," should be re-examined for verification that it is the present species and not one of the many from South America. Modern collections are on

hand from Guadeloupe and Martinique, but only from elevations of 1200 to 1467 m. in altitude. The species might also be expected in Dominica.

Camp (Bull. Torrey Bot. Club **66**: 19. 1939) noted that *Gaultheria sphagnicola* (= *G. swartzii*) and *G. domingensis* are very similar. Small (N. Am. Fl. **29**: 74. 1914) distinguished the two species on the basis of the glabrous corolla with leaf blades manifestly toothed in *G. sphagnicola* and the pubescent corolla with leaf blades obscurely toothed in *G. domingensis*. Recent collections from both areas substantiate Camp's observation that a pubescence does occur on the corollas of plants from the Lesser Antilles, although none matches the abundance of hairs on material from Hispaniola. The leaf blade differences are obvious and of specific value. Material of *G. swartzii* from Guadeloupe and Martinique has short blunt teeth, each terminating in a fairly stout seta. Hispaniolan material has leaves with the margin inrolled or thickened but without teeth. Large setae are marginal without noticeable toothlike bases.

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ADDITIONAL NOTES ON THE GENUS FLINDERSIA (RUTACEAE) *

T. G. Hartley and B. P. M. Hyland

Since the publication of a revision of the genus *Flindersia* (Hartley, Jour. Arnold Arb. **50**: 481–526. 1969), a new species of the genus has been discovered in northern Queensland, and the first known flowering specimens of *F. unifoliolata* Hartley have been collected. A description of this new material is given below. Specimens cited as QRS are deposited at the herbarium of the Queensland Research Station, Forest Research Institute, Forestry and Timber Bureau, Atherton, Queensland. The remaining specimens cited are all deposited at the Herbarium Australiense, C.S.I.R.O., Canberra (CANB).

Flindersia brassii Hartley & Hyland, sp. nov.

Arbor usque 30 m. alta; ramulis, foliis et inflorescentiis glabris vel puberulis vel subtiliter adpresse pubescentibus, pilis simplicibus et basifixis vel irregulariter ramosis et centrifixis. Folia opposita vel subopposita, paripinnata vel imparipinnata, 2–4-juga, 7–18 cm. longa; rhachidi basin versus puberula, aliter glabra; petiolulis foliolorum lateralium 2–6 mm. longis, rhachidi ad apicem extensa 0.7–1.6 cm. longa foliolum terminale ferente; laminis subcoriaceis, consperse pellucido-punctatis, subtus costa saepe sparse puberulis, supra glabris, ellipticis vel elliptico-oblongis, aequilateribus vel parum inaequilateribus, 4–8 cm. longis, 1.5–3.7 cm. latis, basi acuta vel cuneata plerumque parum inaequilatera, venis primariis utrinsecus costa 8–11, apice obtuso vel rotundato. Inflorescentia terminalis, usque 15 cm. longa plerumque fere lata quam longa; axibus et ramulis dense puberulis vel subtiliter adpresse pubescentibus. Flores bisexuales, ca. 4.5 mm. longi; pedicellis 2–3 mm. longis; sepalis puberulis, ciliolatis, late ovatis vel suborbicularibus, 1–1.5 mm. longis; petalis cremeis, in sicco pallide brunneis, abaxialiter dense adpresse pubescentibus, adaxialiter tomentulosis, ellipticis, 3.5–4 mm. longis, basi subito contractis; staminibus declinatis, ca. 2.5 mm. longis, filamentis glabris, antheris subdorsifixis, ca. 0.5 mm. longis, mucronulatis; staminodiis ca. 0.7 mm. longis; disco ca. 1 mm. alto; gynoecio ca. 1.3 mm. alto, ca. 1.5 mm. lato, ovulis 1 in quoque latere placentarum. Capsula maturite secedens in valvas distinctas, elliptico-oblonga, 7–11 cm. longa; exocarpio in sicco pallide brunneo, subtiliter adpresse pubescenti, muricato, processibus dense aggregatis, inaequilongis, usque 4.5 mm. longis; endocarpio in sicco luteo. Semina 1 in quoque latere dissepimentorum, utrinque alata, 5.5–7 cm. longa; hypocotylo terminali. Holotypus: *Hyland 2770* (CANB). Figure 1.

* This is the seventh in a series of papers on the Rutaceae of Malesia and Australasia.

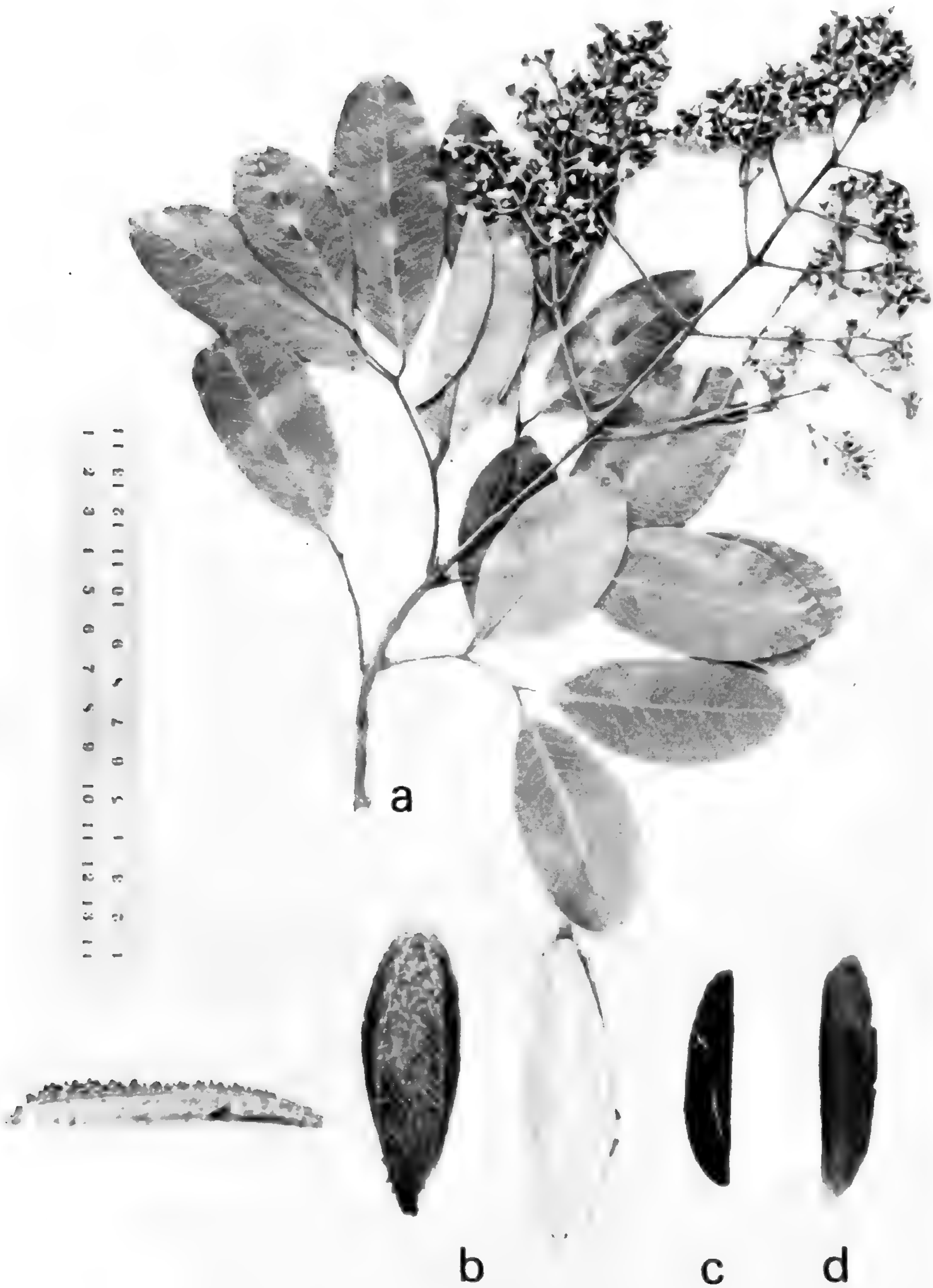

FIGURE 1. **Flindersia brassii** Hartley & Hyland. Photograph of the holotype (CANB): a, flowering branchlet; b, three of the valves of the fruit in lateral, abaxial, and adaxial views; c, dissepiment of the fruit; d, seed.

FIELD CHARACTERS. Medium to rather large tree 13–30 m. tall, 20–40 cm. d.b.h., without conspicuous buttresses. Bark thin (less than 2.5 cm. thick), bitter when chewed, pale brown, smoothish or minutely tessellated, lenticels vertically elongated, often inconspicuous; subrhytidome layer red, pink, or green; outer blaze pink to red, granular to fibrous; inner blaze red to cream, fibrous. Heartwood pale pinkish brown, with odor like that of scented maple (*Flindersia laevicarpa* White & Francis var. *laevicarpa*).

SEEDLING. (Description based on dried specimen of a 4-month-old plant grown from seed of *Hyland 2737*.) Plant about 25 cm. high, stem with five nodes above the cotyledons, youngest growth and petioles sparsely to densely puberulent with simple, basifixed trichomes. Cotyledons chlorophyllous, chartaceous, oblong, about 2.5 cm. long, base sagittate, apex obtuse. Leaves opposite at the first node (i.e., the first above the cotyledons), otherwise alternate; simple at the first four nodes, imparipinnate and unijugate at the fifth node. Petioles of simple leaves 0.3–2 cm. long (gradually increasing in length from the first to the fourth node). Blades of simple leaves subcoriaceous, broadly elliptic, entire, equal-sided, 4.5–8.5 cm. long (also gradually increasing in length from the first to the fourth node), base acute, main veins (in the largest leaf) 8 on each side of the midrib, apex obtuse. Imparipinnate leaf immature, 4 cm. long.

ECOLOGY. Dry, rocky rain forest, 60 to 360 meters. Associated species: *Podocarpus neriifolius*, *Licuala muelleri*, *Grevillea pinnatifida*, *Xanthophyllum octandrum*, *Halfordia kendack*, *Quassia bidwillii*, *Vavaea amicorum*, *Euroschinus falcatus*, *Eugenia* (*Syzygium*) *cormiflora* vel aff., *Metrosideros tetrapetala*, *Rhodamnia blairiana*, *Vitex acuminata*, and *Antirhea tenuiflora*.

Queensland. COOK DISTRICT: Cape York Peninsula, Upper Claudie River, Iron Range, *Hyland 2734* (CANB, QRS), *2735* (CANB, QRS), *2736* (CANB, QRS), *2737* (QRS), *2738* (CANB, QRS), *2740* (QRS), *2743* (QRS), *2770* (CANB, holotype; QRS, isotype), *6663* (CANB, QRS), *Irvine 248* (CANB, QRS).

This species is named in honor of Leonard J. Brass (1900–1971), one of the outstanding plant explorers of the Australasian region.

Flindersia brassii is related to *F. fournieri* Panch. & Sebert, an endemic to New Caledonia; *F. laevicarpa* White & Francis, with two varieties, one endemic to northern Queensland and one restricted to New Guinea and to Misool Island; and *F. brayleyana* F. Muell., an endemic of northern Queensland. It shares with these species the characteristic of a terminal hypocotyl in the embryo. This is a unique (and apparently primitive) feature, the hypocotyl being lateral in the embryos of the remaining species of the genus. Other similarities and differences between these four species are summarized in TABLE I.

In having abruptly narrowed petals and muricate capsules, *Flindersia*

TABLE 1. **Characteristics of Flindersia brassii and related species.**

	F. brassii	F. fournieri	F. laevicarpa	F. brayleyana
TRICHOMES	simple and basifixed or irregularly branched and centrifixed	simple and basifixed	simple and basifixed	simple and basifixed
LEAVES	opposite or subopposite; imparipinnate or paripinnate; 7–18 cm. long	alternate or (occasional leaves) opposite or subopposite; paripinnate; 6–13 cm. long	opposite; paripinnate; 6–30 cm. long	opposite or subopposite; paripinnate; 27–45(–75) cm. long
PETIOLULES OF LATERAL LEAFLETS	2–6 mm. long	4–9 mm. long	2–13 mm. long	10–28 mm. long
PETALS	abruptly narrowed at the base	abruptly narrowed at the base	gradually narrowed at the base	gradually narrowed at the base
STAMINAL FILAMENTS	glabrous	sparsely to rather densely villous	glabrous to densely pubescent	villous subapically
OVULES	1 on each side of the placentae	2 on each side of the placentae (one of each pair is smaller and apparently aborts)	1 or 2 on each side of the placentae (where there are two, one is smaller and apparently aborts)	1 on each side of the placentae
CAPSULE	7–11 cm. long	4–4.7 cm. long	2.9–5.2 cm. long	6–10 cm. long
EXOCARP	finely appressed-pubescent; muricate	glabrous; muricate	glabrous; almost smooth to bluntly short-muricate	glabrous; almost smooth
ENDOCARP	yellow	yellow-brown to brown	pale brown and sometimes flecked with orange	cream to reddish brown
SEEDS	1 on each side of the dissepiments; winged at both ends	1 on each side of the dissepiments; winged at both ends	1 on each side of the dissepiments; winged at both ends	1 on each side of the dissepiments; winged at both ends

brassii appears to be most closely allied to *F. fournieri*. This close relationship indicates that the New Caledonian species is of Australian ancestry, since the center of diversity of *Flindersia* is clearly in eastern Australia.

Flindersia unifoliolata Hartley, Jour. Arnold Arb. **50**: 498. 1969.

Inflorescences from the axils of the upper leaves and terminal, 5–7 cm. long and about one-half as wide, upper axes and branches puberulent to finely pubescent with simple trichomes. Flowers bisexual, about 4 mm. long; pedicels puberulent, obsolete to 0.5 mm. long; sepals 5, puberulent and ciliate, ovate, 1.2 mm. long; petals deep red, rather sparsely strigose abaxially, glabrous adaxially, elliptic, 3.5 mm. long; stamens declinate, 3.5 mm. long, filaments rather stiffly pubescent subapically, anthers dorsifixed, obtuse, 0.8 mm. long; staminodes about 1 mm. long; disc 0.5–0.7 mm. high; gynoecium about 1.5 mm. high and 1.1 mm. wide, ovules 2 on each side of the placentae.

Additional collection. **Queensland.** Cook District: Mt. Bellenden Ker, montane rain forest, 1550 m., *Hyland 6569* (canb, qrs).

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THE MAYACACEAE IN THE SOUTHEASTERN UNITED STATES [1]

JOHN W. THIERET

MAYACACEAE Kunth, Abh. Akad. Wiss. Berlin Phys. **1840**: 93. 1842, "Mayaceae," nom. cons.

(BOGMOSS FAMILY)

A monotypic family of herbaceous aquatic monocotyledons distinguished by "mosslike" habit; perfect, hypogynous, regular (actinomorphic) flowers with 2 perianth whorls; 3 stamens; unilocular gynoecium with three parietal placentae; loculicidal capsular fruit; and seeds with starchy endosperm, a minute apical embryo, and a "stopper" or "embryostegium" formed from the inner integument of the ovule.

Characteristic anatomical features cited by Tomlinson include the lack of hairs except in the leaf axils; the presence of longitudinal air canals in root, stem, and leaf segmented by transverse diaphragms of stellate cells; the absence of mechanical tissues, the reduced stelar tissues being sheathed in both stem and root by an endodermis (thickened in the stem); and the absence of secretory elements.

The Mayacaceae are of somewhat uncertain taxonomic position. Even their familial status has been questioned (Grisebach included them in the Xyridaceae). They share various features with one or more of several families: Centrolepidaceae, Commelinaceae, Eriocaulaceae, Rapateaceae, Restionaceae, and Xyridaceae. A convincing argument for closest relationship with Commelinaceae is presented by Hamann (1961). Tomlinson concluded that "it is probable that *Mayaca* originated from the same stock that has produced Eriocaulaceae, Commelinaceae, and Xyridaceae."

1. **Mayaca** Aublet, Hist. Pl. Guiane Franç. **1**: 42; **3**: *pl. 15*. 1775.

Simple or branched "mosslike" aquatic herbs with copiously leafy stems.

[1] Prepared for a generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of the National Science Foundation (Grant BMS74-21469, principal investigator, Carroll E. Wood, Jr.). This treatment follows the format established in the first paper in the series (Jour. Arnold Arb. **39**: 296–346, 1958). The area covered includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. References that I have not seen are marked with an asterisk.

I am indebted to Dr. Wood for his careful review of the manuscript and for other aid and to the staff of the Lloyd Library, Cincinnati, for help in bibliographic matters. The illustration was drawn by Karen S. Velmure, under the direction of Kenneth R. Robertson, from preserved material collected by J. D. Ray, C. E. Wood, Jr., C. E. Smith, Jr., and R. J. Eaton in Seminole County, Florida, and from a kodachrome taken by C. E. Smith, Jr. at the same time.

Transverse diaphragms in roots producing in dried specimens the appearance of cross-striations. Leaves alternate, spirally arranged, sessile, lanceolate or linear-lanceolate to filiform, 1-nerved, commonly notched at the apex. Inflorescence of solitary axillary flowers [or of terminal simple umbelliform clusters]. Flowers perfect, regular, hypogynous, with 2 perianth whorls, the pedicels short to long, each bracteate at its base, the bracts ("spathes" or "hypsophylls") broad, membranaceous, delicate, shorter than the leaves. Calyx persistent, of 3 distinct, ovate or ovate-lanceolate to lanceolate sepals. Corolla of 3 distinct, ovate to rotund, white to pink petals. Androecium of 3 distinct stamens, these opposite the sepals; filaments linear, slightly widened at the base; anthers basifixed, 2(?)- or 4-sporangiate, 2- [or 4-] loculate at anthesis, opening through an apical or subapical pore or slit [or through an apical tube or cup]; pollen 1-sulcate, tenui-exinous, elliptic to broadly ovate. Gynoecium syncarpous, 3-carpellate; [2] stigma undivided [or 3-lobed]; style 1, elongate, linear, persistent; ovary unilocular, with 3 parietal placentae; ovules 6–30, orthotropous. Fruit a 3-valved, loculicidal capsule; seeds ovoid or globose, reticulate-scrobiculate, with an apical "stopper" or "embryostegium," the endosperm starchy, the embryo minute and apical. TYPE SPECIES: *M. fluviatilis* Aublet. ("Aboriginal American name," according to Fernald; perhaps related to the Mayaca or Mahica region of Brazil, according to Lourteig, 1952.) — BOGMOSS.

A genus of four species (Lourteig, 1952), three of these in tropical and warm-temperate America and one (*M. Baumii* Gürke) in southern Africa (Angola, Zaïre, Zambia). One or two (?) species are found in our area: *M. fluviatilis* Aublet (including *M. Aubletii* Michx.?) occurs on the Coastal Plain of the southeastern United States (North Carolina to Florida, west to eastern Texas [3]), in the West Indies and Central America, and in South America, south to Bolivia, northeastern Argentina, and Uruguay. It grows submersed or floating in water or creeping on soil or moss mats at margins of ditches, streams, ponds, lakes, swamps, and bogs.

Lourteig, the most recent reviser of the genus, recognizes only 4 species, other workers as many as 10. Such differences in taxonomic opinion derive in part from the great phenotypic plasticity of the bogmosses in response to different environmental conditions.

Like many aquatic genera, *Mayaca* shows great variation between emersed and terrestrial forms. Submersed plants of *M. fluviatilis*, for ex-

[2] A specimen of *Mayaca* from Wayne Co., Georgia (*W. H. Duncan 7861*, GH) bears the statement "ovary usually 3 carpellate (occasionally 4 or 5 carpellate) with usually 3 (occasionally 4 or 5) parietal placentae." The occurrence of supernumerary flowers in *Mayaca* seems not to have been noted in literature.

[3] Reports of *Mayaca* from Virginia, dating back to Pursh, are ascribed by Fernald to misidentification of *Lycopodium inundatum* var. *Bigelovii*. Gleason's report of *Mayaca* from Ohio, for which I have been unable to locate a supporting specimen, may be based on similar confusion. Ulbrich's incidental mention of Kentucky in the range of *M. Aubletii* may safely be ignored, as may Muenscher's report of Pennsylvania in the range of this species.

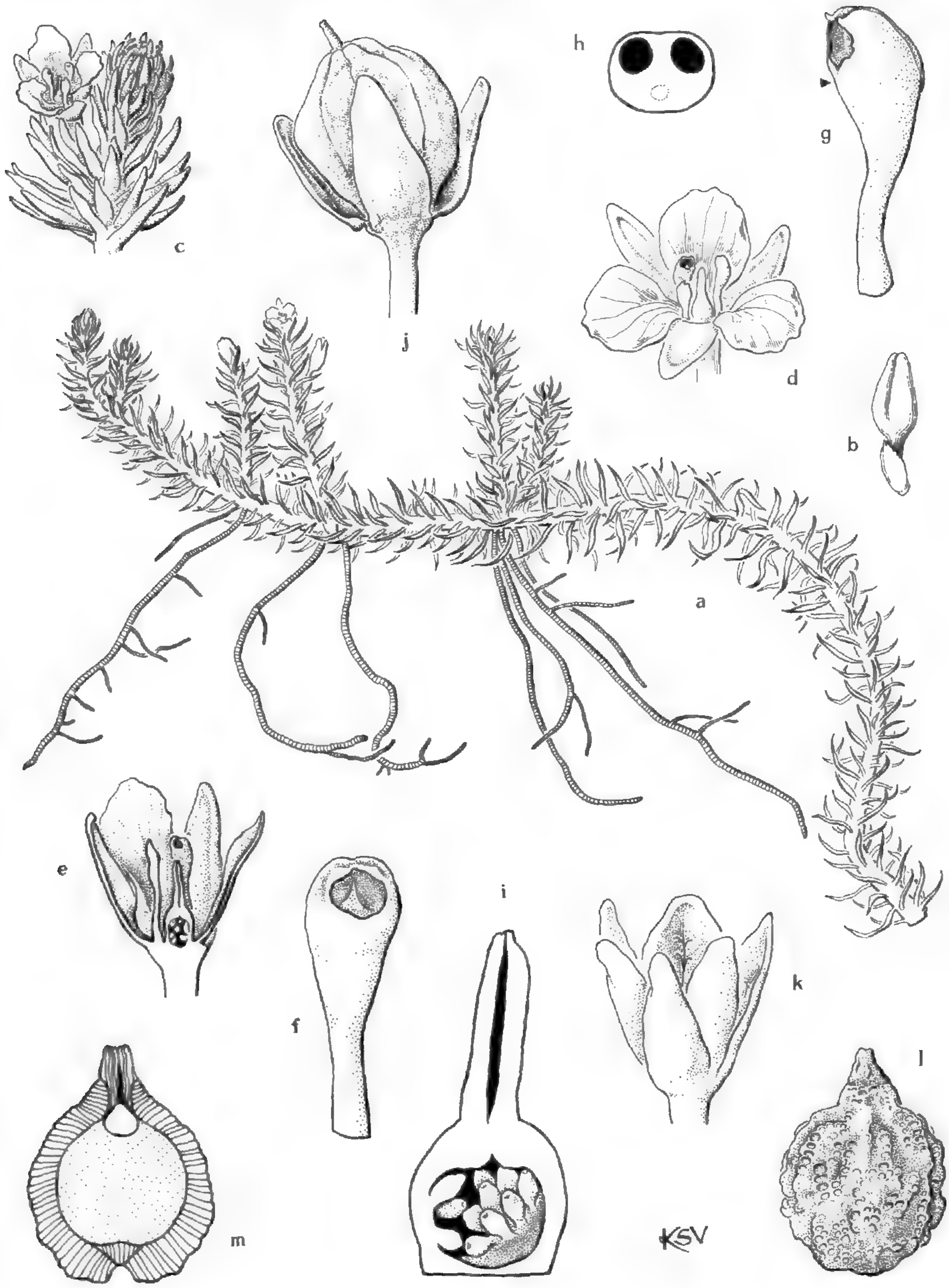

FIGURE 1. **Mayaca.** a–l, *M. fluviatilis* (*M. Aubletii*): a, apical part of flowering plant — note cross-striated roots, × 1; b, flower bud with subtending bract, × 3; c, tip of stem with open flower, × 3; d, flower, × 6; e, flower in vertical section, × 6; f, adaxial side of stamen — note dehiscence by apical pore, × 20; g, lateral view of stamen, × 20; h, cross section of stamen at level shown in "g," anther locules in black, vascular bundle in dots, × 25; i, gynoecium in vertical section, one parietal placenta in section, one uncut — note orthotropous ovules and stylar canal, × 20; j, nearly mature capsule, × 5; k, dehisced capsule — note remains of placentae on valve, × 6; l, seed, the micropyle up, × 25; m, seed in vertical section, outer integument hatched horizontally, inner integument forming "stopper" hatched vertically, endosperm evenly stippled, embryo unshaded, × 25.

ample, tend to have elongate stems with long-tapering, translucent, obviously spirally arranged leaves, while emersed plants generally have short stems with shorter, thicker, very closely imbricated leaves. Submersed forms have a thicker endodermis and a greater amount of aerenchyma than do emersed forms. *Mayaca* in the southeastern United States should be studied under controlled conditions to determine whether *M. fluviatilis* is the only representative of the genus there, as Lourteig concluded, or whether *M. Aubletii* is distinct, as claimed by some. The two taxa have been supposed to be distinguishable on the basis of weak, trailing, often submerged stems usually more than 40 cm. long in *M. fluviatilis* versus tufted or matted emersed stems only 2–20 cm. long in *M. Aubletii*; leaves 4–20 mm. long *vs.* 3–5 mm. long; pedicels shorter than the leaves *vs.* longer than the leaves; and capsules oblong-ellipsoid, nearly twice as long as broad, *vs.* subglobose or ovoid, nearly as broad as long. At least some of these characteristics are known to be environmentally influenced.

Of basic taxonomic value in *Mayaca* is the variation in the mode of dehiscence of the anthers, which open through an apical or subapical pore or slit (*M. fluviatilis*) or through an apical tube (*M. longipes, M. Sellowiana*) or cup (*M. Baumii*). A detailed developmental study of the stamens of *M. fluviatilis* is needed to determine whether the anthers are indeed 2-sporangiate and thus different from the usual 4-sporangiate condition in *Mayaca*, a claim made by Horn af Rantzien but denied by Lourteig (1952). Kenneth R. Robertson, in a series of freehand sections made for FIGURE 1, found "no evidence of four locules" (C. E. Wood, *in litt.*). The Mayacaceae are unknown cytologically and embryologically.

The broadly ovate bract subtending each pedicel splits longitudinally into halves when it is still relatively young, often even before the pedicel elongates fully. Literature reports of the pedicels of *Mayaca* being *bi*bracteate at the base derive from misinterpretation.

Pollination mechanisms in *Mayaca* have been little investigated. Uphof (1933) noted no insect visitors to the flowers of *M. fluviatilis* in Florida and suggested the possibility of anemophily. He reported fruit development both from aërial and from submersed cleistogamous flowers.

The seeds of *Mayaca* are characterized by an "embryostegium" (or "stopper") at their micropylar end (FIGURE 1, k–l). This structure, just distal to the embryo, is apparently developed from the inner integument, the growth of which exceeds that of the outer. The cells of the "stopper" are thinner walled than those of the testa, which is formed from the outer integument. Hamann (1961) suggests that disintegration of the "stopper" may provide a canal for emergence of the seedling.

The seeds are dispersed, so far as is known, by water. In one experiment (Ludwig), seeds of *M. fluviatilis* germinated promptly in water after six weeks of drying, but seeds kept submerged had not begun to germinate even after twelve weeks.

Mayaca fluviatilis and perhaps other species of the genus fare poorly in competition with other plants.

Mayaca may rarely be used as an aquarium plant. Other than this, the genus has no economic importance.

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DEVELOPMENT OF THE DIGITATELY DECOMPOUND LEAF IN CUSSONIA SPICATA (ARALIACEAE)

W. F. REYNEKE AND H. P. VAN DER SCHIJFF

EVEN THOUGH LEAF FORM is one of the earliest and most common characteristics used in descriptions of plants, the interpretation of the leaf form in most species of *Cussonia* has still to be clarified. These include South African *Cussonia* species such as *C. spicata* Thunb., *C. sphaerocephala* Strey, *C. arenicola* Strey, *C. nicholsonii* Strey, *C. zuluensis* Strey, and *C. gamtoosensis* Strey.

In all six species the leaves have long petioles and are digitately compound, with 5 to 13 digits radiating from a single point, the compacted rachis. These digits are homologous to the pinnae of a pinnately compound leaf. Since each digit is further once or several times vertebrately divided, the entire leaf is thus digitately decompound.

At the present time interpretations of what the parts of each digit represent vary. For example, Strey (1973) refers to an individual digit as a "vertebrate leaflet" consisting of pinnules arranged along a winged rachilla. In contrast, Van der Schijff (1971) divides each digit (pinna) into leaflets of the first, second, and third order.

In order to clarify this problem, the external morphology of the leaf of *Cussonia spicata* was studied at progressive stages of development. Since the leaf form of *C. spicata* varies considerably, the form that appeared to be the most complex was examined. This would make interpretation of less complex leaf forms relatively easy.

MATERIALS AND METHODS

Leaves of *Cussonia spicata* are formed in clusters at the apex of branches during a growth flush. As a result, all stages of leaf development are present in a single actively growing shoot apex. Such shoot apices were fixed in formalin-acetic-acid-alcohol and examined under a dissection microscope. All apices were collected from one plant growing in the Loskop Dam Nature Reserve in the Northern Transvaal (*W. F. Reyneke, 280*), where specimens of this plant occur in quite large numbers. The leaves of these plants differ from those of other members of *C. spicata* in that they have a considerably more complex form and are gray-green in contrast to the dark green leaves of other plants in the same and other localities.

OBSERVATIONS

The leaf development of *Cussonia spicata* can be divided into two phases: (1) the development of the digitately decompound leaf in its entirety and (2) the development of an individual vertebrately (de-)compound digit.

Development of the digitately decompound leaf

Following the initiation of the pyramidal leaf primordium (Figure 1A), limited apical growth occurs while the two stipular primordia differentiate laterally. At this stage the leaf primordium is approximately 230 μm. long (Figure 1B) and comprises a median petiolar-midrib region (Foster, 1936) and two lateral stipular primordia.

The stipular primordia develop rapidly, so that at a very early stage they are already very much wider and longer than the petiolar-midrib region. During their development the young stipules extend toward each other behind the petiolar-midrib region, and the leaf axis then lies against the stipules (Figure 1C–G).

As in the leaf development of most Angiospermae, the apex (tip) of the petiolar-midrib region matures very early, and when the leaf axis is approximately 300 μm. long, the first digit primordia have already been initiated (Figure 1C). The initiation of the digit primordia resembles that of the pinnae in most pinnately compound leaves, which arise basipetally as a result of localized marginal growth. Since the future rachis of the digitately decompound leaf is reduced or compacted in *Cussonia spicata*, the digit primordia appear to emerge at the same level (Figure 1D). A single apical digit primordium (I), which is homologous with the apical leaflet of imparipinnate leaves, develops first. This is followed by two lateral digit primordia (II, II^1), and the subsequent pairs of lateral digit primordia (III, III^1, IV, IV^1, etc.) are formed on either side of the preceding pair in a similar manner. Eventually this leads to an uneven number of digits in a mature leaf (Figure 4), with the single apical digit (I) the oldest and the most lateral pair the youngest. The apical digit (I) and the first pair of lateral digits (II and II^1) usually are at maturity the most complex, while the digits most laterally situated are less complex. In some leaf forms of *Cussonia spicata*, the most lateral digits can even be simple.

Immediately after their initiation, the first five digit primordia lie in the same vertical plane, but as the leaf matures, more digits are initiated anteriorly on either side of the first five digit primordia. The young leaf then eventually has its digits arranged in a semicircle around the reduced rachis, with the adaxial surfaces of the digits facing one another. It is because of this arrangement that the first differentiated digit is often referred to as the posterior or central digit and the last differentiated digits as the anterior or most lateral digits.

The further development of a single digit was studied using the posterior digit from leaves of different ages.

Development of the vertebrately (de-)compound digit

Once the digit primordium has reached a length of about 0.5 mm. (Figure 1F), it elongates rapidly. Apical growth here is also of short duration, and the first pair of lateral leaflets soon appear as rod-shaped structures on the adaxial leaf surface (Figure 1G). Their appearance is

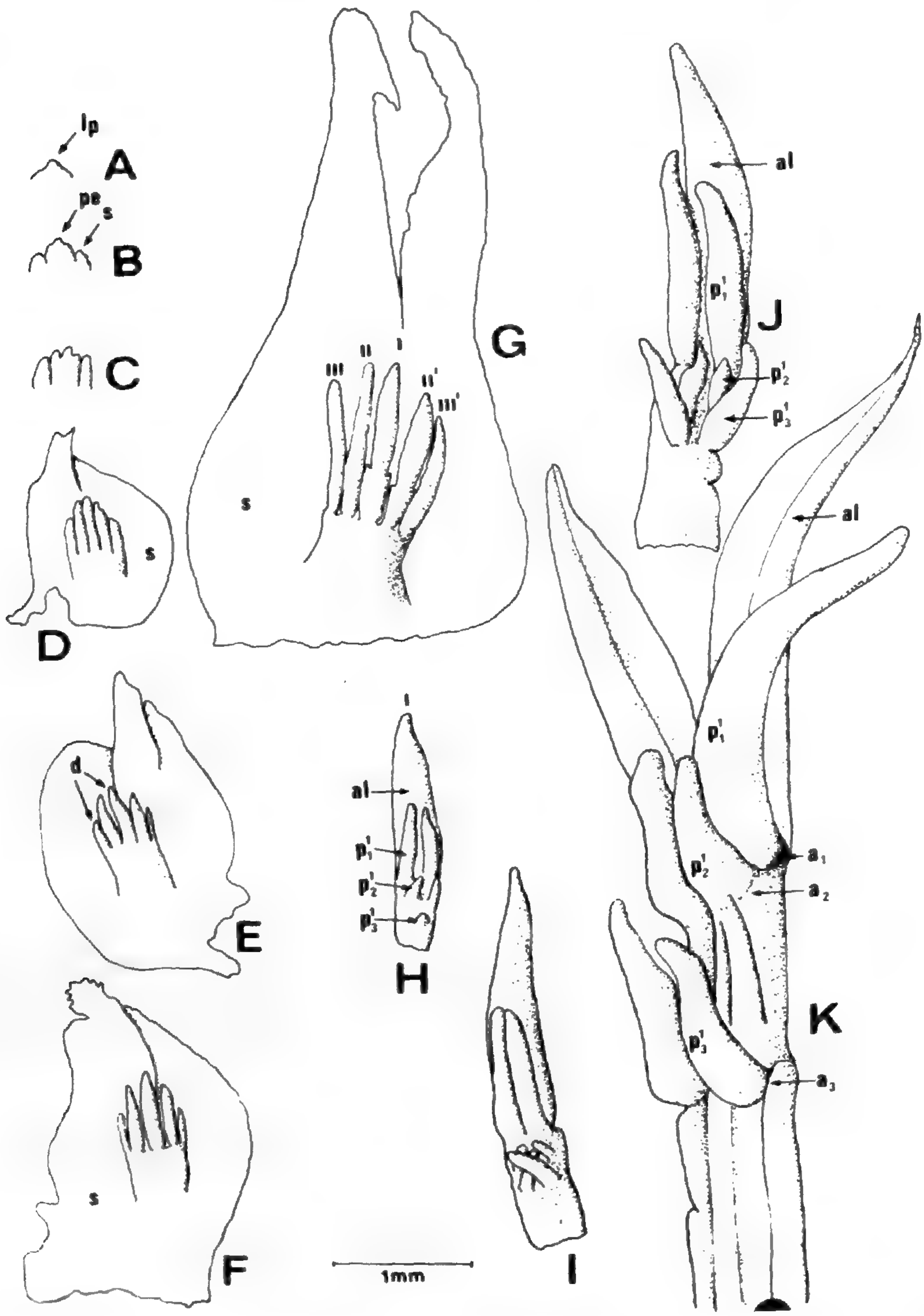

FIGURE 1. A–G. Different stages in the development of the digitately decompound leaf of *Cussonia spicata* (abaxial surface): A, initiation of pyramidal leaf primordium (lp); B, differentiation of two stipular primordia (s) on either side of the petiolar-midrib region (pe); C, initiation of digit primordia at the apex of the petiolar-midrib region. D–G. Further development of the young stipules and digit primordia (d); I, II, II^1, III, and III^1 show the sequence in which the digits initiate. H–K. Different stages in the development of a single digit (adaxial surface): a_1 = articulation no. 1; a_2 = articulation no. 2; a_3 = articulation no. 3; al = apical part of digit primordium; p_1^1 = first leaflet pair of first gene = ration at articulation no. 1; p_2^1 = second leaflet pair at articulation no. 2; p_3^1 = third leaflet pair at articulation no. 3.

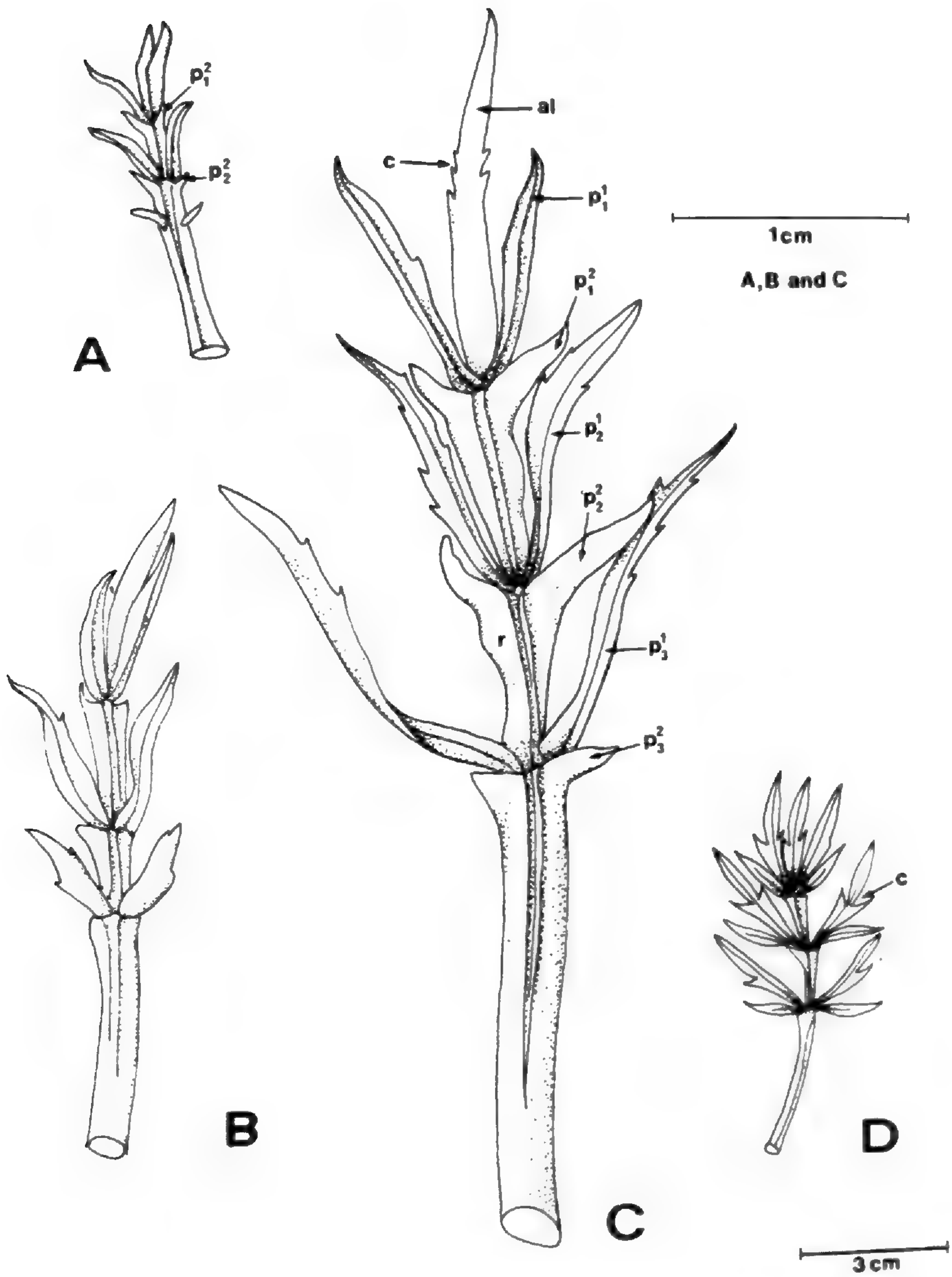

FIGURE 2. A–D. Different stages in the development of a digit of *Cussonia spicata*: al = apical part of digit primordium; c = constriction; p_1^1 = first leaflet pair of first generation; p_2^1 = second leaflet pair of first generation; p_3^1 = third leaflet pair of first generation; p_1^2 = first leaflet pair of second generation; p_2^2 = second leaflet pair of second generation; p_3^2 = third leaflet pair of second generation.

followed by the basipetal differentiation of an additional one or two pairs of leaflet primordia (FIGURE 1H). These lateral pairs of leaflets on the digit are called leaflets of the first generation and are able to subdivide by forming constrictions (FIGURE 2D). The apical part of the digit primordium above the first pair of lateral leaflets gives rise to an apical leaflet which can also constrict (FIGURE 2C).

Those parts where the different pairs of lateral leaflets of the first generation arise basipetally are termed articulations 1, 2, and 3, i.e., leaflet pair no. I arises at articulation 1 and pair no. II arises at articulation 2, etc. (FIGURE 1K). If the apical part of the digit primordium does constrict, the articulation is called no. 4 (FIGURE 3) and a pair of lateral leaflets may even originate here. Although only four articulations have been observed during this study, there may be up to five in some digits (Strey, 1973).

During subsequent development a rapid elongation of the rachilla and an increase in size of the apical and lateral leaflet primordia take place (FIGURE 1I–K), together with a flattening of these structures. When the young leaflet reaches a length of approximately 1 cm., the lateral leaflets of the second generation appear and develop at the articulations, with the leaflets directly proximal to those of the first generation, and according to Strey (1973), leaflets of a third generation may even develop (FIGURE 2A-D). Similar to the leaflets of the first generation, these second generation leaflets arise in basipetal succession at articulations 1, 2, and 3. In contrast to the leaflets of the first generation, which arise as distinctly rod-shaped primordia, those of the second generation appear to have been formed by a prominent widening of the rachilla directly below the articulations (FIGURE 2C). At a later stage of development individual leaflets originate from these widened parts (FIGURE 2D). At some articulations these leaflets of the second generation may not constrict at all, may constrict incompletely, or may not even develop. Leaves have also been observed on which only one of a possible pair of leaflets develops.

The development of leaflets of the first and second generations is accompanied by an elongation and broadening of the digit axis and eventually results in a winged rachilla. These wings, which extend along the entire length of the digit, are not only between articulations but are also beyond the first and below the most basal articulations (FIGURE 3). In most cases the wings appear V-shaped, with the broadest part directly below the articulations. The wings themselves can sometimes also form constrictions (FIGURE 3).

CONCLUSION AND SUMMARY

According to these observations, it is apparent that the development of the digitately decompound leaf of *Cussonia spicata* corresponds, in general principle, to that of a pinnately compound leaf. In *Cussonia*, however, apical growth of the petiolar-midrib region ceases at a very early stage. Consequently, the digits that develop on this axis emerge at the

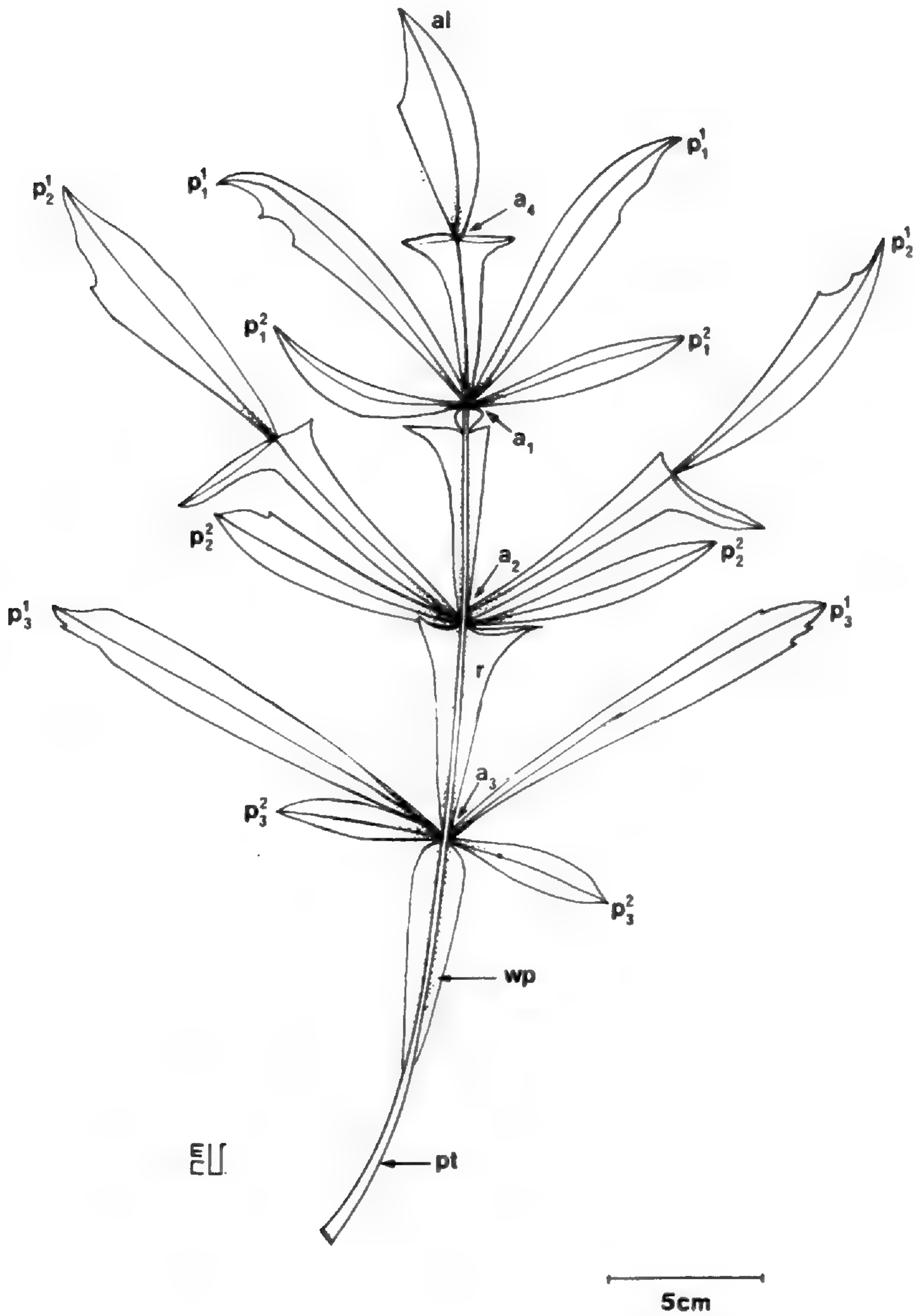

FIGURE 3. Fully developed digit: a_1 = articulation no. 1; a_2 = articulation no. 2; a_3 = articulation no. 3; a_4 = articulation no. 4; al = apical leaflet; p_1^1 = first leaflet pair of first generation; p_2^1 = second leaflet pair of first generation; p_3^1 = third leaflet pair of first generation; p_1^2 = first leaflet pair of second generation; p_2^2 = second leaflet pair of second generation; p_3^2 = third leaflet pair of second generation; pt = petiolule; r = winged rachilla; wp = winged petiolule.

same level, thus resulting in a palmate arrangement of digits about the reduced rachis (FIGURE 4).

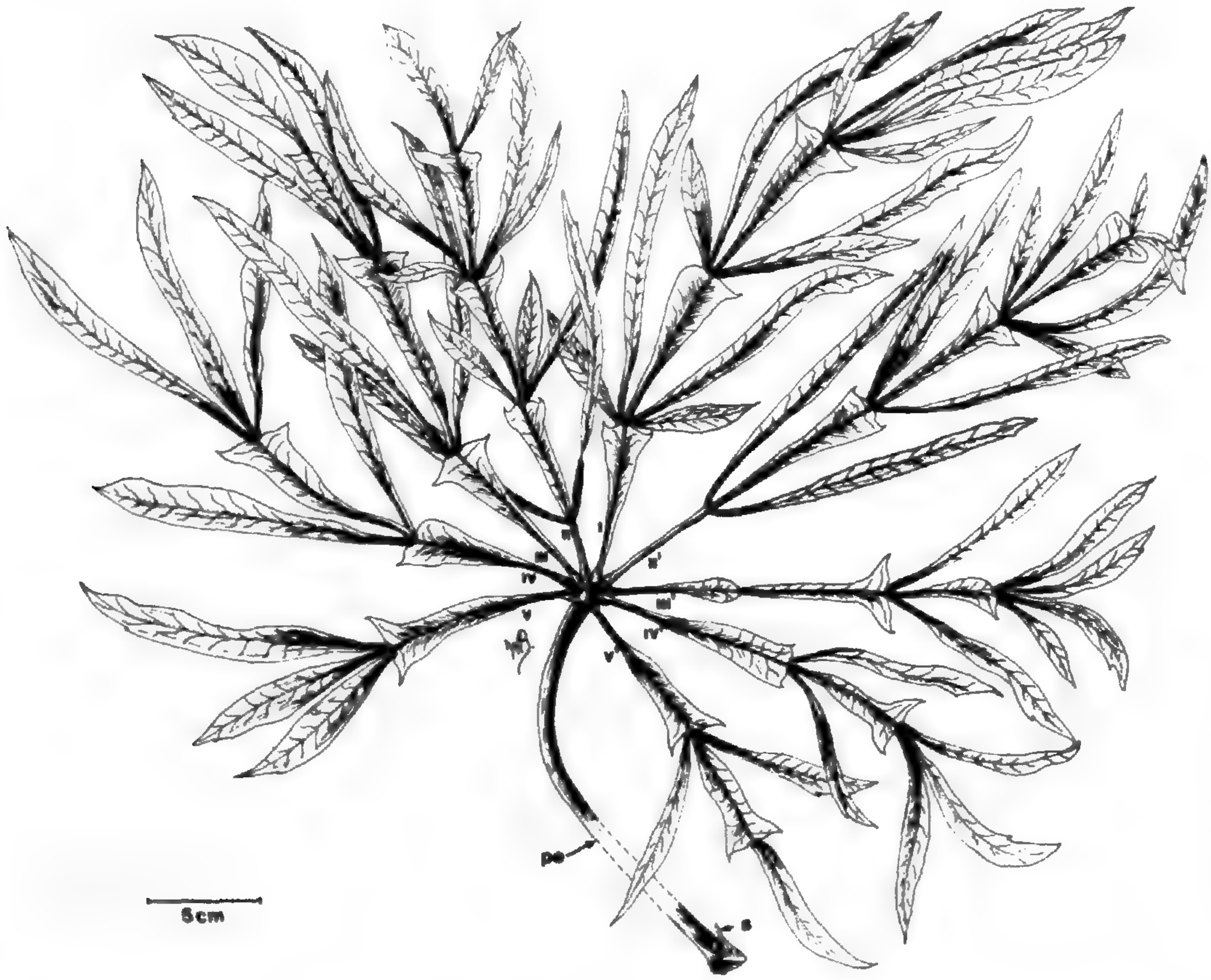

FIGURE 4. Digitately decompound leaf of *Cussonia spicata*: I–V = digits; pe = petiole; s = stipules.

Even though apical growth of the digit is also of short duration, the rachilla continues to elongate. The lateral leaflets, which differentiate at the different articulations in a basipetal direction, therefore become spaced at intervals along the rachilla.

The shape of the entire fully developed leaf of *Cussonia spicata* is digitately decompound, with the different digits (homologous with the pinnae of a pinnately compound leaf) arranged palmately about the reduced rachis. The individual digits vary in complexity. The posterior or central digit, which differentiates first, is the most complex, while the anterior or most lateral digits, which develop last, are the least complex. There is a gradual decrease in complexity from the apical leaflet to the most lateral leaflets. Although most digits are vertebrately compound, the apical digit, as well as those adjacent to it, may be vertebrately decompound, while the most lateral digits may be simple. Depending on the complexity of the digit, one or two generations of lateral leaflets differentiate basipetally at articulations along the rachilla, resulting in a vertebrately compound digit.

In some cases the lateral leaflets of the first generation may constrict, thus forming a vertebrately decompound digit.

Although leaf development has not been investigated in other species of *Cussonia* with compound leaves, their leaf development does appear to correspond quite closely to that of *C. spicata*. In most other species of *Cussonia* the mature leaf is not as complex as in *C. spicata*, since there is usually only one articulation, no articulation, or occasionally no leaflets of the second generation at all.

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Pawling, New York — April 7, 1904

Chapel Hill, North Carolina — April 6, 1975

We record with regret the death of Dr. Caroline K. Allen, member of the staff of the Arnold Arboretum from 1933 to 1948 and student of the Lauraceae.

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THE GENUS CLADOCOLEA (LORANTHACEAE)

JOB KUIJT

THE NEOTROPICAL GENUS *Struthanthus* (Loranthaceae) has never, in its existence of nearly a century and a half, been monographed or even surveyed in its entirety. Except for a few regional treatments of the genus, none of which extend north of Costa Rica, there has been little more than rather casual listing of species and the sporadic addition of what adds up to a great number of new names. Van Tieghem's work at the turn of the century added many new generic names to Loranthaceae in the Americas and elsewhere, and some of these genera are within what is now generally called *Struthanthus*. Little note has been taken of Van Tieghem's profusion of new genera except in rather isolated instances.

A scrutiny of materials in most of the major herbaria of Europe and North America has shown that the insights of Van Tieghem and his nomenclatural creations can by no means continue to be ignored. This fact is well illustrated by the present study. I have discovered that there exists, mostly in central and southern Mexico, a group of related mistletoes which are so unusual, especially in their inflorescence morphology, that generic status is fully deserved. The resultant genus, through the consistent use of accepted nomenclatural procedure, receives the name *Cladocolea* Van Tieghem. Although Van Tieghem correctly perceived some of the unusual structural features of this genus, I hasten to point out that my conception of the outlines of *Cladocolea* has little in common with Van Tieghem's. Be that as it may, the present work embodies a monographic treatment of *Cladocolea*.

In the original description of *Cladocolea* (Van Tieghem, 1895a) some unusual features were listed. The flowers, unlike those of *Struthanthus* and most others, are single and develop in axillary positions. The spikes are axillary and often appear to break through the cortex of the main stem, leaving an irregular craterlike rim. Van Tieghem erroneously described the flowers as hermaphroditic. While this condition exists in some other species, the species referred to by Van Tieghem are dioecious, although the flowers have rather large aborted organs of the opposite sex. Van Tieghem also failed to observe that the inflorescence of at least his type species, *C. andrieuxii*, was a determinate inflorescence, i.e., it ter-

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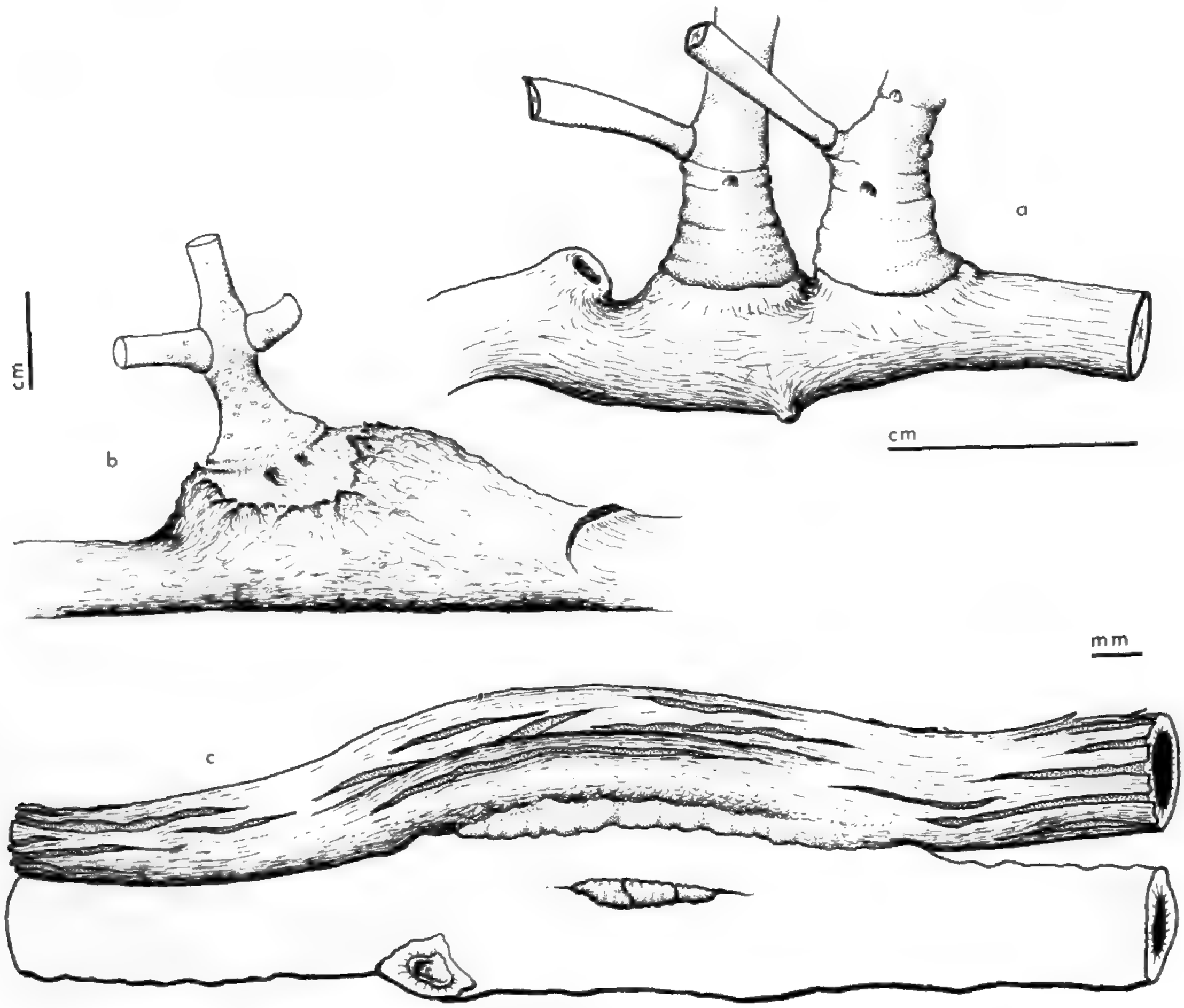

FIGURE 1. Some haustorial connections of **Cladocolea:** a, primary haustoria of two plants of **C. inconspicua** (*Hinds 346*, K); b, primary haustorium of **C. loniceroides** (*Converse 83*, UBC); c, secondary haustorium of **C. pringlei** (*Pringle 4697*, P).

minated in a single flower. He did observe this condition in a second species, which, however, he assigned to *Loxania* Van Tieghem (Van Tieghem, 1895b). As will be seen below, nearly every species in the present treatment is characterized by determinate inflorescences. The existence of determinate inflorescences in Loranthaceae is an important fact which was not even known to Eichler (1878).

As no member of *Cladocolea* has been studied in the field, we know nothing of its germination. From mature fruits of several species it appears that the seedling is always dicotyledonous and green, surrounded by a whitish endosperm and some viscous tissue. The haustorial (radicular) pole of the embryo seems little differentiated in comparison to embryos of *Struthanthus*, *Phthirusa*, and *Oryctanthus*. A rather exceptional embryo is present in *C. inconspicua* (see FIGURE 19c).

In most mistletoe collections only a few twigs are gathered, and the base of the plant is left behind. This is rather unfortunate, as the presence or absence of basal epicortical roots is an important character. In only five species has the base of the plant been seen (*Cladocolea gracilis*,

C. inconspicua, *C. inorna*, *C. loniceroides*, and *C. oligantha*), and in all but the first species epicortical roots were lacking, the primary haustorium being a simple, graftlike union (FIGURE 1a & b). It should be noted, however, that none of these four species have such roots from the branches, while both basal and cauline epicortical roots characterize *C. gracilis*. Stem roots with secondary haustoria have been observed in a number of species (*C. archeri*, *C. gracilis*, *G. grahami*, *C. harlingii*, *C. mcvaughii*, *C. pringlei*, and *C. tehuacanensis*; FIGURE 1c). It is quite possible that many if not all of the latter group also develop epicortical roots from the base of the plant, as does *C. gracilis*.

Cladocolea stems show little variation in shape. In one species (*C. inconspicua*) there is a tendency toward flattened stems, but in others stems are normally terete. The leaves may be strictly paired or completely alternate, or they may vary between these two situations.

Many species of *Cladocolea* share an unusual feature in that lateral branches, either vegetative or flowering, seem to be endogenous. They break through cortical tissues of the mother stem, leaving an irregular craterlike rim of dead cortical tissue around the base of the lateral branch. This feature was observed by Van Tieghem both in the type species of *Cladocolea*, *C. andrieuxii*, and in the plants he called *Loxania* (Van Tieghem, 1895a & b). Earlier a similar observation had been made by Eichler (1878, p. 551) for *Psittacanthus*, in which the condition is not nearly as obvious as in *Cladocolea*.

The situation is illustrated in FIGURE 2 for *Cladocolea microphylla*. The leaf base of a young, leafy shoot is surrounded by a cushion consisting of papillar hairs. These hairs seem to grow together or coalesce in the axillary area, forming a hard cushion. When the axillary shoot develops, this cushion cracks open and the first leaves emerge. The more mature stem, then, is invested by a black or brownish calluslike growth. This condition and the associated branching pattern are strikingly similar to those in the quite unrelated genus *Myzodendron* of the Myzodendraceae (Kuijt, 1969, *figs. 3–25*). It may be mentioned that this situation in some *Cladocolea* species is not only difficult to recognize but indeed often very deceptive as well. In *C. glauca*, for example, the leaves visible along older branches are not primary leaves but rather secondary ones attached to the base of short lateral inflorescences.

There are two general branching habits in the genus, the sympodial and the percurrent, which may give a strikingly different appearance to otherwise closely related species, such as *Cladocolea microphylla* and *C. loniceroides*.

The distribution of inflorescences provides further systematic distinctions. In the percurrent species, such as *Cladocolea loniceroides*, there is a gradual, sequential appearance of inflorescences. In many others, however, inflorescences are limited to year-old growth, which at that time has dropped its leaves. This condition is well illustrated in *C. microphylla* (FIGURE 25a & b). In two remarkable cases (*C. dimorpha* and *C. oligantha*) current growth produces one type of inflorescence and year-old

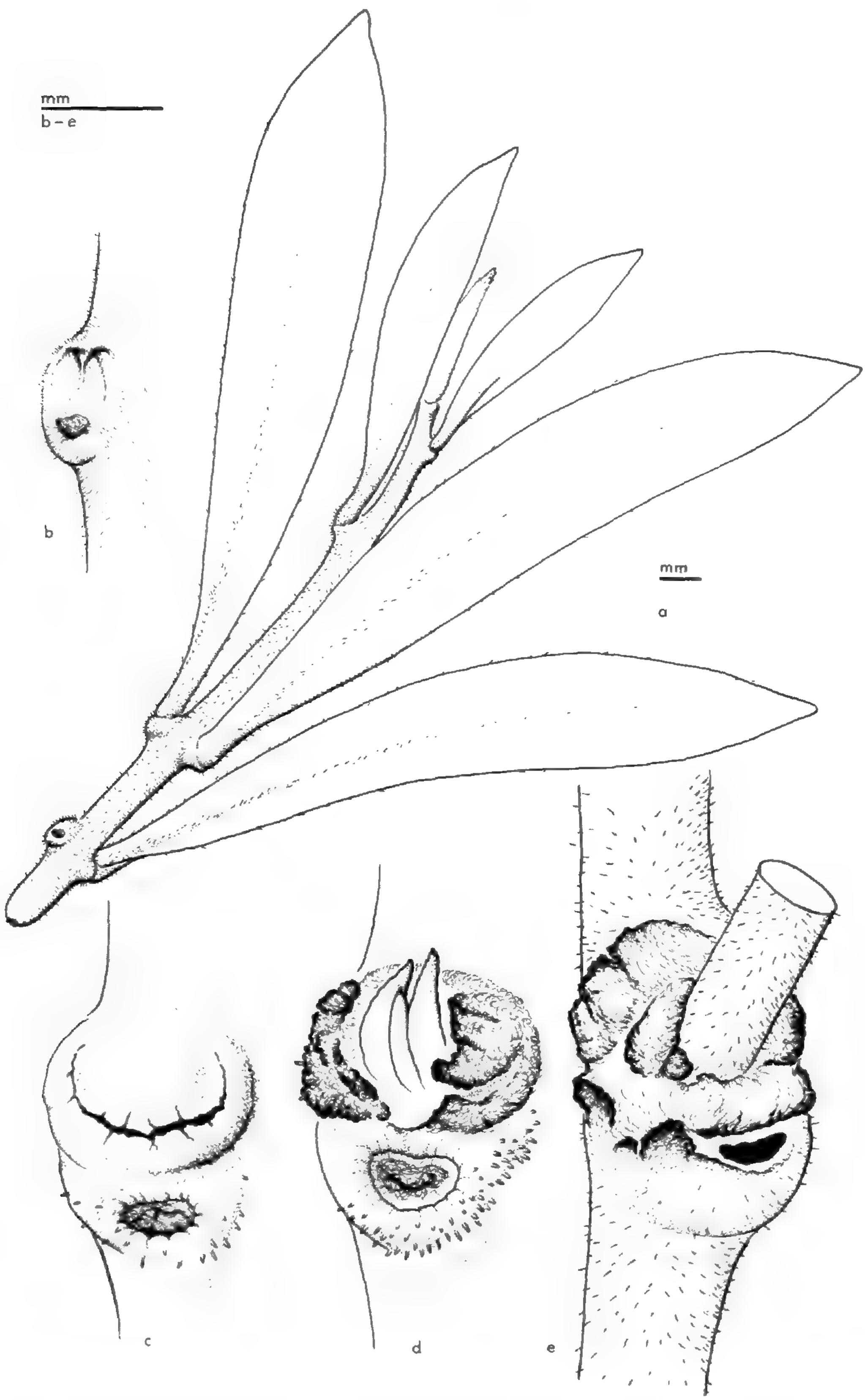

FIGURE 2. Emergence of lateral shoots in **Cladocolea microphylla** (*Troll 593*, M): a, expanding innovation; b, young axillary cushion above leaf scar; c, mature axillary cushion rupturing, leaf scar below; d, young leaves of the axillary shoot or inflorescence emerging from the axillary cushion, which has cracked wide open; e, a blackish-brown craterlike formation has developed around the base of the lateral shoot.

growth a quite different type. These are the only instances known to me of inflorescence dimorphism in the Loranthaceae. It is important to note that this dimorphism is not related to sex distribution.

The flower of *Cladocolea* may have four, five, or six petals, each of which bears a stamen or its aborted remnant fused with the abaxial surface. As in other Loranthaceae, a small calyculus crowns the ovary. In a number of species the stamens are all inserted at the same height. Monomorphic stamens are also known from the unrelated American genera *Desmaria* and *Tristerix* (Barlow & Wiens, 1973), but in most there is a clear dimorphism. Most species are dioecious, but several have hermaphroditic flowers. A high degree of correlation exists between tetramerous flowers, hermaphroditic flowers, straight styles, and monomorphic stamens (TABLE 1). This correlation is so strong that it is perhaps not too adventurous to speak of a constellation of primitive characters, the

TABLE 1. **Correlation of tetramery with hermaphroditic flowers, straight styles, and monomorphic stamens.***

	PETAL NUMBER	FLOWERS ♂/♀ OR ☿	STYLE STRAIGHT	STAMENS MONOMORPHIC
C. archeri	4(5)	☿	+	−
C. clandestina	4	☿	+	+
C. coyucae	4	?	−	+
C. dimorpha	4	?	−	+
C. harlingii	4	☿	+	+
C. inconspicua	4	☿	+	+
C. inorna	4	☿	+	+
C. oligantha	4	♂/♀	+	+
C. roraimensis	4	?	?	−

* All *Cladocolea* species having tetramerous flowers, hermaphroditic flowers, or monomorphic stamens are included in this list.

more so since the dioecism and stamen dimorphism of all other known *Cladocolea* species must surely be regarded as derivative conditions. It is particularly interesting that all four South American species are present among this possibly primitive group of species (*C. archeri, C. clandestina, C. harlingii,* and *C. roraimensis*).

The contorted or sometimes geniculate style of many Mexican species is a very peculiar feature which does not appear to occur elsewhere in Loranthaceae except in *Struthanthus* (see below). In some species the style is merely somewhat undulating in its middle or upper portion. The style of the staminate flower tends to be much straighter than that of the pistillate flower. The extreme is illustrated in the pistillate flower of *Cladocolea pedicellata,* where a great many twists occur. In at least some species (for example, the pistillate flower of *C. glauca*), these convolutions effectively double the total length of the style. Such contorted styles show no evidence

of later straightening, as they fall off after anthesis still in the original condition. The biological significance of these peculiar styles is unknown. The same feature is seen in several Mexican species of *Struthanthus* and the possibility of intrageneric affinities in these areas cannot be excluded. One of the early Mexican genera of Loranthaceae, *Spirostylis* Presl, was based on this stylar feature (Kuijt, in press).

Pollen has not been studied adequately in *Cladocolea*. It tends to be of the rounded, smooth tricolporate type typical of many Loranthaceae. In a number of species, however, a triradiate groove has been noted, as in *C. grahami* (FIGURE 13c), sometimes with a triangular central prominence.

The systematic position of *Cladocolea* with regard to other genera of small-flowered Loranthaceae, particularly *Struthanthus*, is a complex one, which may not be amenable to a completely satisfactory solution. This difficulty becomes clear when considering *C. harlingii*. There is little question that it must be assigned to *Cladocolea*; in its single, ebracteolate lateral flowers, determinate inflorescence, monomorphic stamens, and hermaphroditic flowers it agrees with a number of other *Cladocolea* species and with no known *Struthanthus* species. Yet its remarkable similarity in habit and mode of parasitism with *Struthanthus orbicularis* (H.B.K.) Blume (Kuijt, 1964) leaves one with a strong feeling that these similarities are more than superficial. This feeling is reinforced by the discovery of an as yet undescribed species from Peru, also of the same habit, which is characterized by an inflorescence with triads in its lower portion and by single flowers (including a terminal flower) in its upper part. This species represents the perfect intermediate between *C. harlingii* and *S. orbicularis*, and a position in either *Cladocolea* or *Struthanthus* would therefore seem justified for the Peruvian plant.

However, this is not the only "bridge" between the two genera. *Struthanthus polystachyus* (Ruiz & Pavón) Blume is paired in almost precisely the same way with *Cladocolea archeri* (see discussion under that species). At least one Mexican *Struthanthus* species, probably undescribed, also has an intermediate inflorescence. Inflorescence and floral details of some other Mexican *Struthanthus* species strongly suggest even further, possibly older, intergeneric connections. The unique stylar convolutions in some representatives of both genera thus assume additional evolutionary meaning and may yet be useful as an index of affinity.

It is clear that if the above suggestions are substantiated, *Struthanthus* as it is currently recognized becomes a polyphyletic entity, its several component units traceable back to separate branches of a *Cladocolea*-like group. The indeterminate, triad-bearing inflorescence of *Struthanthus* has been derived along various independent paths from determinate, *Cladocolea*-like inflorescences. These guiding principles can scarcely be defended adequately within the context of the present monograph; in fact, it is unlikely that such a defense can be made without a monographic treatment of *Struthanthus* itself.

If the postulated evolutionary relationships between the two genera are

even partly correct, the precise delimitation of *Cladocolea* and *Struthanthus* becomes somewhat arbitrary, at least where "bridging" species are located. In groping for the most useful separation, I am suggesting that *Cladocolea* be restricted to species with determinate inflorescences and single lateral, ebracteolate flowers, or obvious derivatives thereof, such as the species where the "inflorescence" is reduced to a single apical flower (for example, *C. clandestina* and *C. inconspicua*). *Struthanthus* is thus characterized by triads and (usually) an indeterminate inflorescence. Where difficulties arise (in species with mixed inflorescences), the situations should be individually evaluated.

The genus *Ixocactus* (Kuijt, 1967) may also be visualized as a derivative of *Cladocolea*-like ancestors. Indeed, in general habit its only species, *I. hutchisonii* Kuijt, is close to several *Cladocolea* species. The uniqueness of its quadricolpate, spinulose pollen, however, guarantees its survival as a separate genus.

With respect to the internal taxonomic structure of *Cladocolea*, it is first necessary to deal with Van Tieghem's division of the genus into two subgenera: subg. EUCLADOCOLEA, characterized by the presence of foliage leaves on the lower part of the spike (*C. andrieuxii*), and subg. STACHYCOLEA, in which such foliage leaves are absent (*C. tehuacanensis*, *C. grahami*, and *C. oerstedii*, the latter being a *Struthanthus*). The species added in the present work, including the two species which Van Tieghem placed in his new genus *Loxania*, render Van Tieghem's subgeneric dichotomy obsolete.

The genus as presently constituted, however, does not allow for a simple, convincing subdivision. It is possible, nevertheless, to define several groups of species which show strong affinities among themselves. It has been mentioned above that there is a very high degree of correlation between tetramery, monomorphic stamens, and hermaphroditic flowers. The nine species thus characterized (TABLE 1) undoubtedly form a closely related cluster. It is further possible to say that the three most closely related species of this group are *C. inconspicua*, *C. inorna*, and *C. clandestina*, notwithstanding the surprising geographical isolation in Brazil of *C. clandestina*.

Those species with expanded leaves on the inflorescences, either at the base or as floral bracts above, also seem to form a natural group. This is particularly convincing with *Cladocolea loniceroides* and *C. microphylla* (which have often been confused with each other), the rare *C. hintonii*, and *C. gracilis*. *Cladocolea andrieuxii* is also a member of this group. The relationships of these species to *C. pedicellata* are uncertain, the affinity with *C. glauca* and *C. tehuacanensis* being fairly remote.

A third species cluster consists of *Cladocolea grahami*, *C. mcvaughii*, and *C. pringlei*. These species undoubtedly form a natural group, but are rather distant from other *Cladocolea* species.

VERNACULAR NAMES. Only two vernacular names have been recorded by collectors: "sileno" and "malojo" (*Mexia 321, 970*), both applied to

Cladocolea inconspicua. It would be surprising, however, if the common Latin American appellation "matapalo" were not used for at least some of these mistletoes.

HOSTS. A tabulation of hosts that have been recorded is provided at the end of this paper. While several *Cladocolea* species are known only from *Quercus*, this should not mislead the reader into reaching conclusions with regard to host specificity. The possibility always exists that other ecological factors quite unrelated to hosts limit a mistletoe species to a zone or area where oaks are predominant. It is only when many collections are provided with such information that tentative ideas of this sort may be formulated. Thus it is clear that *C. loniceroides* has little host specificity; conversely, the fact that 13 out of 14 collections of *C. microphylla* are on oaks is suggestive of a very limited host range.

ACKNOWLEDGMENTS

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Cladocolea Van Tieghem, Bull. Soc. Bot. France **42**: 166–168. 1895.

Loxania Van Tieghem, Bull. Soc. Bot. France **42**: 386–389. 1895.
Phthirusa Martius, Flora **13**(7): 110. 1830, not Eichler, Flora Brasil. **5**(2): 52–67. 1868.[1]
Loranthus L. p.p., *Oryctanthus* Eichler p.p., *Phthirusa* Eichler p.p., *Struthanthus* Martius p.p.

TYPE SPECIES: *Cladocolea andrieuxii* Van Tieghem, Bull. Soc. Bot. France **42**: 166–168. 1895.

Erect or scandent parasitic shrubs, glabrous or short-pubescent; lateral branches (including inflorescences) often emerging in a pseudo-endogenous fashion; epicortical roots may occur on stems or at the base of the plant, or are absent. Leaves decussate, alternate, or irregularly arranged, simple, with pinnate venation, sometimes reduced to scales. Plants dioecious or with flowers hermaphroditic; in the former case aborted organs of the opposite sex usually present. Inflorescence normally a determinate spike, capitulum, dichasium, or raceme, in some species having undergone loss of the terminal flower or having been reduced to a single flower with one pair of bracts; lateral flowers ebracteolate, single in the axils of squamate (sometimes caducous) or foliaceous bracts. Flowers pale green

[1] See KUIJT, JOB. Proposal for the conservation of the generic name *Phthirusa* Eichler (1868) over *Phthirusa* Martius (1830) and *Passowia* Karsten (1852). Taxon (in press).

to pale yellow, sessile or pedicellate, 4-, 5-, or 6-partite; stamens fused with perianth members, dimorphic or monomorphic, with 4 thecae; pollen rounded-triangular, sometimes with triradiate groove and included triangular prominence, otherwise smooth; style often contorted or geniculate, especially in upper portion. Fruit a one-seeded berry with endosperm; embryo dicotyledonous, elongate, or globular, the haustorial disk weakly developed.

The genus *Cladocolea* is distinguished from *Dendropemon*, *Oryctanthus*, *Phthirusa*, and *Struthanthus* by the terminal flowers (determinate inflorescences) and by its lack of any bracteoles; from *Ixocactus* mostly by the unique pollen grain of the latter; and from *Struthanthus* and *Phthirusa* by its single, ebracteolate lateral flowers. The genus, however, shows clearly definable affinities with a number of *Struthanthus* species, such as *S. orbicularis* (H.B.K.) Blume, *S. polystachyus* (Ruiz & Pavón) Blume, possibly *S. johnstonii* Standley & Steyermark, and several as yet undescribed *Struthanthus* species.

Geographically *Cladocolea* is concentrated north of the Isthmus of Tehuantepec. One species, *C. oligantha*, is known from Mexico, as well as from Guatemala and Panama, and is likely to occur in intermediate areas also. Four species, three of which have previously been placed in other genera, are found in rather separate stations in South America, all but *C. clandestina* at high elevations (*C. archeri*, *C. harlingii*, and *C. roraimensis*). It is of considerable interest, furthermore, that all species occurring south of Mexico belong to the apparently primitive group delineated in the introduction.

Key to Species of Cladocolea

1. Inflorescences absent, the flowers occurring singly, axillary to leaves on main stem.
   2. Calyculus fimbriate, style conical; known from Brazil. ..... 3. *C. clandestina*.
   2. Calyculus not fimbriate, style straight, not conical; known from Mexico.
      3. Stem cylindrical even when young; anthers without connectival horn; most leaves acicular, some narrowly oblanceolate. ..... 14. *C. inorna*.
      3. Young stems somewhat compressed; connectival horn of anther prominent; leaves obovate to oblanceolate, never acicular. ..... 13. *C. inconspicua*.
1. Inflorescences present.
   4. Inflorescence subtended by several pairs of acute scale leaves.
      5. Petiole 8 mm. long or more; leaf apex obtuse; known only from Mt. Roraima. ..... 21. *C. roraimensis*.
      5. Petiole 5 mm. long or less; leaf apex acute, even-attenuate; known from Ecuador, Colombia, and Peru. ..... 2. *C. archeri*.
   4. Inflorescences not so subtended.
      6. Inflorescences in leaf axils of current growth, but sometimes also on older growth.
         7. Inflorescences on current growth simple dichasia.

8. Bracts on primary inflorescences caducous, small; secondary inflorescences with basal foliage leaves only; dioecious. .... 18. *C. oligantha.*
8. Bracts on primary inflorescences persistent, as large as the flowers; secondary inflorescences with foliage leaves along axis; flowers probably hermaphroditic. ..... 6. *C. dimorpha.*
7. Inflorescences on current growth more than 3-flowered.
9. Leaves at least 10 times as long as wide. ..... 5. *C. cupulata.*
9. Leaves no more than 5 times as long as wide.
10. Flowers pedicellate. ..... 10. *C. harlingii.*
10. Flowers sessile.
11. Plants with at least the young growth pubescent, puberulent, or with short, stiff epidermal hairs.
12. Plants sparsely branched, sympodial.
13. Flowers 4-partite, style contorted or geniculate. ..... 4. *C. coyucae.*
13. Flowers 5-partite, style nearly straight. .... *22. C. stricta.*
12. Plants profusely branched, not sympodial. .... 15. *C. loniceroides.*
11. Plants with even the young growth always glabrous.
14. Flowers nearly perpendicular on inflorescence axis, widely spaced. ..... 16. *C. mcvaughii.*
14. Flowers differently arranged.
15. Leaves approximately twice as long as wide. ..... 12. *C. hondurensis.*
15. Leaves more than 3 times as long as wide.
16. Spikes always determinate; staminate buds obovate; fruit 10 mm. long or more. ..... 9. *C. grahami.*
16. Spikes determinate or indeterminate; staminate buds obovate; fruit about 5 mm. long. ..... 20. *C. pringlei.*
6. Inflorescences not occurring on current growth; mature inflorescences present only on leafless, older internodes.
17. Mature leaves linear. ..... 8. *C. gracilis.*
17. Mature leaves not linear.
18. Young growth finely puberulent.
19. Spikes with 0–3 foliage leaves on lower half of peduncle. ..... 11. *C. hintonii.*
19. Spikes with involucral foliage leaves near tip of inflorescence. ..... 17. *C. microphylla.*
18. Young growth glabrous.
20. Stems grooved or ridged when young. . . 1. *C. andrieuxii.*
20. Stems always terete.
21. Leaves at least 6 cm. long. ..... 9. *C. grahami.*
21. Leaves less than 5 cm. long.
22. Flowers sessile along a slender, elongate inflorescence rachis. ..... 23. *C. tehuacanensis.*
22. Flowers pedicellate or, if sessile, on a short, crowded inflorescence rachis.

23. Flowers short- or long-pedicellate, rarely sessile; twigs rather straight and stout; buds 6 mm. or more long, acute. .... 19. *C. pedicellata.*

23. Flowers sessile; twigs often voluble, slender; buds 5 mm. long or less, more or less rounded. ..... 7. *C. glauca.*

1. **Cladocolea andrieuxii** Van Tieghem, Bull. Soc. Bot. France **42**: 167. 1895. FIGURES 3 & 4.

Oryctanthus andrieuxii (Van Tieghem) Engler in Engler & Prantl, Nat. Pflanzenfam., Nachtr. zu **III**: 135. 1897.
Struthanthus alni Bartlett, Proc. Am. Acad. **44**: 630. 1909.

TYPE: *Andrieux 345* (see below).

Plant dioecious, completely glabrous, dark and shiny when dry, with sympodial growth; stems somewhat grooved or ridged; stem craters conspicuous. Leaves alternate, with primary leaves only on current year's growth, up to 3.5 × 1.5 cm., more usually 3 × 1 cm., lanceolate-oblanceolate, somewhat rounded to acute at apex, the base tapering into a petiole 2–4 mm. long; the pinnate venation clearly visible above. Inflorescences only on year-old wood, consisting of a short spike with about 2 leaves below, the 5 or 6 sessile flowers crowded at the tip, bracts caducous, one flower in a terminal position. Staminate flowers nearly 10 mm. long in bud, the bud pointed; petals 6; anthers nearly sessile, dimorphic, upper series attached above middle of petal, lower series attached about ⅓ the distance from the base; anthers 2–2.5 mm. long, lacking a conspicuous connective; filament cushion absent below the anther, an even ridge taking its place; pollen lacking triradiate groove, glabrous; ovary 2 × 2 mm.; style only slightly undulant, reaching to base of upper anthers, where slightly contorted; stigma not differentiated; nectary well developed, glabrous. Pistillate flowers 7–8 × 1.5 mm., 6-merous; staminodia very slender and inconspicuous; ovary 2 mm. long, calyculus irregularly dentate; petals sometimes with tufts of hairs on incurved tips; style ranging from nearly straight to strongly convolute in middle region; stigma capitate, with somewhat angular, papillar surface; nectary well developed, more or less smooth. Fruit 9 × 5 mm., ellipsoid, smooth; embryo dicotyledonous, half the length of the fruit.

There is no sign of any epicortical roots, but the base of the plant has not yet been seen.

C. andrieuxii is the type species of *Cladocolea* Van Tieghem.

Mexico. GUERRERO: Chichihualco, Cerro de Pastilla, near Camotla, on *Quercus*, 2300 m., *Rzedowski 16436* (MICH). OAXACA: Mt. S. Felipe, on *Quercus*,

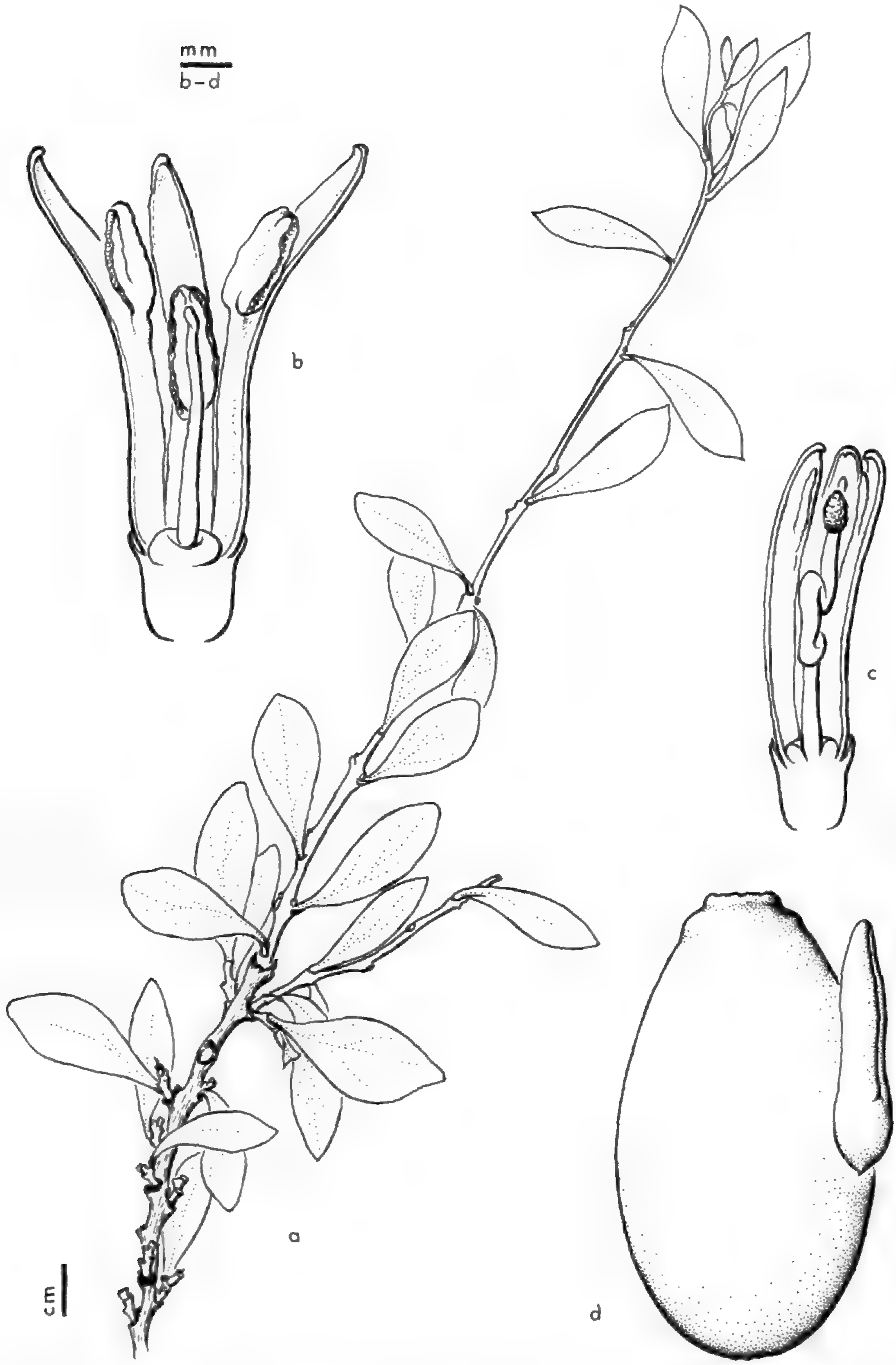

FIGURE 3. **Cladocolea andrieuxii**: a, habit, pistillate plant? (*Andrieux 345*, K); b, staminate flower, longitudinal section (*Pringle 10244*, SMU); c, pistillate flower, longitudinal section (*Pringle 10244*, SMU); d, fruit and embryo (*Camp 2609*, NY).

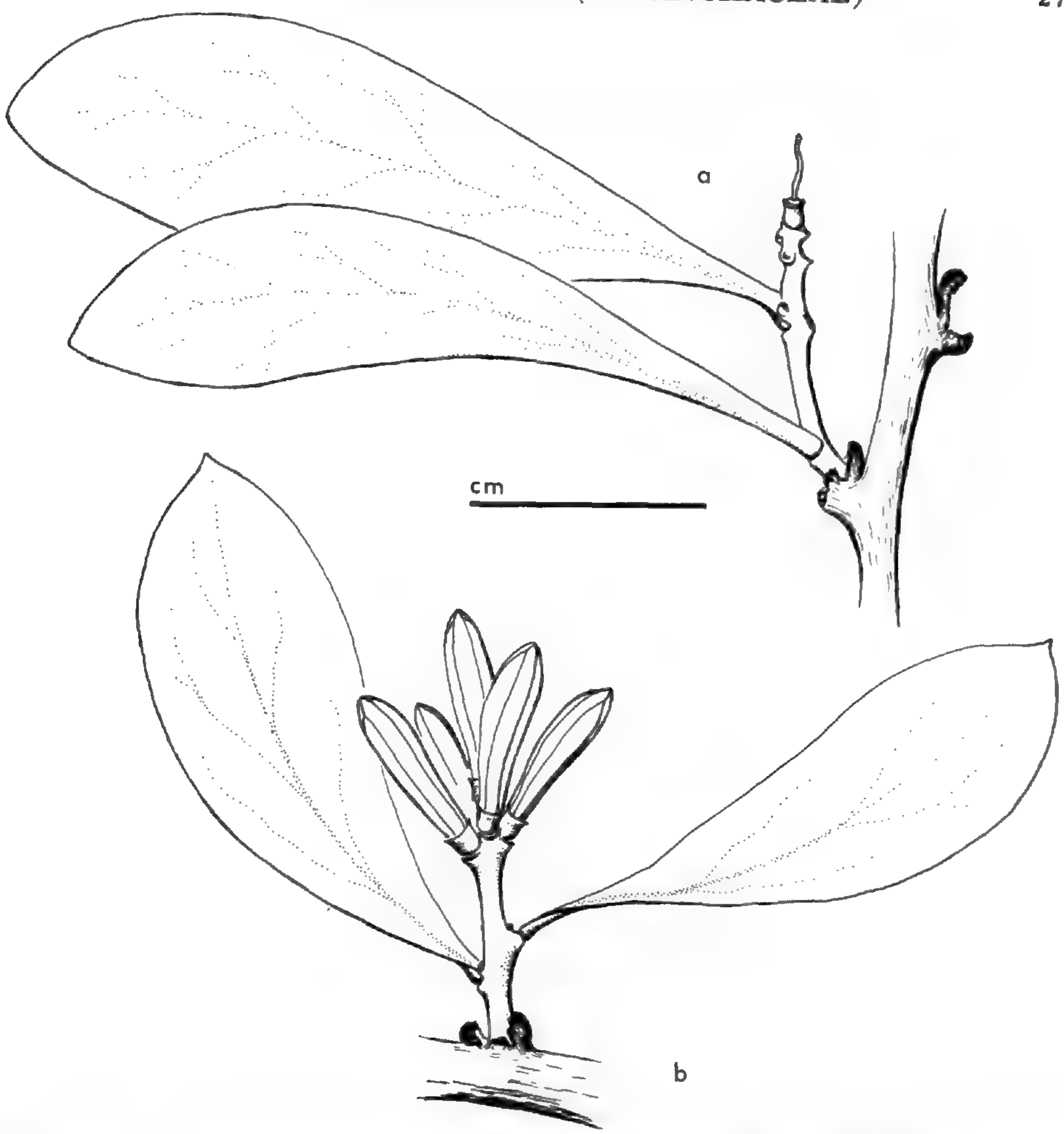

FIGURE 4. **Cladocolea andrieuxii:** a, inflorescence, pistillate? (*Andrieux 345*, G); b, inflorescence, staminate? (*Pringle 10244*, SMU).

Andrieux 345 [2] (P, holotype of *C. andrieuxii*; G, K, M, isotypes); Cerro de San Felipe N of Oaxaca, on *Alnus*, *Camp 2609* (NY); summit ridge, Sierra de San Felipe above city of Oaxaca, on *Alnus jorullensis* var. *exigua*, 10,000 ft., *Pringle 10244* (GH, holotype of *Struthanthus alni*; CAS, MICH, UC, US, UT, isotypes).

2. **Cladocolea archeri** (A. C. Smith) Kuijt, comb. nov. FIGURE 5.

Oryctanthus archeri A. C. Smith, Bull. Torrey Bot. Club **59**: 516, 517. 1932.

TYPE: *Archer 1521* (see below).

Rather large, glabrous plant strikingly similar to *Struthanthus polystachyus* (Ruiz & Pavón) Blume, with apparently sympodial growth;

[2] There is some confusion concerning *Andrieux 344*, which appears to be a mixed collection. It is accompanied by the same data as *Andrieux 345*. At K and P the specimen clearly belongs to the present species, but at M it would seem to be *C. tehuacanensis* instead (as, in fact, indicated by an annotation to that effect in Van Tieghem's hand). *Andrieux 344* is not mentioned in Van Tieghem's note on *C. andrieuxii*.

stems long and straight, branching only from older wood, angular and smooth when young, becoming stout and terete, with numerous conspicuous, round lenticels of uniform size; internodes 4.5–8 cm.; stem roots rare. Leaves decussate, the leaf blade 3–10 × 2–5 cm., ovate, somewhat attenuate at apex and rounded to truncate at base; petiole 4–8 mm. long, canaliculate; midvein prominent as a groove, running into apex, with

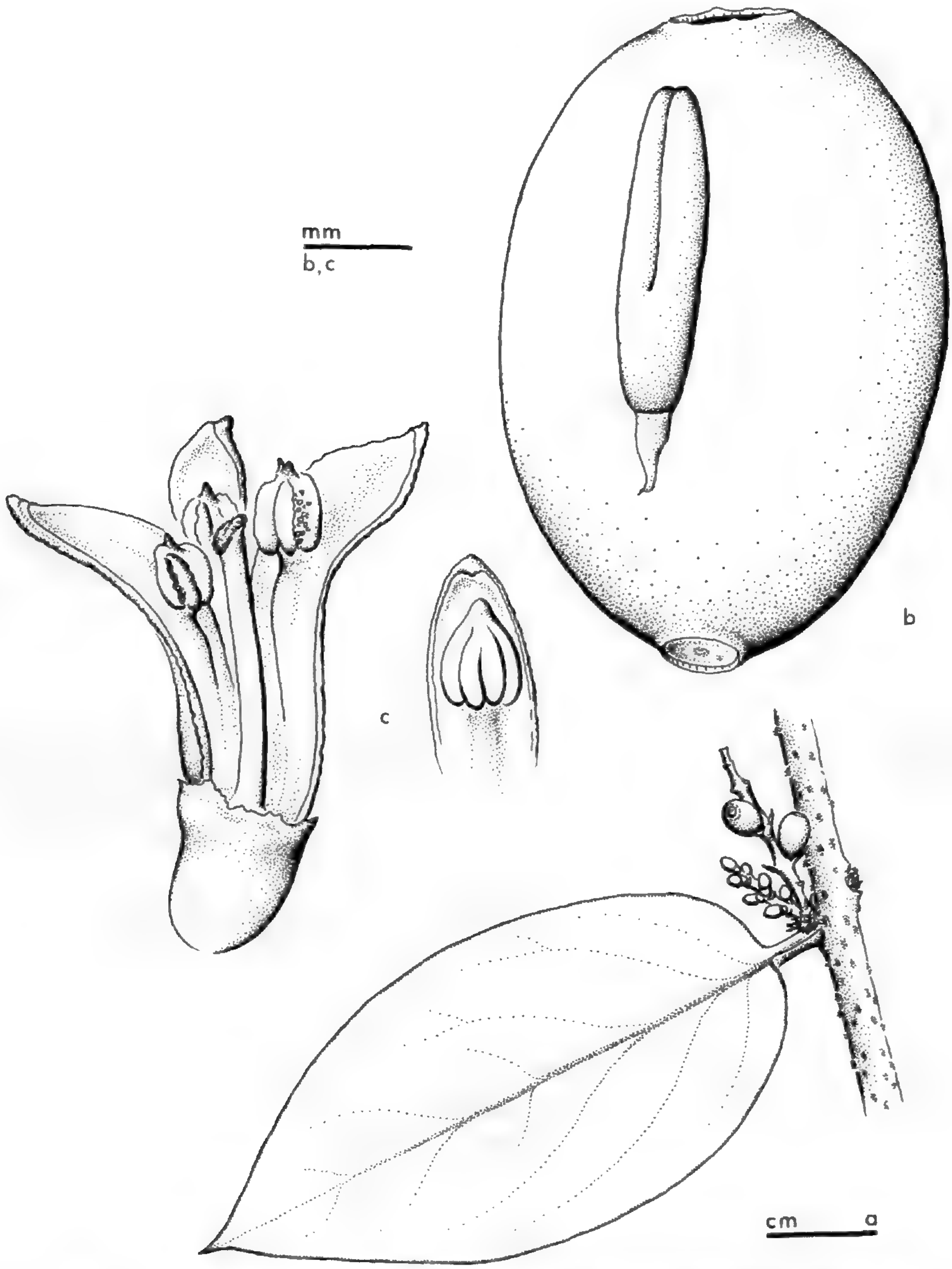

FIGURE 5. **Cladocolea archeri**: a, portion of twig with two inflorescences of different ages (*Archer 1521*, US); b, fruit and embryo of same collection; c, anther and flower, two petals removed (*Dodson & Thien 1852*, UBC).

regular and prominent lateral veins. Inflorescence subtended by several pairs of small, chartaceous scale leaves, several per leaf axil; each inflorescence with ca. 5 pairs of ebracteolate, sessile flowers and one terminal one; floral bracts acute, up to nearly 3 mm. long, naviculate, mostly caducous but some persisting. Flowers yellow-green, hermaphroditic, the mature bud nearly 6 mm. long, blunt; petals 4.5 mm. long, 4(5), each with one anther, the filament fused with its petal; anthers attached at two different heights, both above middle of petal, but all similar in shape, having 4 pollen sacs with blunt, projecting connective; pollen smooth, somewhat 3-lobed but lacking evident surface markings; ovary 1.5 × 1.5 mm., with irregularly denticulate calyculus; style straight and rather stout, 3 mm. long; stigma weakly differentiated, oblique. Fruit "rose red when young, becoming blue with a greyish bloom" (collector's notes, type specimen), 4 × 6 mm., ovoid, with blunt apex; embryo dicotyledonous, 3 mm. long.

Assignment of this species to *Cladocolea* is logical but by no means inevitable. The closest relative of *C. archeri*, in fact, would seem to be *Struthanthus polystachyus*. The general similarity between these two species survives closer scrutiny. Except for *C. roraimensis*, no other known species of either *Cladocolea* or *Struthanthus* have basal, chartaceous inflorescence bracts; fruit color changes are identical; and, most importantly, the inflorescence of *S. polystachyus* has two or four paired single flowers (rather than triads) and a single, terminal flower (Kuijt, 1964). Indeed, the relationship of these two species is so close that it is tempting to postulate a derivation of the dioecious one (*S. polystachyus*) from *C. archeri*, which has hermaphroditic flowers. A completely parallel situation exists in the relationship between another *Cladocolea*, *C. harlingii*, and *Struthanthus orbicularis* (H.B.K.) Blume and its immediate relatives. It is worth mentioning that in both instances the *Cladocolea* species involved has hermaphroditic flowers and is very localized geographically, while the corresponding *Struthanthus* species is dioecious and widely distributed. *S. orbicularis* ranges from Brazil and Peru through all Central American republics to southern Mexico, while *S. polystachyus* is more cordilleran, ranging from northern Peru to Costa Rica (Kuijt, 1964).

If the relationships are as sketched above, it can be seen that no completely satisfactory assignment at the generic level may be possible at this time. Both *Cladocolea archeri* and *Struthanthus polystachyus* might be included in either *Cladocolea* or *Struthanthus*. A third possibility, which has much to recommend it from the point of view of the recognition of natural affinities, is the establishment of a separate genus to include both species, i.e., the genus *Peristethium*, which Van Tieghem (Bull. Soc. Bot. France 42: 175. 1895) erected for *S. polystachyus* (*S. leptostachyus* (H.B.K.) G. Don). Such an arrangement, however, would not only belie the affinities which *C. archeri* shows to the remainder of *Cladocolea*, but it would also, to be consistent, necessitate the creation of a similarly new genus for *C. harlingii* and its close relatives in *Struthanthus*. The effect would be to split *Struthanthus* into units which, while perhaps represent-

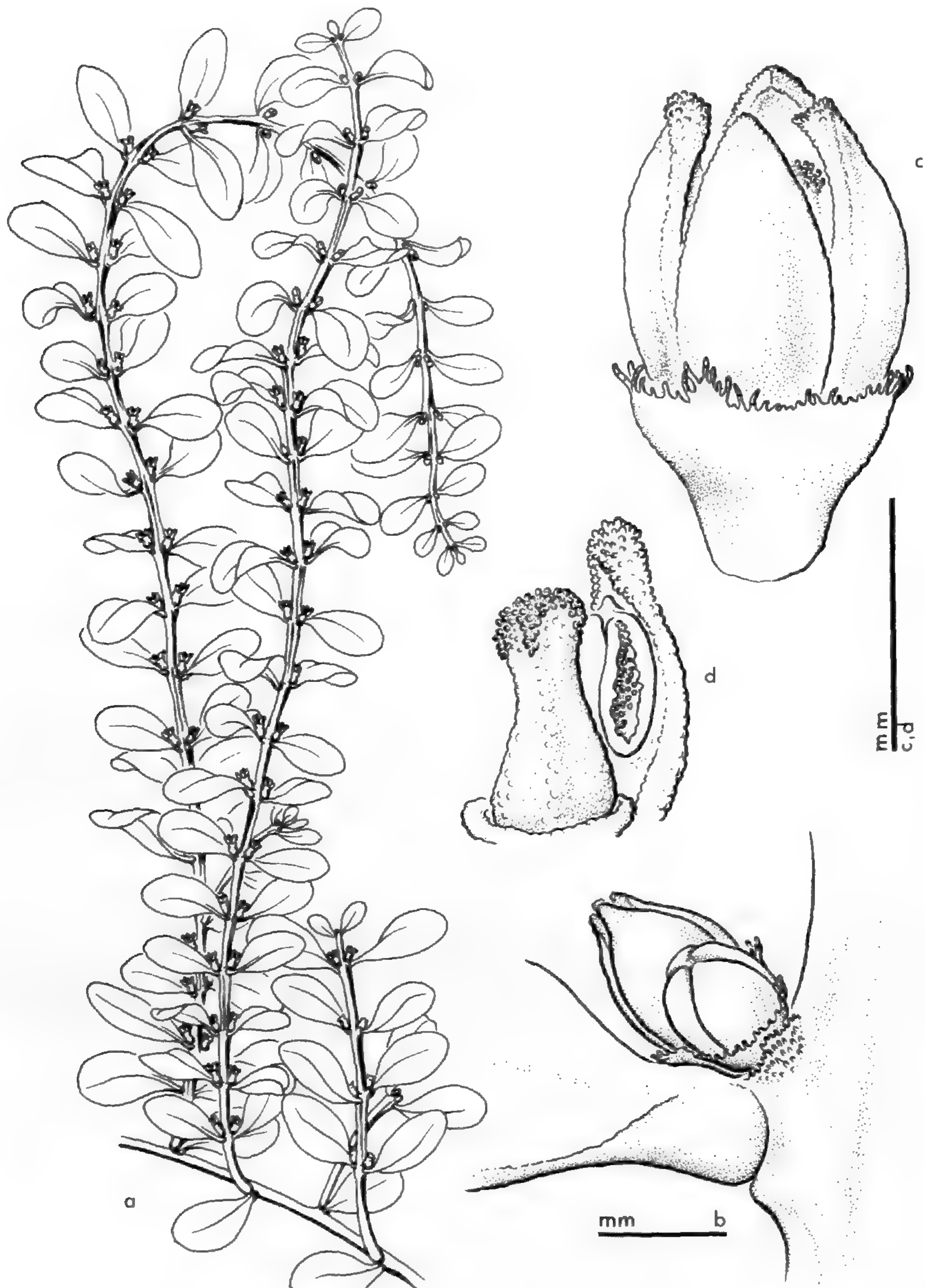

FIGURE 6. **Cladocolea clandestina** (*Martius s.n.*, M): a, habit, redrawn from Eichler, Flora Brasil. 5(2): *pl. 18.* 1868; b, axillary group of flowers; c, mature flower; d, style and anther-bearing petal.

ing the most natural groups possible, could nevertheless not always be adequately distinguished from each other. At any rate, as *Struthanthus* has never been monographed, such action is at present quite premature, and

the inclusion of *C. archeri* in *Cladocolea* would seem to be the most reasonable alternative.

Ecuador. PROV. IMBABURA: Lita, 500 m., *Acosta Solis 12200* (F); PROV. TUNGURAHUA: Chaupi, 2400 m., *Dodson & Thien 1852* (UBC, UC). **Colombia.** DEPT. ANTIOQUIA: La Sierra, 18 km. N of Medellín, on *Tournefortia fuligunosa*, 2000 m., *Archer 1058* (US), *Archer 1521* (US, holotype, *Oryctanthus archeri*); Cordillera Central, near Porcesito, Río Medellín Valley, 1100 m., *Hodge 6842* (US). DEPT. VALLE: Cordillera Occidental, Hoya del Río Digua, La Elsa, ravine La Cristalina, 1000–1150 m., *Cuatrecasas 15244* (F, UC); Cordillera Occidental, Hoya del Río Cali, Quebradahondo, arriba de La Glorieta, camino a Miralindo, 2100–2250 m., *Cuatrecasas 18430* (F); Cordillera Central, shores of Río Bugalagrande, Calamar, 1680 m., *Cuatrecasas 20506* (F). **Peru.** DEPT. HUANUCO: SW slope of Río Llulla Pichis watershed, ascent of Cerro del Sira, below summit, on Melastomataceae, 2100 m., elfin forest, *Dudley 13450* (F).

3. **Cladocolea clandestina** (Martius) Kuijt, comb. nov. FIGURE 6.

Loranthus clandestinus Martius in Schultes & Schultes, Syst. Veg. **7**: 96. 1829.
Phthirusa clandestina (Martius) Martius, Flora **13**: 110. 1830.

TYPE: *Martius* (see below).

Young leafy stems quadrangular, smooth, green; older stems terete, developing longitudinal lenticels which are often in long series. Leaves regularly decussate, 2.5 × 1.5 cm. or slightly smaller, obovate to broadly elliptical, with rounded apex and acute base; petiole ca. 1 × 1 mm.; venation pinnate but obscure, with two large lateral veins at base of blade. Inflorescence with flowers single or in threes (two laterals in axils of scale leaves beneath primary, median flower), in the axils of foliage leaves, margin and back of scale leaves covered with short hairs. Flowers 2 × 1 mm., calyculus glabrous but with fringed margin, the projecting hairs mottled with brown; petals 4, slightly more than 1 mm. long, each with papillate tip but otherwise glabrous; anthers on extremely short filaments, less than 1 mm. long, placed at uniform heights on the middle of the petal; petals differing only slightly in width, otherwise both petals and stamens monomorphic; anther connective projecting slightly; pollen broadly triangular, smooth, with very faint triradiate marking; style 1 mm. long, somewhat quadrangular, base very heavy; stigma very conspicuously papillate, dark-colored; nectary rather smooth. Fruit 2 × 4 mm., ellipsoid, dark-colored(?).

This species is the type species of *Phthirusa* Martius, a generic name recently superseded by *Phthirusa* Eichler (Kuijt, in press). Its affinities are clearly with *Cladocolea inconspicua*, as already suggested by Eichler (1868, p. 67).

There is no real evidence for the floral dimorphism described by Eichler; the two "forms" described by Eichler may represent two stages in maturity.

Brazil. PROV. RIO DE JANEIRO: *Glaziou 1429* (F), *Martius* (M, holotype of *Lo-*

ranthus clandestinus; this specimen very faithfully drawn in Eichler, Flora Brasil. **5**(2): *pl. 18.* 1868).[3]

4. **Cladocolea coyucae** Kuijt, sp. nov. FIGURES 7 & 8.

TYPE: *Hinton 3958* (see below).

Gracilis, dioecia?, parce ramosa, sympodialis; caules ut videtur sine radicibus, teretes, juveniles breviter albo-pubescentes, vetustiores lenticellis manifestis vel fissuris epidermalibus longis. Folia alterna, solum in innovationibus vertentibus, oblanceolata, basi longe attenuata, 35 × 8 mm. Inflorescentiae singulares in axillis foliarum ad ramos novellos, subsessiles vel pedunculis ad 10 mm. longis; flores 5–7, ad apicem congesti, foliis squamiformibus parvis suffulti; ca. 3 mm. longi, tetrameri; antherae monomorphicae vel submonomorphicae connectivum obtusum. Stylus medio semel conspicue contortus. Fructus ca. 5 × 3 mm.

Plant possibly dioecious, slender, sparsely branched, with sympodial growth; twigs straight, terete, apparently rootless, the young growth with very short, stiff, white epidermal hairs; year-old stems with longitudinal or roundish lenticels or long epidermal cracks. Leaves alternate, occurring only on current growth, up to 35 × 8 mm., oblanceolate with fairly blunt apiculate apex and long, tapering base; petiole very short or lacking; venation pinnate, the midrib running into apex. Inflorescence one per leaf axil on current growth, only occasional on year-old growth, leafless, peduncles as long as 10 mm. but sometimes much shorter, rarely nearly lacking; flowers 5–7, crowded at apex, subtended by small scale leaves, either paired or alternate, terminal flower always present. Flowers about 3 mm. long, 4-merous; anthers monomorphic or nearly so, 4-loculate, nearly sessile; filament buttress thick, the free upper part continuing in an extremely slender, short filament; connective blunt; ovary 1 × 1 mm., somewhat frayed at calyculus; style with a single, prominent contortion in the middle; stigma well differentiated, capitate, with papillar surface, sometimes lobed, reaching above pollen sacs. Fruit 5 × 3 mm., somewhat obovate, smooth; embryo ca. 3 mm. long, clavate, cotyledons 2 mm. long.

I am not completely satisfied that *Hinton 4777* is the staminate plant of this species or even that the species is dioecious. *Hinton 3958* is a fruit-bearing plant, and its flowers have apparently fully matured anthers; yet I have not been able to find pollen. *Hinton 6688* is also fruit-bearing but has clearly degenerate anthers. As these conditions at least theoretically could coexist in one species, and as some very striking and close similarities exist between these specimens, they are treated together provisionally.

Mexico. GUERRERO. Distr. Coyuca: Coyuca, on a chirimo, *Hinton 5554* (K,

[3] The following material is cited in Rizzini, Rodriguésia **28–29**: 130. 1956. PROV. RIO DE JANEIRO: Tijuca, *Brade 10461*; Corrocado, Schwacke *1411*; PROV. ALAGOAS: Maceió, *Gardner 1322*.

Two further collections, by Mikan and Riedel, both from Prov. Rio de Janeiro, are cited by Eichler (*loc. cit.*) but have not been seen.

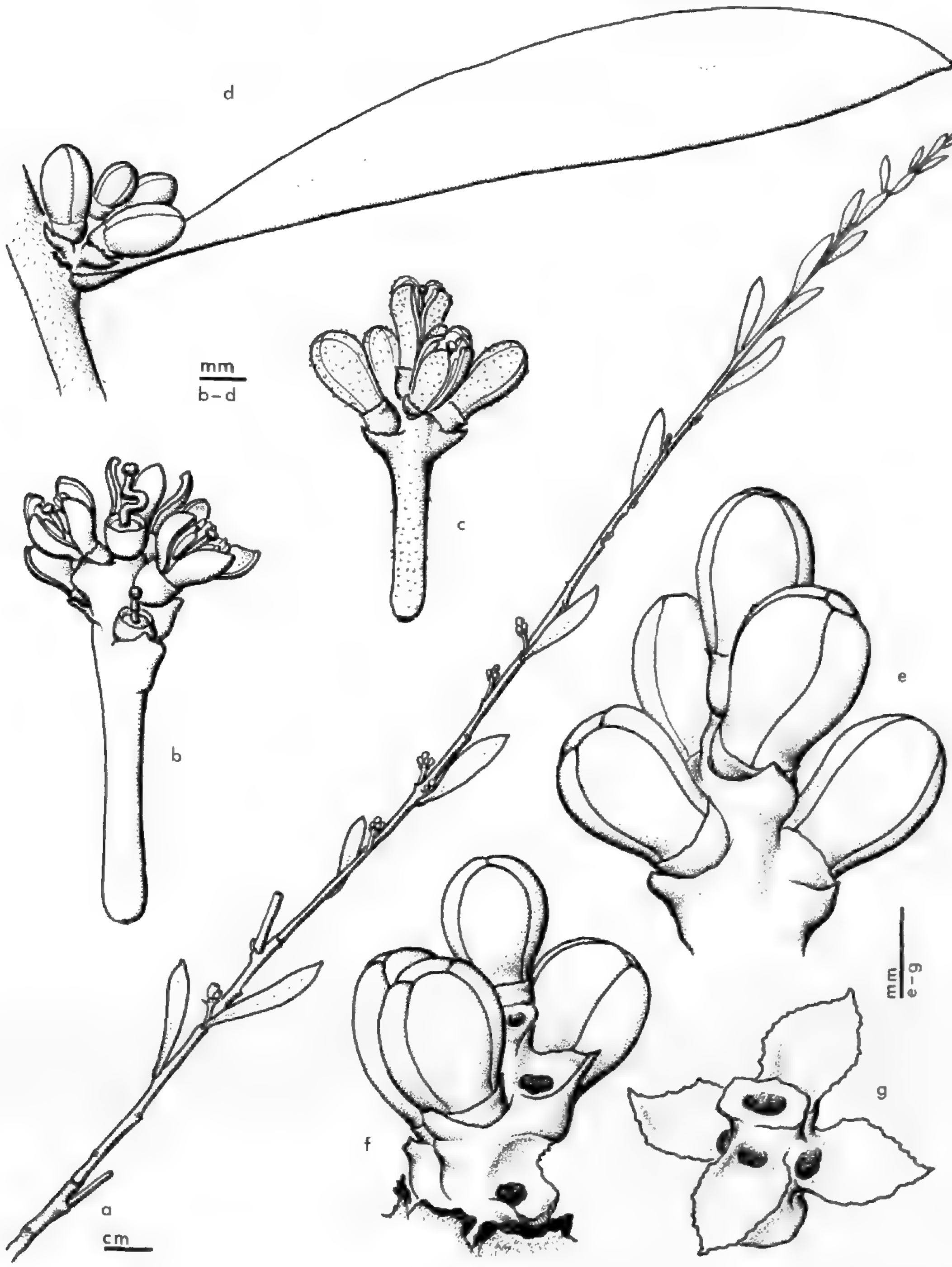

FIGURE 7. **Cladocolea coyucae:** a, habit (*Hinton 3958*, K); b, inflorescence, same collection; c, inflorescence, pistillate (*Hinton 6688*, K); d, inflorescence of sessile type (*Hinton 4777*, G); e–g, inflorescence details of same collection.

MICH, NY, US); Santa Barbara, *Hinton 6688* (K, MICH, NY, UC, US). MEXICO. Distr. Temascaltepec: Bejucos, on a guaje, 610 m., *Hinton 3958* (K, holotype of *C. coyucae*; MICH, NY, UC, US, isotypes); Bejucos, on a brazil, *Hinton 4777* (F, G, K, MICH, NY, P, S, UC, US, W). MICHOACÁN: Tancitaro region, arid slopes above Apatzingán, on *Thevetia*, 2000 ft., *Leavenworth & Hoogstraal 1513*[4] (F,

[4] The Leavenworth and Hoogstraal specimen is sterile, and it is assigned to *C. coyucae* on the basis of vegetative similarity only. The Purpus collection is a broad-leaved plant with hermaphroditic flowers, and its placement here is provisional.

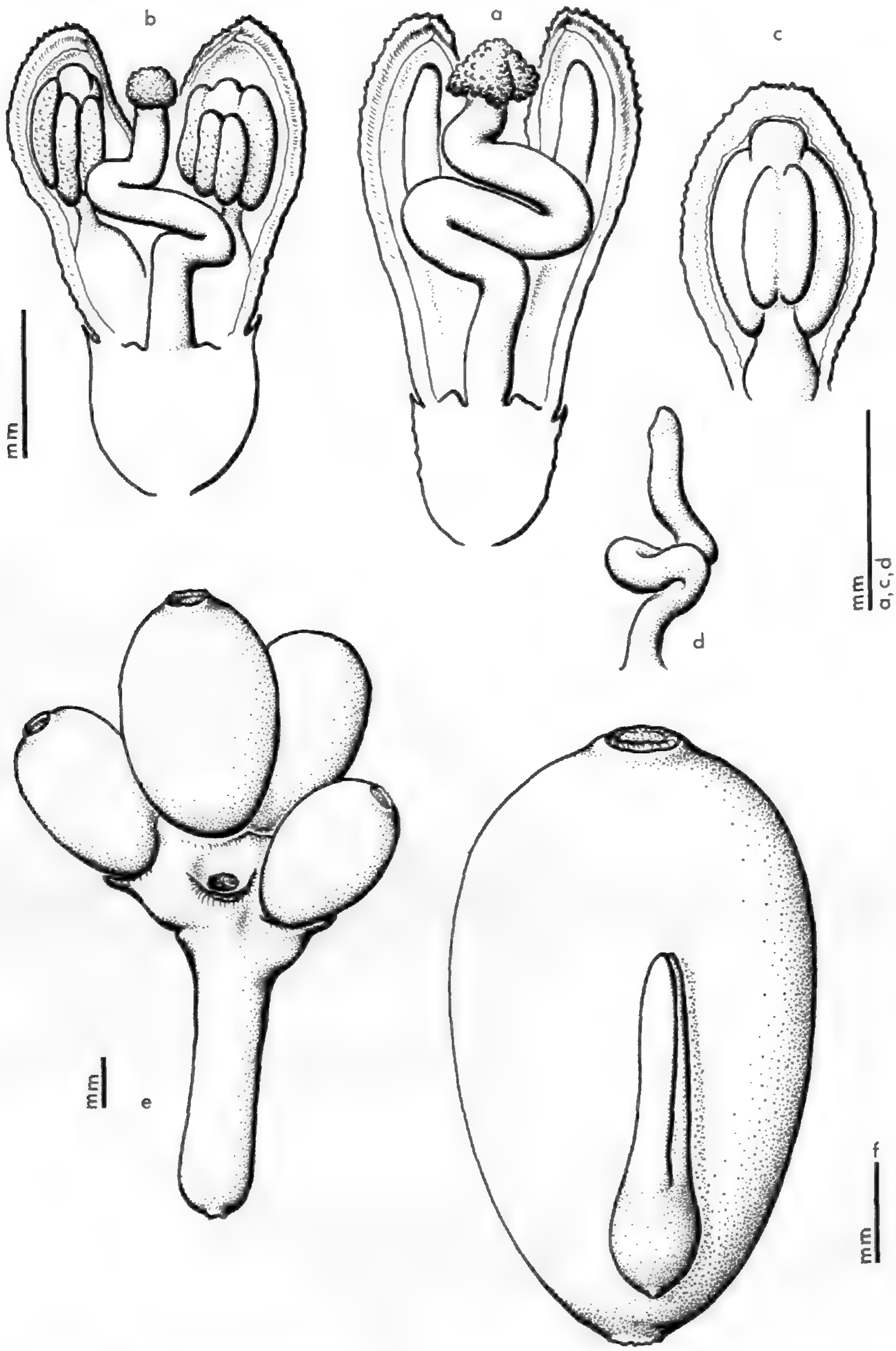

FIGURE 8. **Cladocolea coyucae:** a, pistillate flower, longitudinal section (*Hinton 6688*, K); b, staminate or hermaphroditic flower, longitudinal section (*Hinton 3958*, K); c, stamen and subtending petal (*Hinton 4777*, G); d, style of same collection; e, mature infructescence (*Hinton 3958*, K); f, fruit and embryo (*Hinton 5554*, K).

GH, MICH, MO, NY). PUEBLA: Coxcatlán, on *Heliocarpus*, *Purpus 4191* (BM, F. UC).

5. **Cladocolea cupulata** Kuijt, sp. nov. FIGURE 9.

TYPE: *McVaugh 21127* (see below).

Dioecia, pendula, sympodialis; rami vetustiores scabri. Folia decussata, pendula, coriacea, taeniata vel falcata, ad 140 × 10 mm., apice

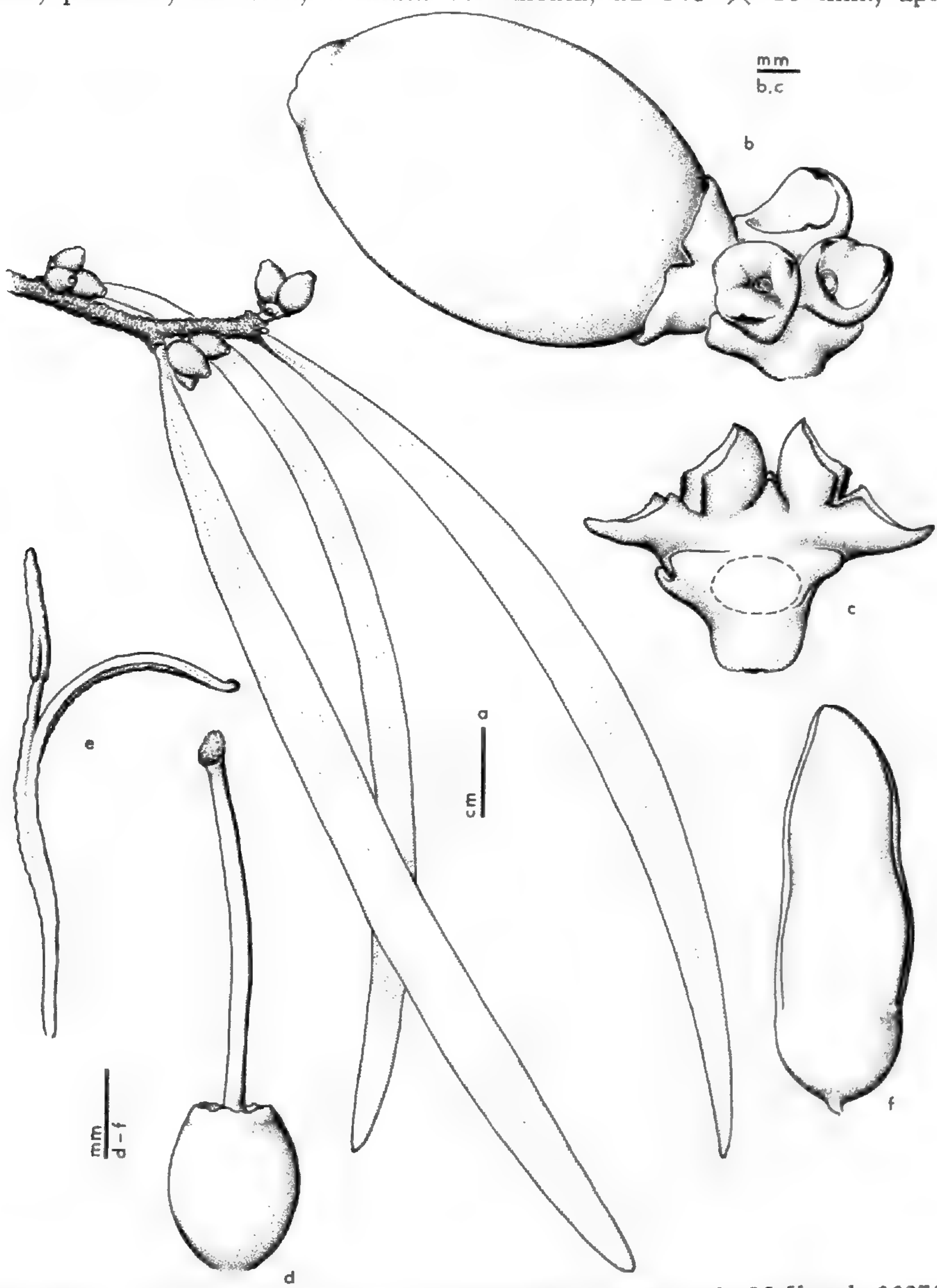

FIGURE 9. **Cladocolea cupulata** (a, *McVaugh 21127*; b–f, *McVaugh 23273*; both MICH): a, habit, pistillate plant in fruit; b, infructescence, three fruits removed; c, same, all fruits removed and lowest cupule cut away (broken line); d, gynoecium; e, petal and aborted anther; f, mature embryo.

basique acuta. Inflorescentia pistillata brevis validaque, axis 3–5 mm. longa, floribus binis ad quaternis, structuris cupulatis insidentibus. Flos femineus fere 8 mm. longus; stylus rectus, 4.5 mm. longus; stigma capitatum; staminodia magna. Fructus ovoideus, 10 × 7 mm., cupula accreta suffultus.

A dioecious, pendent, rather coarse mistletoe 50–70 cm. long, with sympodial growth; older branches terete with rough, gray and cinnamon-brown surface; no basal or stem roots seen; craters conspicuous. Leaves opposite, up to 140 × 10 mm., rather thick, pendent, ribbon-shaped, often somewhat falcate, tapering gradually into an acute apex and base; petiole lacking; leaf margin thickened; venation obscure except for several parallel veins near base. Pistillate inflorescence short and stout, 1–3 per axil of persistent leaf on year-old growth, developing only after full expansion of branches; axis 3–5 mm. long with 2–4 flowers, each flower in a cuplike structure, the cups decussate. Pistillate flowers nearly 8 mm. long, probably hexamerous; petals very slender, with large staminodia which have clearly discernible filaments; ovary 2 mm. long, calyculus somewhat dentate; style straight, 4.5 mm. long, almost as long as the petals; stigma capitate, well differentiated. Fruit 10 × 7 mm., ovoid, smooth, the enlarged, subtending cupule usually rupturing in two places; embryo 4.5 mm. long, the two cotyledons 3.5 × 1.5 mm., very flat, rather blunt-tipped. Staminate plant unknown.

Cladocolea cupulata is an extremely clearly marked species with a puzzling inflorescence morphology. The peduncle is a saddlelike structure, holding the four flowers in bays. I have not been able to identify the bracts which one would expect below the flowers; however, between the upper two cupules and alternating with them are two triangular organs which may be leaflike. The young cupules may consist of a bract. The inflorescence as a whole, therefore, is an indeterminate one. A staminate plant is unfortunately not available. *C. cupulata* would seem to be related to *C. grahami* and *C. pringlei*.

Mexico. JALISCO: pine forests on rolling mountain summits 6 mi. NW of Cuautla, on *Pinus*, 1700 m., *McVaugh 21127* (MICH, holotype of *C. cupulata*), pine-oak forest, hills 7–8 km. NW of Cuautla, on *Pinus*, 1850 m., *McVaugh 23273* (MICH).

6. **Cladocolea dimorpha** Kuijt, sp. nov. FIGURE 10.

TYPE: *Smith, Peterson, & Tejeda 4127*. **Mexico.** PUEBLA: Tehuacan area, Leucho Diego, S of Coxcatlán on Cerro Ajuereado and in the adjacent valley, 1000–1800 m. (G, holotype; F, NY, US, isotypes).

Sympodialis, caules teretes, ut videtur sine radicibus, recti, juveniles capillis brevibus remotis. Folia alterna, primaria solum in innovationibus vertentibus, 20 × 30 mm. vel minora, lanceolata, apex acutus, apiculo parvo; folia secundaria paulo minora, solum ad ramos anniculos. Inflorescentiae primariae permanenter orientes ad innovationes vertentes,

singulae axillares, simpliciter dichasiales; flores sessiles, laterales bracteis persistentibus; inflorescentiae secundariae ad ramos anniculos; folia bina ad quaterna ad partem inferiorem pedunculi, flores 3–5 in capitulum par-

FIGURE 10. **Cladocolea dimorpha** (*Smith, Peterson, & Tejeda 4127*, G): a, diagrammatic representation of the distribution of primary inflorescences (current growth) and secondary inflorescences (year-old growth); b, primary inflorescence and axillant leaf; c, secondary inflorescence, with leaf scar below; d, flower, longitudinal section.

vum congesti. Flos 3 × 1 mm.; petala 4; antherae petalaque monomorphica. Stylus ipsum supra antheras acute contortus, praeterea plus minusve rectus.

A branched plant at least 40 cm. long, with sympodial growth; stems terete, straight, with widely spaced, short hairs when young, but from second season smooth, light brown, and with many lenticels; apparently without roots. Leaves alternate; primary leaves only on current growth, 20 × 30 mm. or less, glabrous but with somewhat granular surface, narrowly lanceolate, the apex acute with small tooth and the base narrow and tapering; discrete petiole absent; secondary leaves along year-old stems, similar but smaller, more oblanceolate, and with more rounded apex. Inflorescences of two types: (1) primary, developing continuously on current growth, one in the axil of all except the first several leaves of a twig, being simple dichasia of 3 sessile flowers, the 2 lateral flowers each subtended by a slightly shorter lanceolate bract, and (2) secondary, on year-old growth only, leaving craters; 2–4 leaves on lower part, one often at very base, the 3 to 5 flowers in a small capitulum, the lowest flowers subtended by foliar or smaller bracts. Flowers 3 × 1 mm. in bud; anthers and petals monomorphic, the 4 petals seemingly sessile but attached nearly half-way up the anther by a very short and slender filament; filament cushion or ridge below anther; pollen sacs 4, the inner ones half the size of the outer ones; connective not extended; pollen trilobate, lacking obvious triradiate groove or triangle; ovary ca. ⅔ mm. long, calyculus slightly dentate; style reaching to above the anthers, more or less straight up to that point but then bent sharply; stigma well developed, capitate, minutely papillate; nectary ring smooth.

Although no fruits are present on the single known collection, the well differentiated style, stigma, and anthers suggest that the flowers of *Cladocolea dimorpha* are hermaphroditic. If this is true, a degree of affinity to *C. inconspicua* and *C. inorna* would seem to be indicated; both of these species also have 4-partite flowers with monomorphic stamens, as does *C. dimorpha*. The only other *Cladocolea* with dimorphic inflorescences is *C. oligantha*, where the differences are less striking than in *C. dimorpha*.

7. **Cladocolea glauca** Kuijt, sp. nov. FIGURE 11.

TYPE: *Arsène 1749/2* (see below).

Tenuis, volubilis, glabra, dioecia; rami vetustiores radices gerentes. Folia primaria glauca, lanceolata, ad 25 × 7 mm.; folia secundaria bina in inflorescentia, oblanceolata-obovata. Inflorescentia ad ramos anniculos, spicam breviter pedunculatam, vulgo solitariam efformans; bracteae caducae. Flores in inflorescentia ca. 6, 5 mm. longi, hexameri; stamina dimorphica; stylus florum pistillatorum valde flexuosus. Fructus 4 × 5 mm.

Dioecious, slender, completely glabrous plants with voluble twigs; bark light brown, smooth, later peeling off in long, gray patches revealing brown,

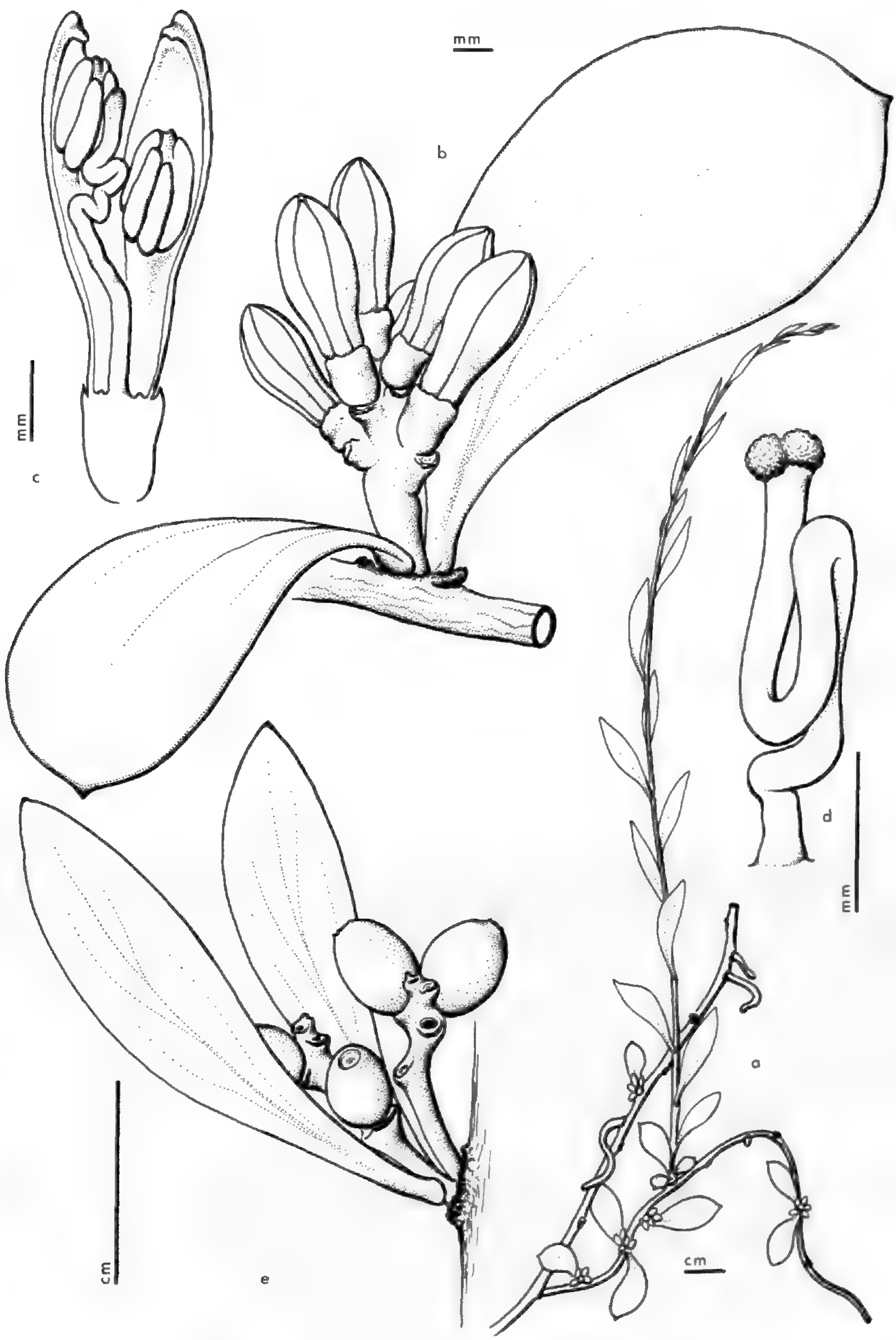

FIGURE 11. **Cladocolea glauca:** a, habit, staminate plant (*Arsène 1749/2*, BM); b, inflorescence, same collection; c, staminate flower, longitudinal section, same collection; d, style of pistillate flower (*Nicolas s.n.*, BM); e, two infructescences, one leafless, same collection.

reticulate, subdermal tissue; some stem roots on year-old and older growth; axillary cushions nearly indistinguishable, but craters on older twigs fairly conspicuous. Primary leaves apparently dropped at end of first growing season or soon after, up to 25 × 7 mm., glaucous, lanceolate, with acute apex and base; petiole ca. 2 mm. long; venation pinnate but only midvein visible; secondary leaves oblanceolate to obovate, with obtuse apex and acute base; petiole 1 × 1 mm., usually 2 leaves per spike; both primary and secondary leaves with narrow, leathery margin. Inflorescences only on year-old wood and (few) on two-year-old wood: staminate inflorescence a pedunculate (1–2 mm.) spike, solitary, the foliage leaves completely basal and seemingly emerging from crater; pistillate inflorescence resembling staminate, but peduncles up to 5 mm. long, at least 1 mm. thick, a superposed, second spike sometimes developing; in both cases flowers ca. 6 per spike, sessile, and subtended by caducous scalelike bracts, spikes determinate. Staminate flowers: mature bud ca. 5 mm. long, obovate; petals 6, with hooded apex; anthers 1.5 mm. long, inserted ½ or ⅔ the distance from the base (stamens dimorphic), filament very short or lacking; connective not projecting, the 2 outer pollen sacs slightly longer than the 2 inner ones; the ovary 1 mm. thick and slightly longer, calyculus irregularly dentate to smooth; style reaching to middle of upper anthers, distal half much convoluted; stigma not differentiated. Pistillate flowers: petals 6, 3 mm. long; style doubled back upon itself for nearly its entire length; stigma capitate, well differentiated, papillate. Fruit ca. 4 × 5 mm., smooth, ellipsoid.

A rather small species related to both *Cladocolea tehuacanensis* and *C. pedicellata*, differing from the former in its fleshy, broad leaves and short spikes and flowers, and from most of the latter in its sessile, small flowers which are obtuse in bud and have a much convoluted style. The material available, as in many *Cladocolea* species, is unfortunately inadequate. Thus I cannot be certain that the superposed pistillate spikes have any foliar leaves; it seems to me that they are leafless. The fruits drawn are not quite mature.

Mexico. PUEBLA: Huejotzingo, near Puebla, on *Crataegus*, 2900 m., *Arsène 1749*(2) (US, holotype of *C. glauca*; BM, GH, NY, isotypes); vicinity of Puebla, Cerro Tepoxuchil, 2330 m., *Arsène 2268* (US); Tepoxuchil, on *Acacia*, *Nicolas* (BM).

8. **Cladocolea gracilis** Kuijt, sp. nov. FIGURE 12.

TYPE: *Rzedowski 17518* (see below).

Dioecia, glabra, sympodialis; rami tenues, teretes. Folia alterna, linearia, 10–20 × 1–2 mm., impetiolata. Inflorescentia determinata, ad partes anniculos vel vetustiores, basi foliis ca. 6; pistillata axi gracillima attenuata, fructifera ad 20 mm. longa, floribus 3–4; staminata brevior, floribus ad 6. Flos hexamerus, ca. 5 mm. longus; stylus floris pistillati valde convolutus, staminati subrectus. Staminodia floris pistillati lori-

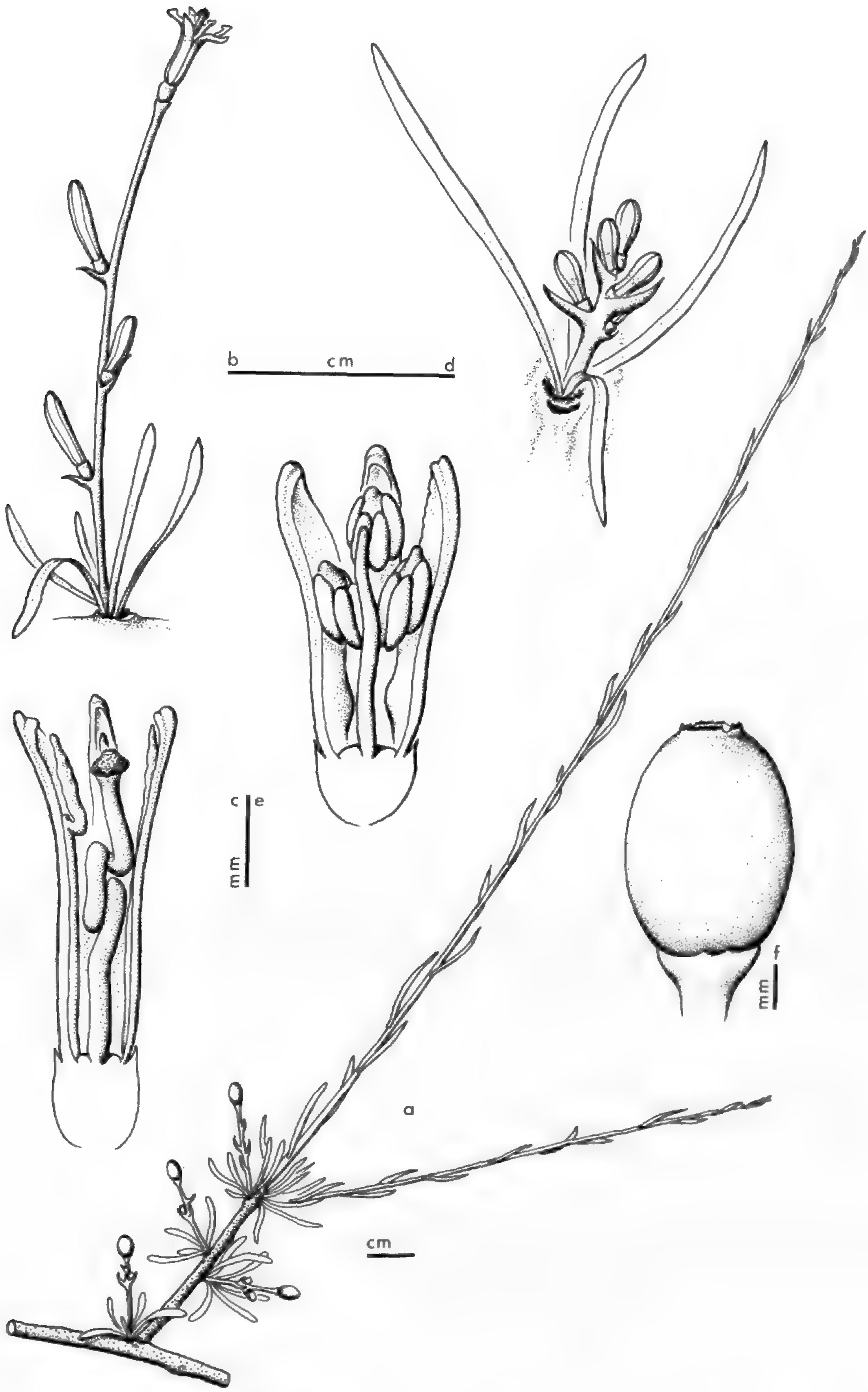

FIGURE 12. **Cladocolea gracilis:** a, habit, pistillate plant (*Rzedowski 17518*, MICH); b, pistillate inflorescence (*Rzedowski 22618*, MICH); c, pistillate flower, longitudinal section, same collection; d, staminate inflorescence, same collection; e, staminate flower, same collection; f, fruit (*Rzedowski 17518*, MICH).

formia; antherae floris staminati planis duobus, inaequalibus. Fructus ovoideus, 6 × 4 mm.

Dioecious, completely glabrous mistletoe about 1 m. in size, pendent, with sympodial growth; branches rather straight, terete, brown, dotted with small lenticels above in the first season, with occasional stem roots on older growth and larger roots at base of plant; craters discernible but not striking. Leaves alternate, with primary leaves only on current growth, 10–20 × 1–2 mm., linear, with acute or somewhat rounded apex; petiole absent. Inflorescences on one-year-old growth and older, with up to half a dozen secondary leaves crowded at the base of the peduncle: pistillate inflorescence with very slender and elongated axis up to 15 mm. long at anthesis, reaching up to 20 mm. in fruit; flowers 3–4, ebracteolate, sessile in axils of acicular bracts spaced along upper half of inflorescence, except for the very prominent terminal flower, which is sessile in a small cuplike structure at the tip of a 2–4 mm. pedicel; staminate inflorescence shorter, with up to 6 flowers, the bracts larger, sometimes almost foliaceous. Staminate flowers yellow, hexamerous, 4.5 × 1 mm., the bud oblong; anthers sessile or nearly so, at two different heights, both above middle of petal but of the same shape; filament buttress prominent; pollen trilobate, smooth, with faint triradiate groove but no triangular prominence; ovary 0.5 mm. long; style more or less straight; stigma undifferentiated. Pistillate flowers greenish, hexamerous, nearly 5 mm. long, very slender; petals very narrow, ca. 3.5 mm. long, staminodia narrow, strap-shaped, reaching the petal tips, their filaments often twisted at anthesis; ovary less than 1 × 1 mm., calyculus smooth; style ca. 2.5 mm. long, strongly convoluted in upper ⅔; stigma capitate, somewhat pointed and lobed, with tubercular, dark surface reaching nearly to the petal tips. Fruit 6 × 4 mm., smooth, ovoid, but with rather blunt apex.

This extraordinary species at first sight reminds one of a larch because of its very narrow leaves and its clearly separated long shoots and short shoots, the latter being reproductive.

Mexico. GUERRERO: road above Canyon de Zopilote 8 km. E of Xochipala on way to Filo del Caballo from Milpillas, 850 m., *Breedlove 35998* (CAS); Canyon de Zopilote, near Milpillas, municipality of Zumpango del Río, on *Randia*, 750 m., *Rzedowski 22618* (MICH). JALISCO: municipality of Tecalitlán, near Gallardo, 10 km. NW of Tepalcatepec (Michoacán), on *Colubrina*, 500 m., *Rzedowski 17518* (MICH, holotype of *C. gracilis*). MICHOACÁN: Tancitaro region, municipality of Apatzingán, La Majada, 1200 ft., *Leavenworth & Hoogstraal 1410* (F, MO); old lava flow 4 mi. NW of Apatzingán, 300 m., *McVaugh 17937* (MICH); Tepalcatepec, flat areas near settlement, on *Podopterus mexicanus*, 400 m., *Rzedowski 16623* (MICH).

9. **Cladocolea grahami** (Bentham) Van Tieghem, Bull. Soc. Bot. France 42: 167. 1895. FIGURES 13 & 14.

Loranthus grahami Bentham, Plantae Hartweg. 62, 63. 1845.

FIGURE 13. **Cladocolea grahami:** a, habit, staminate plant (*Pringle 6987*, P); b, fruit and embryo (*Graham 235*, K); c, pollen grain (*Pringle 6987*, G).

Struthanthus grahami (Bentham) Standley, Contr. U. S. Natl. Herb. **20**(6): 212. 1919.

Oryctanthus grahami (Bentham) Engler in Engler & Prantl, Nat. Pflanzenfam. ed. 2. **16b**: 174. 1935.

TYPE: *Graham 235* (see below).

Large, coarse, dioecious plants, glabrous throughout, with possibly sympodial growth; stems terete, chestnut brown, straight or voluble, with stem roots on year-old growth and older; young, voluble shoots originating subterminally or laterally, growing out for 40–50 cm., not immediately producing stem roots or inflorescences; stem epidermis first smooth, in second year and later exfoliating in irregular, long strips, revealing a fine, brown, honeycomblike subdermal cellular structure; older stems sometimes with low ridges and with round lenticels; craters extremely conspicuous at base of innovations and inflorescences. Leaves irregularly decussate to quite irregular, yellow-green when fresh, 7 × 2(–4) to 14 × 3 cm., leathery, lanceolate, usually with attenuate apex and base; petiole ca. 5 × 2 mm.; margin distinct; venation pinnate, midrib reaching apex or nearly so, often multiple at base. Staminate inflorescence up to 20 mm. long, peduncle 5 mm., first solitary in leaf axils, later in crowded groups of 4–6 per leaf axil; inflorescence bracts mostly caducous but persistent above, very small; 10–12 flowers per spike, the lowest paired, the upper ones alternate, and one flower in a terminal position, subtended by one or sometimes 2 unequal bracts, the other flowers oblique; pistillate inflorescence up to 15 mm. long, peduncle 1–2 mm., basic structure as in staminate, flowers 7–11, usually paired. Staminate flowers sessile, 4–7 × 2–3 mm., 6-merous, the buds ovate; calyculus with smooth edge; stamens strongly dimorphic; anthers at middle or near apex of petals, with 4 approximately equal pollen sacs; connective terminating in a very short cone; pollen with triradiate groove and included triangular prominence (FIGURE 13c); style somewhat undulate; stigma undifferentiated, reaching to base of upper anthers. Pistillate flowers ca. 5 mm. long; petals 6, with strap-shaped aborted anthers; ovary 1 × 1 mm.; style much contorted in mid-portion; stigma capitate, well differentiated, somewhat lobed. Fruit ca. 12 × 6 mm., dark-colored, ellipsoid, calyculus prominent; embryo clavate, ca. 7 mm. long, dicotyledonous, the cotyledons ⅔ the length of the embryo.

A striking species which can be confused only with *Cladocolea pringlei* or *C. mcvaughii*, and with these only superficially. There seems to be a certain amount of variation in some floral features. Commonly, the tips of petals are held together in the bud by a papillate crest. In one instance (FIGURE 14f), a remarkable tuft of long hairs was observed just above the anthers, a tuft very similar to that in santalaceous flowers (Kuijt, 1969).

Mexico. *Graham 235* (K, holotype of *Loranthus grahami*). GUERRERO. Distr. Mina: Laguna, on oak, 1860 m., *Hinton 10149* (GH, K, MO, NY, US). JALISCO: NW slopes of Nevado de Colima, above Jazmín, 3 mi. below El Isote, on *Quercus*, 2500–2700 m., *McVaugh 10143* (MICH). MEXICO. Distr. Temascaltepec: Nanchititla, on oak, *Hinton 3107* (GH, K, MICH, NY, US); Pantoja, on oak, 1500

m., *Hinton 3550* (GH, K, MICH, US); Cumbre-Trojas, *Hinton 9021* (GH, K, MICH, US). MICHOACÁN: 8–10 mi. NW of Ciudad Hidalgo, a few mi. N of village of San Pedro Aguaro, on *Quercus*, 2500–2700 m., *McVaugh 9999* (MICH). MORELOS:

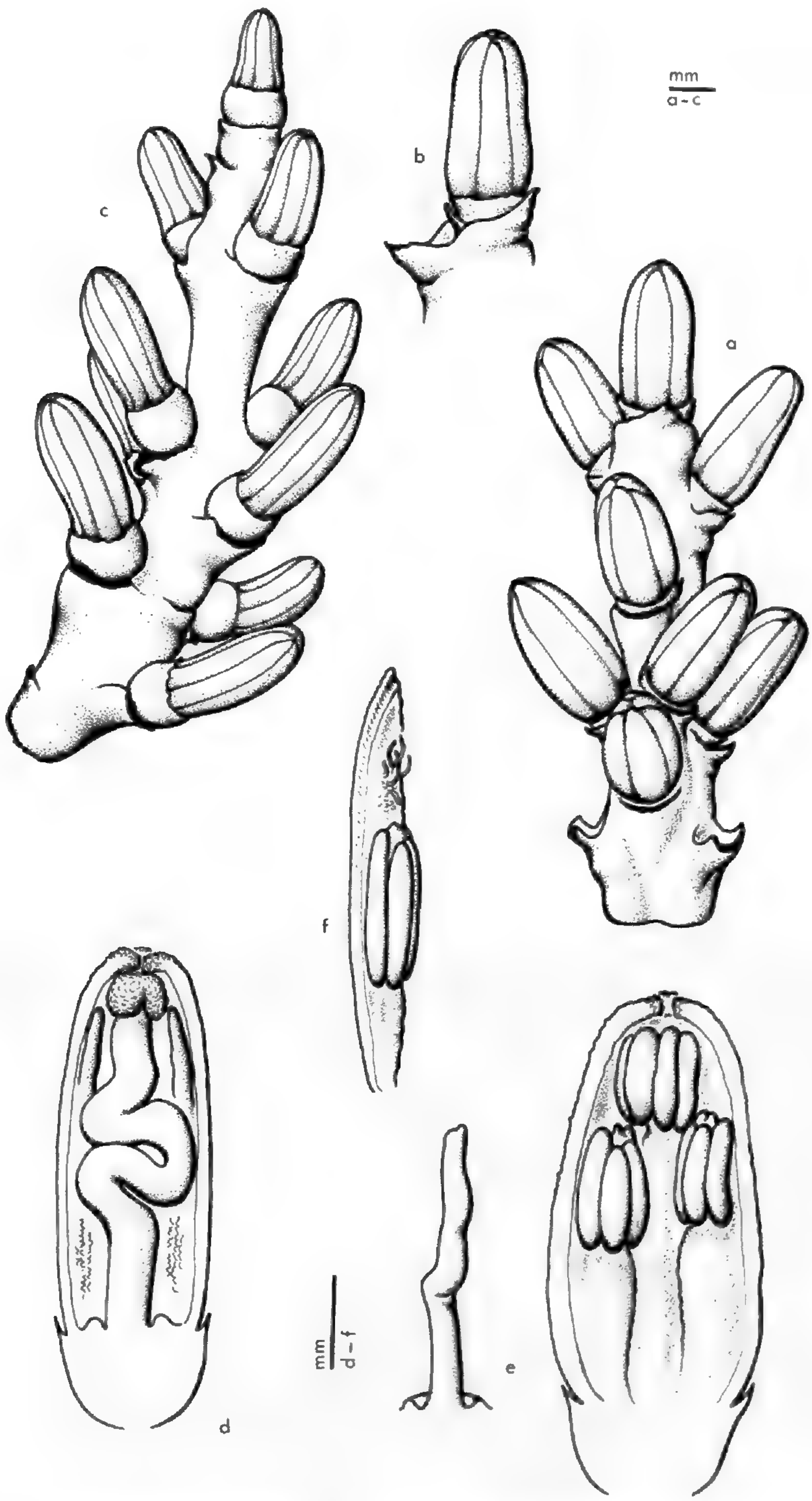

FIGURE 14. **Cladocolea grahami:** a, staminate inflorescence (*Pringle 6987*, G); b, terminal flower of another inflorescence, same collection; c, pistillate inflorescence (*Graham 235*, K); d, pistillate flower, longitudinal section, same collection; e, staminate flower and style, longitudinal section (*Pringle 6987*, G); f, petal and stamen, showing tuft of hairs above anther (*Hinton 3550*, K).

Sierra de Tepoxtlán, on oak, 7500 ft., *Pringle 6987* (BR, C, F, G, GH, GOET, K, M, NY, P, PR, S, UC, US).

10. **Cladocolea harlingii** Kuijt, sp. nov. FIGURE 15.

TYPE: *Harling 6094* (see below).

Scandens, flexuosa, ramosissima, glabra, haud sympodialis; caules quadrangulares, virides. Folia juvenilia prehensilia, matura 3 × 1 cm., obovata; petiolus 4–5 mm., canaliculatus. Inflorescentiae pro axilla 1–4; axis tenuis, quadrangularis; flores ca. 15 pro inflorescentia, singulares, pedicellis ca. 1 mm. insidentes, unus terminalis, reliqui laterales, omnes bractea caduca sub pedicello subtenti. Flores bisexuales; petala 4, 2.5 mm. longa; antherae petalaque monomorphica; stylus rectus, planum antherarum superans. Fructus 4 × 2 mm., ovoideus.

A sinuous, scandent, profusely branching plant, superficially very similar to, but much smaller than, *Struthanthus orbicularis*, completely glabrous, branching not sympodial; stems somewhat quadrangular, green; young leaves on slender branches stiffly recurved, prehensile as in *S. orbicularis*, i.e., the petioles swelling upon contact, allowing the leaf to grasp other objects; epicortical stem roots produced near such grasping leaves and elsewhere. Leaves 3 × 1 cm., blade lanceolate with acute base and apex; leaves occasionally up to 5 × 3 cm., then obovate; petiole 4–5 mm. long, canaliculate; venation pinnate, the single midvein running into apex, very prominent below. Inflorescences 1–4 per axil, one primary, 2 lateral, and one superposed, lacking basal scale leaves or evident craters; axis rather slender, ca. 0.5 mm. thick, quadrangular; flowers single, on 1 mm. long pedicels, in about 7 decussate pairs, and with one terminal, short-stalked flower (inflorescence development acropetal), equally spaced along axis, each lateral flower subtended by a caducous bract, the scar remaining evident below the pedicel. Flowers hermaphroditic, said to be yellowish-green or orange; petals 4, 2.5 mm. long, monomorphic, pointed; anthers also monomorphic, ½ as long as petals, on very slight filament buttress, apparently lacking filament; pollen sacs 4, the inner 2 smaller than the outer 2; pollen with obvious triradiate groove; ovary slightly more than 1 mm. long, less than 1 mm. wide, calyculus smooth; style straight and rather stout; stigma well differentiated, capitate, papillate, reaching to just above the anthers; nectary fleshy, glabrous. Fruit at least 4 × 2 mm., ovate, apparently dark in color, the nectary ring forming a conspicuous "button" at apex.

This remarkable, geographically isolated species must undoubtedly be counted to *Cladocolea*, as indicated by inflorescence morphology, hermaphroditic 4-merous flowers, and monomorphic anthers. Paradoxically, its nearest relative (possibly its derivative) would seem to be *Struthanthus orbicularis*, as shown partly by general appearance, but particularly by the unique mode of parasitism in both mistletoes, where young leaves are used as grappling hooks to capture new host branches.

Ecuador. PROV. LOJA: road from Loja to La Tuna, km. 13–34, 1600–2600 m., *Dodson & Thien 1507* (UBC, UC, US); 16 km. S of Loja, lower than Cajanuma, 2000–2200 m., *Espinosa 16366* (NY); Cariamanga, road to Gonzanamá, 1700 m., *Harling 6015* (S); San Pedro, 2200 m., *Harling 6094* (S, holotype of *C. harlingii*);

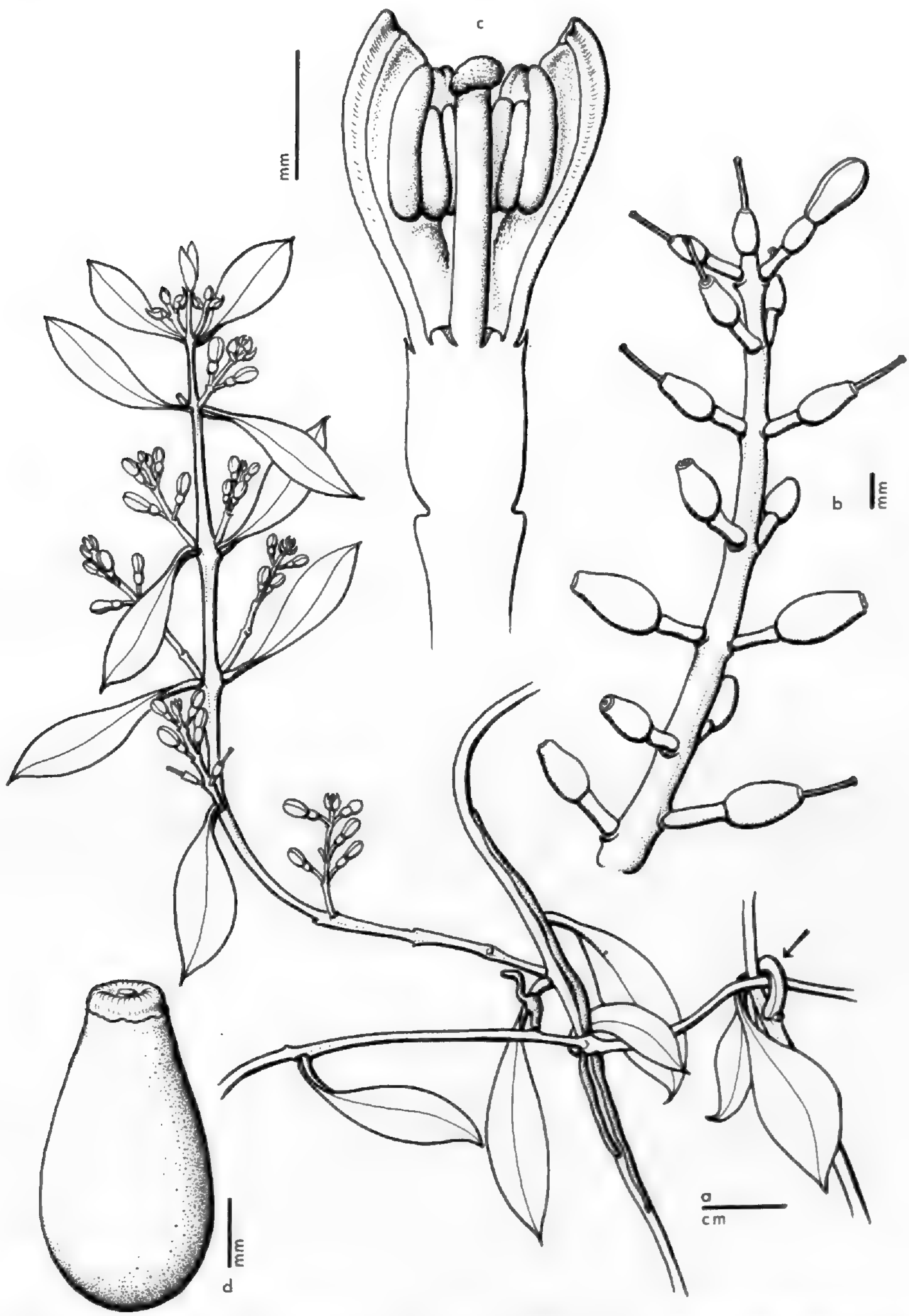

FIGURE 15. **Cladocolea harlingii** (*Harling 6094*, S): a, habit, showing prehensile petiole (arrow), epicortical stem roots, and flowering branch; b, inflorescence with young fruits; c, flower, longitudinal section; d, mature fruit.

Cerro Villonaco, 7–12 km. W of Loja, 8000–9000 ft., *Sparre 16295* (S); Cariamanga, 7210 ft., *Townsend a-27* (US); 46 km. SE of Cariamanga, 1750 m., *Wiens 3800* (UT); 70 km. SE of Pinas, 1500 m., *Wiens 3781* (UT); 28 km. S of Catamayo on road to Macara, on Compositae, 2020 m., *Wiens 3792* (UT); Cerro Villonaco, 7–12 km. W of Loja, 8000–9000 ft., *Wiggins 10964* (UT).

11. **Cladocolea hintonii** Kuijt, sp. nov. FIGURE 16.

TYPE: *Hinton 10148* (see below).

Dioecia, sympodialis; rami teretes, recti, puberuli. Folia decussata vel alterna; folia primaria secundariaque ad 20 × 12 mm., late lanceolata vel obovata, puberula. Inflorescentia pistillata spica pedunculata ad 25 mm. longa; flores 3–5, ad apicem sessiles; folia secundaria nulla vel 1–3, alterna, parte inferiore pedunculi; inflorescentiae solum ad partes anniculos. Flores dense puberuli, 4 × 1 mm., hexameri; petala anguste linearia; stylus tenuis, 3 mm. longus, parte exteriore convolutus.

A dioecious, relatively small mistletoe with sympodial growth, straight, terete, puberulent branches, and puberulent leaves; innovations subterminal, slender; craters fairly obvious; no stem roots seen. Leaves decussate to alternate; primary and secondary leaves approximately the same, the former perhaps somewhat narrower, up to 20 × 12 mm., broadly lanceolate to obovate, the apex usually acute and the base tapering into a petiole ca. 2 × 1 mm.; venation pinnate but obscure. Pistillate inflorescence a spike up to 25 mm. long with 3–5 sessile flowers on distal portion, usually alternate but sometimes subopposite, always with terminal flower; spikes only on year-old growth where primary leaves no longer persist, some spikes lacking foliage leaves, but nearly all with 1–3 alternate leaves on lower half of peduncle. Pistillate flowers densely puberulent, mature bud 4 × 1 mm.; the 6 petals 3 mm. long, narrowly linear, bearing a small, aborted anther above the middle; ovary ca. 1.5 × 1 mm. or narrower; style slender, 3 mm. long, convoluted in distal half; stigma clearly differentiated, somewhat lobed and tubercular; nectary with short hairs. Staminate plant unknown.

It is a pleasure to honor Mr. G. B. Hinton, who seems to have had a special eye for mistletoes in his collecting in southern Mexico. The major set of his mistletoe collections is deposited at Kew and forms the most significant single source, by far, in the present monograph.

Although *Cladocolea hintonii* has clear affinities with *C. loniceroides* and *C. microphylla*, the distinctions are very considerable. *C. hintonii* is sympodial and lacks the involucral leaves or bracts of *C. loniceroides*, while the latter difference also separates it consistently from *C. microphylla*. The fruit and male plant of *C. hintonii* await description.

Mexico. GUERRERO: Distr. Mina, Laguna, on oak, 1860 m., *Hinton 10148* (K, holotype of *C. hintonii*), 1800 m., *Hinton 10151* (NY).

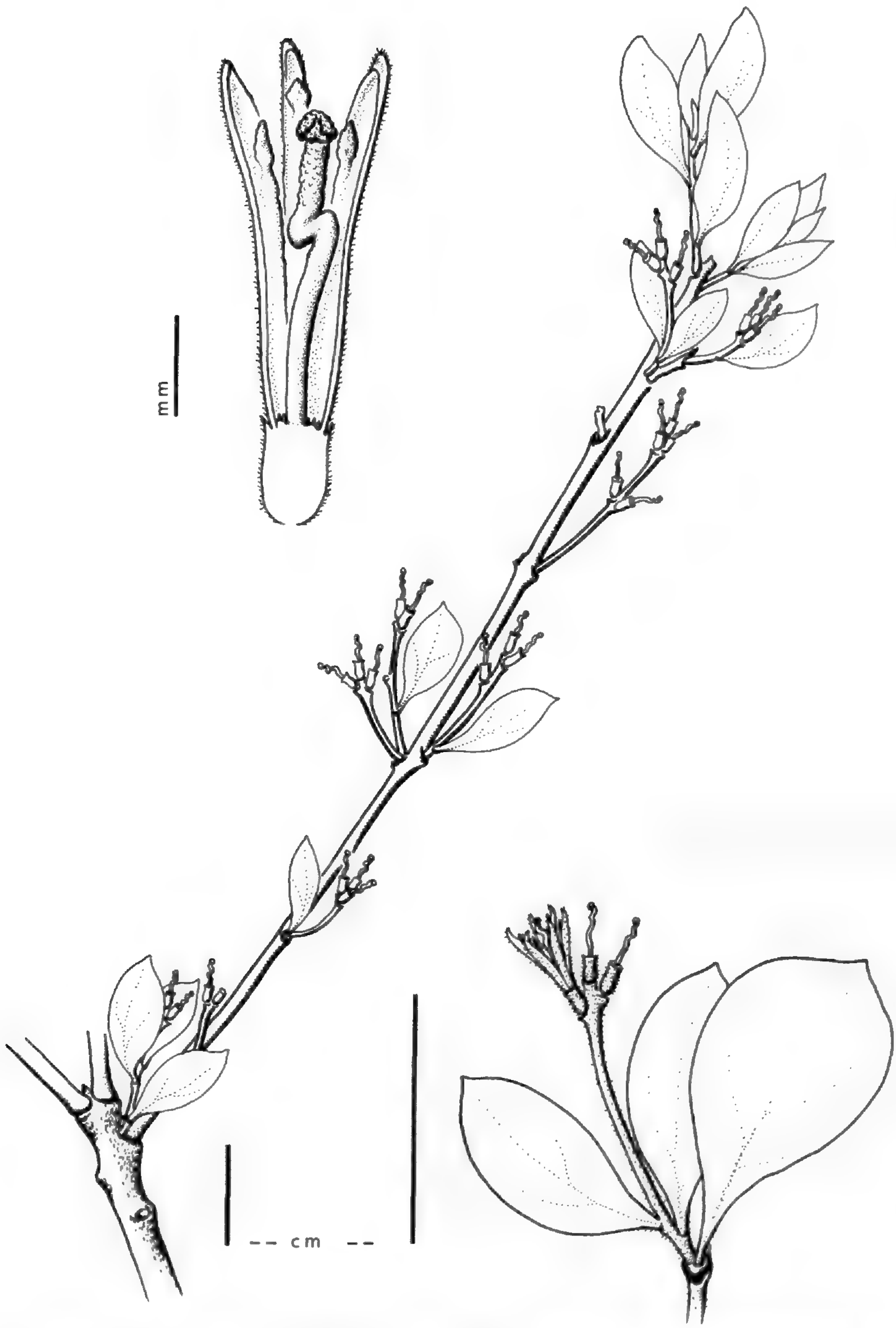

FIGURE 16. **Cladocolea hintonii,** pistillate plant (*Hinton 10148*, K): habit, inflorescence, and sectioned flower.

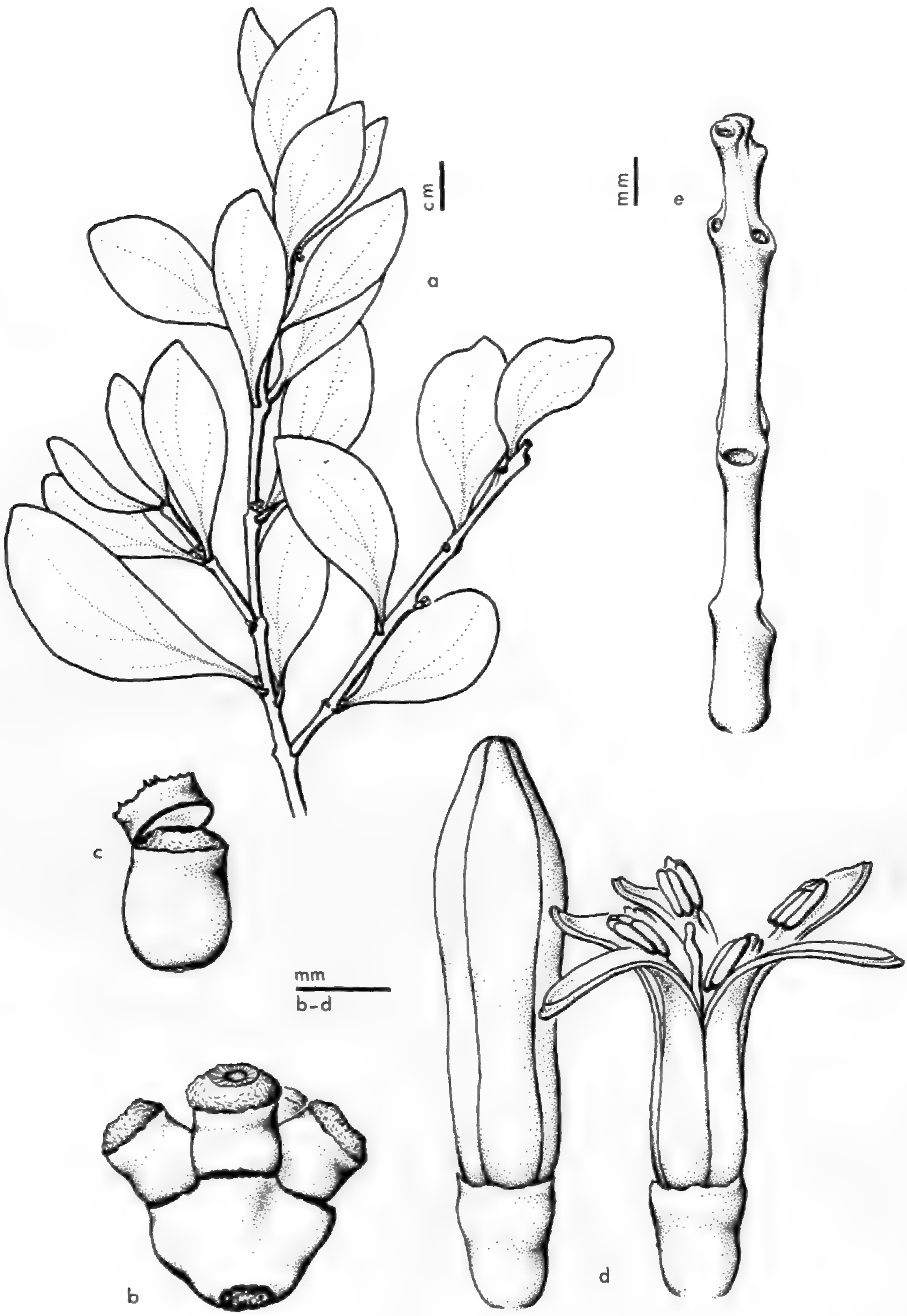

FIGURE 17. **Cladocolea hondurensis:** a, habit (*Yuncker, Dawson, & Youse 6220*, K); b, very young fruit on nearly sessile inflorescence, same collection; c, same, showing circumscissile calyculus; d, staminate flower and bud (*Molina & Molina 13922*, F); e, inflorescence axis, same collection.

12. **Cladocolea hondurensis** Kuijt, sp. nov. FIGURE 17.

TYPE: *Yuncker, Dawson, & Youse 6220* (see below).

Dioecia, glabra, sympodialis. Folia irregulariter decussata vel alterna, subcoriacea, obovata vel lanceolata, rotundata, basi acuta; lamina 40 × 25 mm. Inflorescentia pistillata axillaris, subsessilis, solitaria, floribus ca. 4 sessilibus geminatis. Inflorescentia staminata ad 15 mm. longa, floribus sessilibus, decussatis, paribus ca. 4; flos 6 mm. longus; petala 5; antherae biseriatae, sacculi polliniferi quaterni; stylus fere rectus.

Plant dioecious, leafy, and glabrous, with sympodial growth; young stems straight, somewhat grooved or ridged; craters conspicuous around vegetative laterals, scarcely so around spikes; no stem roots or basal roots seen. Leaves irregularly decussate to alternate, rather leathery, the leaf blade ca. 40 × 25 mm., obovate to lanceolate, the apex rounded and the acute base tapering into a petiole 4–5 mm. long and at least 1 mm. thick; venation pinnate but rather obscure. Staminate inflorescence up to 15 mm. long, with about 4 pairs of decussate, sessile flowers, lacking terminal flower(?). Pistillate inflorescence axillary, on year-old wood only, virtually sessile, solitary, with apparently 4 sessile flowers arranged in two decussate pairs, the flowers in axils of caducous scale leaves. Staminate flowers: mature bud 6 mm. long; petals 5; anthers at two heights, just above middle and near tip of petals, each with 4 equal pollen sacs; connective scarcely protruding; pollen smooth, trilobate, with faint triradiate groove; ovary 1 mm.; calyculus smooth; style more or less straight; stigma undifferentiated, nearly reaching the upper anthers. Pistillate flowers: ovary slightly longer than 1 mm., the flaring, dentate calyculus apparently deciduous in circumscissile fashion, leaving a rough, circular scar; no other pistillate flower or fruit details known.

This species, although very imperfectly known, may be rather distantly related to *Cladocolea mcvaughii*. In superficial appearance it reminds one of an *Antidaphne*, or even *C. andrieuxii*, but the few inflorescences seen leave no doubt that we are concerned with a distinct species of *Cladocolea*. Indeterminate spikes are also known from *C. cupulata*, *C. mcvaughii*, and *C. pringlei*.

Honduras. DEPT. LA PAZ: Cordillera Guajiquiro, 5 km. from Sabanetas, on *Quercus*, 2100 m., *Molina & Molina 13922* (F). DEPT. COMAYAGUA: hills above plains of Siguatepeque, near El Achote, 1350 m., *Yuncker, Dawson, & Youse 6220* (GH, holotype of *C. hondurensis*; F, K, isotypes).

13. **Cladocolea inconspicua** (Bentham) Kuijt, comb. nov. FIGURES 1a, 18, 19.

Loranthus inconspicuus Bentham, Bot. Voy. Sulphur. 102. 1844 [1845].
Phthirusa inconspicua (Bentham) Eichler in Martius, Fl. Brasil. **5**(2): 67. 1868.

Struthanthus inconspicuus (Bentham) Standley, Contr. U. S. Natl. Herb. **20**: 212. 1919.

TYPE: *Hinds 346* (see below).

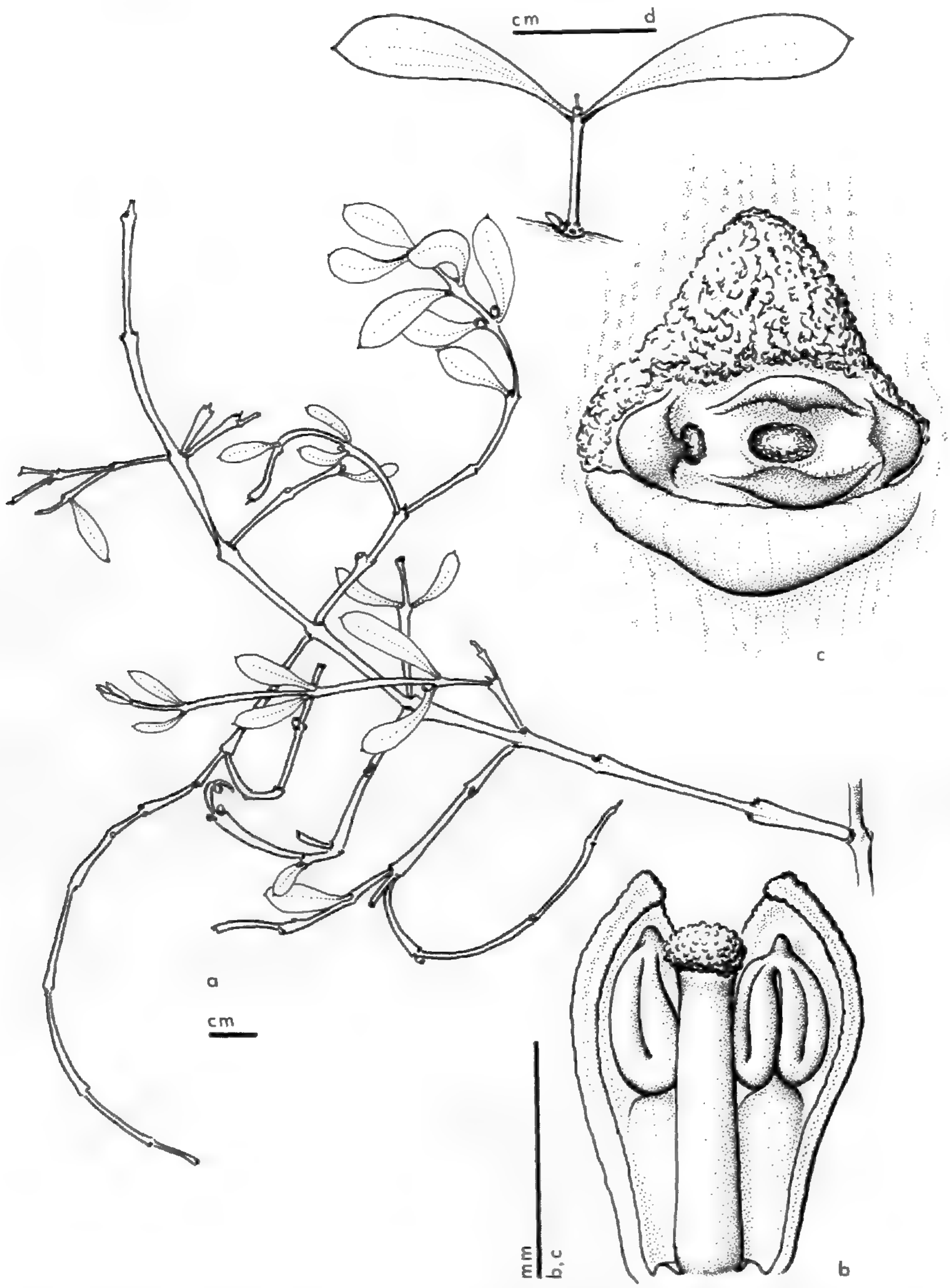

FIGURE 18. **Cladocolea inconspicua:** a, habit (*Hinds 346*, K); b, flower, longitudinal section (*Ortega 632*, K); c, axillary cushion, bracts, and flower scars (*Palmer 531*, BM); d, lateral branch with two leaves and single, terminal flower (*Wiens 2494*, WTU).

Plant a small, much branched, stiff mistletoe with simple graftlike haustoria lacking any sign of other roots (FIGURE 1a), with sympodial growth, each twig with up to 12 internodes, more commonly with about 6, the lateral branches paired; stems somewhat compressed ancipitally when young, becoming terete in age, then with irregular, longitudinal cracks; young stems greenish-gray, essentially glabrous but for papillar bulges of epidermal cells; stomata (and other epidermal cells) in regular longitudinal files, the guard cells transversely oriented; axillary cushions distinct (FIGURE 18c), triangular, light brown and somewhat hairy, on young twigs only, but craters scarcely discernible. Leaves decussate, up to 22 × 9 mm., usually much smaller, glabrous, oblanceolate to obovate, with rounded to acute or mucronate apex, often with callose "nail," the latter a remnant of the densely hairy scalelike tip visible in young, expanding leaves, tapering at base into a petiole 2–3 mm. long; midvein running into the apex, sometimes with 2 additional veins standing out. Flowers hermaphroditic, occurring singly in the axils of foliage leaves, sometimes followed by 2 more developing in the axils of the paired scale leaves of the first flower; each flower sessile but subtended by 2 minute scale leaves with white-hairy margins and papillate dorsal surfaces; some older nodes showing evidence of further flower production. Mature bud 2.5 mm. long; petals 4, rarely 3; anthers 1 mm. long, monomorphic on very short filaments attached at the middle of the petal with conspicuous buttresses below, connective projecting well above the 4 pollen sacs; pollen smooth, with three rather bulbous lobes, each with a circular, shallow depression; ovary 1 mm.; style straight; stigma just above anthers, well differentiated, papillate; nectary smooth. Fruit 2 × 3 mm., red, smooth, broadly ellipsoid; embryo nearly spherical but for the 2 cotyledons, 1.5 × 1 mm.

It is indeed tempting to compare *Cladocolea inconspicua* with the remarkable *Ixocactus* (Kuijt, Brittonia 19: 62–67. 1967), which is similar in general appearance, though leafless. *Ixocactus*, however, has a pollen grain which is unique not only in Loranthaceae but also in the Santalales in general; it also has dimorphic anthers, each of which has only 2 pollen sacs, and a conical, short style. The closest relatives of *C. inconspicua* are *C. inorna* and *C. clandestina*.

It is of some interest that an occasional flower develops in a terminal position, between two normal foliage leaves, on a small lateral branch one internode long (FIGURE 18d). The occurrence of such "inflorescences" lends support to the contention that single, axillary flowers represent the final stage in reduction from a several-flowered, determinate inflorescence.

Mexico. Between Tepic and Mazatlán, *Gregg 1116* (MO). GUERRERO: Acapulco and vicinity, *Palmer 531* (BM, F, GH, K, MO, NY, UC, US). NAYARIT: near Mexcaltitlán, *Ortega 6162* (GH, UC, US). SINALOA: vicinity of Culiacán, Yerba Buena, *Brandegee* (UC); Culiacán, *Brandegee* (UC); above Cofradia, NE of Imala, 450 m., *Breedlove 35588* (CAS); vicinity of Labradas, on *Croton niveus*, *Ferris & Mexía 5166* (CAS); Imala, on *Zanthoxylum*, *Gentry 4996* (GH, MICH, NY); Capadero, Sierra Tacuichamona, on *Mimosa palmeri*, *Gentry 5636* (GH, NY); Culiacán and vicinity, 150–500 ft., *Gentry 7056* (CAS, F, GH, MICH, NY, UC, US); San

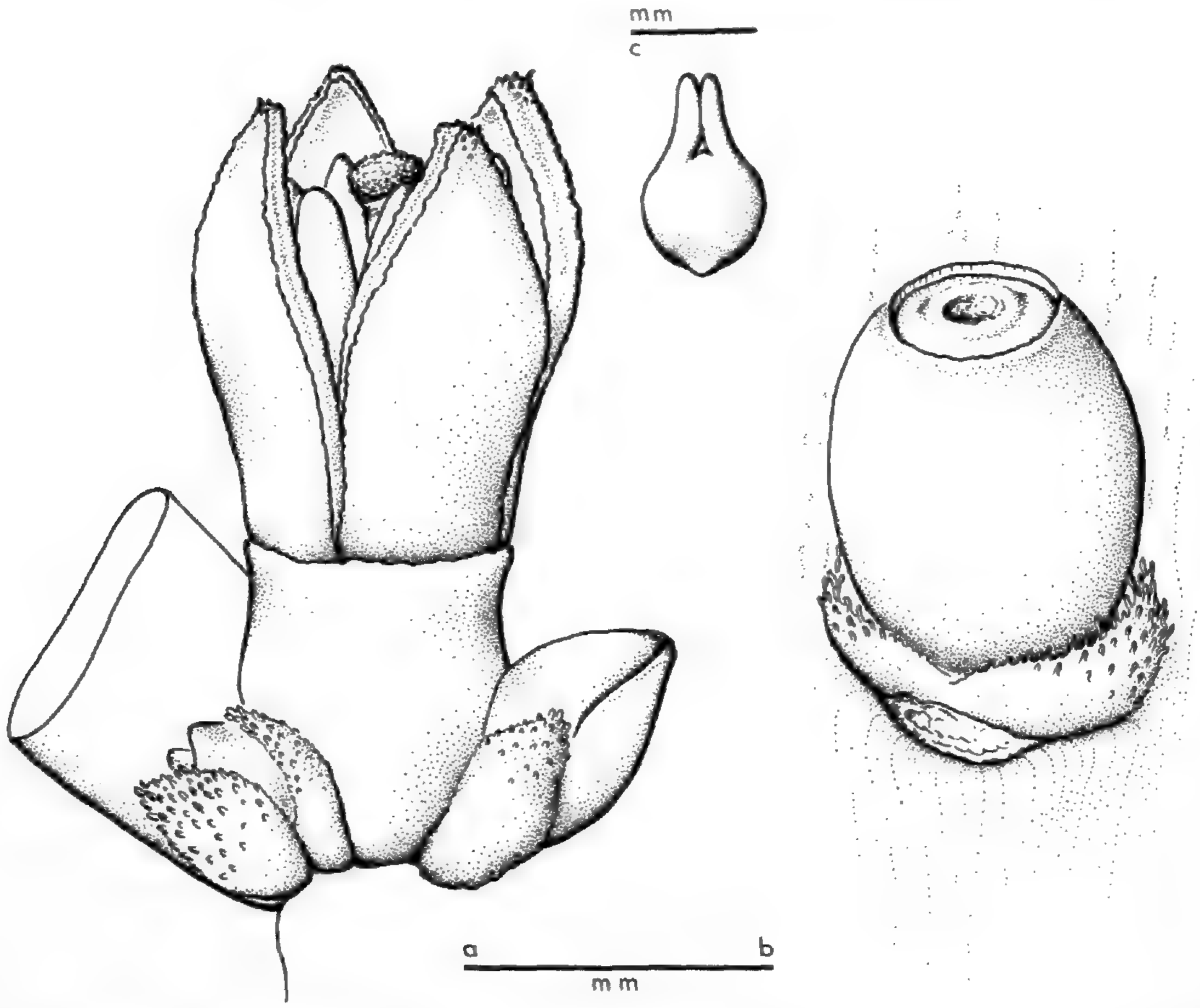

FIGURE 19. **Cladocolea inconspicua:** a, flower with two lateral flower buds (*Ortega 632*, K); b, mature fruit (*Palmer 531*, BM); c, embryo, same collection.

Blas, *Hinds 346* (K, holotype of *Loranthus inconspicuus*); "La Noria" foothills, wooded N slope S of village, 800 ft., *Mexía 321* (C, CAS, MO, UC); trail from Los Labrados to Marisma, 5 m., *Mexía 970* (CAS, F, GH, MO, NY, UC, US); San Ignacio, San Agustín, 185 m., *Ortega 632* (F, K); Culiacán, *Palmer 1796* (GH, US); vicinity of Mazatlán, on *Randia, Rose, Standley, & Russell 13746* (US); ca. 40 mi. N of Mazatlán on Mex. route 15, thorn forest, sea level, *Wiens 2494* (CAS, UC, US, UT; voucher, $n = 8$).

14. Cladocolea inorna (Robins. & Greenm.) Kuijt, comb. nov.

FIGURE 20.

Loranthus inornus Robinson & Greenman, Am. Jour. Sci. **50:** 163, 164. 1895.
Struthanthus inornus (Robins. & Greenm.) Standley, Contr. U. S. Natl. Herb. **20**(6): 212. 1919.

TYPE: *L. C. Smith 122* (see below).

Extremely slender, brittle, profusely branching mistletoe, 56–60 cm. in size, with sympodial branching (no lateral branches formed within each season); stems terete, glabrous, gray-green, with fine longitudinal ridges when dry, apparently lacking both stem roots and basal roots. Leaves irregularly alternate-decussate, the former arrangement predominating, gray-green, the largest leaves up to 15 × 3 mm., oblanceolate, with acute

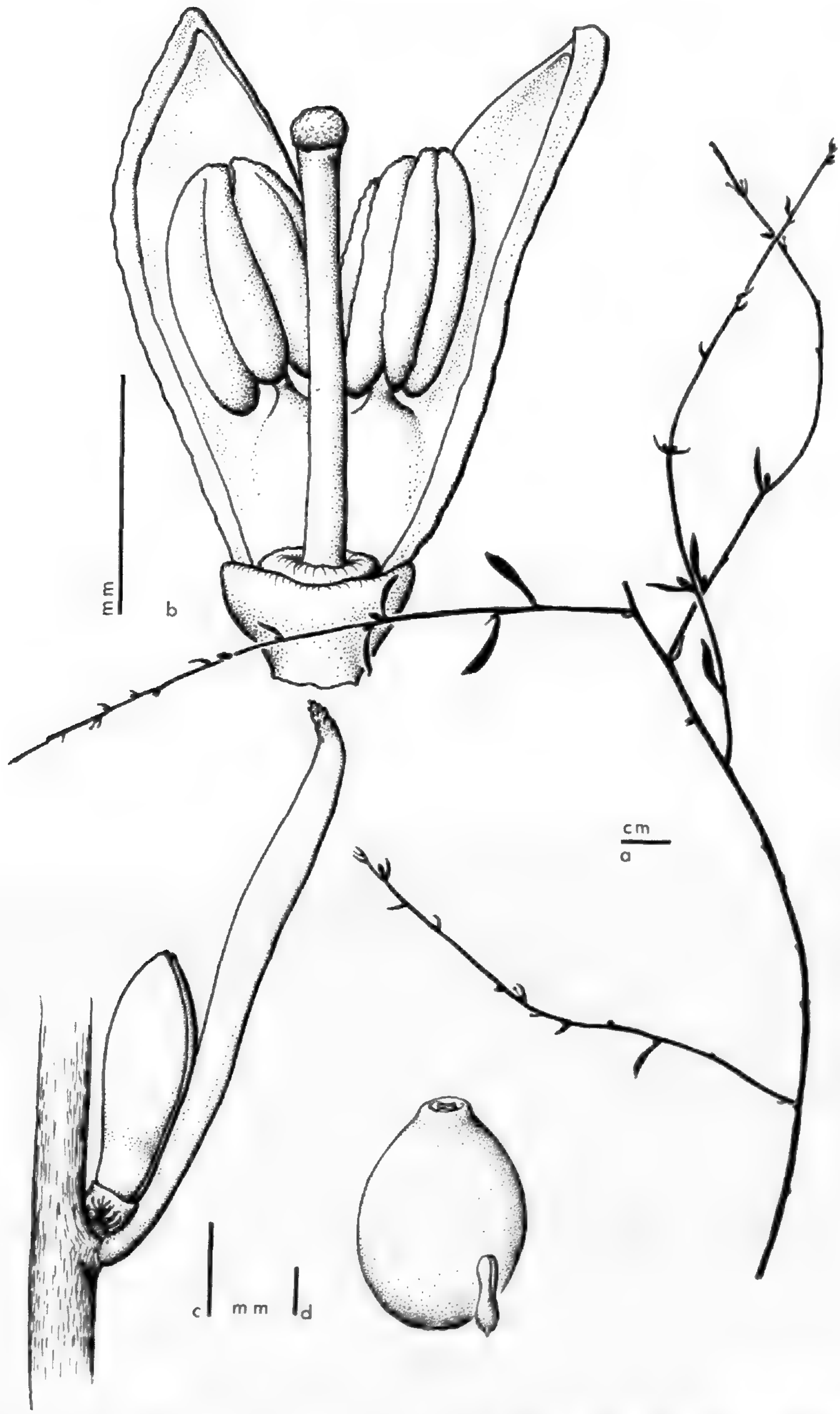

FIGURE 20. **Cladocolea inorna**: a, habit, b, flower with two petals removed, and c, axillary flower bud (all from *Smith 122*, GH); d, fruit and embryo (*McVaugh & Koelz 1019*, MICH).

base and acute, sclerotic, and papillate apex; petiole indistinct or absent; most leaves, however, acicular and about 5 × 1 mm.; youngest leaves, at least on lower portion of each branch, with a fringe of brownish hairs, as on scale leaves; the scale leaves several at very base of laterals, 1 mm. long or less, sclerotic and with reddish-brown laciniate margins. Flowers hermaphroditic, sessile in axils of leaves, commonly single, sometimes followed by later flowers, either in axils of subtending scale leaves or in a superposed position, often flanking the base of lateral branches. Mature buds acute, 3 mm. long, of which ca. ⅙ is ovary; calyculus more or less smooth; petals 4; both petals and stamens monomorphic; filament short, slender, attached about ⅓ the distance from the base of the petal; anther 1 mm. long, with 4 elongate pollen sacs which reach beyond the connective; pollen either of two types or with two faces, one with 3 obscure, circular depressions, the other with faint triradiate line; style straight, 2–2.5 mm. long; stigma small, capitate, just above anther tips; nectary smooth, inconspicuous. Fruit 5 × 3.5 mm., ovoid, smooth and black at maturity, calyculus not prominent; endosperm nearly spherical, embryo dicotyledonous, 1.5 mm. long, both endosperm and cotyledons pink.

Cladocolea inorna is undoubtedly closely related to *C. inconspicua*, as Robinson and Greenman recognized. At the same time there cannot be any question as to the distinctness of the two. *C. inorna* has predominantly alternate leaves that are lanceolate to acicular; terete, smooth stems; and pollen sacs which extend beyond the connective. In contrast, *C. inconspicua* shows consistently paired leaves that are elliptic-obovate; compressed stems with a papillate epidermis; and a projecting connective. Several other minor differences could be added. Another close relative is *C. clandestina*, which, surprisingly, grows in Brazil.

Mexico. JALISCO: mountainsides 6.5 mi. NE of Autlán, near highway pass, on legumes, 925 m., *McVaugh & Koelz 1019* (MICH); N-facing slope 2 mi. W of Autlán, *Wilbur & Wilbur 1666* (MICH); 8 mi. S of Autlán toward La Resolana, on *Cassia*, *Wilbur & Wilbur 2400* (MICH). MICHOACÁN: between Río Tepalcatepec and Arteaga, along highway S from "Cuatro Caminos," 3 km. S of Nueva Italia and 30 km. E of Apatzingán, 225 m., *McVaugh 22521* [4] (MICH). OAXACA: Cuicatlán, 2000 ft., *Smith 122* (GH, holotype of *Loranthus inornus*).

15. **Cladocolea loniceroides** (Van Tieghem) Kuijt, comb. nov.

FIGURES 1b, 21, 22.[5]

Loxania loniceroides Van Tieghem, Bull. Soc. Bot. France **42**: 387. 1895.
Struthanthus loniceroides (Van Tieghem) Engler in Engler & Prantl, Nat. Pflanzenfam. ed. 2. **16b**: 173. 1935.

[4] The collection *McVaugh 22521* is added provisionally only, as it shows some significant differences (densely puberulent; leaves obovate, up to 10 mm. wide, with truncate, mucronate apex; fruit red at maturity) and may, when further material becomes available, warrant nomenclatural distinction.

[5] See also Calderón & Rzedowski, Cact. y Sucul. Mex. **17**: *fig. 59*. 1972.

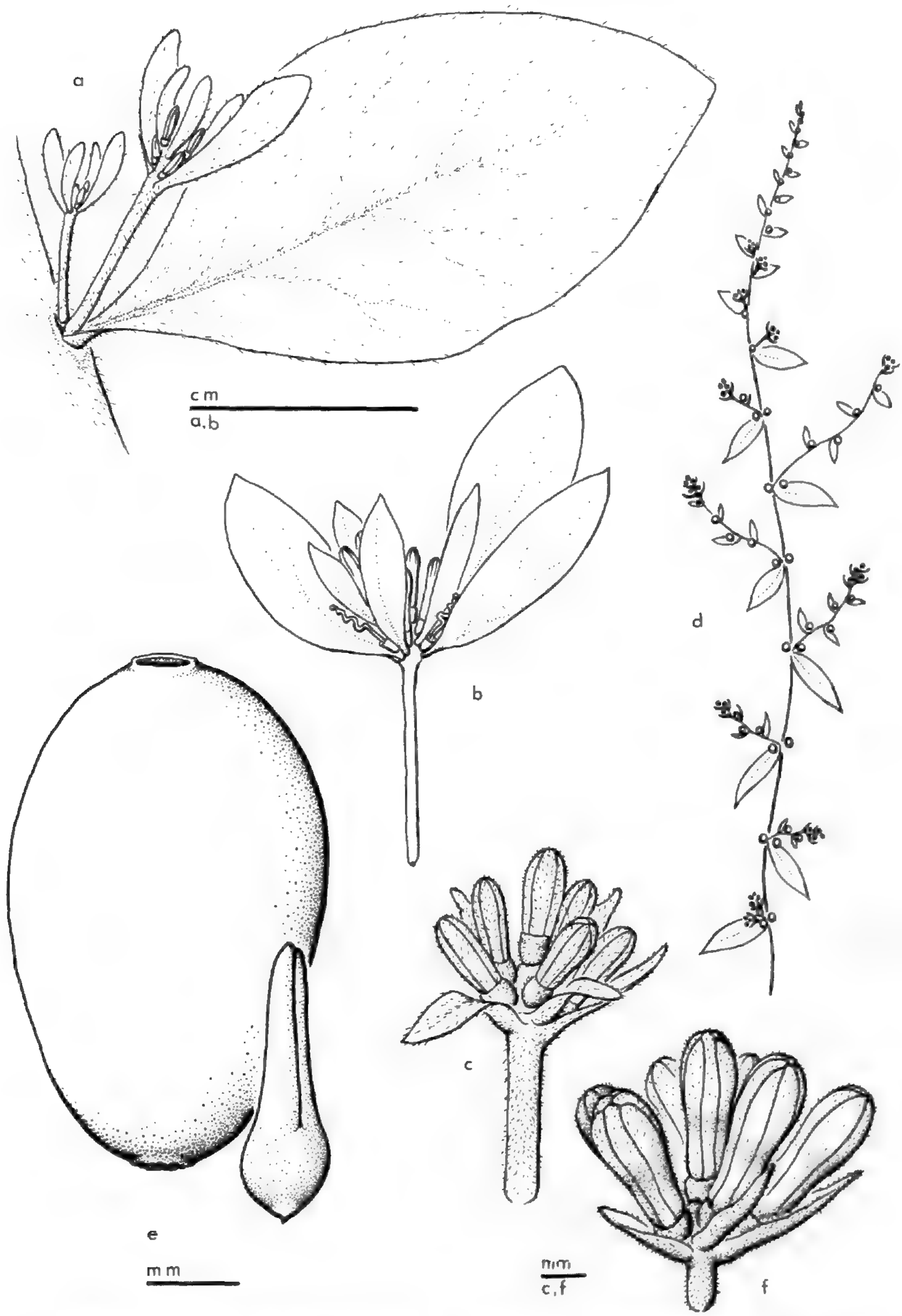

FIGURE 21. **Cladocolea loniceroides:** a, pistillate inflorescences and leaf (*Hinton 3796*, G); b, pistillate inflorescence, large-bracted type (*Hinton 4112*, K); c, pistillate inflorescence, small-bracted type (*Pavón, s.n.*, P); d, diagrammatic representation of a complex flowering branch, staminate (*Hinton 10458*, K), black dots = flowers, small circles = young inflorescences; e, fruit and embryo (*Hinton 3152*, K); f, staminate inflorescence, small-bracted type (*Hinton 3840*, K).

Struthanthus hunnewellii I. M. Johnston, Contr. Gray Herb. **95**: 53, 54. 1931.
Struthanthus mexicanus Calderón, Cact. y. Sucul. Mex. **17**: 99–102. 1972.

TYPE: *Pavón* (see below).

Dioecious, leafy, profusely branching plants reaching 2 to several m. in size, pubescent or finely puberulent throughout, with growth percurrent and continuously branching, only exceptionally tending to sympodial habit; stems slender, terete, light tan-colored, not exfoliating even when older; plants lacking stem roots or basal roots; craters inconspicuous. Leaves decussate to alternate, soft and thin, up to 35 × 15 mm. (more usually 25 × 10 mm.), broadly lanceolate with acute (sometimes slightly attenuate) apex and acute base; petiole very short or lacking; venation pinnate, midvein running into apex. Inflorescences sometimes in compound groups (FIGURE 21d), where they show transitions between larger lateral branches and individual inflorescences. Staminate inflorescences one or 2, sometimes more per axil, superposed and/or lateral, or flanking vegetative laterals; peduncle 1–several mm. long, topped by an involucre of bracts 4 mm. long or less, each one with one axillary flower, terminal flower always present; 6–10 flowers per inflorescence. Pistillate inflorescence in same position as staminate; peduncle 3 mm. or longer, occasionally up to 15 mm. long, slender; involucral bracts extremely variable, ranging from squamate organs or linear 4 mm. bracts to foliaceous organs more than 10 × 5 mm. (outer bracts), decreasing in size inwardly; numbers of flowers same as in staminate. Staminate flowers said to be yellow, 4 mm. long; petals more than 3 mm. long, 6 (rarely 5) per flower; anthers less than 1 mm. long, at two different heights on the petals, dorsifixed more or less in middle of anther by slender, short filament; the inner 2 pollen sacs lower but not smaller than the outer 2; pollen smooth, with a faint central, triangular prominence; ovary less than 1 mm. long; style 3 mm. long, straight except for slight undulation near anthers; stigma little differentiated; base of style invested by pubescent nectary. Pistillate flowers said to be white, at least 3 mm. long; staminodia strap-shaped; ovary less than 1 mm.; style contorted in middle or upper ⅔, reaching to tip of petals; stigma fairly well differentiated; nectary pubescent. Fruit ca. 5 × 3 mm., obovoid, glabrous, turning red at maturity; embryo dark green, clavate, the 2 cotyledons linear.

This seems to be the most commonly collected species of *Cladocolea*, even though its geographic range is limited. The holotype at Paris is a small pistillate specimen with rather small bracts (FIGURE 21c). *C. loniceroides* is the type species of *Loxania* Van Tieghem.

Several of the collections at MICH from Jalisco are very delicate in all structural details and have only squamate floral bracts. The main characteristics of *Cladocolea loniceroides* apply, however, and the specimens are here included. Also unusual is the Guerrero collection *McVaugh 150*, which, besides having squamate bracts, has leaves that are nearly orbicular. A further questionable specimen is *Rzedowski 16372*. It has extremely fine branches and foliage, squamate inflorescence bracts, and, in apparent

contrast to other collections of *C. loniceroides*, secondary haustoria from a thick basal root.

"Attracts large numbers of bees" (*Wilbur & Wilbur 1838*).

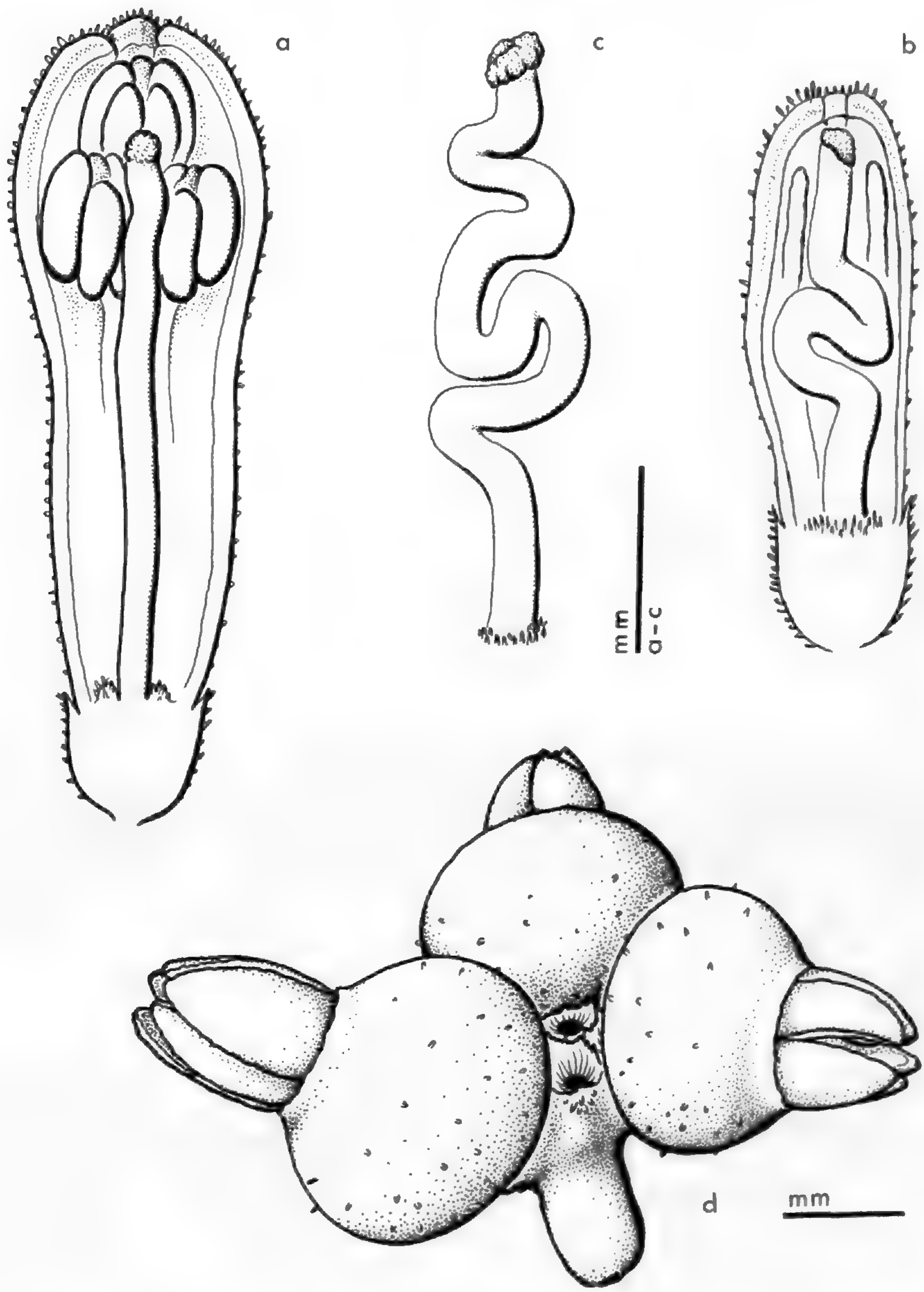

FIGURE 22. **Cladocolea loniceroides:** a, staminate flower, longitudinal section (*Hinton 3840*, K); b, pistillate flower, longitudinal section (*Pavón s.n.*, P); c, style of pistillate flower (*Hinton 4112*, K); d, insect galls resembling small fruits on staminate plant (*Hinton 10689*, K).

Mexico. *Pavón* (P, holotype of *Loxania loniceroides*); *Sessé, Mociño, Castillo, & Maldonado 927, 4957* (F). GUERRERO. Distr. Mina: Manchón, on oak, *Hinton 10458* (K, MO, NY, US); Aguazarca-Filo, on oak, *Hinton 10500* (GH, K, US); Pilas, 1600 m., *Hinton 10689* (K, WTU); 2 km. NE of Campamento El Gallo, estribaciones suroccidentales del Cerro Teotepec, on *Alnus*, 2650 m., *McVaugh 150* (MICH); Chichihualco, near Camotla, Campo de Aviación, 2250 m., *Rzedowski 16372* (MICH); Chichihualco, Cerro de la Pastilla, near Camotla, on *Quercus*, 2300 m., *Rzedowski 16437* (MICH); same, on *Ostrya virginiana*, *Rzedowski 16451* (MICH); Puerto Chico, Chichihualco, 10 km. W of Camotla, on *Alnus*, 2500 m., *Rzedowski 18000* (MICH); 16 km. E of Aserradero Aqua Fría, Tlacotepec, on road to Chilpancingo, on *Populus*, 2400 m., *Rzedowski & McVaugh 270* (CAS, MICH); below Omiltemi, on *Ostrya*, 6400 ft., *Sharp 441572* (GH); vicinity of Omiltemi, ca. 60 km. W of Chilpancingo, on Compositae, 2000 m., *Tillett 637–153* (GH, US). JALISCO: mountains N of Autlán, 3–5 mi. above Mina San Francisco, on Malvaceae, 1500–1650 m., *McVaugh 19918* (MICH); Sierra de Manantlán, 25–30 km. SE of Autlán, 8–10 km. E of La Cumbre between El Chante and Cuzalapa, on *Eupatorium mairetianum*, 2000–2250 m., *McVaugh 23159* (MICH); Sierra de Halo, 7 mi. SSW of Tecalitlán, on lumber road to San Isidro, on *Baccharis*, 2000–2200 m., *McVaugh & Koelz 1129* (MICH); wooded slopes S of road above pass 10 mi. S of Autlán toward La Resolana, on Compositae, *Wilbur & Wilbur 1420* (MICH); mountains E of Mamantlán ca. 15 km. SSE of Autlán by way of Chante, on *Alnus*, 8300 ft., *Wilbur & Wilbur 1838* (MICH); Pacific slopes 10 mi. S of Autlán, 5200 ft., *Wilbur & Wilbur 2162* (MICH). MEXICO: Tiloxtoc, below Valle de Bravo, edge of river, on *Salix*, *Converse 83* (UBC); Mexico City, corner of Marsella and Nápoles streets, on *Ligustrum*, *Gimate Leyva* (MICH); 4 km. SSE of Luvianos, 1500 m., *Roe, Roe, Mori, & Rzedowski* (UT); Distr. Temascaltepec: Temascaltepec, 1750 m., *Hinton 636* (K, US); Bejucos, 610 m., on brazil, *Hinton 930* (K, MICH, NY, US); Acatitlán, on a cirian, *Hinton 3152* (K, MICH, NY, US); Calera, 770 m., *Hinton 3796* (G, GH, K, MICH, NY, S, UC, US); Rincón, 1960 m., on peach, *Hinton 3840* (K, NY, US); Nanchititla, on oak, *Hinton 4112* (K, MICH, NY, UC, US); same on "espino," *Hinton 4115* (K, NY, US); Telpintla, 1840 m., on peach, *Hinton 4255* (K, MICH, MO, NY, US); 10 km. S of Temascaltepec, *Moreno 164* (CAS, US). MICHOACÁN: km. 150 S of Zitácuaro, 8600 ft., on *Alnus*, *Barr & Barr 64–553* (CAS, US); El Salto S of Morelia, on *Alnus*, *Barr & Dennis 64–304A* (UC); S. Torricillas, Coalcomán, 2400 m., *Hinton 15022* (GH, MO, NY, US); road N of San Felipe Los Alzati to San Cristóbal, 12 km. N of Zitácuaro, on *Alnus*, 2300–2500 m., *Iltis, Iltis, & Koeppen 318* (MICH); S-facing slopes of mountains between Río del Salto and La Polvilla, ca. 18 mi. E of Morelia, 7200–8000 ft., on leguminous tree, *King & Soderstrom 5105* (MICH, NY, SMU, UC, US); steep mountain sides NW of Aguililla 6–7 km. S of Aserradero Dos Aguas, on *Baccharis* and *Vernonia*, 2000 m., *McVaugh 22732* (MICH); near summits 8–12 km. SW of Aserradero Dos Aguas, nearly W of Aguililla, on *Alnus*, 2250–2400 m., *McVaugh 22791* (MICH); 3–6 km. S of Aserradero Dos Aguas, nearly W of Aguililla, on *Baccharis*, 2000–2100 m., *McVaugh 24662* (MICH); same, on *Rumfordia*, *McVaugh 24681* (MICH); Las Manzanillas, near Zitácuaro, on *Alnus*, 2150 m., *Rzedowski 28122* (ENCB, holotype of *Struthanthus mexicanus*; CAS, MICH, isotypes); same, *Rzedowski 28123* (CAS, MICH). MORELOS: woods N of Cuernavaca, on *Alnus*, 2100 m., *Hunnewell 11854* (GH, holotype of *Struthanthus hunnewellii*); Cuernavaca, on *Quercus*, *Kenoyer A-501* (MICH); km. 59 of Mexico City — Cuernavaca road, *Lundell & Lundell 12328* (MICH, NY, UC, US); ca. 6 mi. N of edge of Cuernavaca on old road to Mexico City, on *Alnus*, 6500 ft., *Mickel*

1678 (NY, UBC); lava beds near Cuernavaca, on *Solanum refractum*, 5000 ft., *Pringle 7362* (F, US); 10 km. N of Cuernavaca (km. 65), on *Alnus*, *Rzedowski 18481* (CAS, US). OAXACA: road between Juquila and Napala, *Nelson 2421* (US).

16. **Cladocolea mcvaughii** Kuijt, sp. nov. FIGURE 23.

TYPE: *McVaugh 15008* (see below).

Dioecia, sympodialis, glabra, caulibus rectis vel sat volubilibus, interdum radicibus. Folia alterna vel decussata, 50–100 × 30–30 mm., lanceolata, basi apiceque saepe aliquantum attenuata. Inflorescentiae pistillatae 10–20 mm. longae, floribus 8–12, staminatae ad 35 mm. longae, floribus 10–14, ut videtur, indeterminatae; flores sat remoti. Flores pistillati 4 × 1 mm., staminati 5–6 × 1.5 mm., hexameri, stylus pistillatorum valde convolutus, staminatorum fere rectus. Stamina staminodiaque dimorphica.

Dioecious, completely glabrous mistletoe, with sympodial growth; stems straight or voluble, terete, light cinnamon-brown when young, becoming gray-brown with age and often crowded with small, transverse lenticels; craters obvious; stem roots occasional on older growth. Leaves alternate to decussate, 50–100 × 20–30 mm., lanceolate, acute to rounded or sometimes slightly attenuate at apex, acute at base, tapering into a dorsiventrally flattened petiole 5–10 mm. long, 1–3 mm. wide; leaf margins smooth, not brown or callose; venation obscurely pinnate, lower midrib never multiple. Inflorescences developing axially after branches fully expanded(?), also on previous year's growth. Staminate inflorescence seen only axillary to foliage leaves (midsummer), one per axil, up to 35 mm. long, only sometimes terminating in a (bracteate) flower; flowers 10–14, widely spaced or paired along upper ¾ of inflorescence, nearly perpendicular to axis; bracts mostly persistent, acute. Pistillate inflorescence 10–20 mm. long at anthesis, 1–several per axil, axis 1.5 mm. thick, the 8–12 flowers mostly paired but often irregularly so, terminal flower often but not always lacking, when present, subtended by small scale leaves with acute, caducous tip. Staminate flowers light yellowish green, hexamerous, 5–6 × 1.5 mm.; anthers 0.5 mm. wide, dimorphic, attached to petals at middle and ⅔ the distance from the base, 1 mm. long; pollen smooth, trilobate with triradiate groove and triangular prominence. Pistillate flowers yellow-green, 4 × 1 mm., hexamerous, the petals narrow, strap-shaped and provided with pale yellow staminodia at two slightly different levels, attached at and slightly above the middle; ovary 1 mm.; style much convoluted along its entire length; stigma well differentiated, obliquely capitate, reaching ¾ the length of the petals. Fruits not seen, infructescence axis elongating up to 40 mm. long before fruits mature.

This species is reminiscent of *Cladocolea grahami* and *C. pringlei*, with which *C. mcvaughii* undoubtedly has affinities. It can be distinguished from them on the basis of the elongated (and, in the pistillate, elongating) inflorescence axis; the orientation and shape of the staminate buds; and the lack of the "multiple vein" character typical of the leaves of *C. gra-*

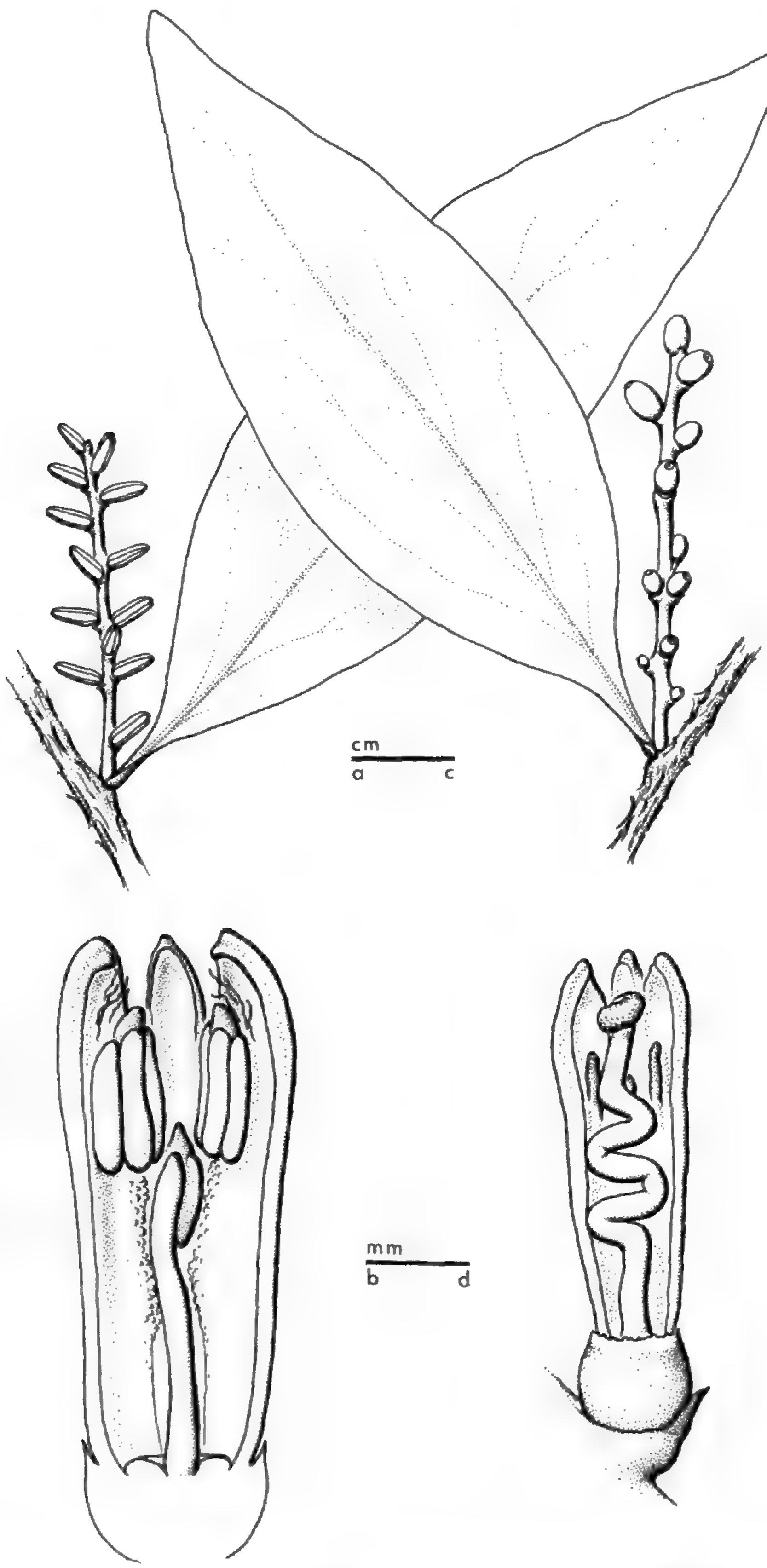

FIGURE 23. **Cladocolea mcvaughii**: a & b, staminate inflorescence and flower, the latter in longitudinal section (*McVaugh 15008*, MICH); c, pistillate inflorescence (*Rzedowski 17404*, MICH); d, pistillate flower in longitudinal section (*McVaugh 12193*, MICH).

hami and *C. pringlei.* One of the most consistent vegetative distinctions is the smooth leaf margin, which in the above two species is invariably brown, and callose or corklike.

It is a pleasure to name this species after Dr. Rogers McVaugh of the University of Michigan, long-time student of the flora of Jalisco (one of the most crucial *Cladocolea* areas) and collector of some of the most important material not only of the species named for him, but also of several other species of *Cladocolea.*

Mexico. JALISCO: oak-pine forest near summit of pass 7–8 mi. NW of Los Volcanes, along road between Ayutla and Mascoto, on *Quercus*, 1800–1900 m., *McVaugh 12193* (MICH); near summits, Sierra del Cuale, SW of Talpa de Allende, SW of Piedra Rajada, on *Quercus*, 1800–2250 m., *McVaugh 14353* (MICH); Sierra del Halo, near lumber road leading to San Isidro, 2–5 mi. from Colima highway 7 mi. SSW of Tecalitlán, on *Quercus*, 1400–1500 m., *McVaugh 15008* (MICH, holotype of *C. mcvaughii*); same, but 13–16 mi. from Colima highway, on *Quercus*, 2000–2200 m., *McVaugh & Koelz 1211* (MICH); municipality of Jilotlán, Sierra del Coral, on *Quercus*, 1400 m., *Rzedowski 16635* (MICH); Llano Verde, near Los Corales, municipality of Tecalitlán, Sierra de Los Corales, on *Quercus macrophylla*, *Rzedowski 17404* (MICH). MEXICO: W of Toluca, hills W of Jordana, on *Quercus*, *Gregg 722b* (MO); 2 km. NW of Nanchititla, municipality of Tejupilco, on *Quercus*, 1900 m., *Rzedowski 22120* (MICH). NAYARIT: 3 km. W of Mazatlán, on *Quercus aristata*, 800 m., *Rzedowski 17914* (MICH). SINALOA: Pacific Coast Highway, on Highway 40 near Porterillos, on *Quercus*, 4600 ft., *Wiens 4415* (UT).

17. **Cladocolea microphylla** (H.B.K.) Kuijt, comb. nov.

FIGURES 2, 24, 25.

Loranthus microphyllus H.B.K., Nov. Gen. Sp. Pl. 3: 439 (*quarto ed.*), *pl. 300.* 1820.

Phthirusa microphylla (H.B.K.) Blume, in Schultes & Schultes, Syst. Veg. 7(2): 1730. 1830.

Struthanthus microphyllus (H.B.K.) G. Don, Gen. Hist. Dichlam. Pl. 3: 413. 1834.

Loxania microphylla (H.B.K.) Van Tieghem, Bull. Soc. Bot. France 42: 387. 1895.

TYPE: *Bonpland* (see below).

Plant dioecious, white-puberulent, half a meter or more in size, with sympodial growth; stems terete, straight, primary leaves only on current growth, year-old growth often with many reddish-brown lenticels; craters very obvious, also reddish-brown; stem and basal roots absent. Leaves alternate to decussate, mostly the former, 5–30 × 2–10 mm., lanceolate, acute at apex and base; petiole 2 mm. or less; leaf margin and base puberulent. Inflorescences only on year-old growth (rarely a few on older twigs), one (pistillate) or 1–2 (staminate) per axil, the latter in a superposed position where it occurs; peduncle 2–12 mm. (rarely nearly lacking), terminated by capitulum with several foliar involucral bracts which subtend the lowest flowers; upper flowers with minute bracts or (the ter-

minal flower) ebracteate; flowers usually about 6; some individuals consistently with 1–2 leaves on lower peduncle, these leaves lacking flowers. Staminate flowers pale yellow to orange, 3–4 × 1–2 mm. in bud, 6-partite; anthers with 4 pollen sacs, the inner 2 somewhat lower than the outer 2;

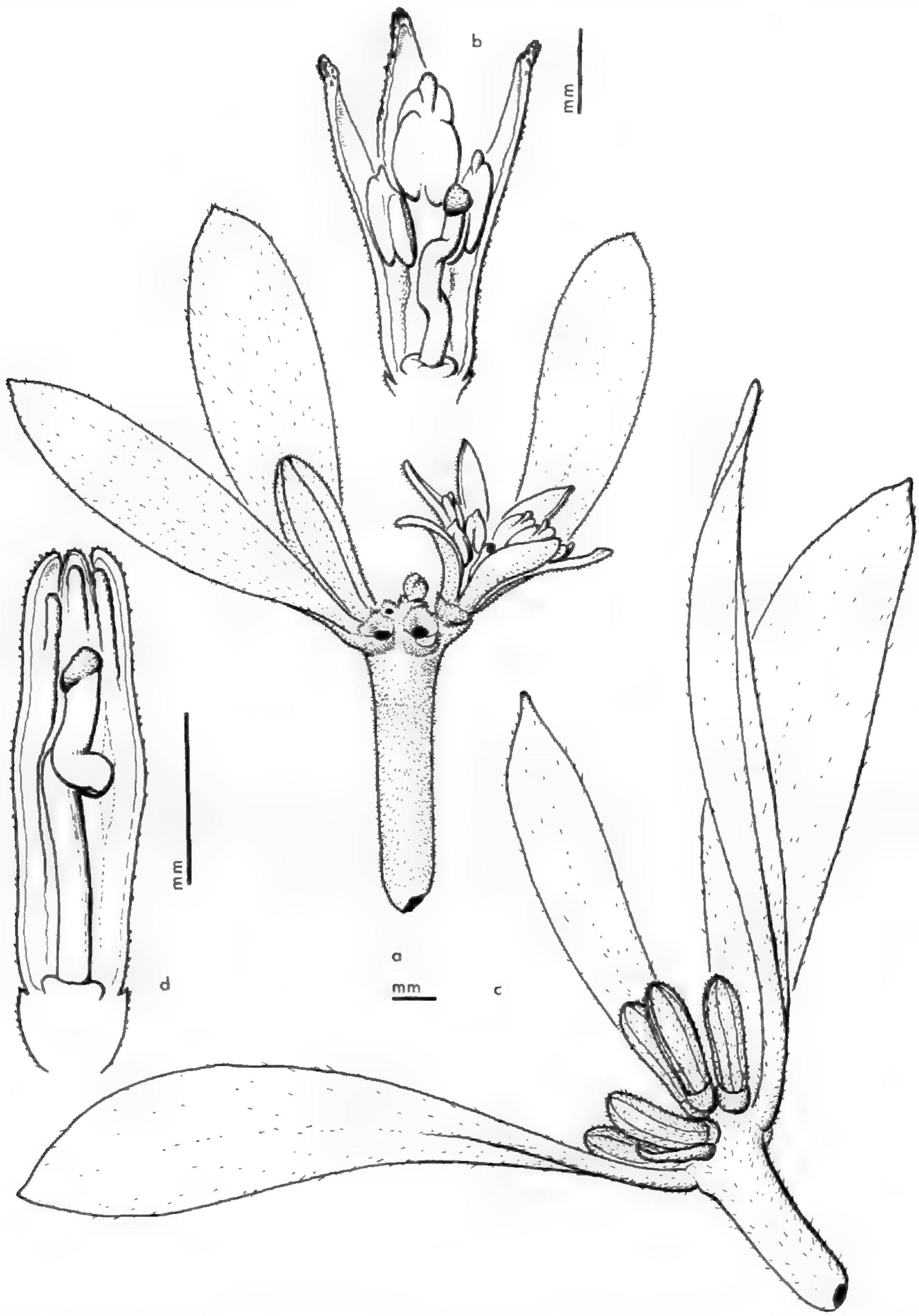

FIGURE 24. **Cladocolea microphylla:** a & b, inflorescence and longitudinal view of staminate flower (*Pringle 4369*, M); c, pistillate inflorescence, d, pistillate flower in longitudinal section (both from *Troll 593*, M).

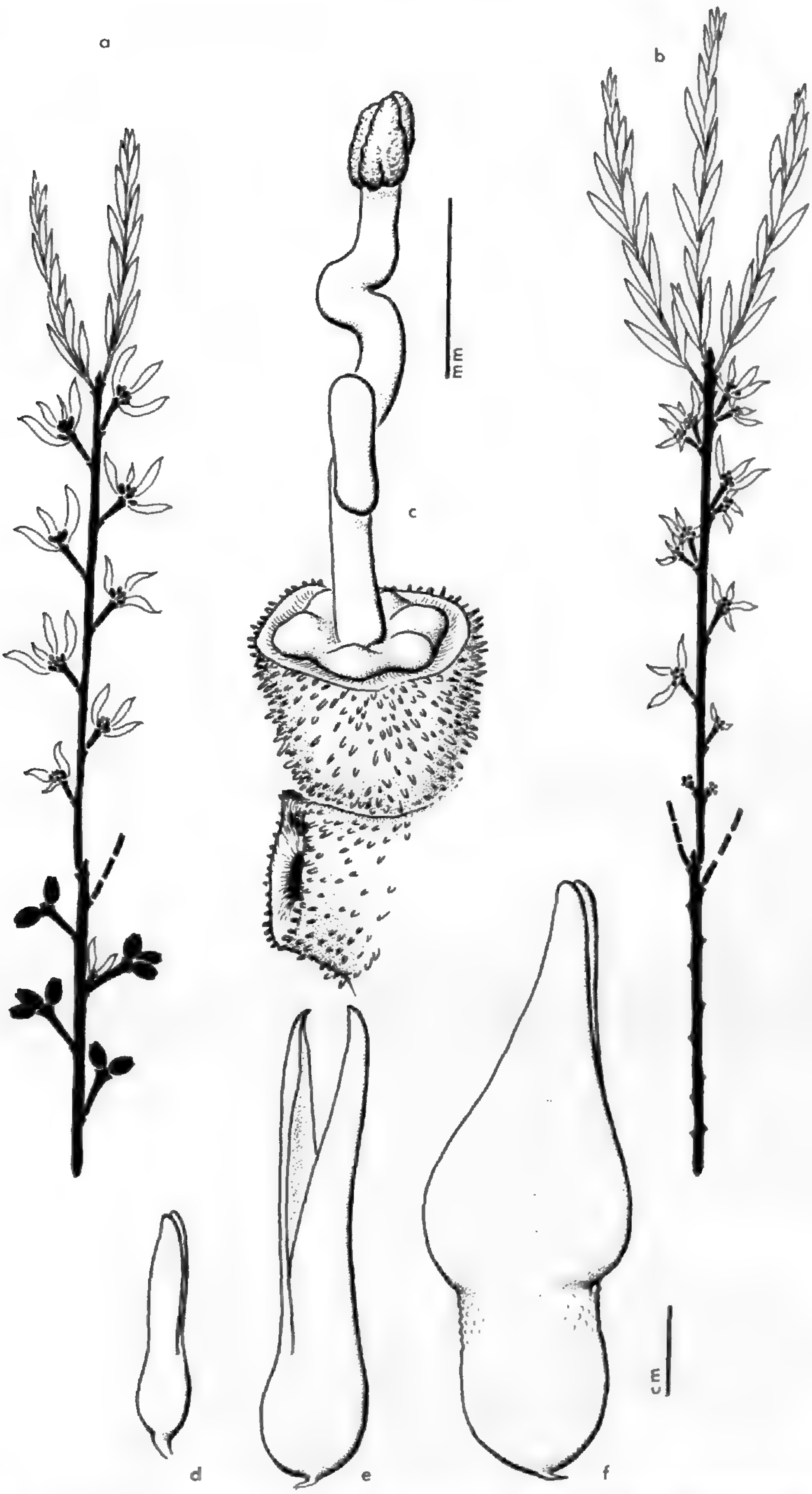

FIGURE 25. **Cladocolea microphylla:** a & b, diagrammatic representation of branching pattern of pistillate (*Troll 593*, M) and staminate (*Pringle 4369*, M) plants respectively; c, gynoecium, pistillate flower with highly convoluted style (*Frye & Frye 2601*, SMU); d–f, stages in embryo development (*Troll 593*, M).

the anthers dimorphic, upper ones above, lower ones at or slightly below middle of petal; ovary 0.5 mm.; style slightly twisted in middle; stigma capitate, situated half-way up the flower. Pistillate flowers greenish-yellow, 4–5 × 1 mm.; petals 6, very narrow, with very slender inconspicuous staminodia near tips; ovary slightly less than 1 mm.; style slightly or much convoluted above the middle; stigma capitate, often somewhat lobed and acute, reaching ¾ the distance from the base of the flower. Nectary in both types of flowers glabrous; all flowers puberulent on ovary and back of petals. Fruit ca. 7 × 4 mm., an orange to scarlet, ellipsoid berry; embryo dicotyledonous, the tips of the cotyledons emerging from the spherical endosperm.

This is one of the three *Cladocolea* species previously illustrated (H.B.K., Nov. Gen. Sp. Pl. 3: 439 (*quarto ed.*) *pl. 300.* 1820). The illustration is generally accurate but gives no hint of the long shoots with primary leaves. The type specimen is in exceedingly poor condition.

As far as I can discover, flowering takes place in late spring and early summer. Innovations develop at the same time. Both primary and secondary leaves remain on the plant all summer. By late November or early December the first inflorescences begin to break through the cushions in the axils of primary leaves. All leaves are still on the plant at this time, but they are apparently dropped more or less simultaneously with the resumption of vegetative and inflorescence growth (April ?); none remain at the next flowering season. Mature fruits are on the plant during the flowering season, but they may well ripen earlier, as a full year seems a rather long period for maturation.

A more detailed and illustrated account of emergence of lateral shoots is given in the introduction.

The species is often confused with *Cladocolea loniceroides*, which, however, does not share the peculiar periodicity of *C. microphylla* and seems to flower more or less continuously. The two are nevertheless closely related.

Mexico. "Nouvelle Espagne," Moricand (G, possibly an isotype instead); "Nova Hispania," *Sessé, Mociño, Castillo, & Maldonado 926* (F). JALISCO: N slopes, Nevado de Colima, on *Quercus*, 2400 m., *McVaugh 10146* (MICH); Sierra del Halo, 5 km. toward San Isidro on lumber road, Colima highway 11–12 km. SW of Tecalitlán, on *Quercus*, *McVaugh 24492* (MICH); base of Nevado de Colima, on oaks, *Pringle 4369* (F, G, GH, GOET, K, M, MICH, NY, P, S, UC, US). MEXICO: 5 km. WSW of Villa Victoria, on road to Zitácuaro, on *Quercus mexicana*, 2550 m., *Rzedowski 28127* (MICH); La Ciénaga, 4 km. S of Sultepec, on *Quercus*, 2350 m., *Rzedowski 30389* (CAS, US), *30390* (CAS); Distr. Temascaltepec, Comunidad, on *Quercus*, *Hinton 7689* (GH, K, MICH, US). MICHOACÁN: Lake Pátzcuaro, 3 km. W of Quiroga, on oak, *Frye & Frye 2601* (GH, MO, NY, SMU, UC, WTU); ca. 18 mi. S of Pátzcuaro, 8900–9000 ft., on *Quercus*, *King & Soderstrom 5196* (MICH, NY, SMU, UC, US, WTU); 6 mi. N of Tancitaro, mountain slope, on *Alnus*, 8500 ft., *Leavenworth 340* (F, GH, MICH, MO, NY); "Cerritos de Agua," 3 mi. below lumber camp at Dos Aguas, nearly W of Aguililla, 2000–2100 m., *McVaugh 17839* (MICH); Los Manzanillas, near Zitácuaro, on *Quercus*,

2150 m., *Rzedowski 28125, 28126* (CAS, MICH); Tangancícuaro, near Cerezos, base of Cerro Patambán, on *Quercus*, 2300 m., *Rzedowski & McVaugh 652* (MICH); Mil Cumbres between Morelia and Ciudad Hidalgo, 2400 m., on *Quercus*, *Troll 593* (G, M). MORELOS: Cuernavaca, *Bonpland* (P, holotype of *Loranthus microphyllus*); El Mirador, near road from Cuernavaca to Mexico City, 2000 m., *Williams 3820* (GH).

18. **Cladocolea oligantha** (Standley & Steyermark) Kuijt, comb. nov. FIGURE 26.

Struthanthus oliganthus Standley & Steyermark, Contr. Field Mus. Nat. Hist. (Bot. Ser.) **23**: 154, 155. 1944.

TYPE: *Steyermark 50672* (see below).

Plant dioecious, sparsely branched, completely glabrous, with sympodial growth; stems rather stout and straight, terete, first light colored, later dark brown and often with a sprinkling of rather large, transverse lenticels; one-year-old wood (bearing secondary inflorescences) with shrunken bark, as if cortex very fleshy; no basal or stem roots seen. Leaves alternate, 20–30(–45) × 8–10(–16) mm., lanceolate to oblanceolate, acute to rounded at apex, long-tapering at base into a petiole 2–4 mm. long and 0.5–2 mm. thick; midvein running into the apex, other veins often obscure, pinnate except for two large, basal lateral veins running half-way down the length of the blade. Inflorescences of two types: (1) primary, on current year's growth, being mostly single (rarely with a superposed inflorescence), axillary, simple dichasia on peduncles 4–5(–10) × 1 mm.; bracts of 2 lateral flowers caducous; the 3 flowers in one plane, and (2) secondary, developing on year-old growth, bearing one or 2 smallish but normal foliage leaves at the very base, deceptively like primary leaves; flowers 4–6, one of which is terminal, the others crowded nearby, spirally arranged. Flowers said to be reddish, ca. 5 × 2 mm. when in (clavate) bud, tetramerous; anthers 1.5 mm. long, inserted in the middle of the petals, with projecting connective and 4 pollen sacs; stamens and petals monomorphic; style straight or nearly so, at least 4 mm. long; stigma inconspicuous. Fruit red, becoming black, 7 × 5 mm., ovoid, smooth; embryo dicotyledonous, nearly 4 mm. long, clavate.

This is one of two *Cladocolea* species with dimorphic inflorescences, the other being *C. dimorpha*. In the present species the two inflorescences are deceptively alike except, of course, for the position of the associated leaves or leaflike organs. Occasionally, leafless inflorescences identical to primary ones may be found in superposed positions above secondary ones.

The staminate and pistillate flowers are also remarkably similar. The aborted stamens in the pistillate flower, for example, are unusually well differentiated.

Cladocolea oligantha is further noteworthy for being the only *Cladocolea* which occurs both north and south of the Isthmus of Tehuantepec.

Guatemala. DEPT. HUEHUETENANGO: rocky dry slopes above San Ildefonso

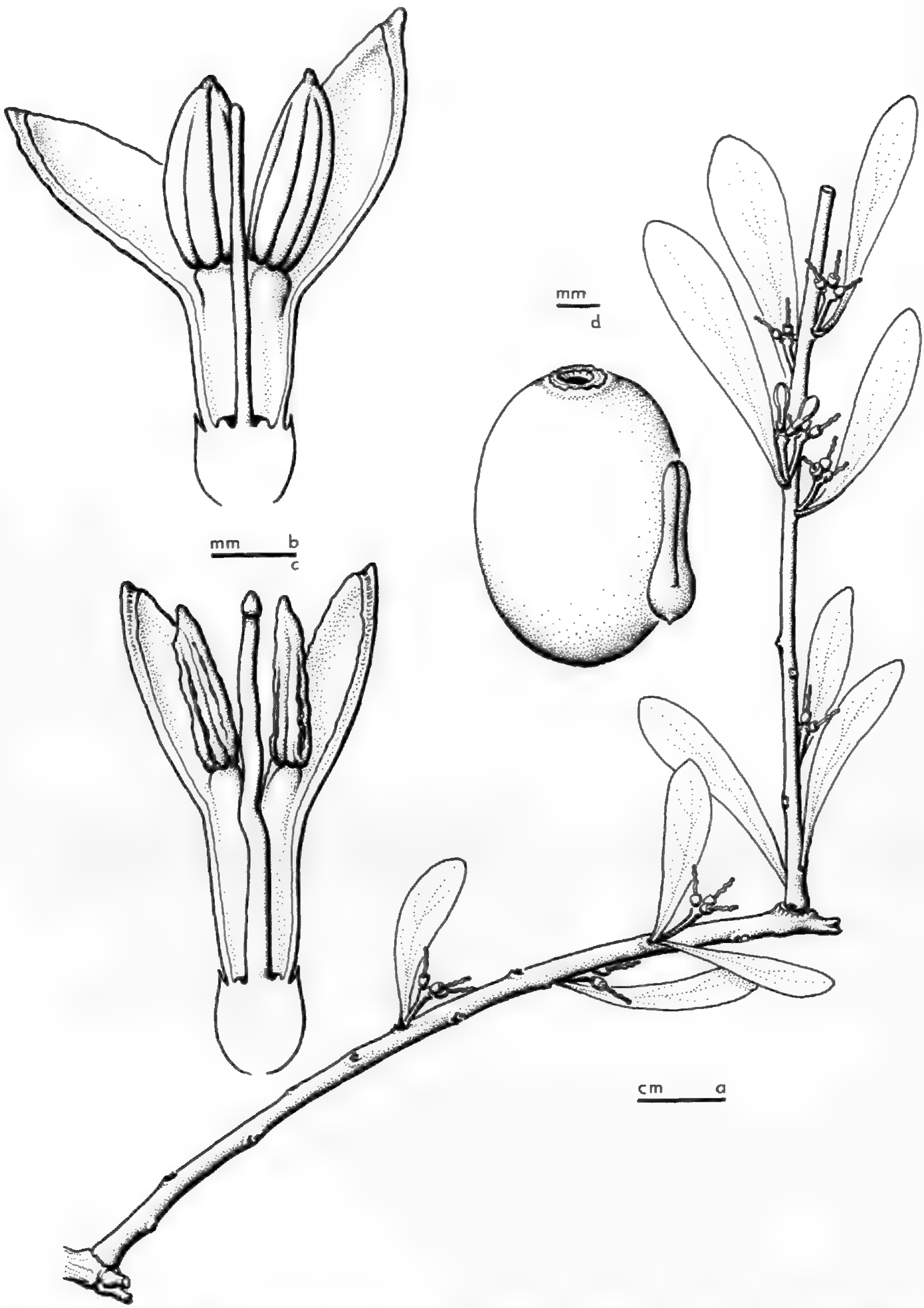

FIGURE 26. **Cladocolea oligantha:** a, habit, showing primary inflorescences (erect portion) and secondary inflorescences (lower, oblique portion) (*Hinton 8146*, K); b, staminate flower, same collection; c, pistillate flower (*Hinton 4730*, K); d, fruit and embryo (*Breedlove 35995*, CAS).

Ixtahuacán, 1600–1700 m., *Steyermark 50672* (F, holotype of *Struthanthus oliganthus*; isotype at US); NW of Cuilco, Cerro Chiquihui above Carrizal, on copal, 1350–2300 m., *Steyermark 50824* (F, US). **Mexico.** COLIMA: Rancho Guerro, *Jones 423* (US). GUERRERO: road above Canyon del Zopilote, 8 km. E of Xochipala on way to Filo del Caballo from Milpillas, on *Lysiloma*, 850 m., *Breedlove 35991* (CAS); 5 km. E of Xochipala, on *Bursera*, 1100 m., *Rzedowski 18649* (CAS); E of Cerro Alquitrán, near Mazatlán, municipality of Chilpancingo, on *Bursera bipinnata*, 1500 m., *Rzedowski 22674* (CAS, MICH); Distr. Coyuca, Pungarabato, on a copal, *Hinton 8146* (K, US). JALISCO: near Chapala, *Rose & Painter 7662* (US). MEXICO: Distr. Temascaltepec, Naranjo, on a cirian, 860 m., *Hinton 4730* (K, MICH, NY, UC, US). OAXACA: Pan-Am. Highway between Oaxaca and Tuxtla Gutierrez, 12.5 km. E of Juchitán, on *Bursera*, 0–50 m., *McVaugh 21853* (MICH). PUEBLA: 12 km. NW of Petlalcingo along Pan-Am. Highway on road to Acatlán, 1350 m., *Iltis & Koeppen 1116* (MICH, US); 7 mi. SE of Izúcar de Matamoros, on *Bursera*, 4950 ft., *Webster, Miller, & Miller 11446* (GH). **Panama.** PROV. PANAMA: vicinity of Las Lajas bridge, Panama National Highway, *Bartlett & Lasser 16645* (MO); near beach at Nueva Gorgona, on *Bursera tomentosa*, *Duke 4504* (GH, US).

19. **Cladocolea pedicellata** Kuijt, sp. nov. FIGURES 27 & 28.

TYPE: *Hinton 4091* (see below).

Dioecia, glabra, sympodialis; caules sat validi; cortex badia, deinde cinereo-brunnea. Folia opposita vel decussata, oblanceolata vel obovata, subsessilia, rotundata, basi attenuata. Inflorescentiae binae in axillis, ad ramos anniculos et vetustiores; axis inflorescentiae pistillatae ad 20 mm. longa; pars inferior foliis 2–6 geminatis vel sparsis. Flores in racemo determinato, 7–9, pedicellis 4–7 mm. insidentes, saepe gracillimi; alabastra acuta, 6 mm. longa vel ultra, hexamera, calyculus extus expansus. Stylus gracilis, parte superiore valde contortus; stigma bene efformatum. Stamina dimorphica; antherae ad 2 mm. longae.

Plant dioecious, glabrous, with sympodial growth, the leafy long shoots developing during late summer, primary leaves being dropped before or staying on during anthesis; stems terete, stout, the bark shredding into strips later, becoming gray and smooth in age; craters evident; stem roots seen only on *Rzedowski 24020* (CAS). Leaves alternate to decussate, up to 60 × 23 mm., lanceolate to oblanceolate or obovate, acute to rounded at apex, at base tapering into flat, short petiole. Inflorescences determinate, only on second season and older stems, one or rarely 2 per axil, consisting of 7–9 flowers on a stout or slender axis; secondary leaves somewhat smaller than primary ones, one or 2 pairs, the lateral flowers in the leaf axils (or slightly above) and in a terminal raceme; flowers with pedicels ranging from extremely slender, 4–7 mm. long, to stout and very short or occasionally (*Rzedowski 16373*) absent. Staminate flowers hexamerous, apparently variable in size, 6–12 mm. in length, narrowly acute to somewhat oblong and blunt; buds acute; stamens strongly dimorphic; anthers up to 2 mm. long, attached at or above middle of petals; pollen sacs 4, more or less equal; style straight or slightly undulating at tip;

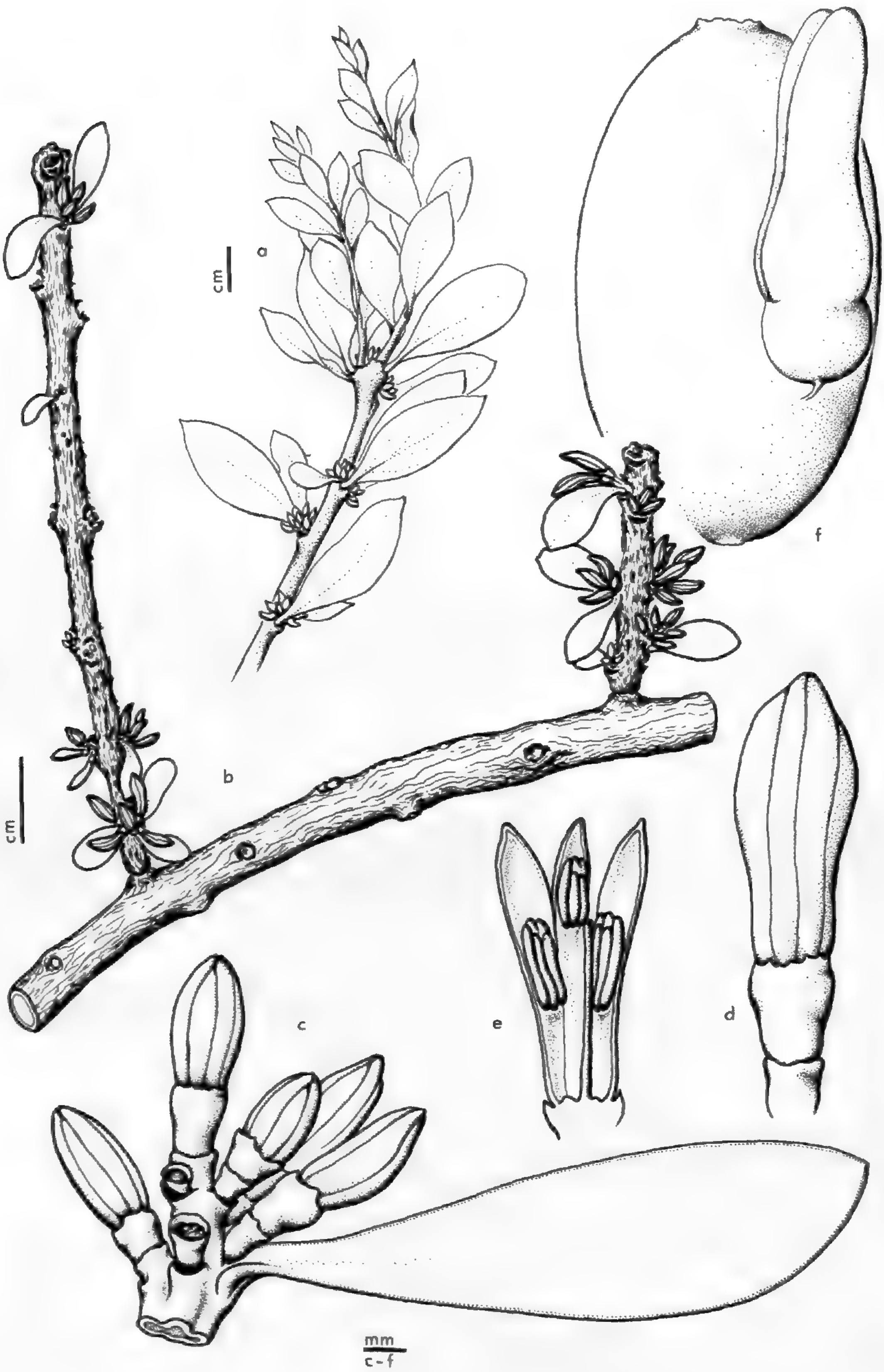

FIGURE 27. **Cladocolea pedicellata:** a, habit, probably staminate plant, primary leaves persisting (*Rzedowski 16373*, MICH); b, habit, staminate plant, primary leaves deciduous (*Nicolas 5158/4*, BM); c–e, same collection, inflorescence, bud, and longitudinal section of flower; f, fruit and embryo (*Rzedowski 22359*, MICH).

FIGURE 28. **Cladocolea pedicellata,** pistillate, long-pedicelled form (*Hinton 4091*, G): a, normal inflorescence; b, rare triad at base of otherwise normal inflorescence.

stigma scarcely differentiated. Pistillate flowers hexamerous, 6 mm. long in bud; bud acute; petals acicular, greenish, with dimorphic staminodia above middle; ovary 1.5 mm. long, only slightly thicker than supporting pedicel, expanding into a flaring, dentate calyculus above; style slender, undulating slightly below, greatly contorted in upper half; stigma clearly differentiated. Fruit ca. 12 × 6 mm., smooth, ovoid; embryo 8.5 mm. long, the 2 cotyledons 6.5 mm. long, very flat, the haustorium scarcely differentiated.

The specimens cited below are placed together with a certain amount of trepidation, as much variation exists, particularly in various inflorescence characters. The type specimen, in particular, has an unusually slender and graceful inflorescence, which is probably unique in the family. Only more extensive collecting can demonstrate whether all the cited specimens may be retained in one species. *Cladocolea pedicellata* is one of the two or three species with pedicellate flowers, the others being *C. harlingii* and (perhaps) *C. cupulata*. These species, nevertheless, are scarcely related to one another except at the generic level. A closer affinity may exist with *C. glauca*, which differs in having stem roots, more slender, scandent stems, sessile flowers, and smaller leaves. It is interesting, nevertheless, that one of the three known collections of *C. glauca* was made by the same person, in the same locality, and on the same host as one collection of the present species.

Mexico. GUERRERO: Campo de Aviación, Chichihualco, near Camotla, on *Quercus*, 2250 m., *Rzedowski 16373* (MICH). MEXICO: Cerro Sacremonte, near Amecameca, *Rzedowski 22359* (MICH); E of Cerro del Pino, near Ayotla, on *Quercus*, 2600 m., *Rzedowski 24020* (CAS, MICH); 5 km. E of Zoquipán, on road to Puebla, on *Quercus*, 2500 m., *Rzedowski 27330* (F, MICH); Distr. Temascaltepec, Nanchititla, on oak, *Hinton 4091* (K, holotype of *Cladocolea pedicellata*; isotypes at G, MICH, NY, UC, US). MICHOACÁN: wooded slopes 8–10 mi. NW of Ciudad Hidalgo, a few mi. N of village of San Pedro Aguaro, 2500–2700 m., on *Quercus*, *McVaugh 10000* (MICH). PUEBLA: Tepoxuchil, near Puebla, on *Acacia*, *Nicolas 5158/4* (BM, US); Cerro del Gavilán, on *Quercus*, 7000–8000 ft., *Purpus 4063* (F, UC, US).

20. **Cladocolea pringlei** Kuijt, sp. nov. FIGURES 1c, 29, 30.

TYPE: *Pringle 4697* (see below).

Dioecia, scandens vel volubilis, glabra, sympodialiter ramosa; rami badii, deinde cinerei. Radices ad partes vetustiores. Folia irregulariter alternodecussata; ad annuum secundum persistentia, coriacea, lanceolata vel obovata, 50–110 × 7–15 mm., apice basique acuta, margine squamosa. Inflorescentiae singulae vel paucae congregatae, axillares, ad partes vertentes vel juniores; plerumque determinatae; bracteae caducae; flores 6–13. Alabastra ca. 5 × 2 mm.; petala 6; stamina petalaque dimorphica; antherae sessiles. Stylus parte superiore paulum vel multum flexus. Fructus ovoideus, 5 × 3.5 mm.

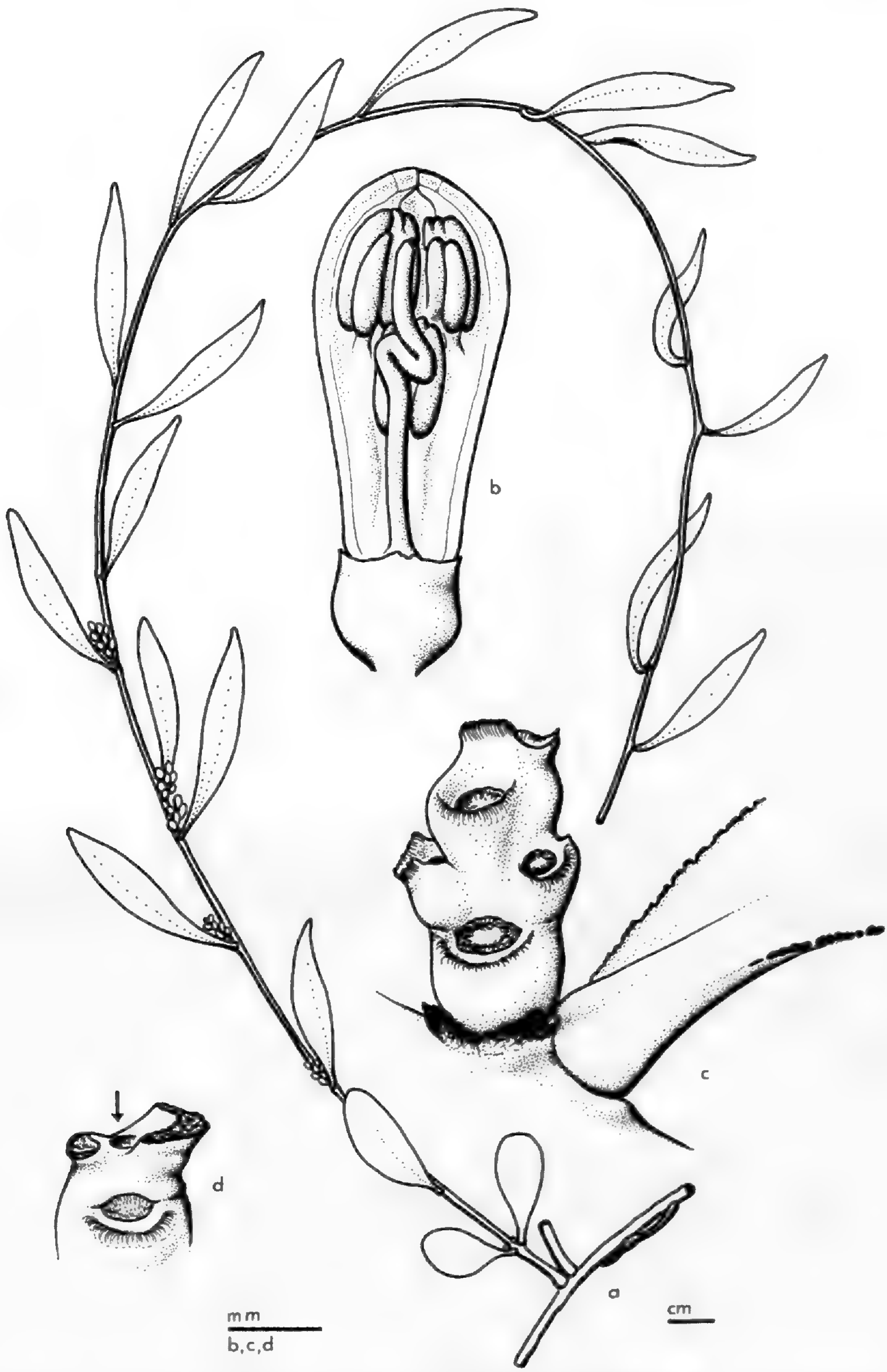

FIGURE 29. **Cladocolea pringlei,** staminate plant (*Pringle 4697*, G): a, habit; b, flower, with three petals removed; c, inflorescence, with all flowers removed to show terminal wedge; d, tip of a second inflorescence showing scar of terminal flower (arrow).

Plants dioecious, scandent to somewhat voluble, often 2 m. or more in size, completely glabrous, with apparently sympodial branching; branches first chestnut-brown, becoming grayish; craters conspicuous; stem roots on older stems only. Leaves sometimes paired, with their arrangement always quite irregular, leathery, 50–110 × 7–15 mm., lanceolate to obovate, with an acute to rounded apex and an acute base often tapering into a petiole 3–8 mm. long; leaf margin brown, of scaly texture; the basal portion of the midrib multiple; venation pinnate. Inflorescences single or in small clusters, in axils of foliage leaves on current or very recent growth; mature infructescences on year-old growth, where leaves persist. Staminate inflorescence a spike with 6–13 flowers, the apex often aborting to form a terminal wedge of sterile tissue, but at other times spike terminated by a bracteate flower; all bracts caducous, leaving a swollen, crescent-shaped scar. Staminate flowers 5.5 × 2 mm. in mature bud which is obovate in shape; petals 6, dimorphic, as are the stamens; filaments very short; upper anthers above, lower anthers at middle of petals; anthers 4-locular, inner pollen sacs slightly shorter than outer ones, connectival horn short and blunt or lacking; pollen with triradiate line and included triangular prominence; ovary ca. 1 × 1 mm., calyculus somewhat dentate; style slightly to considerably bent in upper portion; stigma undifferentiated. Pistillate inflorescence in fruit ca. 13 mm. long, lowest fruits paired, others irregular, 5–8 fruits per spike, at least 5 × 3.5 mm., ovoid, orange-red.

This species is superficially similar to *Cladocolea grahami*, but it is consistently smaller and has fruits and buds of a different form. The papillate petal tips of *C. grahami* have not been seen in *C. pringlei*, while spikes in the former species are always determinate. The two species are nevertheless closely related. Much confusion has existed between *C. pringlei* and the recently described *Struthanthus palmeri* Kuijt (1975), both of which have frequently been misidentified as *Struthanthus "spirostylis"* or *S. haenkei* (Presl) Engler, a synonym of *S. venetus* (H.B.K.) Blume. As with some other *Cladocolea* species, this similarity with a *Struthanthus* species might indicate true affinity. The Rzedowski specimen cited below has lanceolate, distinctly petiolate leaves and is, therefore, placed here provisionally. The same is true for the McVaugh & Koelz specimen, which has extraordinarily large leaves and may well belong to an undescribed species.

Mexico. GUERRERO: vicinity of Omiltemi, 60 km. W of Chilpancingo, on *Quercus*, 2000 m., *Tillett 637–146* (US); Campo de Aviación, near Camotla, on *Quercus*, 2250 m., *Rzedowski 16359* (MICH). MICHOACÁN: Lake Pátzcuaro, 3 km. W of Quiroga, on oak, *Frye & Frye 2600* (GH, MO, SMU, UC, US, WTU); near Pátzcuaro, on oaks, *Pringle 5058* (GH). OAXACA: mountains N of Oaxaca, end of road to TV relay station off Highway 190, 1 mi. S of 490 km. marker, on oak, 7400 ft., *Breckon & Breckon 803* (GH); Cerro de San Felipe N of Oaxaca, lower slopes, on *Quercus*, *Camp 2365* (NY); 15–18 km. WSW of Oaxaca, canyon of the Río Zavaleta near village of San Pablo Quatro Venados, on *Quercus*, *Camp 2550* (NY); Manzanar, E of Oaxaca, on road through San Au-

gustín toward Natividad, on *Quercus*, 7550 ft., *Carlson 1385* (F, MICH); Tecomatlán, Pueblo Viejo, Camino Montelobos, 3000 m., *Conzatti 1898* (F); Cuicatlán, Coyula a Cuyamecalco, 1800 m., *Conzatti & Gomez 2381* (*2081?*) (F); Cañada de San Gabriel, Etla., 2900 m., *Conzatti & Gonzalez 294* (GH); montañas de Mitla, Tlacolula, Cerro de Xaagá, 1850 m., *Conzatti & Ostlund 5178* (K); upper SW slopes of Cerro San Felipe, above San Felipe, 12–14 km. NNW of Oaxaca, on *Quercus*, 2400–2800 m., *Koeppen & Iltis 1242* (MICH); San Felipe, *Liebmann 3117* (C); foothills above Oaxaca, on oaks, 7000 ft., *Pringle 4697* (US, holotype of *Cladocolea pringlei*; isotypes at BR, G, GH, GOET, K, NY, P, PR, S, UC); Mt. Jayacatlán, *Smith 32* (GH); Distr. Nochixtlán, W of Huandilla, 2000 m., *Conzatti 1899* (F); Distr. Inguila, Plan de Minas, 1380 m., *Conzatti 4544* (US).

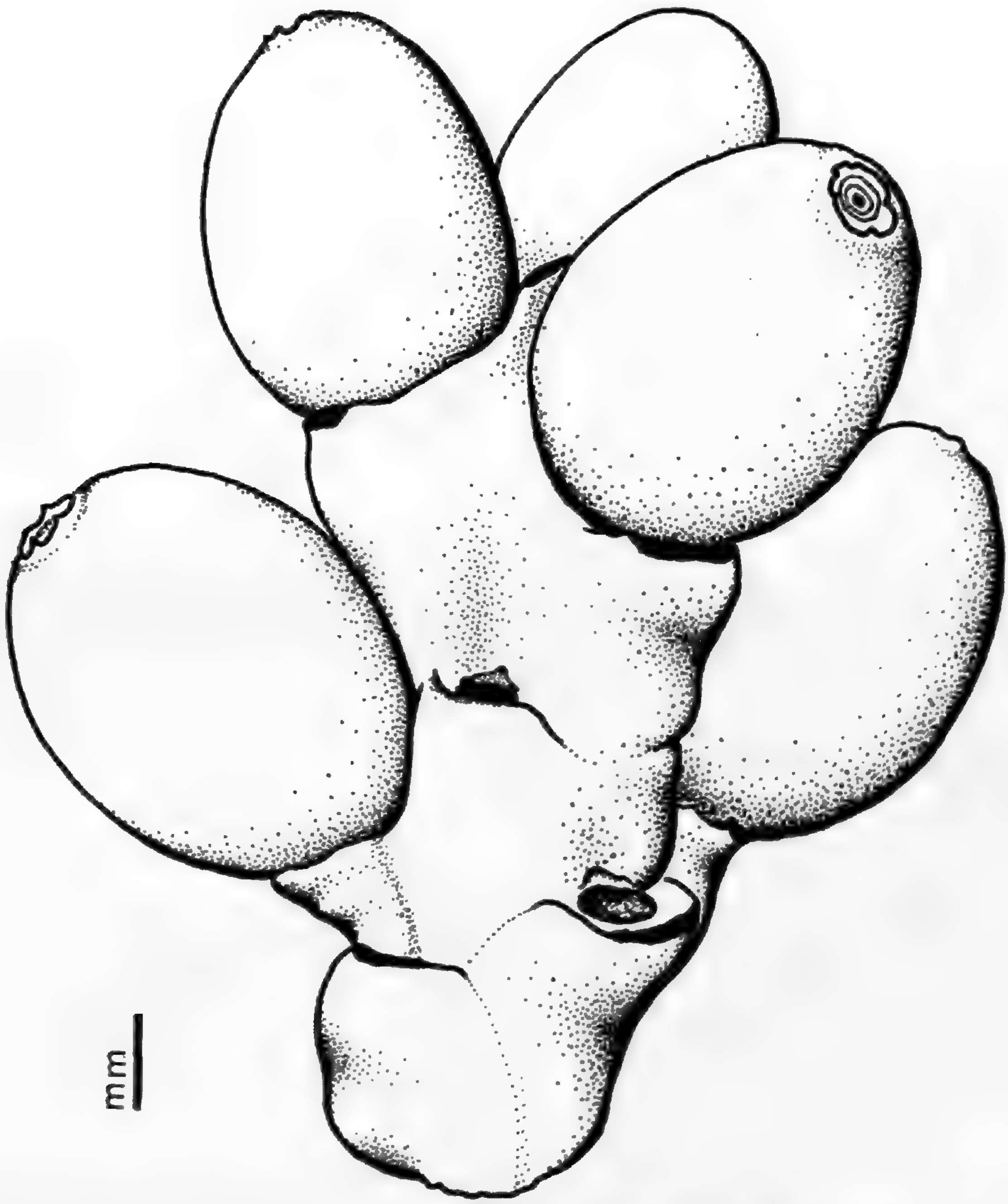

FIGURE 30. **Cladocolea pringlei:** inflorescence with nearly mature fruit (*Conzatti & Ostlund 5178*, K).

21. **Cladocolea roraimensis** (Steyermark) Kuijt, comb. nov.

FIGURE 31.

Phthirusa roraimensis Steyermark, Fieldiana Bot. 28: 224, 225. 1956.

TYPE: *Steyermark 58943* (see below).

A rigid, glabrous, sympodial plant; stems somewhat succulent, 2–5 mm. thick, bark smooth, internodes rather short (1–3 cm.); no stem roots seen. Leaves decussate, olive-green to bronze, very coriaceous, 40–50 × 10–25 mm., elliptic to ovate or obovate, with apex obtuse or more commonly

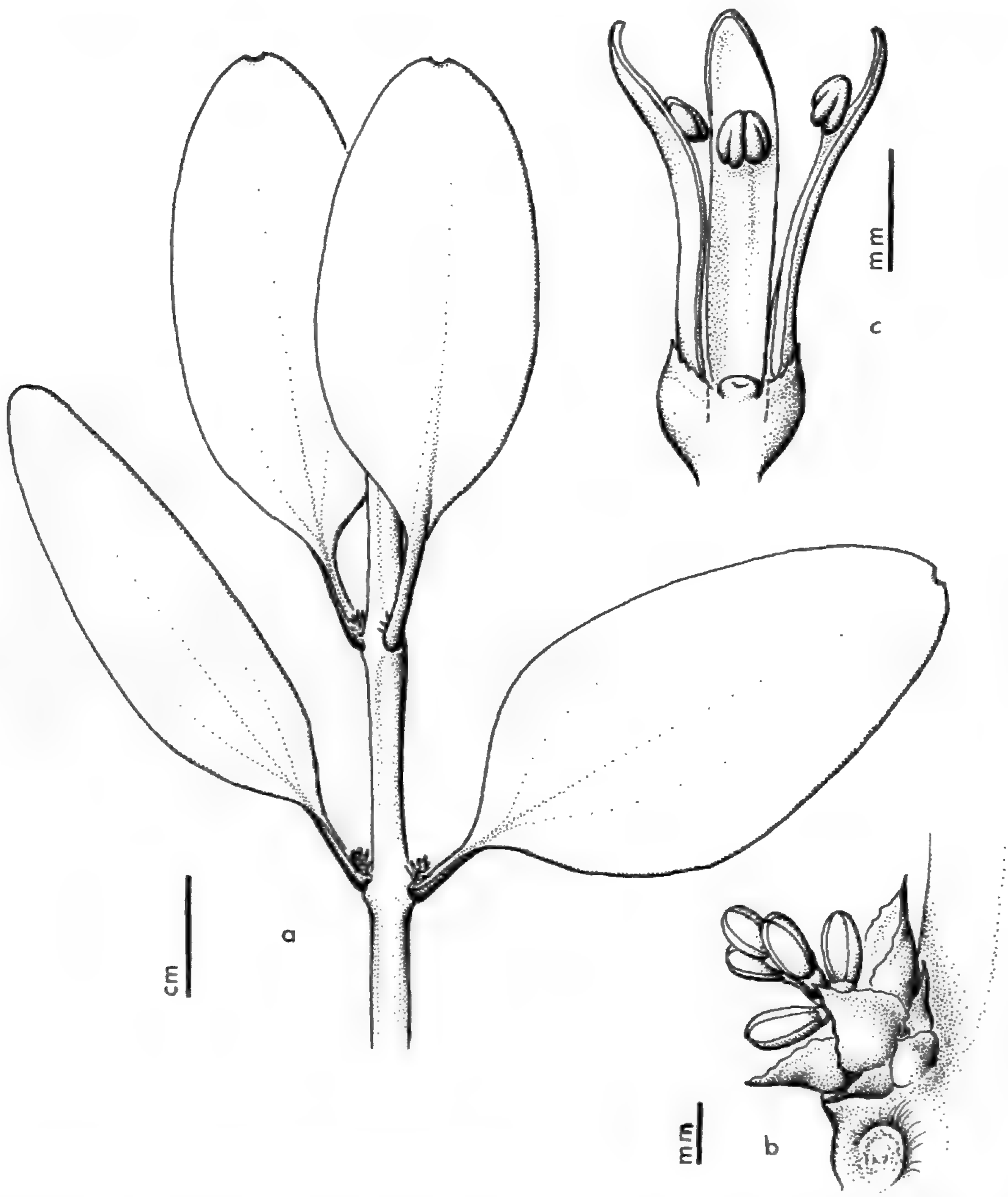

FIGURE 31. **Cladocolea roraimensis** (*Steyermark 58965*, US): a, habit, reconstructed; b, immature inflorescence, leaf scar below; c, mature flower, one petal removed to show central cushion and absence of style.

emarginate through loss of a caducous brown nail-like tip ca. 1 × 1 mm., and base obtuse to acute; petiole ca. 10 mm. long, strongly canaliculate; venation obscure. Much of the mesophyll differentiated into sclereids with many, bulbous arms. Inflorescences one per axil, subtended by several pairs of acute, chartaceous bracts 1–2 mm. long; flowers paired, sessile, ebracteolate, inflorescence terminated by a single, sessile flower; floral bracts caducous; flowers 7 or 9 per inflorescence, yellowish; calyculus prominently 2-dentate; petals 4, 4 mm. long, with a sessile anther above the middle in dimorphic arrangement; pollen smooth, rounded-triangular, with little or no evidence of triradiate grooves; style not seen. Fruit said to be dull blue-green, oblong-ovoid, 7 × 5 mm., the fruiting axis elongating to ca. 12 mm.

Although only two rather inadequate collections exist of this species, the *Cladocolea*-like inflorescence of the material fully warrants transferal of this species to the genus treated here. It is of some interest that Steyermark indicated "*Phthirusa*" *clandestina* as a possible relative, since that species is presently also included in *Cladocolea*. However, *C. archeri* would seem to be much nearer to *C. roraimensis*, as is indicated by the chartaceous inflorescence bracts which, in *Cladocolea*, are known only from the latter two species. All flowers seen, in contrast to Steyermark's statements, are tetramerous. The apparent absence of a style, even in young, unopened flowers, is very surprising. In its place is found a minute cushion with a small central depression. The "floribus. . . . dioicis" in the original description is presumed to indicate unisexual flowers. As in all other Loranthaceae with unisexual flowers, the sexes are likely to be segregated on separate individuals. If this is so, the type is staminate and the other collection pistillate. Unfortunately, no flowers are present on the latter.

Venezuela. BOLÍVAR: Mount Roraima, SW slopes between Rondón Camp and base of sandstone bluffs, 2040–2255 m., *Steyermark 58943* (F, holotype of *Phthirusa roraimensis*); same, *Steyermark 58965* (F, US).

22. **Cladocolea stricta** Kuijt, sp. nov. FIGURE 32.

TYPE: *Hinton 10176* (see below).

Dioecia, sympodialis, folia et rami puberuli, rami teretes. Folia alterna, solum in innovationibus vertentibus, 15 × 7 mm. vel minora, late lanceolata. Inflorescentiae staminatae singulae in axillis foliarum, pedunculis ad 2 mm. longis; flores 5–6 ad apicem congesti, foliis squamiformibus. Stylus rectus, stamina dimorphica.

Plant dioecious, short-pubescent, with sympodial branching; branches terete, straight, up to 25 cm. long for one season's growth, leaves rather dense, but occurring only along current season's growth; branch pubescence persisting into second season; craters conspicuous around base of innovations (which are subterminal), less so around base of inflorescences. Leaves consistently alternate, 15 × 7 mm. or smaller, broadly lanceolate, with acute apex and base, slightly apiculate; petiole 1 mm. or

FIGURE 32. **Cladocolea stricta,** staminate plant (*Hinton 10176,* K): habit and inflorescence.

less; blade rather fleshy, with only the midvein visible, running into apex. Staminate inflorescence solitary in the axils of leaves, being a small, determinate 5–6-flowered capitulum with squamate, persistent bracts and a peduncle ca. 2 mm. long, both bracts and peduncle short-pubescent. Staminate flowers 4 mm. long in bud, including the ovary, commonly 5-merous, sometimes 4-merous or very rarely 6-merous; calyculus and tips of petals short-pubescent; petals and stamens dimorphic; anthers 1 mm. long, attached at or above the middle of the petal; filament 0.5 mm., basifixed, with elongate filament buttress; pollen smooth, without evident grooves; ovary 1 × 1 mm.; style straight, reaching to middle of upper anthers; stigma completely undifferentiated; nectary somewhat pubescent. Pistillate plants not known.

It is with some hesitation that I give this single collection specific status. However, the differences from *Cladocolea microphylla* and *C. loniceroides*, its closest relatives, seem to be such as to make it impossible to do otherwise. *C. stricta* differs from *C. microphylla* in its absence of foliar bracts; its single inflorescence, which, furthermore, is borne in the axil of a persistent leaf; the fact that it flowers along current growth; its 4–5-partite flowers; and by its straight style, at least in the staminate flower. From *C. loniceroides* it differs in the same features (except the flowering along current growth) and, additionally, in its sympodial branching and very rigid, sparse habit.

Mexico. GUERRERO: Distr. Mina, Armenia, on *Salix*, 2340 m., *Hinton 10176* (K, holotype of *Cladocolea stricta*).

23. **Cladocolea tehuacanensis** (Oliver) Van Tieghem, Bull. Soc. Bot. France **42**: 167. 1895. FIGURE 33.

Loranthus tehuacanensis Oliver, Naturhist. Foren. Kjoeb., Vidensk. Meddel. **1864**: 171. 1865.

Oryctanthus tehuacanensis (Oliver) Engler in Engler & Prantl, Nat. Pflanzenfam., Nachtr. zu **III**: 135. 1897.

TYPE: *Liebmann 3129* (see below).

Plant dioecious, slender, sparsely branched, completely glabrous throughout, sympodial, without branching in a single season; youngest twigs very attenuate and whiplike, bearing narrowly lanceolate (immature?) leaves; stems somewhat sinuous, terete, light brown, with fine longitudinal lines, later with small, rounded lenticels; craters rather conspicuous; stem roots abundant locally but seen only on fruiting twigs. Leaves alternate throughout, secondary leaves one (rarely 2) per spike, at the very base of the spike, seemingly emerging from the crater, rather thin, up to 35 × 7 mm., lanceolate-oblanceolate, with rounded apex and tapering at base into the 1 × 5 mm. petiole; venation pinnate, midrib not reaching apex. Pistillate inflorescences on year-old wood, not on current growth, one or 2 per axil, up to 30 mm. long, axis somewhat compressed in dried plants only, leafless above crater, the flowers subtended by "shoulders" on which leaf

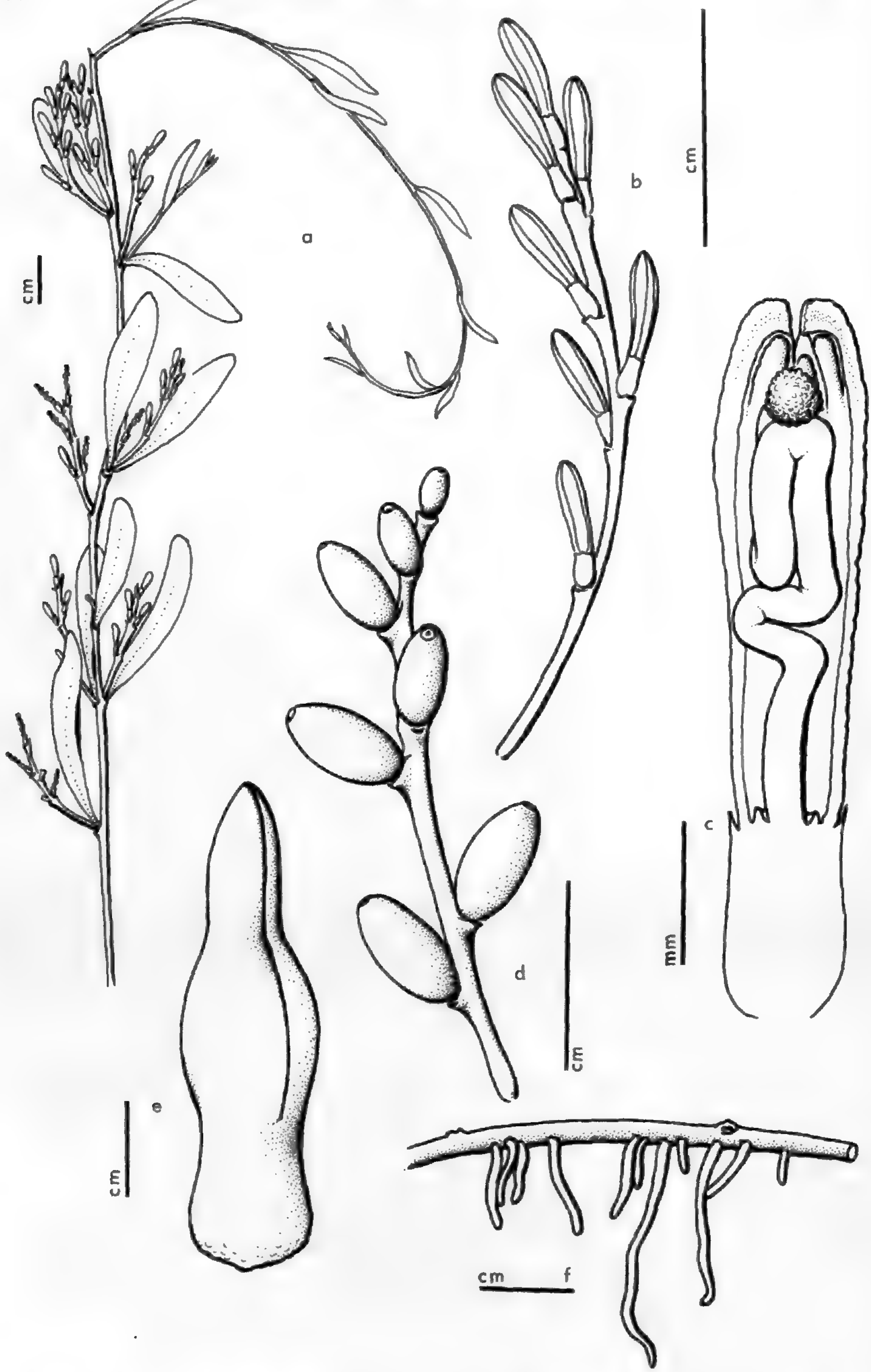

FIGURE 33. **Cladocolea tehuacanensis**, pistillate plant: a, habit (*Liebmann 3129*, C); b, inflorescence, same collection; c, pistillate flower, longitudinal section, same collection; d, infructescence (*Liebmann s.n.*, presumably *3129*, P); e, embryo, same collection; f, roots growing from stem (*Liebmann 3130*, C).

scales are not recognizable; flowers 5–8 per spike, one of which is terminal, in irregular, paired to alternate arrangements. Pistillate flowers: mature bud 5 × 1 mm., somewhat clavate in shape; calyculus smooth except for one or more teeth; petals 5 or 6, very narrow, slightly more than 3 mm. long, with very small staminodia reaching tip of petal, showing a slight but distinct dimorphism; ovary 1.5 mm. long; style highly convoluted in upper ⅔; stigma just below petal tips, capitate, well differentiated, with papillar surface; nectary smooth. Fruit at least 7 × 3 mm., ellipsoid, dark-colored; embryo dicotyledonous, slightly more than 5 mm. long, ⅔ of which is cotyledons, the radicular end rather blunt. Staminate plant unknown.

There is some unfortunate confusion in the very sparse collections of this species. In Copenhagen three sheets exist, each labelled "6. *Loranthus Tehuacanensis* Oliv." Two of these sheets bear the Liebmann number *3129* but have different collection dates (May and December, 1841; the latter is considered the holotype). The third sheet bears the number *3130* and was also collected in December, 1841, in Tehuacán. The two unnumbered Liebmann sheets at Paris, dated Dec. 1841, are presumed to be *3129*.

Mexico. "In monte Felipe, prope Oaxacam Julio. Parasitica," *Andrieux 344* (M; at K and P this number is *C. andrieuxii*); Tehuacán, *Liebmann 3129* (C, holotype of *Loranthus tehuacanensis*; isotype at P); same, *Liebmann 3130* (C).

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INDEX TO COLLECTIONS CITED

Numbers in parentheses refer to species as treated in the text.

Acosta Solis *12200* (2)
Andrieux *344* (1, 23), *345* (1)
Archer *1058* (2), *1521* (2)
Arsène *1749/2* (7), *2268* (7)

Barr & Barr *64–553* (15)
Barr & Dennis *64–304A* (15)
Bartlett & Lasser *16645* (18)
Bonpland *s.n.* (17)
Brade *10461* (3)
Brandegee *s.n.* (13)
Breckon & Breckon *803* (20)
Breedlove *35588* (13), *35991* (18), *35998* (8)

Camp *2365* (20), *2550* (20), *2609* (1)
Carlson *1385* (20)
Converse *83* (15)
Conzatti *1898* (20), *1899* (20), *4544* (20)
Conzatti & Gómez *2381* (*2081?*) (20)
Conzatti & Gonzalez *294* (20)
Conzatti & Ostlund *5178* (20)
Cuatrecasas *15244* (2), *18430* (2), *20506* (2)

Dodson & Thien *1507* (10), *1852* (2)
Dudley *13450* (2)
Duke *4504* (18)

Espinosa *16366* (10)

Ferris & Mexía *5166* (13)
Frye & Frye *2600* (20), *2601* (17)

Gardner *1322* (3)
Gentry *4996* (13), *5636* (13), *7056* (13)
Gimate Leyva *s.n.* (15)
Glaziou *1429* (3)
Graham *235* (9)
Gregg *722b* (16), *1116* (13)

Harling *6015* (10), *6094* (10)
Hinds *346* (13)
Hinton *636* (15), *930* (15), *3107* (9), *3152* (15), *3550* (9), *3796* (15), *3840* (15), *3958* (4), *4091* (19), *4112* (15), *4115* (15), *4255* (15), *4730* (18), *4777* (4), *5554* (4), *6688* (4), *7689* (17), *8146* (18), *9021* (9), *10148* (11), *10149* (9), *10151* (11), *10176* (22), *10458* (15), *10500* (15), *10689* (15), *15022* (15)
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Mexía *321* (13), *970* (13)
Mickel *1678* (15)
Mikan *s.n.* (3)
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Moreno *164* (15)
Moricand *s.n.* (17)

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Nicolas *s.n.* (7), *5158/4* (19)

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Pavón *s.n.* (15)
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Riedel *s.n.* (3)
Roe, Roe, Mori, & Rzedowski *s.n.* (15)
Rose & Painter *7662* (18)
Rose, Standley, & Russell *13746* (13)
Rzedowski *16359* (20), *16372* (15), *16373* (19), *16436* (1), *16437* (15), *16451* (15), *16623* (8), *16635* (16), *17404* (16), *17518* (8), *17914* (16), *18000* (15), *18481* (15), *18649* (18), *22120* (16), *22359* (19), *22618* (8), *22674* (18), *24020* (19), *27330* (19), *28122* (15), *28123* (15), *28125* (17), *28126* (17), *30389* (17), *30390* (17)
Rzedowski & McVaugh *270* (15), *652* (17)

Schwacke *1411* (3)
Sessé, Mociño, Castillo, & Maldonado *926* (17), *927* (15), *4957* (15)
Sharp *441572* (15)
Smith *32* (20), *122* (14)
Smith, Peterson, & Tejeda *4127* (6)
Sparre *16295* (10)
Steyermark *50672* (18), *50824* (18), *58943* (21), *58965* (21)

Tillett *637–146* (20), *637–153* (15)
Townsend *a-27* (10)
Troll *593* (17)

Webster, Miller, & Miller *11446* (18)
Wiens *2494* (13), *3781* (10), *3792* (10), *3800* (10), *4415* (16)
Wiggins *10964* (10)
Wilbur & Wilbur *1420* (15), *1666* (14), *1838* (15), *2162* (15), *2400* (14)
Williams *3820* (17)

Yuncker, Dawson, & Youse *6220* (12)

RECORDED HOSTS OF CLADOCOLEA

Number of records in parentheses

C. andrieuxii:	*Alnus jorullensis* (1)
	Alnus (1)
	Quercus (2)
C. archeri:	*Tournefortia fuliginosa* (1)
	Melastomataceae (1)
C. clandestina:	?
C. coyucae:	? *Thevetia* (1)
	Heliocarpus (1)
C. cupulata:	*Pinus* (2)
C. dimorpha:	?
C. glauca:	*Acacia* (1)
	Crataegus (1)
C. gracilis:	*Colubrina* (1)
	Podopterus mexicanus (1)
	Randia (1)
C. grahami:	*Quercus* (7)
C. harlingii:	Compositae (1)
C. hintonii:	*Quercus* (1)
C. hondurensis:	*Quercus* (1)
C. inconspicua:	*Croton niveus* (1)
	Mimosa palmeri (1)
	Randia (1)
	Zanthoxylum (1)
C. inorna:	*Cassia* (1)
	Leguminosae (1)
C. loniceroides:	*Alnus* (11)
	Baccharis (3)
	Eupatorium mairetianum (1)
	Ligustrum (1)
	Ostrya virginiana (1)
	Ostrya (1)
	Populus (1)
	Prunus persica (2)
	Quercus (4)
	Rumfordia (1)

	Salix (1)
	Solanum refractum (1)
	Vernonia (1)
	Compositae (2)
	Leguminosae (1)
	Malvaceae (1)
C. mcvaughii:	*Quercus aristata* (1)
	Quercus macrophylla (1)
	Quercus (9)
C. microphylla:	*Alnus* (1)
	Quercus (13)
C. oligantha:	*Bursera bipinnata* (2)
	Bursera tomentosa (1)
	Bursera (3)
	Lysiloma (1)
C. pedicellata:	*Acacia* (1)
	Quercus (4)
C. pringlei:	*Quercus* (9)
C. stricta:	*Salix* (1)
C. tehuacanensis:	?

INDEX TO ACCEPTED NAMES AND TO SYNONYMS

The numbers refer to the corresponding species in the text.

Cladocolea
andrieuxii = 1
archeri = 2
clandestina = 3
coyucae = 4
cupulata = 5
dimorpha = 6
glauca = 7
gracilis = 8
grahami = 9
harlingii = 10
hintonii = 11
hondurensis = 12
inconspicua = 13
inorna = 14
loniceroides = 15
mcvaughii = 16
microphylla = 17
oerstedii = *Struthanthus*
oligantha = 18
pedicellata = 19
pringlei = 20
roraimensis = 21
stricta = 22
tehuacanensis = 23

Loranthus
clandestinus = 3
grahami = 9
inconspicuus = 13
inornus = 14
microphyllus = 17
oerstedii = *Struthanthus*
tehuacanensis = 23

Loxania
loniceroides = 15
microphylla = 17

Oryctanthus
andrieuxii = 1
archeri = 2
grahami = 9
oerstedii = *Struthanthus*
tehuacanensis = 23

Phthirusa
clandestina = 3
inconspicua = 13
microphylla = 17
oligantha = *Dendropemon*
roraimensis = 21

Struthanthus
alni = 1
grahami = 9

Struthanthus (*cont'd*)

hunnewellii = 15
inconspicuus = 13
inornus = 14
loniceroides = 15
mexicanus = 15
microphyllus = 17
oliganthus = 18

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HYBRIDIZATION AND INTROGRESSION IN QUERCUS ALBA [1]

JAMES W. HARDIN

THE MOST OBVIOUS and most frequent variability in *Quercus alba* L., white oak, is intrinsic; that is, it occurs as random genetic variance, ecotypic or ecophenic variation, as discussed by Baranski (1975). In addition, a significant, although relatively minor, component of the variation is due to hybridization and localized introgression with eleven other white oaks of the subgenus QUERCUS (*Lepidobalanus*) which are sympatric with *Q. alba* in various parts of its range.

During the 27 years since Palmer (1948) summarized the history of American hybrid oaks, there has been continued interest in various crosses or introgressed populations. Most of the studies have been based on gross morphology of natural populations or seedling progeny, and there is still a need for analyses of other characteristics, as well as for experimental work. One of the most perplexing gaps in our knowledge is the need for an understanding of the barriers that either effectively maintain the individual species or are at times weaker and allow limited hybridization and introgression.

The intent of this paper is to summarize the information now available and to answer the basic question of just how important hybridization and introgression are as contributors to the total variation in *Quercus alba*. Field studies were made from southeastern Canada and New England to Illinois and south to Florida and Texas from 1965 to 1973. Herbarium material was examined from A, DUKE, FSU, GA, GH, HAM, IA, ILL, IND, KANU, KY, MICH, MIN, MISSA, MO, NCU, NCSC, OS, PAC, PH, SMU, UARK, US, WISC, and WVA. Acorns from numerous labeled hybrid trees from the Arnold Arboretum and from natural populations were planted in the North Carolina State University greenhouse and the seedlings analyzed. The collections made by M. J. Baranski during 1969 and 1972, as well as his intimate knowledge of the species, have been invaluable to this study. Voucher specimens for the research are the annotated specimens in the herbaria indicated above plus my collections and those of M. J. Baranski deposited in NCSC.

THE WHITE OAK SYNGAMEON OF EASTERN NORTH AMERICA

Gene exchange occurs or at least has the potential for taking place among nearly all species of subg. QUERCUS in eastern North America (albeit to a very limited extent in most cases), and the species can be

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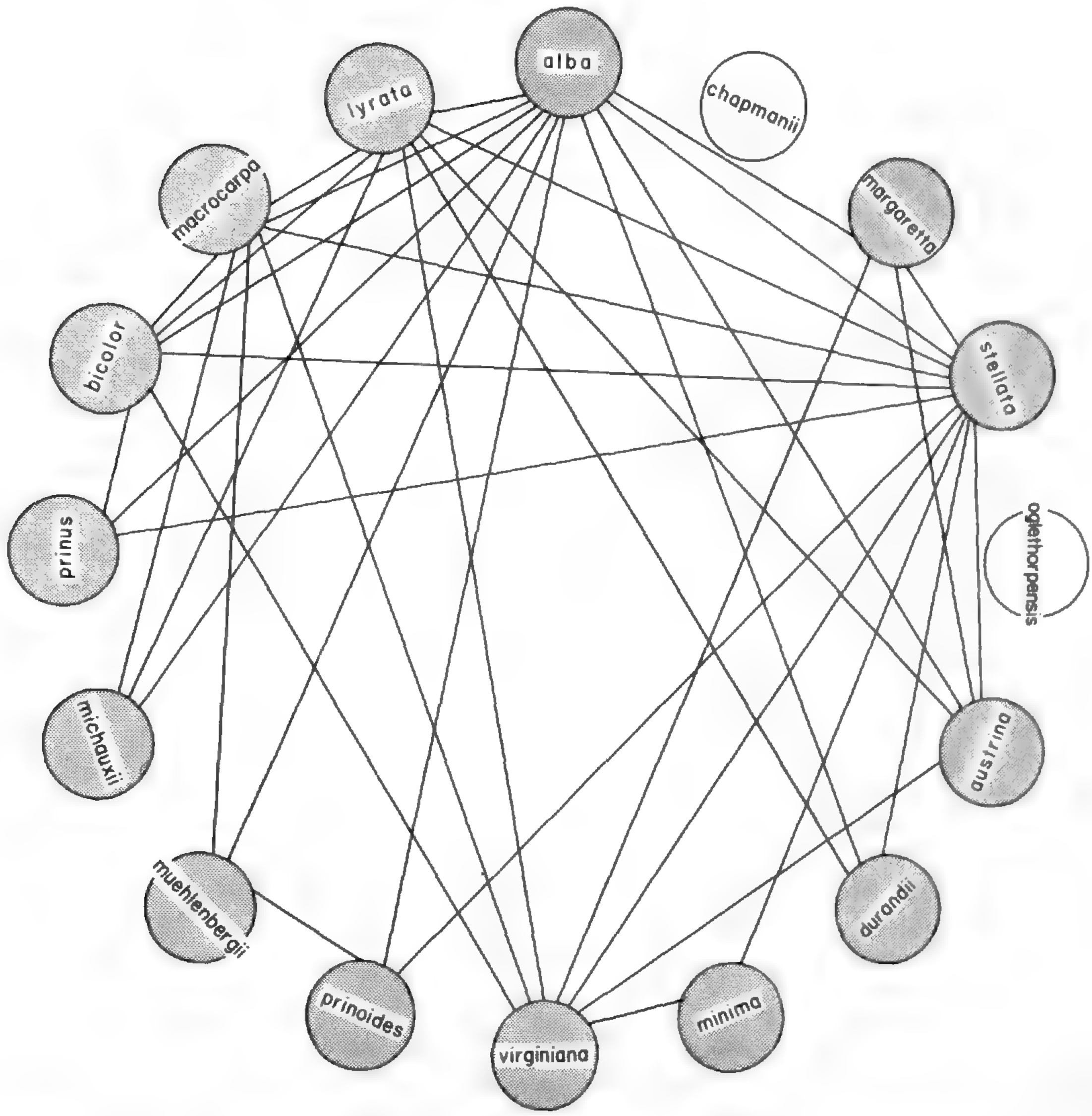

FIGURE 1. The white oak syngameon of eastern North America (shaded areas).

thought of as comprising the most inclusive breeding group or syngameon (Grant, 1971). The syngameon pictured here (FIGURE 1) is arbitrarily limited to the indigenous white oaks that occur east of Oklahoma and Texas. In actuality it is more inclusive because of crosses with *Quercus robur*, which is cultivated in the East, and *Q. gambelii* and *Q. havardii*, which are more western. Various crosses with these more western species form a connecting link between the eastern and western white oaks (Tucker, 1961).

Only the crosses involving *Quercus alba* have been included in this study. The other crosses indicated (FIGURE 1) are from the literature (Palmer, 1948; Correll & Johnston, 1970), from my collections, or from herbarium specimens examined.

It is interesting to note that *Quercus alba* and *Q. stellata* cross with more species than does any other member of this group. This may possibly reflect the relatively broad distribution and ecological amplitude of

these species, which permit them to be sympatric with so many others. The lack of certain hybrids is equally interesting. No crosses involving either *Q. chapmanii* or *Q. oglethorpensis* are known, and for this reason they cannot at present be considered part of the syngameon. In addition, there are a number of species pairs which are frequently sympatric, but between which hybrids have not been found, such as *Q. bicolor–michauxii*, *Q. macrocarpa–prinus*, and *Q. michauxii–prinus*. The reason for the lack of hybrids may be either the presence of strong intrinsic barriers or merely the fact that hybrids have not yet been found or identified. In view of the extensive crossing of other species, the latter explanation appears to be the more likely.

The pattern of crossing within the subgenus substantiates the inclusion of the evergreen species, such as *Q. virginiana*, in this subgenus, but it does not lend support to the sections recognized by either Trelease (1924), Camus (1936–39), or Rehder (1940).

RECOGNITION OF WHITE OAK HYBRIDS

The basic prerequisite for recognizing hybrids is a thorough knowledge of the intrinsic variation within each of the parental species, particularly that due to ecophenic and ecotypic differences, stump sprouting, and juvenility, as well as to stress morphology created by extreme climatic conditions or insect damage (Muller, 1941). Once a total species concept is acquired, hybrid forms can then be recognized with some degree of assurance. However, the designation of hybridity and attribution of parentage are still only opinions based on comparative morphology, often with circumstantial evidence from associated species, ecology, and geography. There is seldom any real proof of the proposed hybridity in nature.

It may be assumed that a first generation hybrid will be more or less intermediate between the parent species in nearly all features — leaves, twigs, acorns, bark, phenology, fall coloration, and ecology. It must be remembered, however, that all of the species are variable and the different forms of the parental types could yield hybrids with slightly different characteristics. There is also the possibility of dominance or epistasis, morphological irregularities, or transgressive segregates.

Continued generations (F_2, etc.) tend to segregate somewhat, and the segregates are often similar to and difficult to distinguish from the parental species. Oaks, in general, have been thought to be rather self-incompatible (Irgens-Moller, 1955; Piatnitsky, 1960), so that selfing would be rare. On the other hand, there is evidence that indicates considerable selfing, at least within *Quercus alba* and hybrids. Isolated trees beyond the effective pollination range of other trees seem regularly to bear large numbers of acorns. Although the effective pollination range for oaks is not precisely known, such normal fruit production would indicate selfing, assuming, of course, that the acorns were not all of hybrid or apomictic origin. The pollen of oaks is small (ca. 35×40 μm.), and judging from work done with pines (Colwell, 1951), the effective pollination range would

probably not exceed 200 meters. In addition, the various progeny tests (Allard, 1932, 1949; Bartlett, 1951; and the analysis of *Q. alba* × *bicolor* reported here) also tend to substantiate selfing and segregation. However, since all of the trees used in these various studies were open grown, one could argue that the individual progeny considered to be "segregates" were in fact the result of backcrosses to the parental species. Without definitive information on the relative degree of self-incompatibility in white oaks, I am assuming that at least some selfing and segregation occurs regularly in the natural populations of the eastern white oaks.

When introgression occurs, there is developed a more or less complete bridge across the morphological and ecological gaps between the two parents, depending upon whether the backcrossing is unilateral or reciprocal. It may then be impossible, at least locally, to recognize any discontinuity between parents and hybrids or to identify correctly certain individuals as backcrosses. All features seem to vary independently, and techniques such as the use of a hybrid index or pictorialized scatter diagrams (Anderson, 1949; Goodman, 1966, 1967) or a discriminant analysis (Ledig *et al.*, 1969) must be employed to analyze complex hybrid populations and detect the subtle "trickle" of genes from one species into another. Differential survival of introgressed genes that affect nonmorphological traits may be nearly impossible to demonstrate. In fact, some of the breadth in ecological amplitude in many species could possibly be due to introgression rather than to something entirely inherent within the species. Therefore it is quite likely that the ecological effects of introgression extend beyond the range for which there is morphological evidence of hybridization. This brings up an interesting and unanswered question. Is the very broad ecological amplitude of white oak a result of introgression with eleven other species, or is it an intrinsic feature which allows such widespread crossing? This needs to be investigated.

White oak hybrids exist at various levels of frequency and importance in the natural populations. The lowest level is represented by a single tree, presumably an F_1, which is fairly easily recognized and whose parentage is readily surmised. Such obvious hybrids often attract local interest, and a herbarium will sometimes contain specimens from one tree that have been collected over many years by many botanists. These numerous herbarium specimens often give a false impression of the frequency of the hybrids in nature. A higher level is represented by a few F_1 or F_2 hybrids, some segregation products, backcross types, or all of these. These again are very local trees, which may have very little or no effect on the variation of white oak in the immediate area. At the other extreme is the hybrid swarm which is a complex mixture of parental forms, F_1 hybrids, or successive generations, including segregation products, introgressants, or crosses between any of these; or it may be an extensive introgressive population developed through repeated backcrossing with one or both parental species. I think the distinction between "hybrid swarm" and "introgressive population" is mainly academic and generally impossible to make in nature. Either situation may be quite local or

may cover rather extensive areas and heighten the variability of white oak in the area. The obvious hybrids in such a population may have been identified and represented in herbaria, but the subtle segregates or introgressants have normally passed as one of the parental species.

The nature of the differences between the parental species increases the difficulty of recognizing or analyzing hybrids. Most differences are quantitative, and in some cases the species are already quite similar. As Palmer (1948) indicated, "the facility and certainty with which any natural hybrid can be identified is in inverse ratio to the similarity of the parent species." This is less of a problem when dealing with hybrids of *Quercus alba*, for the presence of rather loose or appressed branched hairs on the abaxial surface of the leaves is an almost certain clue to hybridization. Nine of the eleven species with which it crosses are rather densely pubescent, and the hybrids maintain a certain number of these hairs. Distinguishing which one of the nine possible parents is involved often becomes more difficult.

Since the form and density of hairs on the abaxial leaf surface is so important, a brief explanation is needed regarding the two main types of trichomes on mature leaves. The more conspicuous (at 10–15×) is a branched type ("non-glandular," according to Dyal, 1936). This type may be erect and "loose" or appressed, sessile, or pedicellate, and it may consist of 2 to 15 branches. The size, color, form, and number of branches are often quite characteristic of certain species. This is the more important trichome type in the recognition of hybrids, since it is common on all species under consideration here except *Quercus alba*, *Q. austrina*, and *Q. robur*. The second type is a stellate hair which is minute, generally appressed, and much less conspicuous except at a magnification of about 40×. These hairs, which give the impression of being somewhat viscid, were designated as "glandular hairs" by Dyal (1936). They are of little diagnostic value.

There is a need for new criteria in the study of eastern white oak hybrids. The chromosome number of $n = 12$ (Duffield, 1940) is the same for all species, and only slight differences in size and morphology of chromosomes (Stebbins, 1950) occur. Although no intensive cytological studies have been conducted on eastern white oak hybrids, this technique is not expected to be of great help. Sax (1930) found no significant differences in pollen sterility between different species and hybrids, but SEM studies of pollen grains may be worth investigating. Chemical analyses may add a new dimension, as indicated by Li and Hsiao (1974), to the investigation of hybrids and introgressed populations and should be made.

ECOLOGICAL CONDITIONS OF HYBRIDITY

Hybrids are found primarily in (1) marginal, (2) intermediate, or (3) disturbed or open habitats. The conditions of these three habitats may, and often do, occur in combination. The disturbed, intermediate habitat is certainly the most frequent site for white oak hybrids.

Palmer (1948) observed that "hybrids are most likely to occur in nature along the margins of the range of one of the parent species where one is locally rare and the other abundant." His general principle stated that "other factors being equal, the chance for the production of natural hybrids between compatible species increases in proportion to the numerical inequality of the parent species in the immediate vicinity." This is generally true if "range" is interpreted to be "ecological" in local physiographic situations as well as "geographical" in terms of total distribution. Hybrids may be found at the margins of the geographical range (FIGURES 15, 16), but they are more frequently found at the margins of the ecological range. Palmer's explanation for this marginal position was based on relative pollen frequencies; i.e., "the chance of the rare parent being pollinated by one of its own kind" is less than "the chance of its pistillate flowers being fertilized by the wind-borne pollen of the dominant species." This assumes some degree of self-incompatibility as well as only weak incompatibility of foreign pollen. There is obviously a balance between these two mechanisms which allows the hybrids to form in these marginal situations.

In addition to this differential pollination, another possible explanation for the marginal location of hybrids may be the greater ability of the hybrid to compete in an area of stress for one of the parents. Theoretically, in an area where both parents are common in a closed community, there would be maximum competition or other interactions from the two species upon the establishment and development of the hybrid. Under such conditions hybrids are rare. However, a species at the edge of its range is not only less frequent, but under stress conditions its seedlings are at a selective disadvantage and it is not able to exert maximum competition against hybrids. The hybrids, presumably more like the dominant parent, are adaptively superior to the marginal species and can compete more favorably in such a situation.

The concept of the "hybridized habitat" has been thoroughly discussed by Anderson (1948, 1949) and by Grant (1971). It is interpreted here to mean "intermediate" or an "array of intermediate conditions" between the optimal habitats for the two parental species. In the case of *Quercus alba* and related species, the intermediacy is primarily in soil moisture or total moisture balance, soil texture, and soil pH. Relative shade tolerance may also be a factor. In certain habitats and regions, related species seemingly co-exist with white oak. But as pointed out above, both parental species exert maximum competition against the hybrid in such an apparently sympatric situation. Examples of apparent ecological sympatry are infrequent, however, since most related species that are geographically sympatric with white oak align themselves along the complex ecological gradient, with the optimum for each species at a slightly different point and with either no overlap or varying degrees of overlap between the ecological ranges of each. Anemophilous species can easily be within effective pollination range and yet be ecologically allopatric, even with a relatively short effective pollination range. The more narrow the ecological

amplitude and the greater the difference between the ecological requirements of the parental species, the greater the likelihood is for a rather broad intermediate habitat in which neither parental species is very common. This concept also assumes that no other species is dominant in this intermediate habitat to the exclusion of both parents and hybrids. In such instances of ecological allopatry, an intermediate habitat is ideal and most often necessary for the survival of the F_1. Backcrosses and segregates have a better chance of occupying either the same habitat as the more similar parent or one of the various niches in the "hybridized" habitat *sensu* Anderson (1948, 1949).

In limited areas of overlap between the ranges of the species along the ecological gradient, the hybrid is likely to compete favorably, not only because of the intermediacy of its genotype and ecological requirements, but also because one or both of the parental types are on the margin of their ecological ranges and are therefore less competitive, as discussed above.

Although hybrid acorns are probably formed occasionally throughout the area of geographical sympatry between species, undisturbed, closed forests contain the parental species, with only a rare surviving hybrid or none at all except in the marginal or intermediate situations described above. In contrast, disturbed or open habitats are frequent locations for the survival of white oak hybrids. The survival of seedlings is obviously greater in areas where there is less interspecific competition and weaker habitat selection. Certainly as long as the eastern white oaks have existed there have been habitats repeatedly disturbed by natural agencies, and man probably has contributed to these during the past few thousand years. As modern man continues at an even faster pace to clear and develop the land, to overgraze, and to overcut, open as well as hybridized habitats will continue to increase. On the other hand, there is no strong evidence to indicate that white oak hybrids are now any more frequent than they were when first described (Engelmann, 1877; Trelease, 1924; Palmer, 1948). In very few populations is there evidence that hybrids are in greater relative abundance in the seedling and sapling class than in the older canopy class.

WHITE OAK HYBRIDS

Quercus alba crosses naturally with eleven other species of the subg. QUERCUS (*Lepidobalanus*) (FIGURE 2). The arrangement of the species in FIGURE 2 is not meant to indicate relationships, but rather to show a trend from the fewest crosses (3) at the top to the most (8) at the botton. Within the twelve species, *Q. alba* crosses with the most. It is placed at the center merely for emphasis. *Quercus durandii* is included here with *Q. austrina*, as will be discussed later.

Seven of the eleven crosses with *Quercus alba* have been given binary names by such authors as Schneider, Trelease, and Palmer. The others have been designated by formula only. Since there is no unanimity of

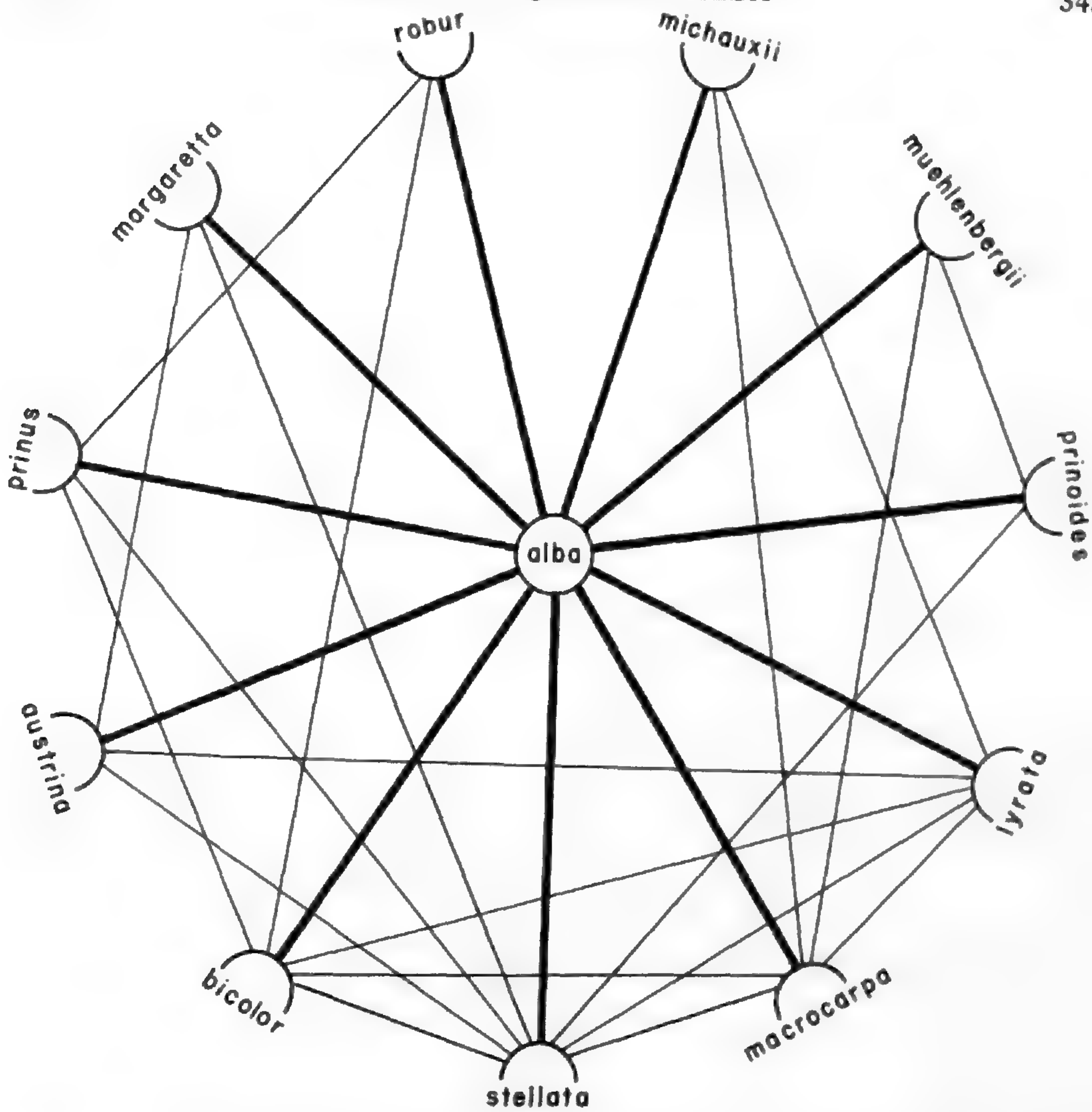

FIGURE 2. Natural hybridization between the eastern white oaks that cross with *Quercus alba*.

opinion regarding the preferable nomenclatural method for naming hybrids (Little, 1960; Rowley, 1961, 1964; Grassl, 1963), I prefer to be consistent throughout and to designate all hybrids by formula with the epithets in alphabetical order. None of the hybrids form large distinct populations or in any way resemble natural species.

Without direct proof of hybridity, the best evidence of hybridization is (1) a demonstration of morphological intermediacy and recombination in nearly all characters analyzed, (2) progeny tests, and (3) a comparison between the natural putative hybrids and those made artificially. Relying primarily on the first of these, analyses of populations (using the hybrid index or pictorialized scatter diagram methods of Anderson, 1949) were made based on various features of the leaf, acorn, twig, bark, and ecology, depending upon the particular cross and the character differences between the putative parents. Foliar features alone were used to analyze the progeny grown in the greenhouse.

The leaf offers the most obvious clue to hybridity, but features of the

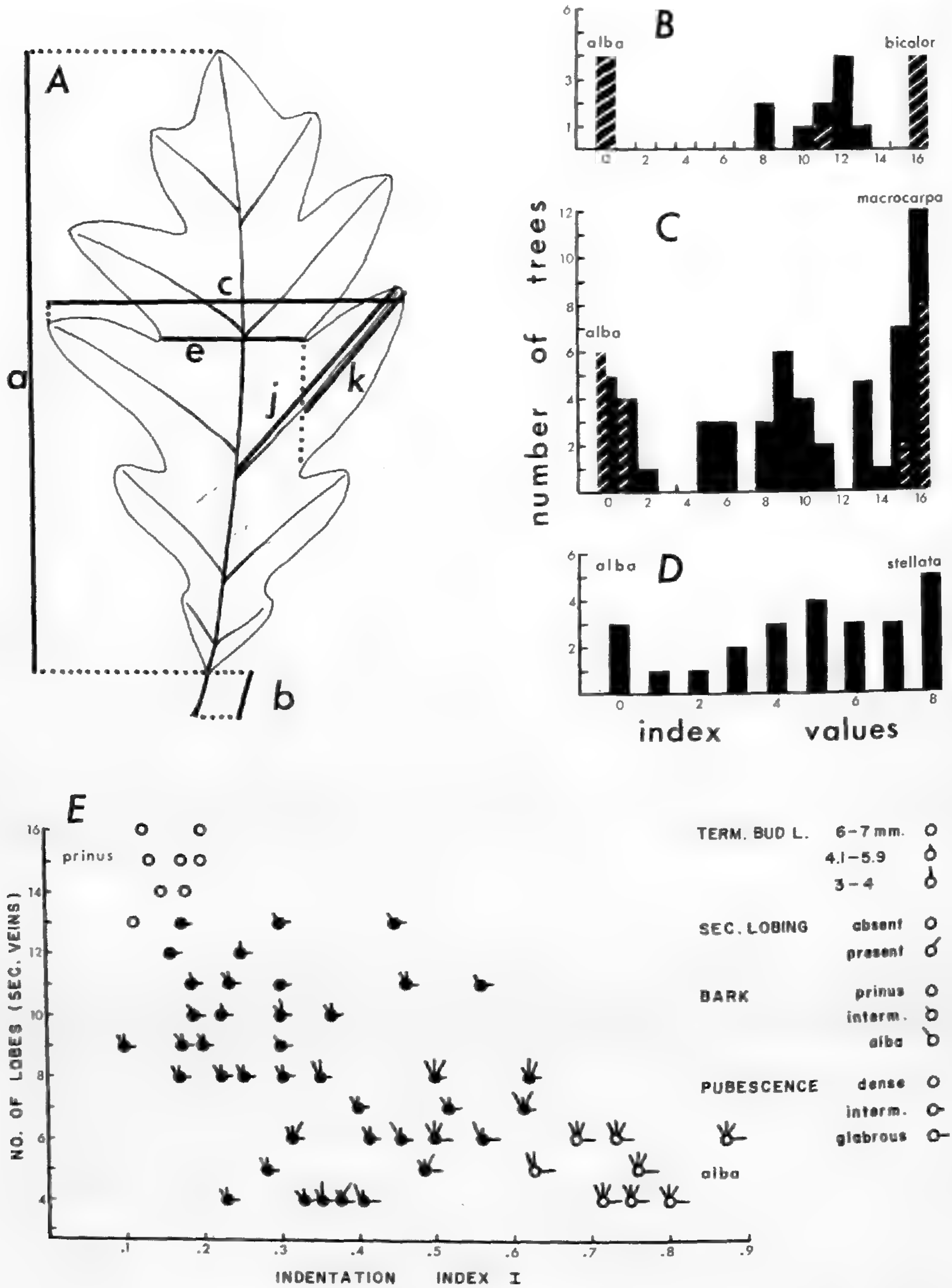

FIGURE 3. Analysis of variation. A, Measurements taken of leaf form (a = length of blade; b = length of petiole; c = width of leaf at widest point; e = intersinus width nearest widest point; j = length of longest lobe from base of vein; k = length of longest lobe from line between sinuses). B, Mature *Quercus alba*, *Q. bicolor*, and the hybrid tree growing at the Arnold Arboretum (hatched bars); progeny from the hybrid tree (solid bars). C, Hybrid population from Livingston County, Michigan (solid bars); typical *Q. alba* and *Q. macrocarpa* from southeastern Michigan (hatched bars). D, Hybrid population (*Q. alba* × *stellata*) from San Augustine County, Texas. E, Hybrid population (solid circles); typical *Q. alba* and *Q. prinus* (open circles); all from Wake County, North Carolina.

acorn, twig, and bark are of great diagnostic value and should always be used when available. The type and relative density of trichomes on the abaxial leaf surface are one of the most important characters. The following variables were used for analysis of leaf form (FIGURE 3A):

1. Length of blade (a).
2. Length of petiole (b).
3. Width of leaf at widest point (c).
4. Length/width ratio (a/c).
5. Intersinus width nearest widest point (e).
6. Position of widest point: below, above, or at the middle.
7. Number of primary lobes on the right edge of the abaxial side, not including the apex.
8. Number of primary lobes above the middle.
9. Presence of secondary lobes.
10. Length of longest lobe from base of vein (j) and from line between sinuses (k).
11. Indentation index I — $\frac{c-e}{c}$
12. Indentation index II — $\frac{k}{j}$

Leaf silhouettes (FIGURES 4–14) represent only a few examples of each cross. The single white oak leaf is more or less typical for the species, but it obviously may not represent the correct parental type for all crosses. Also, the silhouettes represent only leaf form and should never be taken alone to indicate hybridity.

The following variables were used for acorn analysis: (A) nut length and diameter, (B) cup depth, (C) ratio of A/B, and (D) features of

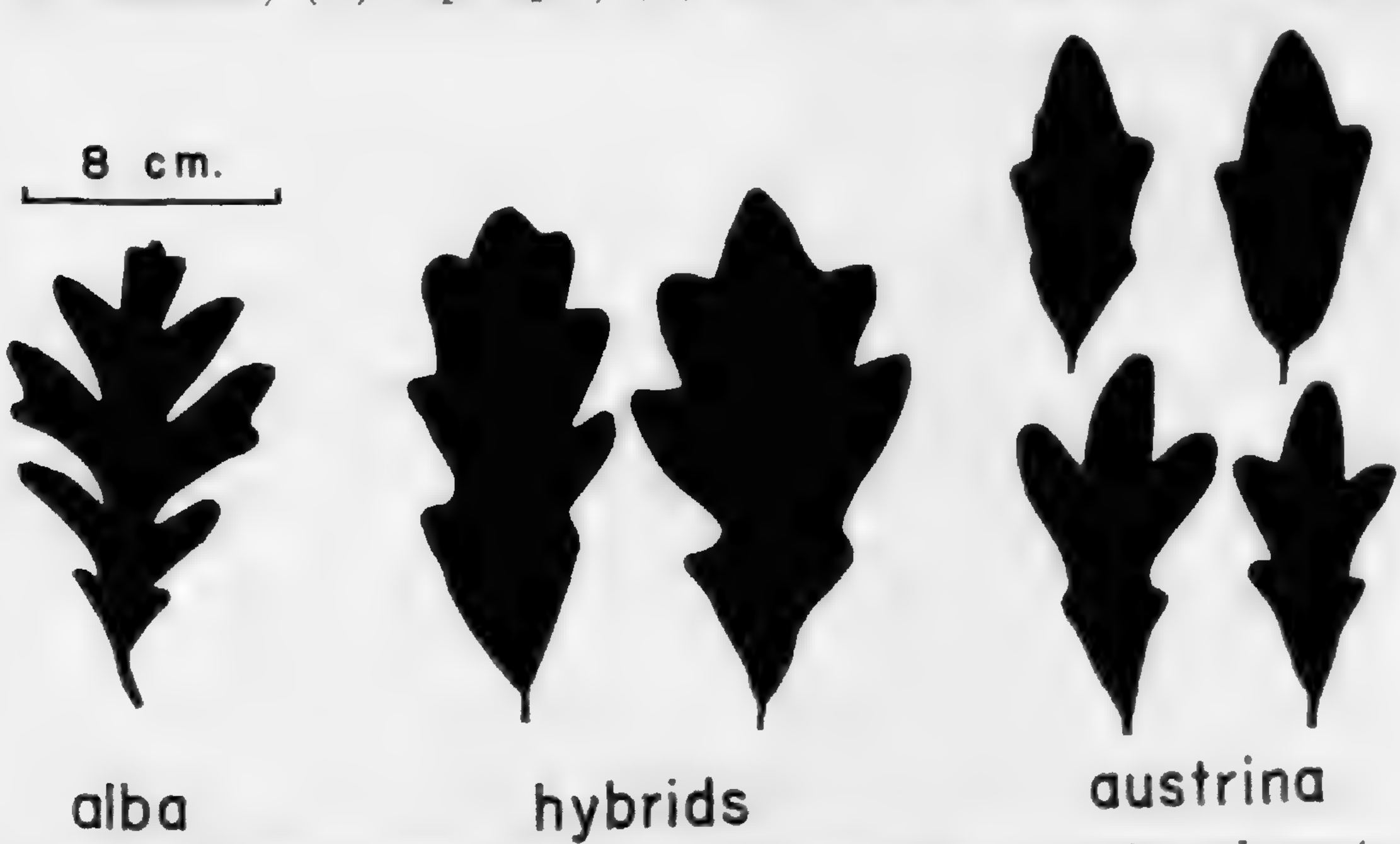

FIGURE 4. Representative leaf forms of *Quercus alba* × *austrina* and parents.

the scales. In some cases the acorn was scored as being like one or the other parent or intermediate, taking all features into consideration.

Twig features such as color, pubescence, form, and size of buds were used as a basis for scoring the twig as being either like one or the other parent or intermediate. Bark of mature trees was scored in a similar manner. Where there was an obvious ecological differentiation between parents in nature, the location of the hybrid was also given a score.

The distribution maps (FIGURES 15, 16) show the location of hybrids identified in the field or from herbarium material. The ranges of the species have been generalized from the detailed maps by Little (1971) in most cases, or very general ranges have been interpreted from various floristic manuals.

1. Quercus alba × austrina

The entire complex involving *Quercus austrina* Small, *Q. durandii* Buckl., and *Q. sinuata* Walt. is in need of a critical re-evaluation and field study before definitive judgments can be made regarding hybridization with white oak. Until the taxonomy of this complex is settled, I am for convenience considering only *Q. austrina*, since most of the hybrids involving *Q. alba* are with this segment of the complex. Rehder (1940) included "*Q. a.* × *Durandii*" in his list of white oak hybrids, but Palmer (1945, 1948) did not mention it. I have found a few examples that may be *Q. alba* × *durandii*, on the basis of intermediate lobing and pubescence, but I prefer to withhold judgment until the complex is better understood.

The differences between *Quercus alba* and typical bluff oak (*Q. austrina*) are so subtle that hybrids are difficult to detect. A few herbarium specimens from Mississippi and Florida are tentatively identified as *Q. alba* × *austrina* (FIGURES 4, 15) on the basis of intermediacy of leaf form, color, acorn features, and habitat. There are also populations in lower South Carolina, northern Florida, and central Louisiana that seem to be mixtures of *Q. austrina–durandii*, *Q. alba*, and *Q. margaretta*, but most have not been analyzed critically. One population in South Carolina is discussed under *Q. margaretta*. All such hybrid and introgressed populations are very local. I am tempted to suggest that what we know as *Q. austrina* may have arisen as a result of the past influence of *Q. alba* on *Q. durandii*. The apparent cline from west to east in this complex approaches *Q. alba* in the southeastern United States. This pattern of variation could, however, reflect strong selection and merely a homoplastic similarity with *Q. alba*.

2. Quercus alba × bicolor

Quercus × *jackiana* Schneider, Ill. Handb. Laubholzk. **1**: 202. 1904.

Jack's oak is scattered in distribution (FIGURE 15) and generally occurs as isolated trees in disturbed or intermediate habitats within populations

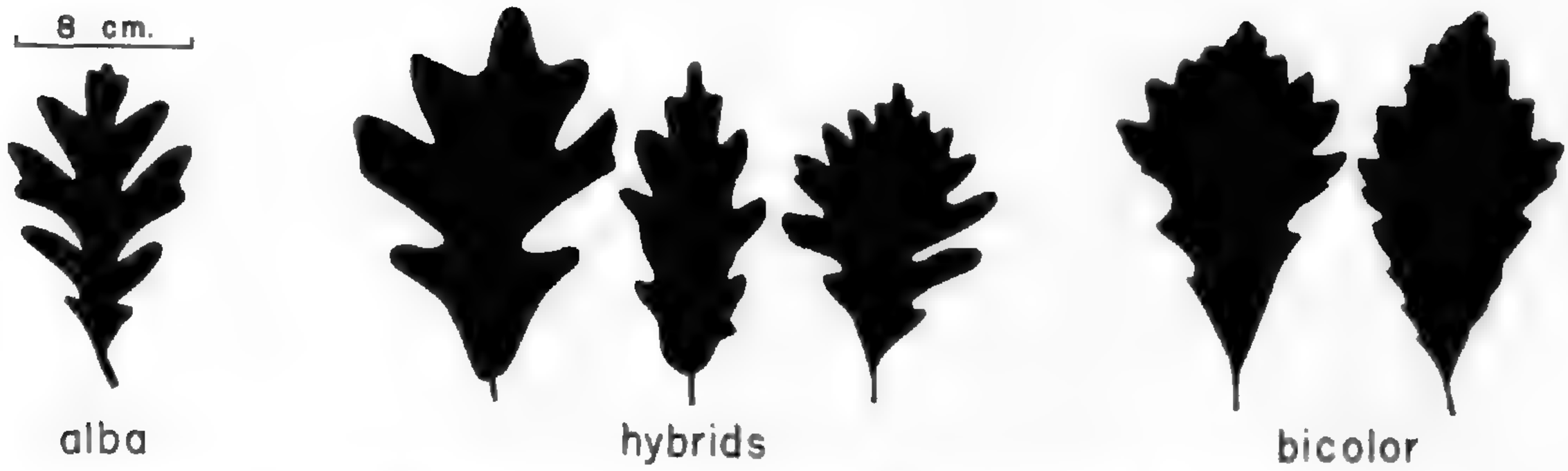

FIGURE 5. Representative leaf forms of *Quercus alba* × *bicolor* and parents.

containing both parental species. It is also quite frequent at the margin of the geographical range of swamp white oak (*Q. bicolor* Willd.).

The leaf outline is more or less intermediate between the leaf outlines of the parental species and is often quite irregular (FIGURE 5). The most distinctive feature is the presence of a mixture of two sizes of branched hairs, a large loose type and a small appressed type (Dyal, 1936), both in less abundance than in typical *Quercus bicolor*.

Acorns collected from a hybrid tree in the Arnold Arboretum were grown in the North Carolina State University greenhouse. The leaves from the seedlings, as well as the parent tree and the typical parental species in the Arboretum, were analyzed with a hybrid index based on number of lobes, indentation index II, general shape, and pubescence; each was scored on a scale from 0 (*Q. alba*) to 4 (*Q. bicolor*). Although the tree was open grown and the pollen parent is unknown, both parental types were in the vicinity. The seedling variation (FIGURE 2B) shows either segregation toward both parents or backcross progeny. The progeny do tend to confirm the parentage of Jack's oak.

This hybrid is infrequent, and gene exchange between the two species seems to be quite limited. Very few populations show more than very limited backcrossing to the more abundant parent species.

3. Quercus alba × lyrata

Evidence for this cross of *Quercus alba* with *Q. lyrata* Walt., overcup oak, is limited to a very few scattered locations (FIGURE 15). Palmer (1948) merely listed it among other crosses suspected on the basis of a few specimens at that time.

The hybrids are recognized on the basis of somewhat intermediate leaf shapes, pubescence, and acorns. Leaf lobing appears to be extremely variable but usually shows the broad sinus below the middle of the blade, in addition to a tendency toward having the three relatively large (although more deeply dissected) upper lobes (FIGURE 6). Sparse pubescence on the young twigs and lower leaf surface is characteristic of the hybrids. The thin acorn cup covers half to two thirds of the nut, and the fringe may either be present or not.

Hybrids occur in bottomlands or low woods where the parents are very

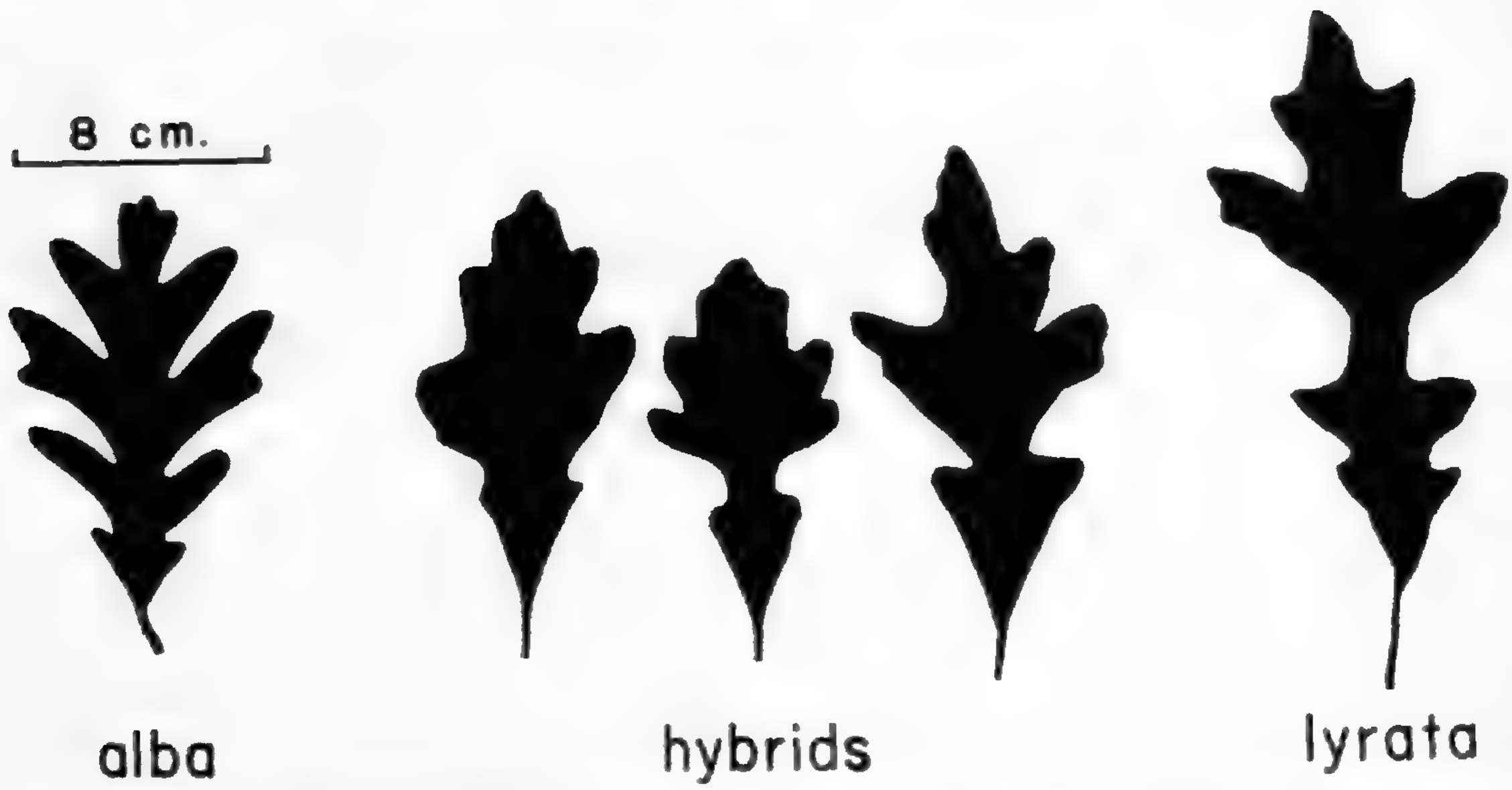

FIGURE 6. Representative leaf forms of *Quercus alba* × *lyrata* and parents.

close to one another and generally where there has been extensive disturbance by past lumbering operations. The hybrids are local, and most backcrossing seems to be with *Quercus lyrata*. Some of the variability of *Q. lyrata* in leaf shape, in pubescence of leaf, twig, and bud, and in depth of acorn cup may reflect a "trickle" of genes from white oak into overcup oak. The influence of overcup oak on the morphology of white oak appears to be very local and negligible.

4. Quercus alba × macrocarpa

Quercus × *bebbiana* Schneider, Ill. Handb. Laubholzk. 1: 201. 1904.

Bebb oak is one of the most frequent of the white oak hybrids, and it is also one of the good examples of introgression. It occurs in scattered locations (FIGURE 15) within the area of sympatry of white and bur oak (*Q. macrocarpa* Michx.).

Although there are "various degrees of transition between parent species" (Palmer, 1948), the hybrids are fairly easily recognized by the intermediacy of features or the mixture of parental characters. Leaf shapes (FIGURE 7) form a continuum between the parental types, but they usually show at least a tendency toward the broad sinus below the middle of the blade and the massive portion above. The hybrids consistently have some degree of pubescence on the lower leaf surface, and the petiole may be pubescent or glabrous. The acorn cup is generally deeper than in white oak, but the marginal fringe, so characteristic of bur oak, may or may not be present. The bark may be intermediate or more like that of one of the parents. Although the ecological ranges of the parental species are somewhat different, the two plants are frequently close associates and appear to occupy similar sites.

A rather large population near Brighton, Livingston County, Michigan, was analyzed in detail. Samples were taken from 56 trees scattered over

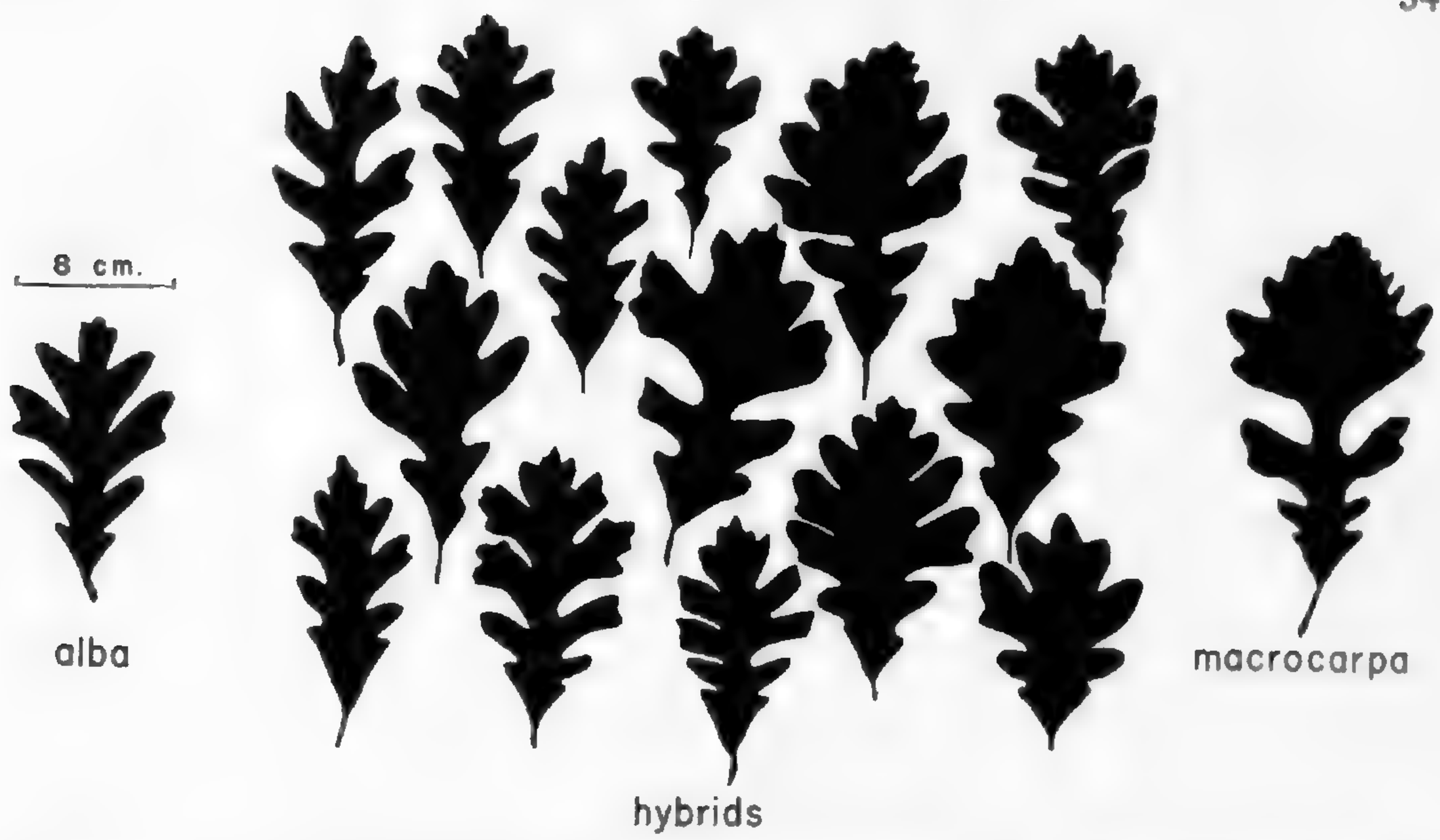

FIGURE 7. Representative leaf forms of *Quercus alba* × *macrocarpa* and parents.

an area of about one square mile. The area was at that time (before construction of two dual-lane highways and a sprawling intersection) covered by an open mixed hardwood forest in small to medium-sized woodlots dissected by pastures and cultivated fields. Some large trees remained along roadsides and in pastures. Much of the area showed signs of extensive disturbance by logging and grazing. Only mature trees greater than 4 inches dbh were sampled. Ten trees of each parental species were sampled from scattered locations in Lapeer and Oakland counties, Michigan. Hybrid indices were constructed using a scale of 0 (*Q. alba*) to 2 (*Q. macrocarpa*) for the following eight diagnostic features: bark (light ashy gray to darker gray and more distinctly ridged), twigs (glabrous to pubescent), acorns (less than 3/4 inches to greater than 3/4 inches, cup less than 1/2 to greater than 1/2 length of acorn, without or with fringe), leaf pubescence (glabrous to densely hairy), and leaf form (oblong to obovate, without and with wide central sinus and massive upper portion).

This hybrid population (FIGURE 3C), in contrast to the typical species, is composed of both parental types plus various hybrid forms. There may be some limited segregation toward both parents, but there is probably more backcrossing, particularly to *Q. macrocarpa,* which is the more frequent parent in the immediate area. This pattern seems rather typical of a number of populations that exhibit limited gene exchange between species. The predominance of forms closer to bur oak is probably due to differential pollination rather than differential selection of seedlings. Presumably any hybrid seedling could compete well in this open, disturbed habitat in which both parental species are well adapted.

Hybrids are nearly always associated with both species. However, a population of hybrids more like bur oak was found near Mora, Kanabec

County, Minnesota. No white oaks were found in the area. The hybrids are large trees, possibly 50 to 75 years old, and white oak has undoubtedly been selectively cut from the area since the hybrids were formed.

Bebb oak exists either as single trees, probably F_1 hybrids, or in mixed populations, which could be either hybrid swarms or introgressed populations. Hybrids are localized, and introgression seems to have rather limited influence on the variability of the parent species in the region.

Li and Hsiao (1974) have shown that the phenolic compounds in a hybrid tree growing at the Morris Arboretum substantiate the suspected parentage of *Quercus alba* and *Q. macrocarpa*.

5. Q. alba × margaretta

The hybrid with *Quercus margaretta* Ashe, sand post oak, is found infrequently in the lower Coastal Plain (FIGURE 15). The habitat of sand post oak is fairly restrictive (Muller, 1952), and white oak generally does not occupy the same sites. Undoubtedly the ecological barrier is very effective where the parental species are close enough for cross-pollination, and an intermediate habitat is necessary for the survival of the hybrid.

This hybrid was included under *Quercus* × *fernowii* (*Q. alba* × *stellata*) by Palmer (1948). The collections from Nansemond County, Virginia, which Fernald (1942) considered to be *Q. alba* × *stellata* var. *margaretta* were cited by Palmer under *Q.* × *fernowii*. I consider *Q. margaretta* to be a distinct species, and likewise the hybrid with white oak is distinct from *Q.* × *fernowii*.

The hybrid between *Quercus alba* and *Q. margaretta* is recognized by the more or less shrubby or small tree habit, smaller leaves, large pedicellate branched hairs (in contrast to the sessile branched hairs in *Q. alba* × *stellata*), and glabrous twigs. Leaf shapes (FIGURE 8) are variable but generally indicate the large lobes of the upper half.

In most cases, these hybrids occur as single individuals or small clones. However, there are populations, particularly in the southwestern part of the range, where presumably reciprocal or unilateral introgression has occurred and heightened the variability of both parental species in the immediate area. A hybrid index for a population in Harrison County,

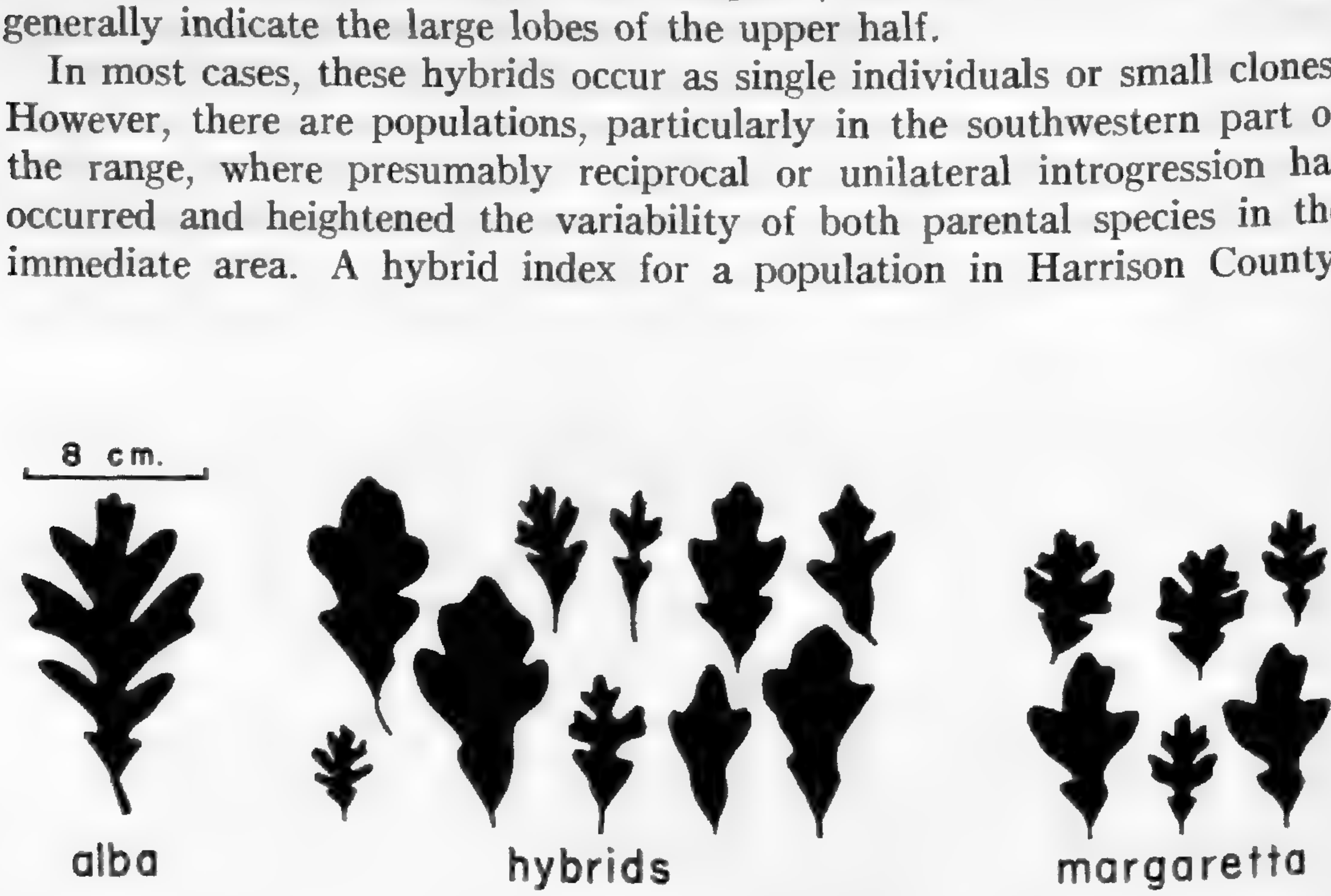

FIGURE 8. Representative leaf forms of *Quercus alba* × *margaretta* and parents.

Texas would appear quite similar to that in FIGURE 3C, owing to the greater backcrossing to *Quercus margaretta.*

As mentioned under *Quercus alba* × *austrina*, there are populations that appear to be mixtures of *Q. alba*, *Q. austrina*, and *Q. margaretta.* One such population near Bluffton, South Carolina is a mixture of a few large white oaks, infrequent sand post oak, and fairly common bluff oak and hybrids. The hybrid forms are either small single trees (more nearly *Q. alba* × *austrina*) or clones of stoloniferous small trees to eight feet tall. The leaves are mostly like *Q. alba* × *austrina* in shape and texture but have scattered pedicellate branched hairs and occasional larger lobes at the apex typical of *Q. margaretta.* The habitat is a low, sandy, pine flatwood, which has been heavily disturbed in the past by lumbering operations. The influence of this mixture appears to be very local.

6. Quercus alba × michauxii

Quercus × *beadlei* Trelease ex Palmer, Jour. Arnold Arb. **29:** 16. 1948.

Beadle oak is found rather infrequently in scattered geographical locations (FIGURE 15) and in low woods, on the lower slopes adjacent to floodplains, or in swamps where the ecological ranges of white oak and swamp chestnut oak (*Quercus michauxii* Nutt.) overlap.

This hybrid is fairly easily recognized by the light gray, flaky bark, the more or less intermediate leaf form (FIGURE 9), the sparse pubescence of loose branched hairs, and acorns of more or less intermediate size, the cups with rather coarse, thick, and loosely imbricated scales. The leaf form (FIGURE 9) appears very similar to *Quercus alba* × *bicolor* (FIGURE 5), *Q. alba* × *prinus* (FIGURE 12), or *Q. alba* × *muehlenbergii* (FIGURE 10), and distinction between these four has to be based on other features, such as bark, pubescence, acorns, and ecology. A number of herbarium specimens were found to be mistakenly identified as *Q. alba* × *prinus* (*montana*).

The hybrids seem to exist as individuals in disturbed, intermediate habitats, and there is no evidence thus far of either extensive hybrid swarms or introgressed populations.

The use of the name *Quercus prinus* L. continues to be a source of con-

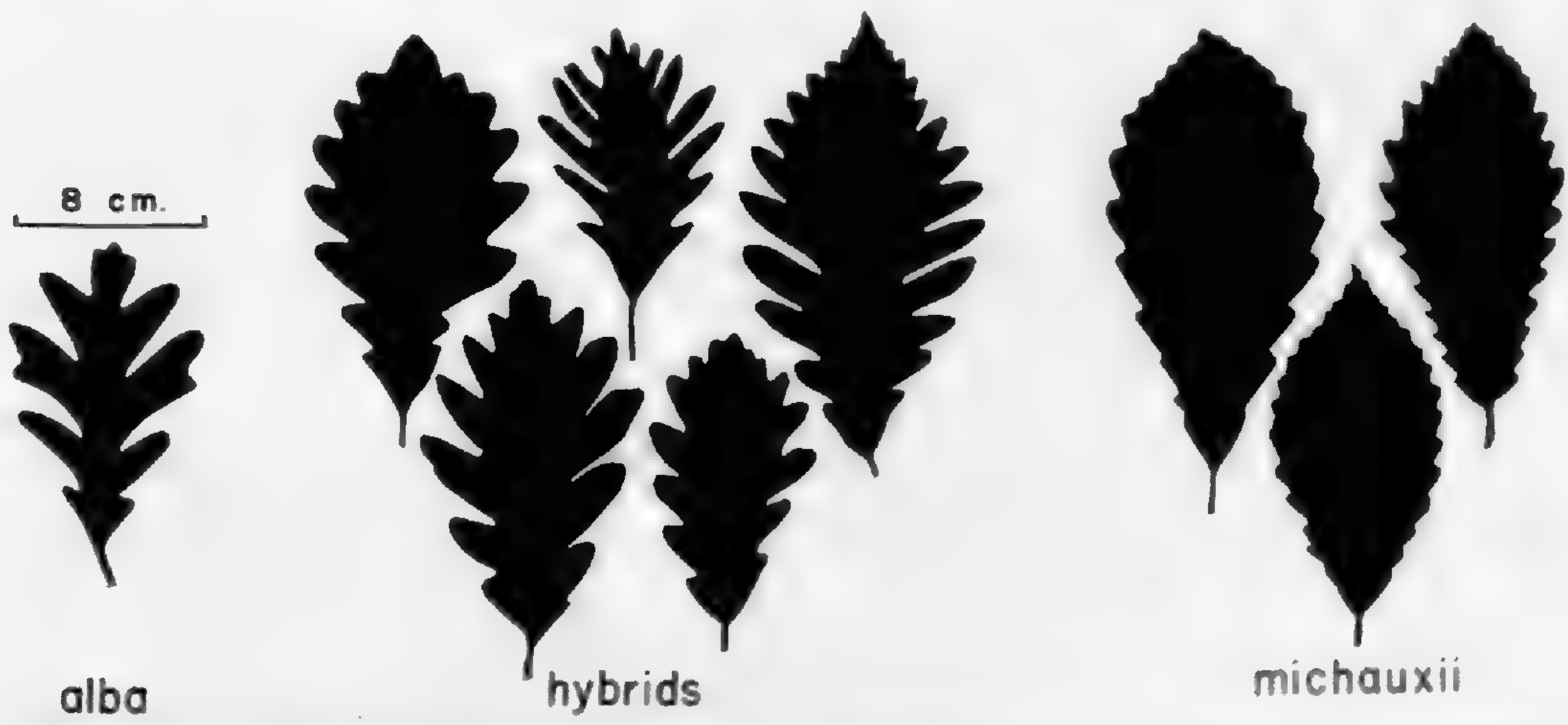

FIGURE 9. Representative leaf forms of *Quercus alba* × *michauxii* and parents.

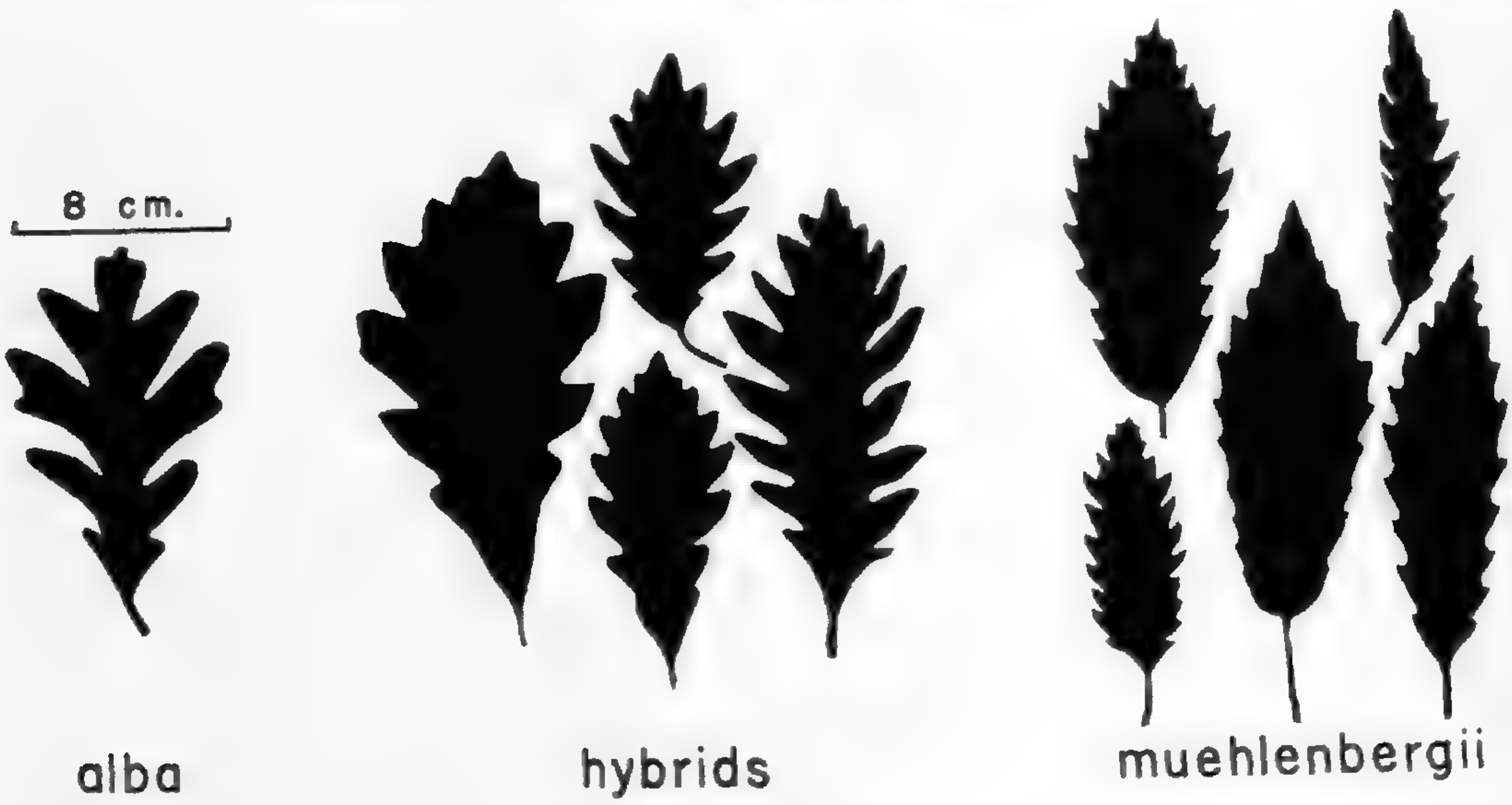

FIGURE 10. Representative leaf forms of *Quercus alba* × *muehlenbergii* and parents.

fusion, and it may be a good candidate for rejection under Article 69 of the *Code*. Standardization of the use of *Q. prinus* for chestnut oak and *Q. michauxii* for swamp chestnut oak did not follow the publication of Little's *Check list* (1953) as was hoped, for many recent publications use *Q. prinus* for swamp chestnut and *Q. montana* Willd. for chestnut oak. C. H. Muller considers the Linnaean type specimen to be the swamp chestnut (Bernard & Fairbrothers, 1967). At this time, no one can be certain of the meaning of the name *Q. prinus* unless it is accompanied by a synonym, common name, habitat, or distribution. However, I prefer, at least for the present, to continue to follow Little (1953) and to use *Q. michauxii* for the swamp chestnut oak and *Q. prinus* for the chestnut oak.

7. Quercus alba × muehlenbergii

Quercus × *deamii* of some authors; not Trelease, Natl. Acad. Sci. Mem. **20**: 14. 1924.

White oak and chinkapin oak (*Quercus muehlenbergii* Engelm.) are frequent associates on calcareous soils, and hybrids between them have been found at the edge of fields or in heavily disturbed woods in scattered locations (FIGURE 16). There is no evidence of extensive introgression, for most hybrids seem to exist either as single trees or at most as a few individuals together in a small area.

This hybrid is recognized primarily by the leaf, which is more or less intermediate in lobing (FIGURE 10), often with the rather sharp points and glandular mucros more characteristic of chinkapin oak, and always with some given density of appressed branched hairs. It can be distinguished from *Quercus alba* × *bicolor* by the lack of the two sizes of hairs mentioned under that cross. It is questionably distinct from *Q.* × *faxonii*, as will be discussed later.

The name Deam oak (*Quercus* × *deamii* Trel.) has often been mistakenly associated with this hybrid cross, since a tree from near Bluffton, Indiana, which was later named *Q.* × *deamii* by Trelease, was originally determined by Sudworth to be *Q. alba* × *muehlenbergii* (cf. Palmer, 1948). Palmer, although he used this binomial for this cross, questioned the parentage of the tree, since seedlings raised from acorns from the type tree included individuals with leaves similar to those of *Q. bicolor*. I collected acorns from *Q.* × *deamii* growing at the Arnold Arboretum and grew them in the North Carolina State University greenhouse for two years. Some leaves had the general shape of *Q. bicolor*, but they all lacked the two sizes of hairs, the lobes were more pointed (like those of *Q. muehlenbergii*), and many had the shape indicative of *Q. macrocarpa*. Bartlett (1951) showed from progeny tests from the type tree that *Q.* × *deamii* represented the cross *Q. macrocarpa* × *muehlenbergii*. The progeny which I grew confirm this, and many herbarium specimens originally identified as *Q.* × *deamii* indicate *Q. macrocarpa* and *Q. muehlenbergii* rather than *Q. alba*. Thus *Q.* × *deamii* applies to *Q. macrocarpa* × *muehlenbergii*, and the cross between *Q. alba* and *Q. muehlenbergii* has no binary name.

8. Quercus alba × prinoides

Quercus × *faxonii* Trelease, Natl. Acad. Sci. Mem. **20**: 14. 1924.

Faxon oak has been identified infrequently from scattered locations (FIGURE 16). Except for generally smaller leaves (FIGURE 11) and a shrubby or smaller tree habit, it is doubtful whether *Q. alba* × *prinoides* can always be distinguished from *Q. alba* × *muehlenbergii*. The leaf often has fewer and shallower lobes, but these features are quite variable. Much of the variation would seem to be due to the intrinsic variation in the parental species, and it is questionable whether the chinkapin oaks represent two distinct species.

There is no indication that this cross leads to any increased variability in the parental species. Hybrids occur rarely, and then usually as indi-

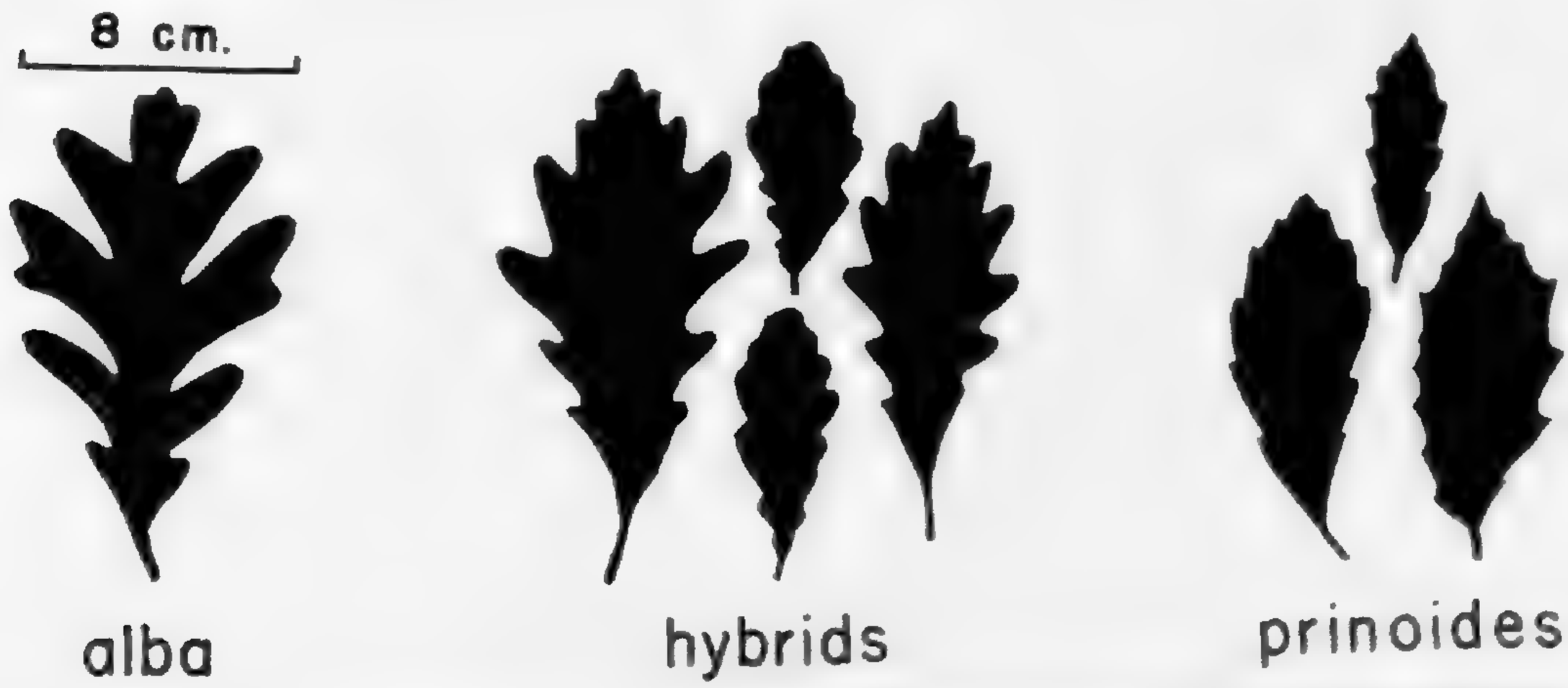

FIGURE 11. Representative leaf forms of *Quercus alba* × *prinoides* and parents.

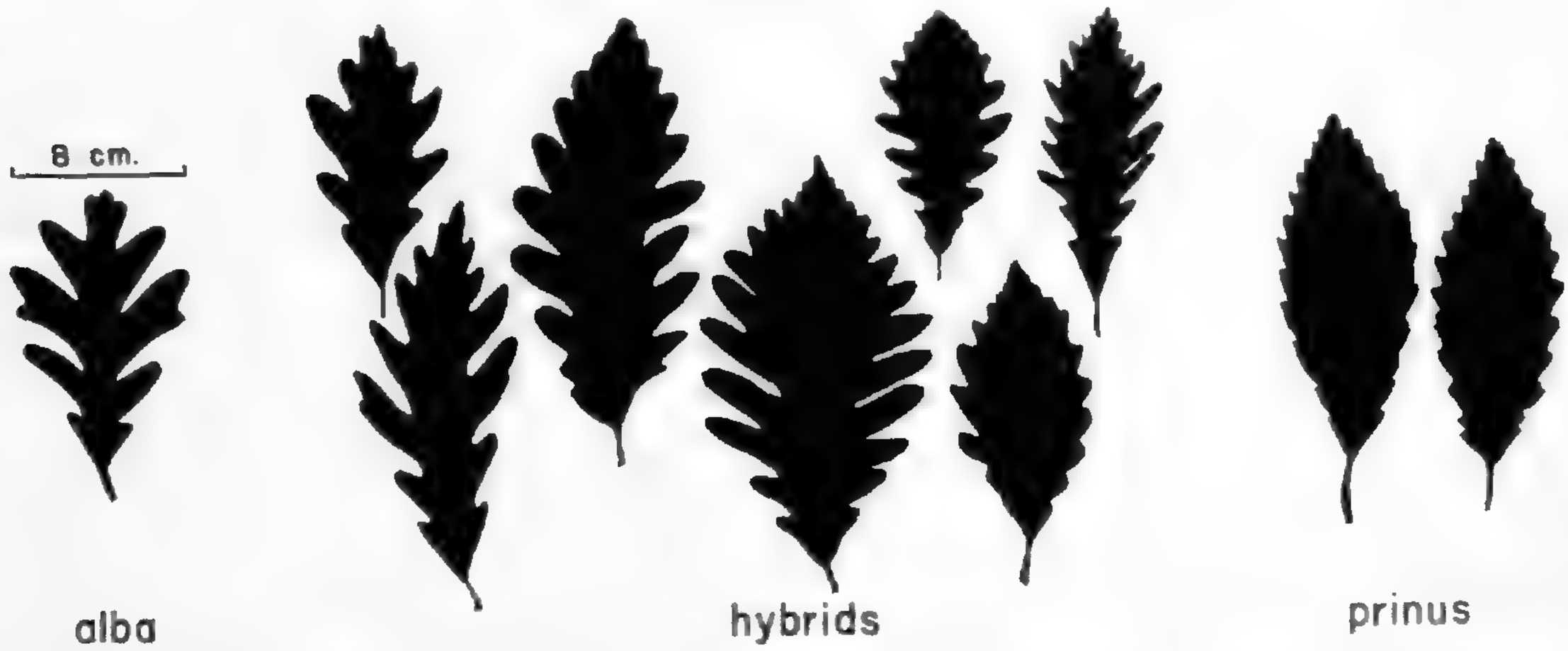

FIGURE 12. Representative leaf forms of *Quercus alba* × *prinus* and parents.

viduals or infrequent backcrosses to the dwarf chinkapin oak (*Quercus prinoides* Willd.).

The map (FIGURE 16) for dwarf chinkapin oak is very general and is probably quite incomplete in some areas.

9. Quercus alba × prinus (montana)

Quercus × *saulii* Schneider, Ill. Handb. Laubholzk. **1**: 203. 1904.

Saul oak is not only one of the most commonly found hybrids (FIGURE 16) but is also one of the best examples of introgression among the white oak hybrids. In addition, it is the best known through progeny tests (Allard, 1932, 1949; Ledig *et al.*, 1969) and population analysis of mature trees (Silliman & Leisner, 1958).

This hybrid is easily recognized by the leaf, which has more lobes than white oak but deeper sinuses than chestnut oak (FIGURE 12), by the varying numbers of branched hairs on the abaxial leaf surface, by the intermediate terminal bud sizes, by the more or less intermediate acorn size and nature of the cup scales, by the intermediate bark, and by its occurrence generally in an intermediate and disturbed habitat where the parental species overlap in their ecological ranges.

The various studies cited above indicate a limited amount of selfing and segregation and a significant amount of backcrossing. The population analyzed by Silliman and Leisner (1958) showed predominant backcrossing with *Quercus prinus* or possibly a selection for these types by the particular habitat. The analysis of hybrid progeny by Ledig *et al.* (1969) indicated backcrossing to both parental species, which may be the expected situation when both parental types are in about equal frequency in the area and when natural selection of the seedlings has not yet occurred. Any deviation from equal backcrossing, as shown by the progeny, would normally be a function of the relative frequency of the parental species in the vicinity. Further deviation from equal numbers of surviving seedlings and mature trees would be a function of natural selection. This model assumes no differential intrinsic barrier to backcrossing.

A population of Saul oak in Reedy Creek Park, west of Raleigh, North Carolina, was analyzed, since it appeared to have hybrids that approached both parental species. The habitat is a rocky northeast- to northwest-facing slope, with *Quercus alba* in the ravine and lower part of the slope and *Q. prinus* on the ridge and upper part of the slope. The hybrids occur throughout the slope, but they are more abundant in the mid-section. Both parental species are present in large numbers, and the habitat appears intermediate and open enough to accommodate all hybrid forms. Forty trees from a transect perpendicular to the contours were selected as probable hybrids on the basis of morphology. For a comparison, samples were taken from eight white oaks from the North Carolina State University Schenck Forest, northwest of Raleigh, and eight chestnut oaks from Hemlock Bluff, southwest of Raleigh. Saul oak is not found in these two locations.

The pictorialized scatter diagram of these populations (FIGURE 3E) probably indicates a more or less equal backcrossing to both parental species, although there may also be some segregation products included. This location is obviously capable of maintaining various products from reciprocal introgression.

This introgressant population at Reedy Creek covers an area of about 70 acres, and the major influence from the gene exchange seems fairly well restricted to that immediate area. A subtle "trickle" of genes from one species into another would be very difficult to detect, although it undoubtedly is occurring. There is certainly no obvious heightened morphological variation in either *Q. alba* or *Q. prinus* in the region as a result of the scattered populations of Saul oak. The heightened ecological variation, although difficult to analyze, may be more extensive.

Several populations of Saul oak in other areas show introgression with the predominant tendency toward backcrossing to the more abundant parental species. In all cases the hybrids are found in intermediate habitats that have been opened up by fire, logging, grazing, highways, or powerline construction.

The name *Quercus prinus* L. is at present meaningless without either an associated synonym, common name, habitat, or distribution, as discussed under *Q. alba* × *michauxii*. Although use of the name *Q. montana* Willd. is less ambiguous and possibly correct, I continue to follow Little (1953) and to use *Q. prinus* until the name is formally designated as a *nomen ambiguum* or officially designated as correct for one of the species.

10. Quercus alba × robur

Quercus × *bimundorum* Palmer, Jour. Arnold Arb. **29**: 18. 1948.

The hybrid between white oak and the English oak (*Quercus robur* L.) was first found in 1923 in Jamaica Plain, Massachusetts, and has since been found only in a few locations in eastern Massachusetts and southeastern Pennsylvania (Palmer, 1948). The habitats have been woods in

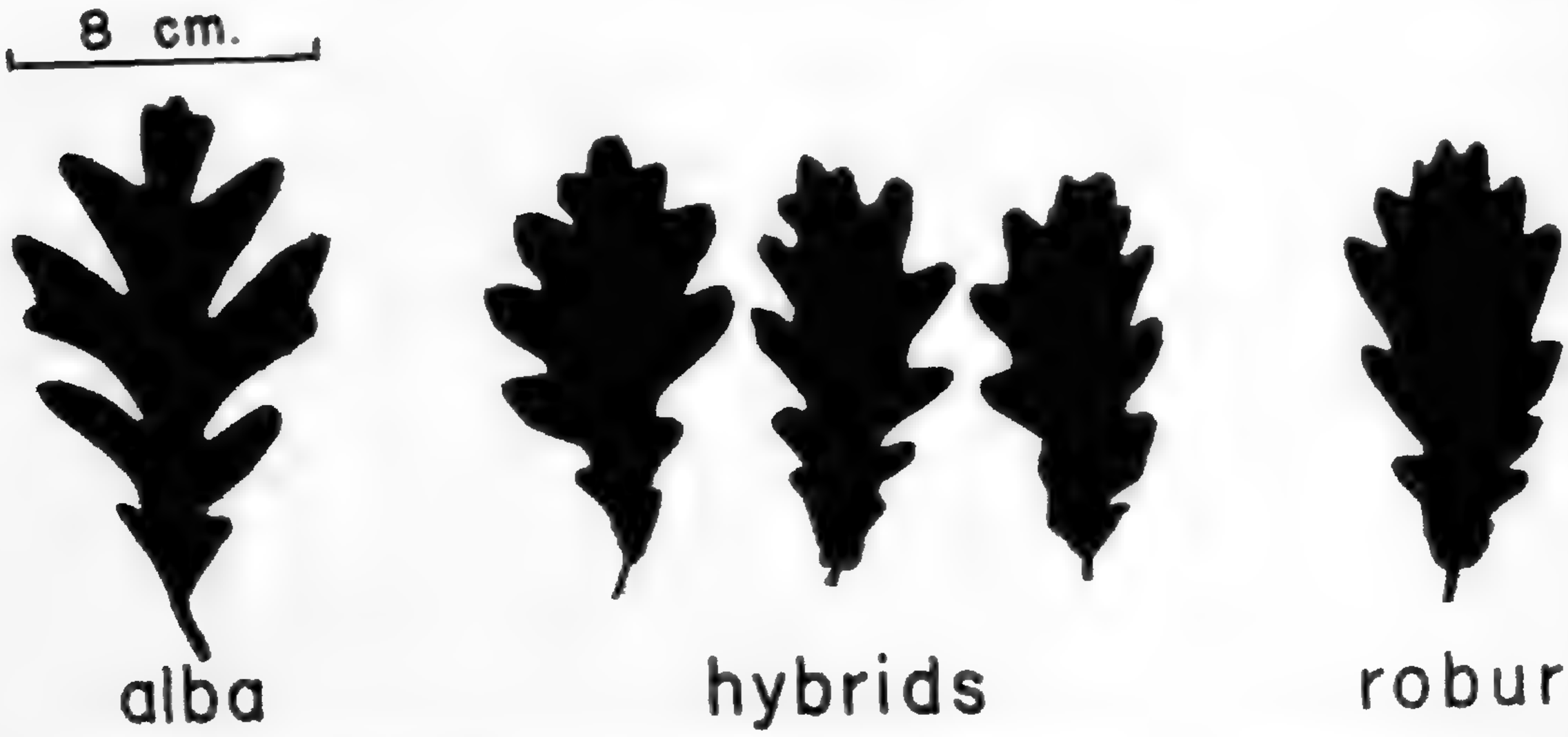

FIGURE 13. Representative leaf forms of *Quercus alba* × *robur* and parents.

or near cities in which the English oak is cultivated. Although none of the populations in the immediate areas have been analyzed, any backcrossing would probably be with the native and more abundant white oak.

This hybrid can be recognized by the bark, which is medium gray and only slightly flaky or furrowed, and by the leaves (FIGURE 13), which are glabrous and usually smaller than those of typical white oak and which show a tendency toward a truncate or narrow cordate base and a very short petiole. The number of leaf lobes and degree of dissection are too similar in the parental species to be used for identification.

An artificial cross between white oak and English oak was reported by Piatnitsky (1960). Schreiner and Duffield (1942) discussed a similar cross and gave an interesting account of metaxenia, in which the pollen parent (*Quercus robur*) had a delaying effect on the maturity of the hybrid acorns. Artificially produced hybrids are very similar to the putative hybrids identified in nature. The progeny of hybrid trees, grown at the North Carolina State University greenhouse, also substantiate this cross.

11. Quercus alba × stellata

Quercus × *fernowii* Trelease, Natl. Acad. Sci. Mem. **20**: 15. 1924.

The cross known as Fernow oak is of scattered occurrence (FIGURE 16). It can be recognized by bark that is lighter and less ridged than in *Quercus stellata*; twigs that are pale and canescent or with scattered hairs; short-stalked acorns with shallow cups and smooth close scales; leaves that are more or less pubescent below with large, erect, sessile, branched hairs and sometimes with minute stellate hairs; and leaf lobes (FIGURE 14) generally indicative of the large wide lobes near the middle of post oak leaf blades. It can be distinguished from *Q. alba* × *margaretta* by the larger leaves, sessile rather than pedicellate branched hairs on the abaxial leaf surface, pubescent twigs, and tree form.

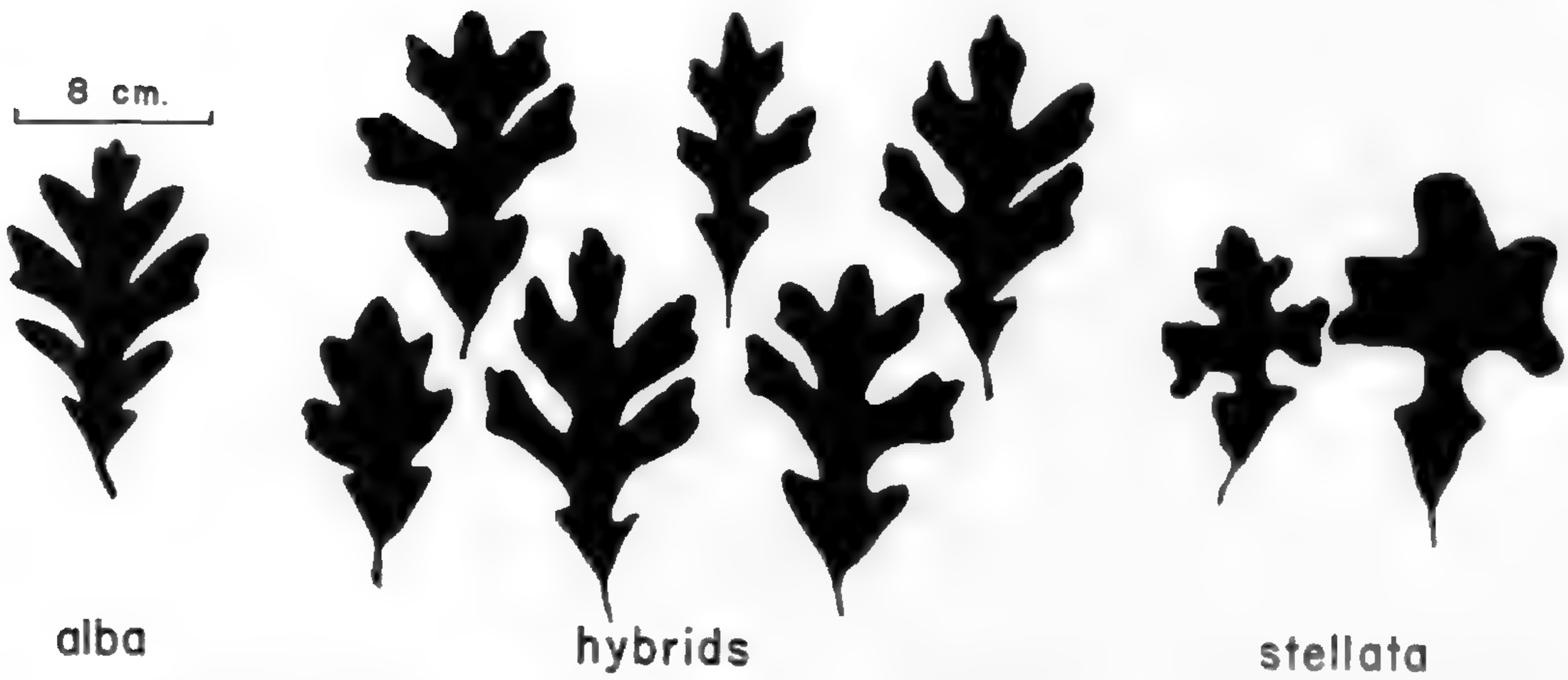

FIGURE 14. Representative leaf forms of *Quercus alba* × *stellata* and parents.

The hybrids generally occur in open, cut-over areas where the parental species are rather closely associated. Intermediate soil conditions are necessary in less disturbed areas. The hybrids are few in number in many localities, but there are some populations in eastern Texas and southeastern Oklahoma that show rather extensive introgression of *Quercus alba* into *Q. stellata* Wang. This is at the margin of the white oak range, so backcrossing could be expected to be to *Q. stellata*.

Samples were taken from a population of 25 mature trees over 4 inches dbh along the eastern edge of Bland Lake, San Augustine County, Texas. A hybrid index was constructed using a scale of 0 (*Quercus alba*) to 2 (*Q. stellata*) for the following four diagnostic features: bark (light ashy gray and flaky — intermediate — reddish brown and longitudinally ridged), twig pubescence (glabrous — scattered hairs — pale and canescent), leaf pubescence (glabrous — scattered branched hairs — densely hairy), and leaf form (even lobing — intermediate — large, wide lobe above middle). All features seemed to vary independently, and from the pattern of variation shown by the population (FIGURE 3D), I suspect a predominance of backcrossing to post oak and possibly some segregation. This pattern seems fairly typical of a number of populations in the southwestern part of the range of *Q. alba*. The white oak of the region shows little influence from this gene exchange away from the local sites of introgression.

Additional crosses — expected and artificial.

Some three-way hybrids among the eastern white oaks undoubtedly exist, but since there are few qualitative characters by which the parent species can be recognized, it is difficult to detect such crosses. Three-way hybrids in *Aesculus* (Hardin, 1957) were easily identified because of distinct qualitative parental features. Tucker (1961) recognizes characters of three or more species in the *Quercus undulata* complex. One example in the east is the *Q. alba–austrina–margaretta* complex mentioned earlier. A specimen from Ashley County, Arkansas, with leaves like those of *Q. alba* × *lyrata*, but with acorns (attached to the twig) more like those

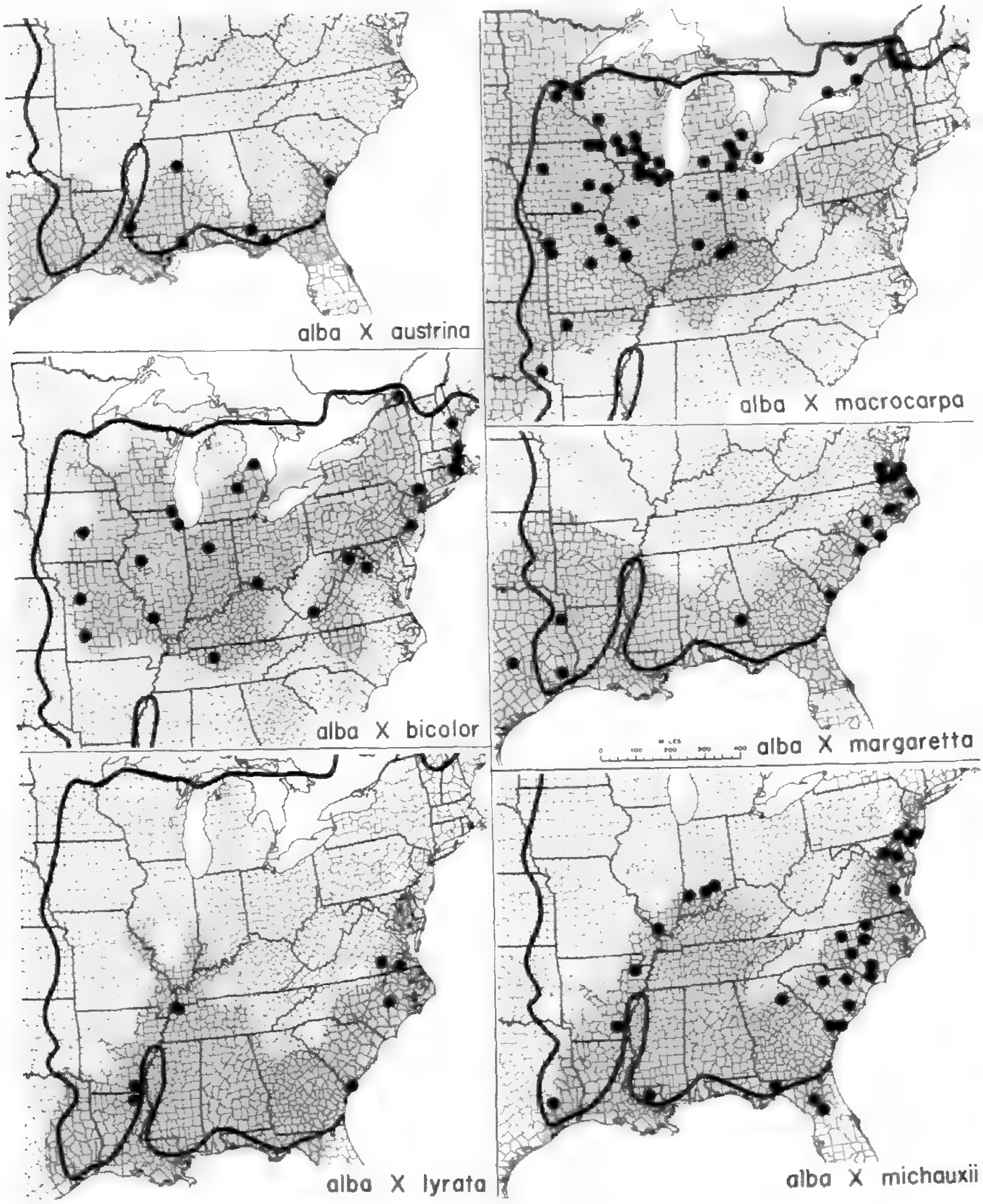

FIGURE 15. Distribution of hybrids (dots) between *Quercus alba* (heavy line) and *Q. austrina*, *Q. bicolor*, *Q. lyrata*, *Q. macrocarpa*, *Q. margaretta*, and *Q michauxii* (shading).

of *Q. michauxii*, may also indicate a mixture of these three species in a low woods. In addition, progeny grown in the North Carolina State University greenhouse from acorns collected at the Arnold Arboretum from a *Q.* × *bimundorum* (*Q. alba* × *robur*) showed a distinct tendency toward *Q. bicolor* in leaf form and pubescence. This could be either the result of crossing there at the Arboretum or a reflection of a three-way parentage of that particular tree. Since a number of oaks are more or less sympatric in many areas, I would certainly suspect that there must be other examples of some limited amount of crossing between three or more parental species.

Within the range of *Quercus alba*, there are four other species of subg. QUERCUS that may be expected to cross with it (FIGURE 1). They are *Q. chapmanii* Sarg., *Q. oglethorpensis* Duncan, *Q. virginiana* Mill., and *Q.*

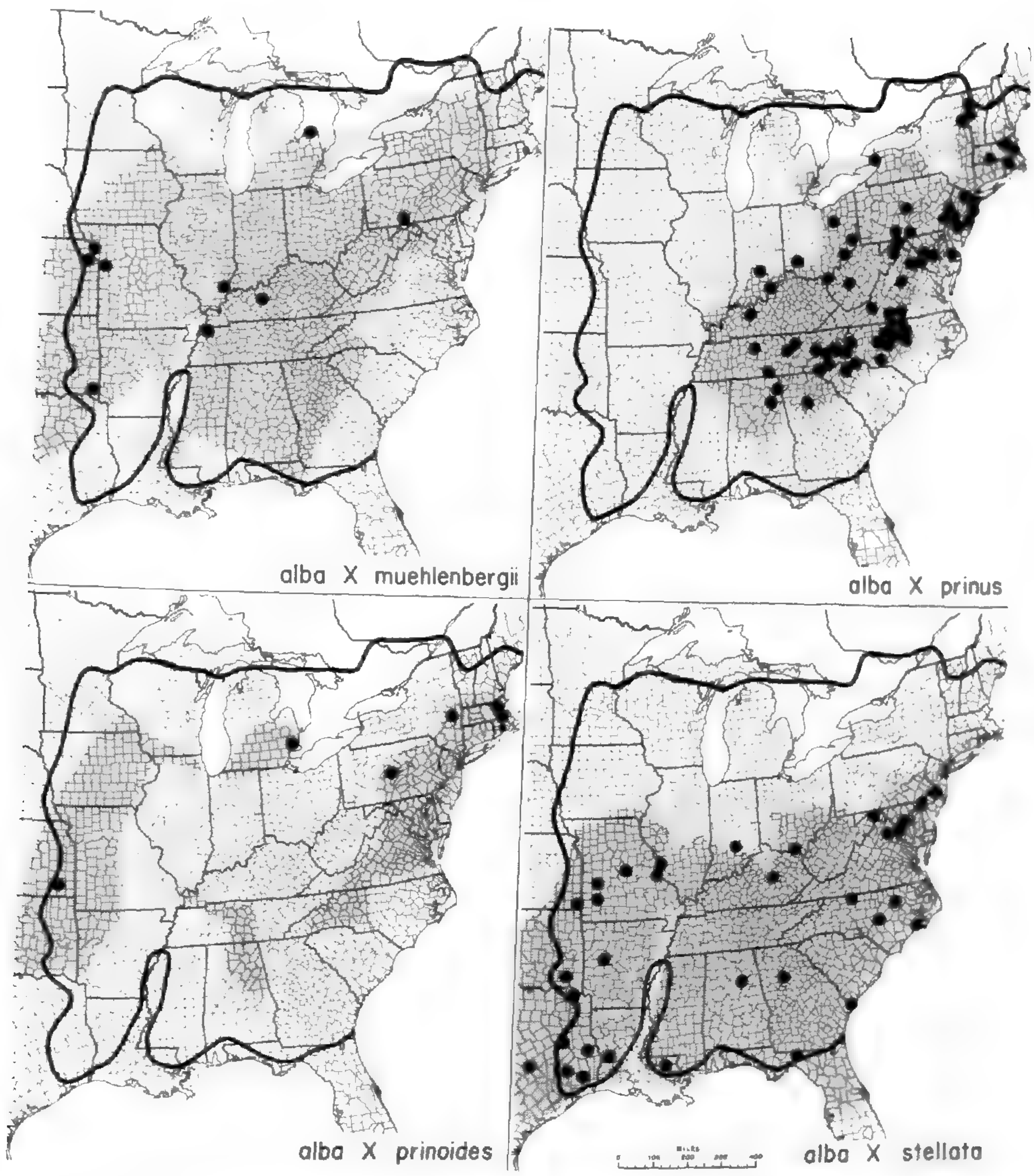

FIGURE 16. Distribution of hybrids (dots) between *Quercus alba* (heavy line) and *Q. muehlenbergii*, *Q. prinoides*, *Q. prinus*, and *Q. stellata* (shading).

minima (Sarg.) Small. Hybrids with Oglethorpe oak in particular should be sought, since it is so closely sympatric with white oak.

Piatnitsky (1960) reports the artificial crosses *Quercus alba* × *suber* and *Q. alba* × *macranthera*. Both species are European members of subg. QUERCUS.

DISCUSSION

The oaks have long had a reputation for being a taxonomically difficult genus owing to intrinsic variability plus frequent hybrids. This survey of hybridization and introgression among the eastern white oaks indicates that although *Quercus alba* crosses naturally with eleven other species, the hybrids are generally quite local single trees and are infrequent in comparison to the abundance of the species in the deciduous forests of eastern North America. Rather extensive hybrid swarms or introgressed popula-

tions occur only with *Q. macrocarpa*, *Q. prinus* (*montana*), and *Q. stellata*, and even these are generally localized. The great variability in *Q. alba* is most often due to ecophenic, ecotypic, and random genetic variances (Baranski, 1975). Neither Baranski nor I agree with Minckler (1965), who thinks that hybridization may mask evidence of races within white oak.

As pointed out by Irgens-Moller (1955), "hybridity [in oaks] apparently seldom affects the distinctness of the species." My use of the term "syngameon" in FIGURE 1 does not imply unlimited and widespread gene exchange between the species. To the contrary, the gene "flow" is but a "trickle" in most cases. Even where hybrid swarms or introgressed populations exist, the effect is still fairly localized, and there is no widespread influence, for example, on the morphology of white oak by genes from the other eleven species with which it crosses. Although in certain cases new genes and gene combinations are slowly being added to the genetic architecture of the introgressed species, the essential integrity is not destroyed. All species have maintained their distinctness in face of this local "contamination," and I see no justification for considering the entities anything less than good taxonomic species. In terms of their biology, they can be considered "semi-species" composing a syngameon (Grant, 1971).

The highly localized gene flow appears to be characteristic of most instances of introgression (Heiser, 1973), and it is in marked contrast to the pattern of dispersed introgression found in *Aesculus* (Hardin, 1957) or *Aronia* (Hardin, 1973), where the morphological influence of one species is detected sometimes hundreds of miles from the site of original hybridization.

It appears that in white oak the greatest effect of introgression may be on the ecology of the species. The broad ecological amplitude may be due to some extent to "ecological genes" acquired from other species. If it is assumed that the morphological features used in distinguishing species are governed by relatively few genes (Stebbins, 1950), while ecological adaptation is controlled by numerous genes, this differential flow of "ecological" versus "morphological" genes may be entirely plausible. The question raised earlier of whether the broad ecological amplitude is a cause or a result of introgression is still unanswered, and without knowledge of the original geographical and ecological ranges of the species, we can only speculate on the significance and origin of the broad ecological diversity seen today in *Quercus alba*.

Also unanswered is the question of the identity of the isolating mechanisms which are so effective among the white oaks. The various barriers have been discussed by Stebbins *et al.* (1947), Muller (1952), Tucker (1963), and others, and actually several mechanisms may act together or in sequence. Without definite information on possible incompatibilities, I suspect that ecological isolation is one of the most important means by which so many related white oak species can co-exist in eastern North America in spite of genetic compatibility. I also suspect that strong

natural selection limits the extent of the introgressants that are produced.

In recent years introgression as an explanation of certain patterns of variation has been called into question (Heiser, 1973). In view of (1) the geographical and ecological locations of the putative hybrids, (2) their close association with the parental species, (3) the nature of the association of characters within the hybrid populations, (4) study of the progeny from hybrid trees, and (5) the close similarity between artificially produced and natural hybrids, I am satisfied that localized introgression does occur among the eastern white oaks.

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THE GENUS ANETANTHUS (GESNERIACEAE)

RICHARD A. HOWARD

THE GENUS *Anetanthus* was described in Bentham and Hooker's *Genera Plantarum* (2: 1025. 1876), where it was attributed to Hiern with the reference "Pl. Bras. Warm. ined." Species were reported to be four or five from Brazil, Peru, and Mexico, with a numbered but unnamed collection, *Lechler 2723*, cited from Peru. No specific names or combinations were used, although three additional taxa, *Dicyrta parviflora*, *Russelia alata*, and *Tapina villosa*, were said to be included in the new genus.

The following year Hiern published a comparable generic description for *Anetanthus* (Warming, Symb. Fl. Bras. 23: 93. 1877) and cited the reference to *Genera Plantarum*. He described a single species as *Anetanthus gracilis* and referred to a Warming collection, without number, from Lagoa Santa, Brazil. In addition, Hiern noted the fact that Bentham and Hooker assigned three other species to the genus, but he also did not use the specific names in combination with *Anetanthus*. Jackson (Ind. Kew. 1: 133. 1893) attributed *Anetanthus gracilis* to Hiern and the binomials *Anetanthus parviflorus*, *Anetanthus alatus*, and *Anetanthus villosus* to Bentham and Hooker. The fifth supplement to *Index Kewensis* also listed *Anetanthus pusillus* Glaziou as a *nomen nudum*.

The four validly published species of "*Anetanthus*" should be assigned to three genera in two families, as the following notes will indicate.

Anetanthus alatus (Chamisso & Schlechtendal) Bentham & Hooker ex Jackson, Ind. Kew. 1: 133. 1893.

Russelia alata Chamisso & Schlechtendal, Linnaea 3: 3, 4. 1828; J. A. Schmidt in Martius, Fl. Bras. 8: 269. *t. 44.* 1862.

I have seen but one specimen of this taxon, that in the herbarium at Kew. A single flower, previously dissected, was in a packet; however, pollen could be obtained from the single anther present for the accompanying SEM photograph. The illustration in *Flora Brasiliensis* must have been drawn from an additional specimen. The type is a Sellow collection, without number, from Brazil.

Carlson, when considering this taxon in her monograph of *Russelia* (Fieldiana Bot. 29: 285. 1957), correctly rejected it as a *Russelia* but referred it to *Anetanthus* without comment. Few morphological details are available in the material on hand for an adequate comparison with *Anetanthus gracilis* except the larger stature, alate stems, and longer calyx.

Chamisso and Schlechtendal (1828) referred *Russelia alata* to the Scrophulariaceae, as did Schmidt (1862). Bentham (in DC. Prodr. 10: 332. 1846) listed *Russelia alata* as a *species dubia* in the Scrophulariaceae be-

fore associating it with *Anetanthus* in the Gesneriaceae in *Genera Plantarum* (1876).

Anetanthus gracilis Hiern in Warming, Symb. Fl. Bras. **23**: 93. 1877.

The type collection, made by Warming in Lagoa Santa, Brazil, is represented by three unnumbered sheets in the herbarium at Copenhagen. A drawing of a dissected flower accompanies one of these sheets and a single flower is in a packet. This specimen has been designated as the lectotype, for the other specimens are in fruit. Other specimens of *Anetanthus gracilis* have been seen from Brazil (Lagoa Santa, Minas Gerais, and Distríto Federál); Colombia (Dept. El Cauca and Meta); Peru (San Martin and Cusco); and Bolivia (San Carlos).

Anetanthus parviflorus (Hooker & Arnott) Bentham & Hooker ex Jackson, Ind. Kew **1**: 133. 1893. (Cited as *Anetanthus parviflora.*)

Trevirania parviflora Hooker & Arnott, Bot. Beech. Voy. 302. 1840.
Dicyrta parviflora (Hooker & Arnott) Seemann, Bot. Voy. Herald 326. *t. 69.* 1856.

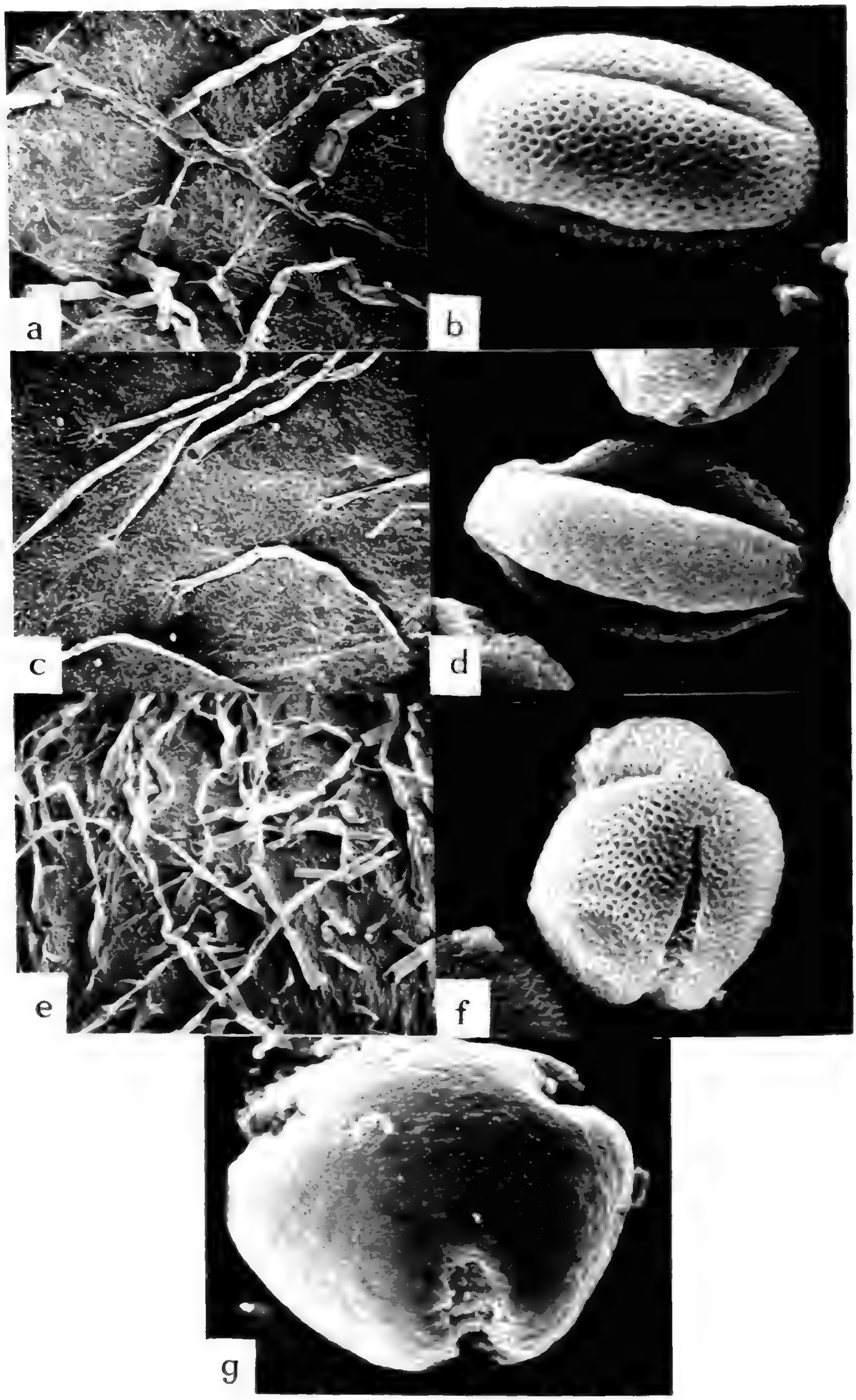
This species was originally described from material collected by Lay and Collie in Mexico. The genus *Trevirania* Willd. was considered a synonym of *Achimenes* P. Br. by Bentham and Hooker (Gen. Pl. **2**: 998. 1876). The genus *Dicyrta* Regel was recognized as related to *Achimenes* by Bentham and Hooker (Gen. Pl. **2**: 1000. 1876), and it is listed as a genus of two species in the Gesneriaceae by Willis (Dict. Fl. Plants & Ferns, 8th. ed. 361. 1973).

In the treatment of the Scrophulariaceae for the Flora of Guatemala (Fieldiana Bot. **24**(Part IX): 406. 1973), Standley and Williams list *Anetanthus parviflorus* in the synonymy of *Stemodia peduncularis* Bentham in DC. (Prodr. **10**: 382. 1846). Dr. L. O. Williams reported (pers. comm.) that he added the synonym to a partially completed manuscript left by Standley, since Standley had so annotated a specimen. The name *Stemodia peduncularis* Bentham must be used for this taxon, since the binomial *Stemodia parviflora* Aiton (Hort. Kew. ed. 2. **4**: 52. 1812) has been used for a different species.

The four stamens of *Anetanthus parviflorus* occur in pairs of unequal length, but these are independent, the anthers not adhering. The connective is globular and the two halves of the anther are clearly distinguishable, as is characteristic of species of *Stemodia.* The transfer of *Anetanthus parviflorus* to *Stemodia* as a synonym of *S. peduncularis* is supported.

Anetanthus pusillus Glaziou, Bull. Soc. Bot. Fr. **58**(Mem. 3f): 515. 1911.

A published list of Glaziou collections associated this name with a collection numbered *19586* from Alto Macahé of Nova Friburgo. A very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brief description of the plant as herbaceous with violet flowers has led subsequent workers to consider this name as a *nomen nudum* (Ind. Kew. Suppl. **5**: 16. 1921). In spite of the discordant reference to the flower color, I believe the Glaziou collection to be a depauperate specimen of *Anetanthus gracilis*.

Anetanthus villosus (Gardner in Hooker) Bentham & Hooker ex Jackson, Ind. Kew. 1: 133. 1893. (Cited as *Anetanthus villosa.*)

Tapina villosa Gardner in Hooker, Icon. *t. 469.* 1842.

The genus *Tapina* Martius was placed in the synonymy of *Sinningia* (Gesneriaceae) by Bentham and Hooker (Gen. Pl. 2: 1004. 1876), but the species *Tapina villosa* was associated with the new genus *Anetanthus*. I have seen two sheets of the original collection (*Gardner 3875*). Data on a sheet in the British Museum indicated that the collection was made from dry cliffs of the rocky summit of the Serra de Natividade, Goyaz Province, Brazil, in February, 1840. The specimens examined differed from *Anetanthus gracilis* in the shape and lobing of the corolla, the adherence of all four anthers, the pubescent ovary, and the scaly rhizomes.

The genus *Goyazia*, described by Taubert (Engler, Bot. Jahrb. **21**: 451, 452. *f. B.* 1896) with a single species, *G. rupicola*, was based on a collection (*Ule 3180*) from Serra Dourado, Brazil. *Anetanthus villosus* shares with it the characteristics of calyx, corolla, adhering anthers, pubescent ovary, and scaly rhizomes and should be transferred to this formerly monotypic genus as **Goyazia villosa** (Gardner in Hooker) Howard, comb. nov. (BASIONYM: *Tapina villosa* Gardner in Hooker, Icon. *t. 469.* 1842.)

Neither *Anetanthus* nor *Goyazia* were mentioned by Ivanina in her paper "Applications of the carpological method to the taxonomy of the Gesneriaceae" (Notes Roy. Bot. Gard. Edinb. **26**: 383–403. 1965). Although *Goyazia* is not known in fruit or with mature seeds, the pubescence type, stomata, and scaly rhizomes suggest that it is a member of the Gesneriaceae. The familial association of *Anetanthus* is more difficult. Fritsch, in a treatment of the Gesneriaceae (Engler & Prantl, Nat. Pflanzenfam. IV. 3b: 156, 157. 1895), placed the genus alone in his Cyrtandroideae-Anetantheae, distinguishing the section from the Beslerieae on the basis of the dry two-lobed or two-valved capsule. The fruits and seeds of *Anetanthus gracilis* are unlike any illustrated by Ivanina.

FIGURE 1. a, **Anetanthus alatus,** pubescence of lower leaf surface, × 25; note the pattern of collapsed cells of the top hair; type, *Sellow s.n.* (K). b, **Anetanthus alatus,** pollen grain, × 2500; type, *Sellow s.n.* (K). c, **Anetanthus gracilis,** pubescence of lower leaf surface, × 25; type, *Warming s.n.* (C). d, **Anetanthus gracilis,** pollen grain, × 2500; *Irwin et al. 14055* (NY). e, **Goyazia villosa,** pubescence of lower leaf surface, × 25; type of *Tapina villosa, Gardner s.n.* (K). f, **Goyazia villosa,** pollen grain, × 2500; type of *Tapina villosa, Gardner s.n.* (K). g, **Stemodia peduncularis,** pollen grain from "*Anetanthus parviflorus,*" × 2500; type of *Trevirania parviflora, Beechey s.n.* (K).

Dr. Umesh Banerjee kindly prepared pollen grains for the accompanying SEM photographs and compiled the descriptions which follow. The distinctness of "*Anetanthus parviflorus*" is evident and the similarity of *Anetanthus gracilis*, *A. alatus*, and *Goyazia villosa* is equally apparent.

Anetanthus gracilis (FIGURE 1d). Pollen grains spheroidal or prolate, tricolpate, colpi long tapering, colpus membrane with warty structures, pores absent, exine sculpture foveolate to reticulate, exine thickness 1.0 μm.

Anetanthus alatus (FIGURE 1b). Pollen grains prolate, tricolpate, colpi narrow and tapering toward the polar region, pores absent, exine sculpture typically reticulate, occasionally luminar areas consisting of small spherical structures, exine thickness 1.0 μm.

Goyazia villosa (FIGURE 1f). Pollen grains prolate to prolate-spheroidal, tricolpate, colpi long tapering, colpus membrane showing distinct spherical warty projections in the pore region of the equatorial plane, pores absent, exine sculpture distinctly reticulate, exine thickness 1.0 μm.

"*Anetanthus parviflorus*" (FIGURE 1g). Pollen grains oblate, tricolporate, colpi short with weakly defined pores in the equatorial plane, colpus membrane with warty structures, exine sculpture foveolate, exine thickness 1.5 μm.

The pubescence of these taxa consists of uniseriate multicellular hairs. Upon drying, adjacent cells commonly collapse at right angles to each other (FIGURE 1a). This characteristic hair type and method of drying has been seen in a great many genera of the Gesneriaceae. In the Scrophulariaceae the same hair type is common, but numerous other types of hairs from simple unicellular to multicellular-stellate or multicellular-uniseriate hairs are found.

On the basis of the material available to me, both *Anetanthus* and *Goyazia* seem appropriately placed in the Gesneriaceae if this family is to be considered as distinct from the Scrophulariaceae.

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A NEW SPECIES OF ZANTHOXYLUM (RUTACEAE) FROM NEW GUINEA *

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SINCE THE PUBLICATION of my revision of the Malesian species of *Zanthoxylum* (1966) and my additional notes (1970), a new species of the genus, collected in eastern New Guinea, has come to my attention. A description of this plant follows.

Specimens were provided for this study by the C.S.I.R.O. Herbarium Australiense, Canberra (CANB) and the herbarium of the Department of Forests, Lae, Papua New Guinea (LAE). Thanks are extended to the curators of those institutions.

Zanthoxylum novoguineense Hartley, sp. nov.

Arbor parva usque 5 m. alta, dioica, sempervirens. Ramuli novelli glabri vel sparse hirtelli. Folia imparipinnata, 34–70 cm. longa; rhachidi glabra vel sparse hirtella, anguste vel late alata (3–11 mm. utrinsecus); foliolis in paribus 2–3(–4), oppositis, sessilibus, chartaceis vel subcoriaceis, pellucido-punctatis, subtus glabris vel sparse hirtellis; foliolis lateralibus anguste vel late ellipticis vel sublanceolatis vel ovatis, 10–34 cm. longis, 5–10 cm. latis, basi acuta vel obtusa vel rotundata, plerumque inaequilatera, venis primariis utrinsecus costa 8–12, margine integra vel interdum parcissime glanduloso-crenata, apice acuminato, acumine 1–3 cm. longo; foliolo terminali oblanceolato, 14–31 cm. longo, 5–12 cm. lato, basi attenuata, aequilatera, venis primariis et margine et apice ut in foliolis lateralibus. Infructescentia terminalis, 4.5–8 cm. longa, paniculata, ramulis patentibus; axe et ramulis glabris vel sparse hirtellis; pedicellis 2.5–4 mm. longis; sepalis persistentibus 4, triangularibus, 0.4–0.9 mm. longis; cicatricibus petalorum delapsorum 4; staminodiis 4. Folliculi subglobosi, 6–9 mm. lati, in pares vel interdum singuli cum carpello abortivo. Flores non visi. HOLOTYPUS: *Pullen 5757* (CANB). FIGURE 1.

DISTRIBUTION. Territory of New Guinea and Papua; lowland and foothill rain forests; sea level to 720 meters. See MAP 1.

Territory of New Guinea. MOROBE DISTRICT: Buso River [about 40 miles S of Lae near the coast], *Foreman LAE 52311* ♀ (CANB, LAE), *Gillison et al. NGF 25690* ♀ (CANB); Kavea Mountain above the Buso River, *Streimann & Foreman*, April 26, 1972 (LAE). **Papua.** NORTHERN DISTRICT: Managalase area, near Pongani Falls [about 25 miles SE of Popondetta], *Pullen 5757* ♀ (CANB, holotype).

There are some rather minor differences between the material from the

* This is the eighth in a series of papers on the Rutaceae of Malesia and Australasia.

FIGURE 1. *Zanthoxylum novoguineense* Hartley. Fruiting branchlet, × 2/5, lower surface of one leaflet shown (drawn from *Pullen 5757*).

Buso River area and the single collection from Pongani Falls, the former being entirely glabrous, as opposed to sparsely hirtellous, and also having shorter pedicels and smaller sepals. Although the two localities are about 140 miles apart, they are connected by continuous lowland and foothill rain forest, so it seems possible that the two populations overlap and that these variants intergrade. Edaphic factors may have something to do with the differences at hand, since the Buso River is in an area of ultrabasic bedrock and Pongani Falls is in an area of volcanic rock and soil.

Zanthoxylum novoguineense appears to be closely related to *Z. megistophyllum* (Burtt) Hartley, known from Papua and the Solomon Islands, and *Z. forbesii* Hartley, known from West Java and Sumatra. It has in common with these species a 2-carpellate gynoecium, a 4-parted perianth and androecium, and a similar habit. In addition, the general appearance of the branchlets, leaves, and infructescences is very similar in the three. The only other species of *Zanthoxylum* in Malesia with 2-carpellate gynoecia and 4-parted perianths and androecia, *Z. backeri* (Bakh. f.) Hartley and *Z. retroflexum* Hartley, are climbers with retrorse prickles and are obviously not closely related to the three species in question.

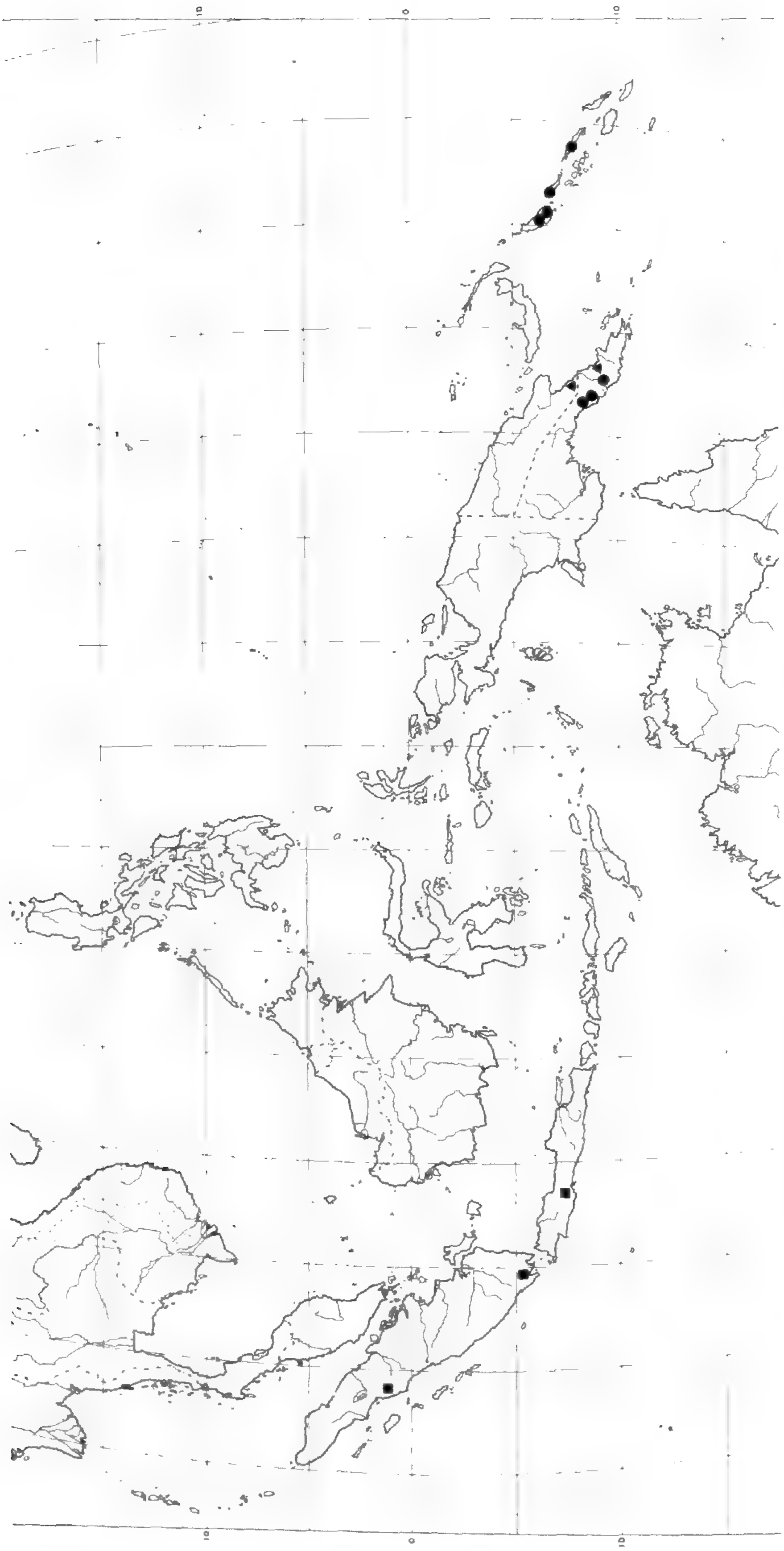
The distant geographic isolation of *Zanthoxylum forbesii* from *Z. novoguineense* and *Z. megistophyllum* (see MAP 1 [1]) may suggest to some that its apparent close relationship is only superficial. While there is no evidence that would definitely refute this, I think it is more likely that the three species share common ancestry and that the present geographic disjunction between West Java and Papua is the result of reduction in the size and continuity of intervening rain forest areas because of past climatic change. Van Steenis (1961) has put forward the idea that low ocean levels, and consequently greater land area, during glacial periods of the Pleistocene resulted in an expansion of monsoonal conditions in Malesia, especially in the regions of Central and East Java and the Lesser Sunda Islands. This is perhaps the best explanation for the discontinuity in question. On the other hand, of course, there are the possibilities that connecting populations remain to be discovered or that they have been destroyed by man's activity.

The most noticeable feature that distinguishes *Zanthoxylum novoguineense* from *Z. megistophyllum* and *Z. forbesii* is its winged leaf rachis. This and other differences between the three species are given in the following key, which also includes the changes required to accommodate *Z. novoguineense* in the key to species that was presented in my revision (pp. 175–177).

The first couplet (p. 175) should be reworded as follows:

1. Branchlets armed, the prickles mostly flattened and predominantly pseudostipular; leaf rachises usually with conspicuous wings extending to as much as 6 mm. on either side; leaves less than 30 cm. long; perianth uniseriate or irregularly biseriate, of 6–8 segments. ..... 2.

[1] A previously unpublished station for *Zanthoxylum megistophyllum* is included here: Papua, Gulf District, junction of the Kapau and Tauri rivers, *Schodde & Craven 4614* (CANB).



MAP 1. Distributions of *Zanthoxylum forbesii* Hartley (squares), *Z. megistophyllum* (Burtt) Hartley (dots), and *Z. novoguineense* Hartley (triangles).

1. Branchlets armed or unarmed, the prickles terete and usually scattered; leaf rachises terete or with narrow wings extending to not more than 1 mm. on either side, *or*, if more broadly winged (to 11 mm. on either side), then the leaves more than 30 cm. long; perianth biseriate, of 4–5 sepals and 4–5 petals. ..... 3.

The twelfth couplet (p. 176) should be reworded as follows and an additional couplet, 12a, added:

12. Leaves more than 30 cm. long; leaflets 2–5 pairs; leaf rachises winged or terete; gynoecium 2-carpellate. ..... 12a.
    12a. Leaf rachises winged; leaflets 2–3(–4) pairs, sessile. .... 6a. *Z. novoguineense.*
    12a. Leaf rachises terete; leaflets 3–5 pairs, sessile or petiolulate. .... 13.
        13. Leaves more than 70 cm. long; leaflets 4–5 pairs, the petiolules obsolete to 5 mm. long. ..... 6. *Z. megistophyllum.*
        13. Leaves less than 70 cm. long; leaflets 3–4 pairs, the petiolules 7–10 mm. long. ..... 7. *Z. forbesii.*
12. Leaves less than 40 cm. long *or* with more than 5 pairs of leaflets; leaf rachises terete; gynoecium 1-carpellate. ..... 14.

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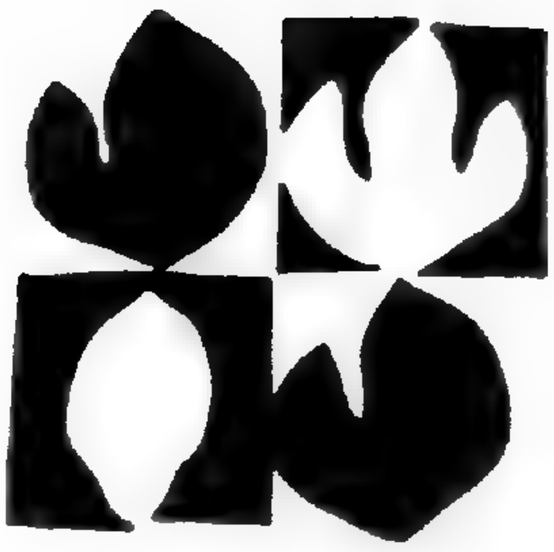

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THE GENERA OF BROMELIACEAE IN THE SOUTHEASTERN UNITED STATES [1]

LYMAN B. SMITH AND CARROLL E. WOOD, JR.

BROMELIACEAE A. L. de Jussieu, Gen. Pl. 49. 1789, "Bromeliae," nom. cons.
(BROMELIA FAMILY)

Perennial, stemless or sometimes caulescent herbs, [terrestrial to] optimally or even obligately epiphytic. Roots usually present, but often serving only as holdfasts in the epiphytic species. Leaves alternate, spirally arranged, in numerous ranks (polystichous) or rarely in two ranks (distichous), rosulate or distributed along and almost always concealing more elongate stems, more or less dilated below into a sheath, the blade varying from narrowly and regularly triangular (with a dense indument) to

[1] Prepared for the Generic Flora of the Southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of the National Science Foundation, currently under Grant BMS74-21469 (Carroll E. Wood, Jr., principal investigator). This treatment, the seventy-fifth in the series, follows the pattern 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 apply primarily to the plants of this area, with supplementary information in brackets. References not seen by either author are marked with an asterisk.

In this collaborative effort the senior author has brought to bear his monographic interest and experience in the Bromeliaceae and the junior author has added observations applicable especially to the southeastern United States. The literature references are intended to sample both the taxonomic and general biological literature, as well as some of the pertinent horticultural references on this fascinating family. We are indebted to Julien Marnier-Lapostille for preserved material of *Guzmania*; to Richard A. Howard for living material of *Catopsis, Guzmania,* and *Tillandsia*; to Loren W. Smoyer for living plants of *Catopsis*; to Daniel B. Ward for information on the blight of Spanish moss in Florida; and to Frank C. Craighead and George Avery for their generosity in sharing their field knowledge of Florida bromeliads at various times. A number of the plants used in the illustrations, all of which were prepared from living material, were grown to flower or fruit in Boston, Massachusetts, in the greenhouse of Theodore J. Schultz. The illustrations were drawn by Dorothy H. Marsh, Virginia Savage, Karen S. Velmure, and Sydney B. DeVore under the direction of the junior author, who prepared the dissections.

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liguliform (with an inconspicuous indument), the indument consisting of peltate scales, the leaf margin entire or spinose-serrate. Inflorescence terminal or lateral or pseudolateral by the elongation of the stem (sympodial), usually scapose, indeterminate, branched or simple, rarely one-flowered, usually bearing brightly colored conspicuous distichous or polystichous bracts, each with an axillary flower. Flowers perfect, 3-merous, regular. Perianth of 2 differentiated whorls, the sepals and petals free or connate. Stamens 6, in 2 series of 3; filaments free or agglutinated or adnate to the petals; anthers basifixed or dorsifixed, introrse, dehiscing by vertical slits; pollen ellipsoid or globose, 1-sulcate or 2- [3- or 4-]porate [or polyporate]. Gynoecium 3-carpellate, syncarpous; style 3-parted; stigmas 3, often spirally twisted; ovary superior or inferior, 3-locular; placentae axile, extending the length of the locule or variously reduced (e.g., apical in *Ananas*); ovules usually numerous, anatropous, the 2 integuments nearly equal. Fruit a capsule [or berry]. Seeds plumose [or winged or naked]. Embryo small, situated at the base of the abundant mealy endosperm. TYPE GENUS: *Bromelia* L.

An almost exclusively neotropical family of about 45 genera with some 2000 species, but including two genera of temperate latitudes in Chile and one species (*Pitcairnia Feliciana* (A. Chev.) Harms & Milbraed) native to westernmost Africa. Three native genera and one introduced genus occur in our area.

The family is delimited by its mealy endosperm, regular (actinomorphic) or subregular trimerous flowers with contrasting sepals and petals (heterochlamydeous), and trilocular ovary usually with numerous ovules. However, Bromeliaceae are identifiable even when sterile, by the curious indument of peltate scales. The flowers are relatively simple, showing scarcely any reduction of parts in the direction of the Eriocaulaceae or any tendency toward zygomorphy in the direction of the higher Commelinaceae and Pontederiaceae. In fact, the Bromeliaceae would seem to be the most primitive family of the order Farinosae, and some recent authors have emphasized this by placing the family in an order of its own.

Division into three nearly equal subfamilies is primarily on the basis of fruit and seed characters, along with some good vegetative correlations. In the Pitcairnioideae [2] the fruit is dry and usually dehiscent, with the

[2] At the rank of subfamily, the name Navioideae Harms (1929) has priority over Pitcairnioideae Harms (1930) when both *Navia* and *Pitcairnia* are included in the same subfamily, as in the present classification. The first use of the rank subfamily in the Bromeliaceae appears to have been by Harms, who in 1930 raised the conventional tribes Pitcairnieae Meisner (1842), Tillandsieae Dumortier (1829), and Bromelieae Dumortier (1829) to subfamilial rank and recognized Navioideae Harms (1929) as a fourth subfamily. In his treatment in *Das Pflanzenreich* (1934), however, Mez used only three subfamilies, Pitcairnioideae, Tillandsioideae, and Bromelioideae, in his classification, reducing Navioideae to the rank of tribe under Pitcairnioideae. These three subfamilial names, which have been used in all of the subsequent literature, tie in with and continue the use of the tribal names that had been previously applied to the same three basic taxa in the Bromeliaceae. Since the introduction of the name Navioideae for the subfamily that includes both *Navia* and *Pit-*

carpels always distinguishable and the seed with entire appendages or rarely with none. The leaves are almost always spinose-serrate, and the arrangement of cells in their scales is quite irregular. With rare exceptions the plants are terrestrial or saxicolous. The Pitcairnioideae do not occur in our area but approach it closely in Cuba and in Texas.

The Tillandsioideae resemble the Pitcairnioideae in the always dry, dehiscent fruit, but the seeds have plumose appendages, and the leaves are invariably entire. The cells of the leaf scales are arranged in a regular geometric pattern with four equal ones in the center (cf. FIGURE 2, 1). The plants generally are epiphytic. All three of our indigenous genera belong to this subfamily.

The Bromelioideae are unique in the family in their baccate fruit with wholly united carpels and are almost unique in their unappendaged seeds. The leaves with their marginal spines and unorganized scales are very similar to those of the Pitcairnioideae and have led some students to consider these subfamilies to be much more closely related to each other than to the Tillandsioideae. The trend toward epiphytism in the Bromelioideae is about midway between the two other subfamilies. *Ananas*, which has some record of persistence in southern Florida but which is included here only tentatively as naturalized, is strictly terrestrial.

The leaf in the Bromeliaceae is considered by some to be a phyllode, but the evidence is not wholly convincing and must be adjusted to the formation of a new sheath, blade, and petiole in the case of a number of species. There is always some distinction between sheath and blade, and usually it is quite marked. The blade usually varies from narrowly triangular to liguliform, with no contraction at base in either form, but occasionally it can be broadly elliptic, with a slender petiole.

In at least the Tillandsioideae and Bromelioideae, the leaf scales have evolved into very effective organs for absorbing water and transmitting it to the interior of the leaf. In the epiphytic species the scales have taken over the function of the roots and absorb organic compounds as well. Their distribution on the leaf surface correlates with the habit and habitat of the two common epiphytic types. In the more or less caulescent xerophytic type with narrow leaf blades, the scales completely cover the blades, protecting them from the sun and giving an even supply of water that is wholly taken up by the leaf tissue. In the rosette mesophytic type, the broad leaf blades carry the water to the tanks formed by the sheaths, and the scales of the blades are reduced, while those of the sheaths become more important in the absorption of both organic and inorganic compounds.

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cairnia would cause needless confusion, it is proposed that the provisions of Article 11 of the *International Code of Botanical Nomenclature* (1972), which allows for the conservation of names from "family to genus inclusive," be invoked, and that Pitcairnioideae be conserved over Navioideae:

Subfam. Pitcairnioideae Harms in Engler & Prantl, Nat. Pflanzenfam. ed. 2. **15a:** 102. 1930, nom. cons. prop. TYPE: *Pitcairnia* L'Heritier.

Subfam. Navioideae Harms, Notizbl. Bot. Gart. Mus. Berlin-Dahlem **10:** 575. 1929, nom. rejic. prop. TYPE: *Navia* Martius ex Schultes f.

This second type of habit, with water stored in the rosette, allows a symbiotic relationship with many more or less aquatic species of plants and animals, furnishing shelter and receiving materials from waste products. In our area this relationship is confined to southern Florida and, to date, has not involved any insects that are carriers of disease, although in a few more tropical areas bromeliads have harbored malaria-carrying mosquitoes, to the detriment of public health. The possibility of the host plant's being directly insectivorous has been explored and disproved.

The primitive type of inflorescence appears to be a many-flowered terminal panicle, which has evolved by reduction to such extremes as the one-flowered pseudolateral (actually terminal) inflorescences of *Tillandsia usneoides* and the spicate compound fruit of *Ananas*. The family is almost unique in its flowering response to chemical stimuli such as carbide, rocket fuel, and even ripening apples.

Pollination is by insects and birds, especially hummingbirds, and by bats in the case of some night-blooming species. Erdtman & Praglowski divide the family into two groups on the basis of pollen morphology (ca. 125 spp. in ca. 40 genera), the first with 1-colpate pollen grains, the second with 2-, 3-, 4-porate to polyporate grains. The pollen of all of the Pitcairnioideae and Tillandsioideae is of the 1-colpate type, but in the Bromelioideae both types occur and both are found in the genus *Aechmea*.

Chromosome counts made for 21 genera and about six per cent of the known species are $2n = 32, 34, 36, 42, 46, 48, 50, 52, 54, 56, 57, 64, 72, 75, 96, 98, 100, 108, 126$, and 150. These counts show little relation to subfamily grouping, except in the Pitcairnioideae, where the base number appears to be 25, and they vary within genera so that little can as yet be inferred from them. In addition, the identification of the plants from which many of these counts were obtained is suspect, and four of six principal papers on chromosome numbers apparently are not backed by voucher specimens. (See McWilliams in Smith & Downs for a review.)

Economically, the family is most noted for the pineapple, *Ananas comosus*, but *Tillandsia usneoides* has been used for pillow and mattress stuffing, especially in our area, and several species furnish strong fibers for cordage. Horticulturally, the Bromeliaceae are enjoying considerable popularity, and some exotic species have been recorded as spontaneous in Florida, although it remains to be seen if they will persist.

For a fuller summary of general information about the family see Bromeliales in *Encyclopedia Britannica*, ed. 15, 1974, and Smith & Downs (1974, introduction).

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KEY TO THE GENERA OF BROMELIACEAE IN THE SOUTHEASTERN UNITED STATES

A. Fruit dry, capsular; seeds plumose; ovary usually superior; leaves always entire. Subfam. TILLANDSIOIDEAE.
  B. Principal seed appendage basal, not outgrowing the capsule and therefore straight; stamens usually equal or nearly so.
    C. Petals free; flowers arranged distichously (in two rows) or solitary [rarely polystichous in a single spike, but the plant then with narrowly triangular leaf blades.] ..... 1. *Tillandsia.*
    C. Petals closely agglutinated in a tube at least to the height of the sepals (when weakly so, the inflorescence simple and the leaf blades liguliform); flowers always arranged polystichously. .. 2. *Guzmania.*
  B. Principal seed appendage apical, growing faster than the capsule and therefore folded over; stamens strongly unequal. ..... 3. *Catopsis.*
A. Fruit fleshy, baccate; seeds naked at maturity (although the ovules often appendaged); ovary inferior or nearly so; leaves nearly always spinose-serrate. Subfam. BROMELIOIDEAE. ..... 4. *Ananas.*

Subfam. TILLANDSIOIDEAE Harms

1. **Tillandsia** Linnaeus, Sp. Pl. 1: 286. 1753; Gen. Pl. ed. 5. 138. 1754.

Mostly epiphytic, caulescent or acaulescent plants of very diverse habit; roots reduced to wirelike holdfasts or completely lost. Leaves rosulate or fasciculate or distributed along a stem, polystichous or distichous, entire; blades liguliform or triangular or filiform. Scape usually distinct. Inflorescence terminal or rarely lateral or pseudolateral by the elongation of the stem, usually of distichous-flowered spikes [or sometimes a single polystichous-flowered spike formed by the reduction of the spikes to single flowers], or rarely the whole inflorescence reduced to a single flower. Sepals usually symmetrical, free or equally joined or only the two posterior ones joined. Petals free, naked. Stamens mostly equal or subequal, of various lengths relative to the petals and gynoecium; pollen 1-sulcate. Ovary superior, glabrous; ovules usually many, apically caudate. Capsule septicidal. Seeds erect, narrowly cylindric or fusiform; the short apical appendage undivided, the large plumose basal appendage straight, white. (*Renealmia* L., 1753, not *Renealmia* L. f., 1781, nom. cons.; *Caraguata* [Plumier] Adanson, 1763; *Dendropogon* Raf., 1825; *Strepsia* Nutt. ex Steudel, 1841; *Diaphoranthema* Beer, 1854; *Phytarrhiza* Vis., 1855.) LECTOTYPE SPECIES: *T. utriculata* L.; see Britton &

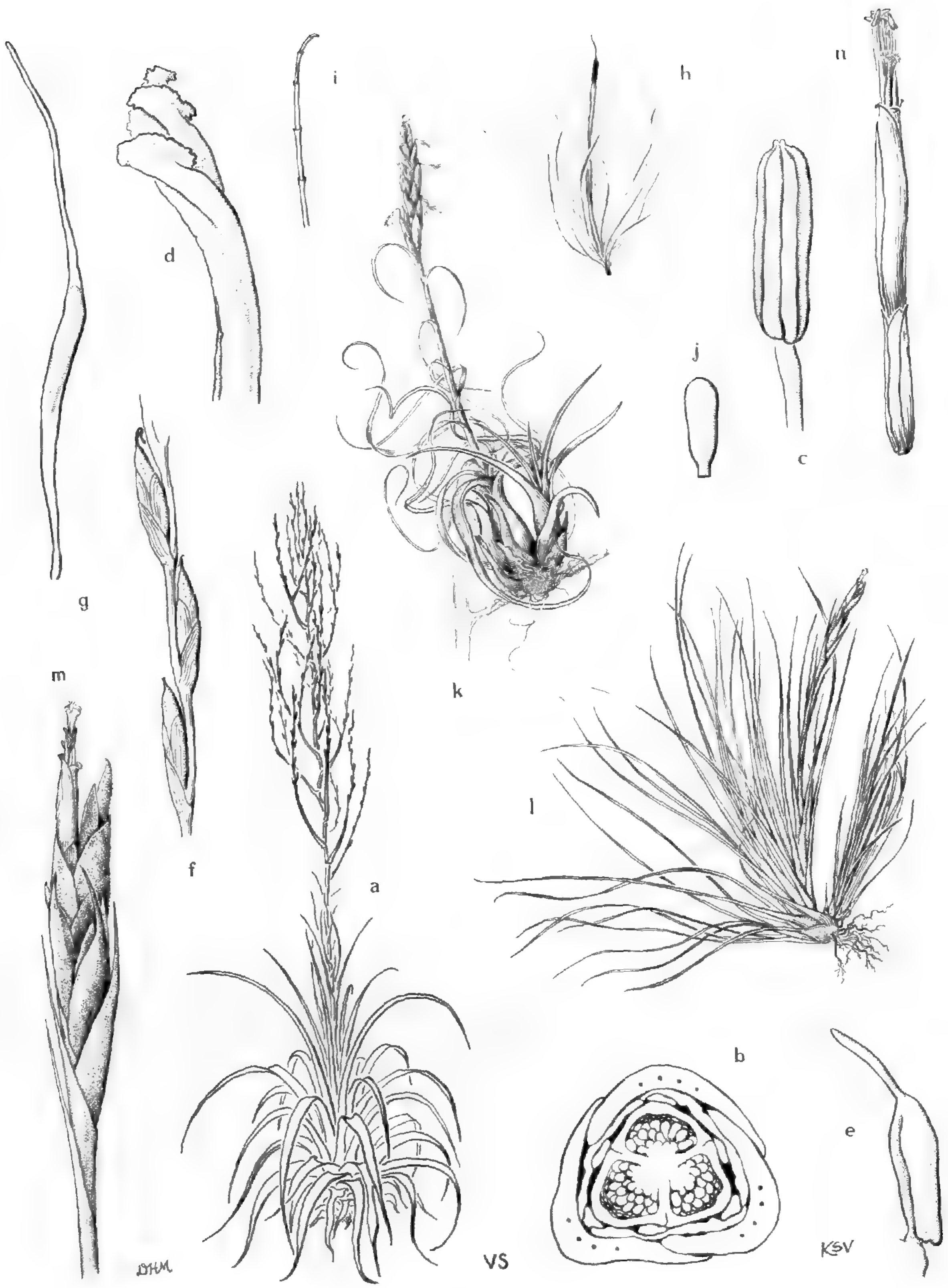

FIGURE 1. **Tillandsia** subgenus **Tillandsia.** a–j, *T. utriculata*: a, plant with flowers and fruit, × 1/20; b, cross section of flower — note three sepals, three free petals, six staminal filaments free from petals, three-loculate ovary with axile placentation, × 6; c, anther, adaxial side, × 6; d, upper part of style with stigmata, × 12; e, ovule at time of anthesis, the apex caudate, the micropyle below (at right), × 25; f, part of inflorescence branch with three nearly mature fruits, × ½; g, partly mature seed oriented as in "e," × 6; h, mature seed with basal appendage of hairs, oriented as in "e" and "g," × 1; i, tip of hair from seed appendage, × 25; j, embryo, oriented as in seed (h), × 12. k, *T. Balbisiana*: plant with developing fruit, × ¼. l–n, *T. Bartramii* (*T. simulata*): l, flowering plant, × ¼; m, inflorescence with open flower, × 1; n, flower, showing tubular corolla and imbricate sepals, × 1 ½.

Millspaugh, Bahama Fl. 64. 1920. (Name in honor of Elias Tillands, professor in Åbo [Turku], Finland, 1640–1693; also a play on words, since the name means "by land," in reference to the professor's abhorrence of travel by water and Linnaeus's mistaken idea that the scales of *Tillandsia* served to shed water.) — WILD PINE.

A genus of over 400 species in seven subgenera, ranging from coastal Virginia, through the West Indies and Mexico, to central Argentina and Chile; represented in our area by 12 native species in two subgenera and a single introduced species in a third subgenus.

The three subgenera of *Tillandsia* in our flora are all widely divergent from the ancestral type of the northern Andes, subg. ALLARDTIA, and presumably have arrived by different routes. Subgenus TILLANDSIA expanded northward, but subg. PHYTARRHIZA moved south to the central Andes and was brought here by man, while its descendant, subg. DIAPHORANTHEMA, developed still farther south but rebounded northward, thanks to the most effective means of dispersal in the Bromeliaceae. Small's *Manual of the Southeastern Flora*, disregarding the complete picture, divides *Tillandsia* into three separate genera. While there may be some grounds for separating *Dendropogon* and *Diaphoranthema* from *Tillandsia* on the floral characters, to take *Diaphoranthema* from *Dendropogon* on a purely habital basis would logically require a genus for each species of *Tillandsia*.

Subgenus TILLANDSIA, with petals erect and forming a long tube, stamens exserted, and style elongate, includes over 100 species distributed from southern Georgia and southern Texas to central Brazil and Bolivia, with the greatest concentration in Mexico. The subgenus is represented in our area by ten species that range in size from *Tillandsia utriculata* L., which may form rosettes 1.2 m. across and paniculate inflorescences 2 m. tall, to *T. pruinosa* Sw., which may be only 7.5–15 cm. tall, with the inflorescence reduced to a 2–5-flowered spike. Other representatives are *T. flexuosa* Sw. (*T. aloifolia* Hooker), *T. Balbisiana* Schult. f., *T. Valenzuelana* A. Rich., *T. circinnata* Schlecht., *T. polystachia* (L.) L., *T. fasciculata* Sw. (*T. hystricina* Small), *T. setacea* Sw. (*T. tenuifolia* of authors, not L.; see Smith, 1962), and *T. Bartramii* Ell. (*T. juncea* of authors, not (Ruiz & Pavon) Poiret, *T. myriophylla* Small, *T. simulata* Small; see Smith, 1966). All except the last species are well known in the West Indies, and some have more extensive distributions.

Tillandsia Bartramii is the most northern species of the subgenus, its range extending from midpeninsular Florida northward well into Georgia (Ben Hill and Liberty counties) and apparently at least formerly into southeastern South Carolina (cf. *Leavenworth* [GH]). *Tillandsia utriculata* reaches southern Georgia, but all of the others, with the possible exception of *T. fasciculata* (see Brooks), are limited to Florida.

At the southern edge of its range in central Florida (e.g., in Polk County), *Tillandsia Bartramii* can be found growing on the same tree with *T. setacea*, there near its northern limit. Although the two are frequently

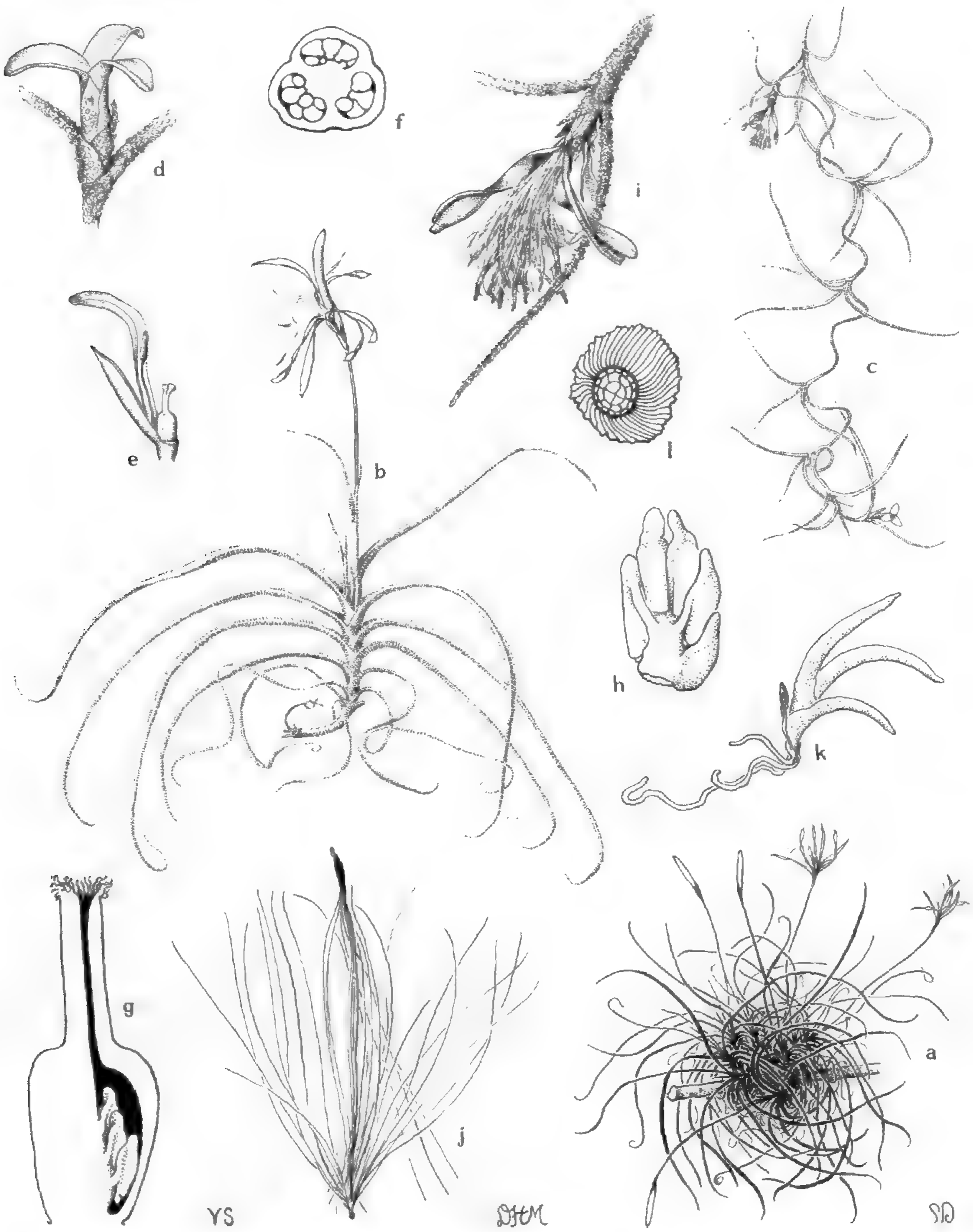

FIGURE 2. **Tillandsia** subgenus **Diaphoranthema.** a, b, *T. recurvata*: a, fruiting plant on branchlet, × ¼; b, single stem with open capsule and seeds — note sympodial growth by axillary shoot at left, × ½. c–l, *T. usneoides*: c, stem with flower and open fruit, × ½; d, flower, × 2; e, flower with 2 sepals, 2 petals, and 5 stamens removed to show gynoecium, × 2; f, cross section of ovary, diagrammatic, × 15; g, gynoecium in vertical section to show placentation and stylar canal, diagrammatic, × 15; h, placenta and ovules from one locule, × 20; i, open capsule with seeds, × 2; j, seed with basal appendage of hairs, × 2; k, seedling, × 4; l, small scale from leaf, × 50.

confused, they are quite distinct (see Smith, 1966), and hybrids between them are unlikely, since *T. Bartramii* flowers in spring, while *T. setacea* flowers in August and September. Another spring flowering species, *T.*

fasciculata, in the northern part of its range in Florida, occurs with *T. Bartramii*, which is extremely variable in this area, strongly suggesting a hybrid swarm. The chromosome number of *T. Bartramii* has not yet been reported, but counts of $2n = 64$ and $2n = 56$ have been recorded for *T. fasciculata* and *T. setacea*, respectively.

Subgenus PHYTARRHIZA (Vis.) Baker, members of which have large and showy, broadly elliptic to orbicular petal blades and stamens that are deeply included but exceed the very short style, comprises 35 species native from Uruguay and northern Argentina to Trinidad and Central America. *Tillandsia Lindenii* Regel, $2n = 64$, of Peru, is widely cultivated and is apparently established in Florida in the Tampa region.

Subgenus DIAPHORANTHEMA (Beer) Baker includes some 26 species of relatively small plants with simple inflorescences; small, narrow, inconspicuous petal blades; and stamens that are deeply included but exceed the very short style. Its species cover the whole American range of the family, and the two in our area, *T. recurvata* (L.) L. (*Diaphoranthema recurvata* (L.) Beer) and *T. usneoides* (L.) L. (*Dendropogon usneoides* (L.) Raf.), are the most widely distributed members of the family. *Tillandsia usneoides*, Spanish moss, long moss, Florida-moss, wood-crape, or crape-moss, $2n = 16$, extends along the Coastal Plain from Virginia to Florida and Texas (rarely entering the Piedmont southward), on into Mexico, and is scattered southward through Central America and the West Indies to central Argentina and Chile, always in relatively humid habitats. Growing on trees in weird-looking, long, gray festoons and often very abundant, it attracts attention in the southeastern United States in a way no other plant does. In 1969 a mysterious blight was reported to be destroying Spanish moss in ten counties in Florida and later on more extensively in Florida, as well as in southeastern Georgia, South Carolina, and Mississippi. Insects, viruses, and air pollution were suspected variously, but Roberts, Jensen, & Weber showed that the blight was caused by a fungus, *Fusarium solani* (Mart.) Appel & Wr. The plant now appears to be recovering in most areas. For details of the structure, life history, and ecology of *T. usneoides*, see especially Billings; Garth; Guard & Henry; Penfound & Deiler; and Tomlinson.

Tillandsia recurvata, ball moss, occurs in more xeric habitats than those of *T. usneoides* in Florida, Louisiana, and Texas, and is the only bromeliad in Arizona. It is widely distributed through the West Indies, Mexico, and Central America to northern Argentina and Chile. Considerable ecotypic differentiation must be involved, since it occupies a variety of habitats from tropical lowland to upland semidesert areas.

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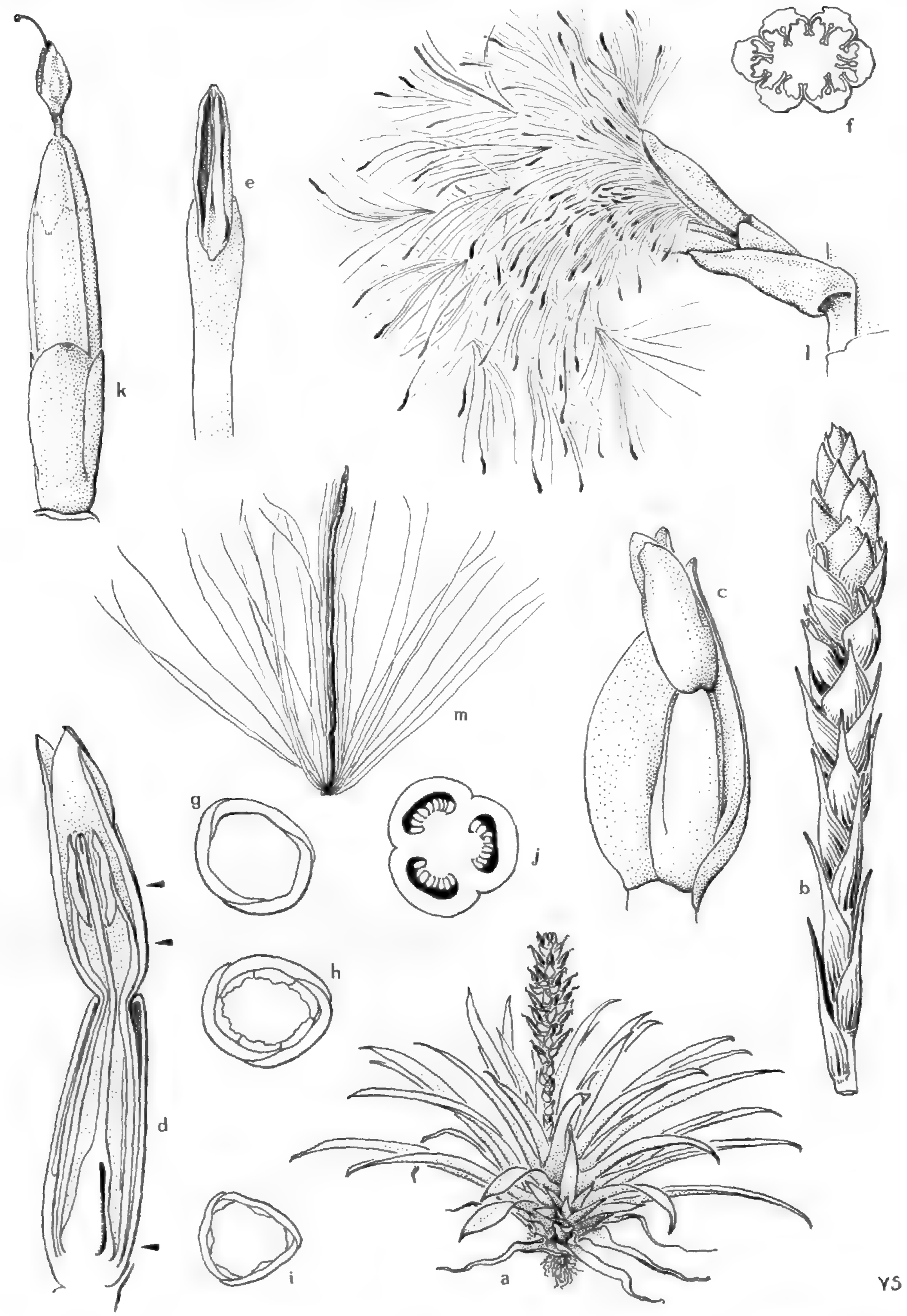

FIGURE 3. **Guzmania.** a–m, *G. monostachia*: a, plant with mature fruit — note new shoot from near base, × ⅙; b, inflorescence, × ½; c, flower with subtending bract seen from adaxial side, × 2; d, flower in vertical section, × 3; e, anther (pollen shed) and upper part of filament, × 5; f, anthers in cross section after anthesis, anthers agglutinated but not connate, × 8; g–i, petals and staminal filaments (h, i) in cross section at levels indicated on "d" — note agglutination of petal margins to each other and of stamens to petals, vascular

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2. **Guzmania** Ruiz & Pavon, Fl. Peru. Chile. 3: 37. 1802.

Acaulescent [or rarely long-caulescent] mostly epiphytic plants. Leaves polystichous, entire; sheaths usually conspicuous; blades mostly ligulate in shape, with inconspicuous scales. Inflorescence simple [or compound], the bracts usually conspicuous and often brightly colored; flowers always polystichously arranged. Sepals usually somewhat connate. Petals with edges overlapping and closely agglutinated, but not truly connate (see FIGURE 3, g–i), naked, white [or yellow]. Stamens usually included; filaments more or less agglutinated to the petals but not truly adnate (see FIGURE 3, g–i); pollen 1-sulcate. Ovary wholly superior, pyramidal, ellipsoid, or ovoid, glabrous; ovules many, densely glomerate. Capsule septicidal; seeds with a long, straight, usually brownish basal coma. (*Caraguata* Lindley, 1827, not Adanson, 1763; *Massangea* E. Morren, 1877; *Sodiroa* André, 1877; *Schlumbergera* E. Morren, 1883, not Lem., 1858.) TYPE SPECIES: *G. tricolor* Ruiz & Pavon = *G. monostachia* (L.) Rusby ex Mez. (Named in honor of Anastasio Guzman, 18th-century Spanish naturalist and apothecary.)

A genus of more than 120 species extending from southern Florida and southern Mexico to central Brazil and Bolivia, with its main con-

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bundles not shown, × 4; j, diagrammatic cross section of ovary to show placentation, × 8; k, nearly mature capsule capped by marcescent corolla and persistent style, × 1 ½; l, opening capsule with seed being extruded by drying and expanding basal appendages, × 1; m, seed with partially expanded basal appendage, × 3.

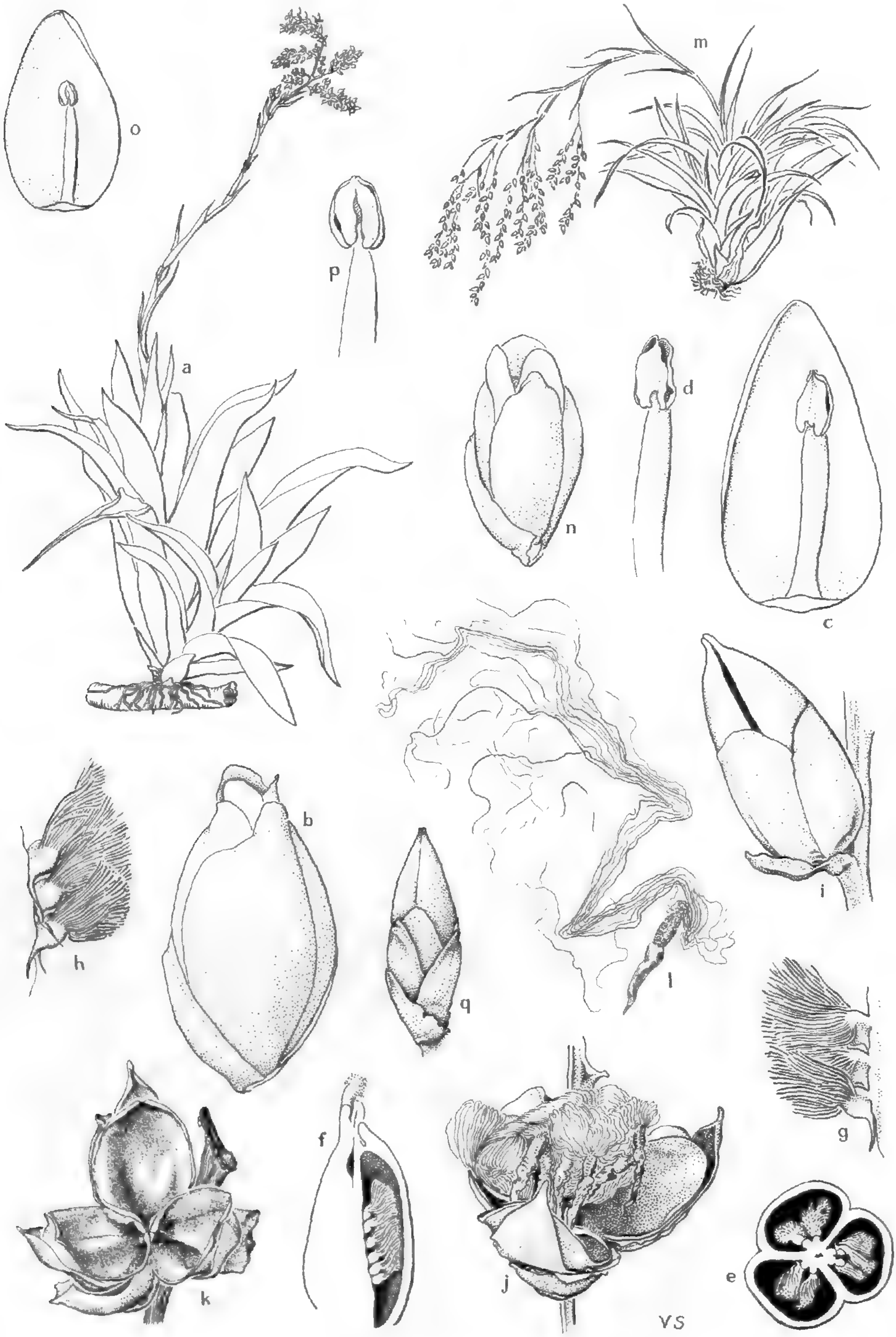

FIGURE 4. **Catopsis.** a–l, *C. Berteroniana*: a, plant in fruit — note new shoot at base, × ⅛; b, flower with subtending bract, × 3; c, petal with stamen adnate at base, × 4; d, antesepalous stamen with dehisced anther, × 4; e, cross section of ovary, showing two rows of ovules in each locule, semidiagrammatic, × 5; f, gynoecium in vertical section, showing one row of ovules in locule at right, × 4; g, h, two views of three ovules, showing elongated integument below and distal tuft of hairs that grows into terminal appendage of seed (l), × 12;

centration in the northern Andes and Central America; one species in our area.

Guzmania monostachia is native to the hammocks and *Taxodium* swamps of southern Florida, extending thence to the West Indies and Nicaragua, northern Brazil, and Peru. In Florida the plant flowers from late May through July (Craighead). The inflorescence is very conspicuous, the upper bracts being pink to salmon [or red], the lower ones pale with dark stripes (see FIGURE 3, b). Each white-petaled flower is open for a single day and, in cultivation at least, is self-pollinated. The plumose seeds are an effective means of dispersal. As the capsules dry and open at maturity, the filamentous basal appendages of the seeds spread out as they dry, and the whole cloudlike mass expands out of the capsule, the inside walls of which are dark brown, shiny, and very smooth (see FIGURE 3, l). The incredibly light seeds are carried even by very weak air currents in the forest interior. The filaments of the appendage catch on almost anything they touch, effectively anchoring the seed. (Obs. C. E. W.).

The most important generic character in *Guzmania* is the pseudo-fusion between the petals and filaments, which simulates a sympetalous corolla with adnate stamens. Although there is no real connation or adnation, the agglutination of petals and stamens is by an adhesive so strong that fresh petals will rupture irregularly under tension, rather than at the lines of meeting.

Harms divided *Guzmania* into five genera and Mez split it into two, largely on the basis of habital characters. These, although striking in the extremes, have so much intergradation that they are quite unusable. The only floral character is the degree of fusion of the sepals, but again there is no firm line of demarcation. In any event, *G. monostachia*, being the type species, would be unaffected.

The chromosome number of *Guzmania monostachia* has been reported as n = ca. 25 and $2n$ = 48. Other counts in the genus are $2n$ = 48, 50, and 56 (see McWilliams in Smith & Downs, 1974).

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Under family references see especially BENZING & RENFROW, CRAIGHEAD, GRAF, HARMS, MEZ, PADILLA, RAUH, RICKETT, and SMITH (1947).

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FOSTER, M. B. New varieties in the Bromeliaceae. Bromeliad Soc. Bull. **3**: 29, 30. 1953. [*G. monostachia* var. *variegata* M. B. Foster described from Big Cypress Swamp near Deep Lake, Collier County, Florida.]

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i, mature capsule beginning to open, × 2; j, same after dehiscence, seeds being released, × 2; k, empty capsule, × 2; l, seed with long terminal appendage of hairs, × 3. m–q, *C. floribunda*: m, plant with fruit, × ⅛; n, flower with subtending bract, × 3; o, petal with stamen adnate at base, × 4; p, anther and upper part of filament of antesepalous stamen, × 12; q, mature unopened fruit, × 2.

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SMITH, L. B. Notes on Bromeliaceae, XXXII. Phytologia **21**: 73–96. 1971. [Key to *Guzmania* and simulators, 73–90; most recent revision of the genus.]

3. **Catopsis** Grisebach, Fl. Brit. W. Indian Islands 599. 1864.

Epiphytic acaulescent herbs. Leaves densely rosulate, entire, minutely appressed-lepidote, often cretaceous-coated, green; sheath large; blade narrowly triangular or liguliform. Scape conspicuous, the paniculate inflorescence usually bipinnate, rarely simple (cf. *C. nutans*) or tripinnate, equaling or exceeding the leaves. Flowers always polystichously arranged, small or minute, mostly sessile or subsessile, uniform and perfect [or dimorphic with some functionally staminate plants]. Sepals free, usually rounded and strongly asymmetric, glabrous. Petals free, naked. Stamens included; filaments unequal; anthers ovate or elliptic. Ovary superior, broadly ovoid or ellipsoid; style shorter than the ovary or lacking; ovules few to several, with an apical tuft of hairs and a potential but normally undivided coma appearing as a spur on the laterally attached funiculus (FIGURE 4, g, h). Capsule septicidal; seeds with principal coma apical and folded over (FIGURE 4, l). LECTOTYPE SPECIES: *C. nutans* (Sw.) Griseb.; see Britton & Millspaugh, Bahama Fl. 66. 1920. (Name from Greek *katoptos*, a view or a place from which a view may be obtained, not explained, but probably in reference to the epiphytism of the plant.)

A genus of some 19 species extending from southern Florida and southern Mexico to Peru and eastern Brazil; three species in our area.

Catopsis Berteroniana (Schult. f.) Mez, distinctive in its chalky-coated yellowish-green leaves, is locally abundant in hammocks in subtropical Florida, where it grows high up in the trees in full or nearly full sunlight. It occurs through the Greater Antilles and Central America to Brazil. *Catopsis floribunda* L. B. Smith (*C. nutans* of authors, including Small) and true *C. nutans* (Sw.) Griseb. (*C. fulgens* Griseb.) are both plants of shadier habitats. The former occurs in scattered hammock locations in southern Florida, southward through the West Indies and Central America to Venezuela. The latter, notable for its slender, usually decurved simple inflorescence, in contrast with the paniculate inflorescences of the preceding two, is found sparingly in the Big Cypress Swamp area of Collier County, Florida, and it occurs in the Greater Antilles, Mexico, and Central America, southward to Venezuela and Ecuador.

Catopsis floribunda flowers in early summer in Florida, while both *C. Berteroniana* and *C. nutans* are fall-flowering (September, October) (see

Craighead). The conspicuous liguliform, bright yellow petals of *C. nutans* contrast strongly with the inconspicuous white petals (hardly longer than the sepals) that characterize most other members of the genus, including the two other species of our area. Because of its conspicuous petals, *C. nutans* can be presumed to be outcrossing, but *C. Berteroniana* and *C. floribunda* are both self-compatible and self-pollinated, at least under greenhouse conditions (obs. C. E. W.). *Catopsis nutans* has dimorphic flowers (staminate-flowered plants and either perfect [?] or functionally carpellate-flowered ones [?]) in Mexico and Central America, but only perfect flowers elsewhere.

The geographical limits of floral dimorphism in *Catopsis* are one of the most interesting features of the genus. The species that are normally dimorphic are limited to Mexico and Central America, but the species that are both perfect-flowered and dimorphic are dimorphic only within that same area. The northern part of this area overlaps that of *Hechtia*, which is the only completely dimorphic genus in the family. So far no explanation of this situation has been found.

An unusual character for many species is a chalky coating on the leaves that is easily brushed off (cf. *C. Berteroniana*). Its exact nature is not understood, but it may be an epidermal excretion similar to the waxy coat in some other families.

In contrast with the large basal appendage of the seeds of *Tillandsia* and *Guzmania*, which is derived from the splitting of the outer layer of the outer seed coat, the principal one of *Catopsis* is composed of apical hairs that increase greatly in length as the ovule matures into seed, while the basal one appears as a spur on the funicle (see FIGURE 4, e–g, l).

Chromosome counts of $2n = 50$ have been recorded for two species of the genus.

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Subfam. BROMELIOIDEAE [Harms]

4. **Ananas** Miller, Gard. Dict. Abr. ed. 4. ord. alph. 1754.

Coarse acaulescent herbs, not producing stolons but short upright shoots or slips. Leaves densely rosulate, scarcely enlarged at base; blades usually spinose-serrate. Scape evident, mostly erect. Inflorescence densely strobiliform, usually terminated by a series of sterile foliaceous

bracts, often producing slips at the base. Flowers sessile. Calyx lobes free above the epigynous tube, obtuse, slightly asymmetric. Petals free, erect, violet or red, each bearing two slenderly funnelform scales. Stamens included; pollen grains ellipsoid, with two pores. Ovaries coalescing with each other and with the bracts and axis to form a fleshy compound fruit; epigynous tube short; placentae apical; ovules caudate. Seeds naked, completely aborted in the cultivated species. LECTOTYPE SPECIES: *Bromelia Ananas* L. = *A. comosus* (L.) Merrill (*Ananas Ananas* (L.) Voss). (Name from that used by the Indians of the Antilles.) — PINEAPPLE.

A genus of some eight species and numerous varieties and forms, probably native to interior South America from the Amazon Basin to Paraguay but now pantropical in cultivation. *Ananas comosus* (*A. sativus* Schult. f.), $2n = 50, 75$, the commonly cultivated species, is reportedly persistent and may possibly be spontaneous in southern Florida. It is included here tentatively.

Like many other cultivated plants, the pineapple is of obscure and controversial origin. There is good evidence that the Indians brought it to the Antilles before the arrival of Columbus, and probably the Portuguese introduced it into the East Indies, although some authors believe it to be native there.

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ISOZYME VARIATION IN SPECIES OF PROSOPIS (LEGUMINOSAE)[1]

OTTO T. SOLBRIG AND KAMALJIT S. BAWA

THE GENUS *Prosopis* — mesquite, algarrobo, screwbean — is comprised of about 40 species (Burkart, in press). They are found primarily in North and South America, but three species grow in East Africa and Asia Minor. The genus *Prosopis* consists mostly of small to large trees, although a few species of shrubs and woody perennial herbs are also known. They inhabit primarily subtropical areas with rainfall regimes of 200–800 mm. and a pronounced dry period. In areas with less than 250 mm. the species are restricted to washes or places with a high water table. Some species (e.g., *P. ruscifolia*, *P. glandulosa*) become obnoxious weedy trees, particularly where man is trying to preserve a grass cover in spite of heavy grazing by his own domestic animals (Morello *et al.*, 1971; Fisher, 1973). Other species (e.g., *P. tamarugo*) are being grown in different parts of the world (India, Chile) as forest species adapted to semiarid conditions.

Several species of *Prosopis* (*P. alba*, *P. nigra*, *P. chilensis*, *P. velutina*, etc.) are the principal riparian trees in the semidesert regions of the "Monte" (Morello, 1958) in Argentina, and the Sonoran Desert (Shreve, 1951) in the United States and Mexico. In conjunction with a comparative ecological study of these areas (Solbrig, 1972a), the genus *Prosopis* was singled out for an in-depth ecological and evolutionary study (Carman, 1973; Solbrig & Cantino, 1975). One of the objectives of the study was to investigate the genetic structure of populations of species of *Prosopis*. Specifically, we asked the following questions: (1) what is the level of genetic variation in species of *Prosopis* and (2) what is the extent of genetic differentiation among species and among populations of the same species? In this paper we attempt to answer these questions by presenting data on variation in isozymes of several species of *Prosopis*.

MATERIALS AND METHODS

Sampling. Twenty to 50 fruits of a tree selected at random were gathered at maturity before they dropped to the ground. Up to ten trees per population were sampled, although only one to three trees per population were used in the assays. The fruits of each tree were kept separate for most species, but they were mixed in a few cases. In the laboratory the

[1] Contribution of the Structure of Ecosystem Program of the U.S./I.B.P.

seeds from the fruits were extracted by hand and 80 undamaged and well-developed seeds were selected for germination. The species sampled and the number of seedlings assayed are listed in TABLE 1. The samples comprise 13 of the 20–25 species in section ALGAROBIA as well as the two species of section CAVENICARPA. In most cases more than one locality was sampled. Altogether, 2145 seedlings belonging to 15 species from 48 localities were analyzed.

Experimental techniques. Seeds were germinated on plastic trays in loamy soil at field capacity at 20° C. The cotyledons of 8–10-day-old seedlings were used for electrophoretic analysis on starch gels. The methods used are those described in Brewer (1970) and modified by Solbrig (1972b). For each seedling, the following six enzymatic systems were assayed: α-esterase, LAP (lucine-amino-peptidase), ADH (alcohol-dehydrogenase), MDH (malic-acid-dehydrogenase), G6DH (glucose-6-phosphate-dehydrogenase), and catalase. The data from the last two systems were ambiguous and are not presented here.

Analysis of data. The isozyme data were analyzed in two ways. In the first method, we obtained the frequency of each isozyme band in the population being analyzed (all seedlings from a tree, or all seedlings from a locality, etc.) and calculated the diversity of the population using the Shanon-Weiner information measure:

$$H' = -\Sigma P_i \log_2 P_i$$

This formula measures the "evenness" of the distribution of the bands in the population. So, for example, if two alleles produce alternate bands, the highest value of H′ in the population is obtained when the bands have a 50:50 distribution, and the lowest value is obtained when the frequency of one of the bands approaches zero. In addition, the larger the number of bands, the higher the value of H′ is. In our context, a high value of H′ therefore signifies populations with many bands, each with a relatively high frequency.

Since different samples possess different numbers of bands (and presumably alleles), the ratio of H′ to H'_{max} (H'/H'_{max}) was calculated (where $H'_{max} = \log_2 P_i$). This expresses how close the sample is to a perfectly even distribution. Unfortunately, populations formed entirely by identical homozygous individuals will also have a H'/H'_{max} ratio of 1. Consequently, a second method of analysis was also used. In this case we scored the frequencies of all the possible combinations of bands (which we will call the "zymogram phenotypes") to get a measure of the number of genotypes in the population. Only the zymogram phenotype data are presented (TABLE 3), since they are representative of the results obtained with the other enzymes.

The number of segregating loci and the allelic frequencies in populations were not calculated, because the sample size was not large enough to produce accurate estimates and such a calculation would be misleading.

TABLE 1. Species and populations of Prosopis sampled.

SPECIES	COLLECTOR & SAMPLE NO.		LOCALITY	NO. OF SEEDLINGS ANALYZED
P. alba	*Solbrig*	*4238*	Argentina, Prov. Formosa, Bartolomé de las Casas	41
	Solbrig	*4272*	Argentina, Prov. Santiago del Estero, Quimilo	15
P. algarobilla	*Naranjo*	*355*	Argentina, Prov. Entre Rios	19
	Naranjo	*369*	Argentina, Prov. Entre Rios	44
	Naranjo	*365*	Argentina, Prov. Entre Rios	31
	Naranjo	*364*	Argentina, Prov. Entre Rios	5
P. alpataco	*Simon*	*449*	Chile, Prov. Santiago, Cuesta de Chacabuco	58
	Simon	*440*	Chile, Prov. Aconcagua, Los Andes	25
	Simon	*445*	Chile, Prov. Aconcagua, La Rinconada	25
	Simon	*461*	Chile, Prov. Santiago, Polpaico	7
P. caldenia	*Simpson*	*1001*	Argentina, Prov. La Pampa, Santa Rosa	39
	Hunziker	*9055*	Argentina, Prov. La Pampa	63
	Hunziker	*9052*	Argentina, Prov. La Pampa	62
P. chilensis	*Simon*	*456*	Chile, Prov. Santiago, Los Andes	26
	Simon	*429*	Chile, Prov. Santiago, Cuesta de Chacabuco	20
P. ferox	*Hunziker*	*s.n.*	Argentina, Prov. Salta, road to Antofagasta	20
P. flexuosa	*Simpson*	*1022*	Argentina, Prov. La Rioja, Arauco	43
	Hunziker	*9199*	Argentina, Prov. Catamarca, Andalgalá	44
	Hunziker	*9107*	Argentina, Prov. Catamarca, Andalgalá	50
	Simpson	*1025*	Argentina, Prov. Catamarca, Andalgalá	48
P. glandulosa	*Simpson*	*2218*	Texas, Hudspeth Co., McNary	142
	Simpson	*2217*	Texas, El Paso Co., Fabens	106
	Simpson	*2215*	New Mexico, Luna Co., Las Cruces	45
P. juliflora	*Hunziker*	*4716*	Colombia, Dept. Tolima, Honda	36
	Hunziker	*4715*	Venezuela, Mérida	24
	Solbrig	*4708*	Venezuela, Mérida, Lagunillas	20
P. laevigata	*Peñalosa*	*3427*	Mexico, San Luis Potosí, Ciudad del Maiz	32
	Peñalosa	*3433*	Mexico, San Luis Potosí, Tula	30
	Peñalosa	*3423*	Mexico, San Luis Potosí, Ciudad del Maiz	29
	Peñalosa	*3422*	Mexico, San Luis Potosí, Ciudad del Maiz	54
P. nigra	*Solbrig*	*4292*	Argentina, Prov. Córdoba, Monteros	26
	Solbrig	*4267*	Argentina, Prov. Formosa, Bartolomé de las Casas	90
	Solbrig	*4248*	Argentina, Prov. Formosa, Bartolomé de las Casas	66
	Solbrig	*4263*	Argentina, Prov. Formosa, Bazan	45
	Simpson	*1024*	Argentina, Prov. Catamarca, Andalgalá	41
P. ruscifolia	*Solbrig*	*4252*	Argentina, Prov. Formosa, Estanislao del Campo	68
	Solbrig	*4240*	Argentina, Prov. Formosa, Bartolomé de las Casas	37
	Solbrig	*4236*	Argentina, Prov. Formosa, Bartolomé de las Casas	46
	Solbrig	*4235*	Argentina, Prov. Formosa, Bartolomé de las Casas	32
	Solbrig	*4249*	Argentina, Prov. Formosa, Bartolomé de las Casas	44
P. sericantha	*Simpson*	*1015*	Argentina, Prov. La Rioja, Chamical	56
P. tamarugo	*Simon*	*171*	Chile, Prov. Tarapacá, Tarapacá	15
	Simon	*183*	Chile, Prov. Tarapacá, Tarapacá	15
	Simon	*173*	Chile, Prov. Tarapacá, Tarapacá	29
P. velutina	*Simpson*	*2200*	Arizona, Pima Co., Tucson	35
	Simpson	*2211*	Mexico, Sonora, Km. 557, Santa Ana	122
	Simpson	*2227*	Arizona, Pima Co., Ajo Way near Tucson	107
	Simpson	*2304*	Arizona, Maricopa Co., Gila Bend	84

TABLE 2. H′ and H′/H′$_{max}$ values for all populations of Prosopis studied.

SPECIES	COLLECTOR & SAMPLE NO.		α-ESTERASE H′	α-ESTERASE H′/H′$_{max}$	LAP H′	LAP H′/H′$_{max}$	ADH H′	ADH H′/H′$_{max}$	MDH H′	MDH H′/H′$_{max}$
P. alba	*Solbrig*	*4238*	2.003	0.870	1.715	0.745	1.573	0.878	1.386	1.000
	Solbrig	*4272*	1.753	0.761	1.098	0.476	1.384	0.772	1.386	1.000
P. algarobilla	*Naranjo*	*355*	0.892	0.910	—	—	1.482	0.827	1.386	1.000
	Naranjo	*369*	1.870	0.899	—	—	1.562	0.872	1.386	1.000
	Naranjo	*365*	1.899	0.913	—	—	1.386	0.773	1.386	1.000
	Naranjo	*364*	1.777	0.854	—	—	1.386	0.773	1.386	1.000
P. alpataco	*Simon*	*449*	1.904	0.866	1.486	0.676	1.386	1.000	1.197	0.863
	Simon	*440*	2.027	0.922	1.776	0.808	1.386	1.000	1.377	0.993
	Simon	*445*	2.133	0.970	1.573	0.719	1.386	1.000	1.299	0.937
	Simon	*461*	1.863	0.847	1.361	0.619	1.386	1.000	1.231	0.888
P. caldenia	*Simpson*	*1001*	1.954	0.889	1.350	0.753	1.859	0.955	1.386	1.000
	Hunziker	*9055*	1.998	0.903	1.337	0.746	1.890	0.971	1.386	1.000
	Hunziker	*9052*	1.986	0.909	1.351	0.754	1.890	0.971	1.386	1.000
P. chilensis	*Simon*	*456*	1.881	0.817	1.374	0.767	1.386	0.773	1.098	0.792
	Simon	*429*	2.199	0.955	1.289	0.719	1.530	0.854	1.098	0.792
P. flexuosa	*Simpson*	*1022*	2.019	0.877	1.475	0.823	1.386	0.773	1.076	0.776
	Hunziker	*9199*	2.089	0.871	1.264	0.705	1.863	0.957	1.098	0.792
	Hunziker	*9107*	2.353	0.981	1.599	0.892	1.887	0.970	1.095	0.790
	Simpson	*1025*	1.686	0.703	1.597	0.891	—	—	1.271	0.917
P. glandulosa	*Simpson*	*2218*	2.000	0.869	—	—	1.406	0.873	1.386	1.000
	Simpson	*2217*	1.949	0.847	—	—	1.410	0.876	1.386	1.000
	Simpson	*2215*	1.997	0.847	—	—	1.386	0.861	1.386	1.000
P. juliflora	*Hunziker*	*4716*	1.834	0.796	1.679	0.937	1.386	1.000	1.386	1.000
	Hunziker	*4715*	1.791	0.778	1.098	0.613	1.386	1.000	1.386	1.000
P. laevigata	*Peñalosa*	*3423*	2.035	0.884	1.098	1.000	1.386	1.000	1.386	1.000
	Peñalosa	*3422*	2.049	0.890	1.098	1.000	1.386	1.000	1.386	1.000
	Peñalosa	*3427*	—	—	1.098	1.000	—	—	1.386	1.000
	Peñalosa	*3433*	—	—	1.098	1.000	—	—	1.386	1.000
P. nigra	*Simpson*	*1024*	—	—	1.530	0.664	—	—	1.098	0.792
	Solbrig	*4292*	—	—	1.335	0.579	—	—	—	—
	Solbrig	*4263*	2.096	0.954	1.918	0.833	1.644	0.845	1.307	0.943
	Solbrig	*4267*	1.951	0.847	1.661	0.721	1.670	0.858	1.133	0.817
	Solbrig	*4248*	—	—	1.743	0.679	—	—	—	—
P. ruscifolia	*Solbrig*	*4252*	1.634	0.785	1.098	0.428	1.527	0.785	1.098	1.000
	Solbrig	*4240*	1.484	0.712	1.728	0.673	1.479	0.760	1.098	1.000
	Solbrig	*4236*	1.564	0.752	1.859	0.739	1.386	0.712	1.098	1.000
	Solbrig	*4235*	1.690	0.812	1.369	0.533	1.386	0.712	—	—
	Solbrig	*4249*	—	—	1.554	0.606	—	—	1.098	1.000
P. sericantha	*Simpson*	*1015*	2.044	0.930	0.864	0.786	1.857	0.845	1.098	1.000
P. tamarugo	*Simon*	*171*	1.096	1.000	1.098	1.000	1.386	1.000	0.693	1.000
	Simon	*183*	1.096	1.000	1.098	1.000	1.386	1.000	0.693	1.000
	Simon	*173*	1.096	1.000	1.098	1.000	1.386	1.000	0.693	1.000
P. velutina	*Simpson*	*2200*	2.047	0.934	1.381	0.858	1.786	0.918	0.693	1.000
	Simpson	*2211*	2.053	0.937	1.385	0.860	1.782	0.916	0.693	1.000
	Simpson	*2227*	2.038	0.931	1.374	0.853	1.788	0.919	0.693	1.000
	Simpson	*2204*	2.121	0.965	1.355	0.842	1.883	0.911	0.693	1.000

RESULTS

DIVERSITY AND VARIATION WITHIN SAMPLES

α-esterase. The number of isozyme bands varied from three to 11 in different species. In most species, two zones of activity can be distinguished: zone 1, with two to four bands, and zone 2, with four to six bands. Bands of zone 1 are thicker and more intensely stained than bands of zone 2. The exception is band 5 of zone 2, which in some species is as intensely stained as the bands of zone 1. The expression of zone 2 bands appears to be modified by minor variations in experimental techniques; occasionally, seedlings from the same sample showed different numbers of zone 2 bands with no consistent pattern from one day to the next. Although such samples were excluded from the data presented here, we are uncertain about the reliability of data on the frequency of zone 2 bands as a whole. Consequently, we have not used such data to make intra- or interspecific comparisons.

Samples of all species showed high H'/H'_{max} ratios (TABLE 2). However, samples of some species had higher ratios than others. For example, in *Prosopis ruscifolia* the H'/H'_{max} ratio ranged from 0.712 to 0.812, whereas in *P. velutina* the range was from 0.931 to 0.965 (TABLE 2).

Samples of all species except *Prosopis juliflora* and *P. tamarugo* showed a large number of zymogram phenotypes (TABLE 3). The frequency of the common classes differed from one species to another. For example, in *P. juliflora* 85% of the individuals sampled belong to one phenotype (TABLE 3). In the other extreme, not more than 35% of the individuals of *P. velutina* belong to one given class.

LAP. The LAP isozymes also appear in two different zones. Zone 1 has one to four bands, which are intensely stained. Most species have one or two bands in this region. The zone 2 bands, which are thin and faintly stained, can be further subdivided into two groups: the slow migrating subgroup *a* and the fast migrating subgroup *b*, with one or two bands in each.

In all species, the samples had a high H'/H'_{max} ratio. There was much variation within samples with respect to the number and frequency of various zymogram phenotypes.

ADH. The ADH isozymes separate into three zones. Most species show only two zones of activity. The number of bands in zone 1 and zone 2 vary from two to three, in zone 3 from two to five.

The diversity measures for ADH bands were generally higher than those for α-esterase and LAP bands (TABLE 2). Again, samples of some species had higher H'/H'_{max} values than other species. For example, the H'/H'_{max} ratio for *Prosopis algarobilla* ranges from 0.773 to 0.872, while for *P. alpataco*, *P. laevigata*, and *P. tamarugo* the ratio is 1.00, indicating that these last species are probably homozygous for various ADH loci.

In contrast to the situation in α-esterase and LAP, the number of band

phenotypes obtained for ADH isozymes within each sample was remarkably uniform throughout. The total number of bands considered for phenotypes was greater than the total for α-esterase isozymes, and almost equal to the total for LAP. Samples of species such as *Prosopis alpataco*, *P. juliflora*, *P. laevigata*, and *P. tamarugo* had only one class of phenotypes for all samples. In *P. algarobilla*, *P. chilensis*, *P. glandulosa*, *P. nigra*, and *P. ruscifolia*, 70 to 90% of the individuals within samples belonged to one class. Only in *P. alba*, *P. flexuosa*, and *P. velutina* did the individuals within samples occur in two or more classes in almost equal proportions.

MDH. All MDH isozymes separate in the same zone and their numbers vary from two to four in different species. Except for *Prosopis alpataco*, *P. chilensis*, *P. flexuosa*, and *P. nigra*, the H'/H'_{max} ratio in samples of all species was 1.00 (TABLE 2).

The level of variation displayed by the distribution of different zymogram phenotypes within the samples was extremely low. The number of phenotypes was rarely more than two in most species and, furthermore, a majority of phenotypes belonged to one class.

DIVERSITY AND VARIATION BETWEEN SAMPLES OF THE SAME SPECIES

α-esterase. None of the species investigated showed significant differences between samples with respect to H'/H'_{max} ratios. However, in regard to the zymogram phenotypes of the first four bands, some differences were observed among samples in a few species. For example, one sample of *Prosopis alpataco* (*445*) showed about one-fourth of its individuals with bands 1 and 2, which were completely lacking in the three other samples of the species. In *P. caldenia*, sample *9055* showed a high frequency of individuals with bands 1, 2, 3, and 4. However, population samples *9052* and *1001* had such individuals in low frequency. Instead, they had a large number of individuals with bands 3 and 4 (TABLE 3). Other species showing such differences between population samples were *P. algarobilla* (with bands 2, 3, and 4) and *P. chilensis* (with bands 1, 2, 3, and 4) (TABLE 3).

LAP. In contrast to the situation in α-esterase, there was considerable variation among samples of several species with respect to H'/H'_{max} ratios. Such species include *Prosopis alba*, *P. alpataco*, *P. juliflora*, *P. nigra*, and *P. ruscifolia* (TABLE 2). Similarly, many species showed much variation among samples with respect to zymogram phenotypes. Because of a possibility that some of the observed variation is the result of experimental techniques, none of these cases are described in detail.

ADH. The H'/H'_{max} ratios were remarkably uniform among samples of all species. However, with respect to phenotypes based on zymograms, samples in several species differed in the frequency of various phenotypes. For example, in *Prosopis chilensis* only population sample *429* had more

TABLE 3. Frequency of various α-esterase patterns in Prosopis species (in %).

SPECIES	COLLECTOR & SAMPLE NO.		N	PATTERNS OF BANDS 4	1,2	3,4	2,3,4	1,2,3,4	OTHER
P. alba	*Solbrig*	*4238*	41	0.243	—	0.487	—	0.048	0.222
	Solbrig	*4272*	15	—	—	1.000	—	—	—
		TOTAL	56	0.178	—	0.660	—	0.035	0.127
P. algarobilla	*Naranjo*	*369*	44	—	—	0.022	0.159	—	0.819
	Naranjo	*364*	5	—	—	—	0.400	—	0.600
	Naranjo	*355*	19	—	—	—	0.894	—	0.105
	Naranjo	*365*	31	—	—	—	0.258	—	0.741
		TOTAL	99	—	—	0.009	0.343	—	0.646
P. alpataco	*Simon*	*449*	58	—	—	0.775	0.019	0.206	—
	Simon	*440*	25	—	—	0.200	0.520	0.040	0.240
	Simon	*445*	25	—	0.240	0.480	—	0.200	0.080
	Simon	*461*	7	—	—	0.428	—	—	0.572
		TOTAL	115	—	0.052	0.565	0.121	0.156	0.106
P. caldenia	*Hunziker*	*9052*	62	—	—	0.580	0.370	—	—
	Hunziker	*9055*	63	—	—	0.822	0.177	—	—
	Simpson	*1001*	39	—	—	0.743	0.179	—	—
		TOTAL	164	—	—	0.711	0.250	—	—
P. chilensis	*Simon*	*456*	26	0.076	—	0.730	0.153	—	0.038
	Simon	*429*	20	—	0.050	0.400	—	0.250	0.300
		TOTAL	46	0.043	0.022	0.587	0.081	0.109	0.152
P. glandulosa	*Simpson*	*2218*	142	0.128	—	0.727	—	0.136	0.083
	Simpson	*2217*	106	0.009	—	0.764	0.122	0.009	0.084
	Simpson	*2215*	45	0.044	—	0.777	0.044	0.066	0.069
		TOTAL	293	0.070	—	0.749	0.053	0.077	0.081
P. juliflora	*Hunziker*	*4716*	36	—	—	—	1.000	—	—
	Hunziker	*4715*	24	—	—	—	1.000	—	—
		TOTAL	60	—	—	—	1.000	—	—
P. laevigata	*Peñalosa*	*3423*	29	—	0.344	0.206	—	0.379	0.068
	Peñalosa	*3422*	54	—	0.166	—	—	0.500	0.333
		TOTAL	83	—	0.313	0.171	—	0.400	0.113
P. nigra	*Solbrig*	*4263*	45	—	—	0.129	0.451	—	0.420
	Solbrig	*4267*	90	0.111	—	—	0.788	0.011	—
		TOTAL	135	0.086	—	0.034	0.734	0.008	0.140
P. ruscifolia	*Solbrig*	*4252*	68	0.985	—	—	0.014	—	—
	Solbrig	*4240*	37	1.000	—	—	—	—	—
	Solbrig	*4236*	46	1.000	—	—	—	—	—
	Solbrig	*4235*	32	1.000	—	—	—	—	—
	Solbrig	*4249*	44	0.272	—	0.136	0.545	—	0.057
		TOTAL	227	0.854	—	0.026	0.110	—	0.011
P. sericantha	*Simpson*	*1015*	56	—	—	0.035	0.767	0.178	0.020
P. velutina	*Simpson*	*2200*	35	—	0.354	0.193	0.193	0.161	0.096
	Simpson	*2211*	122	—	0.254	0.327	0.016	0.270	0.133
	Simpson	*2227*	107	0.037	0.355	0.196	—	0.280	0.291
		TOTAL	264	0.015	0.308	0.256	0.033	0.259	0.192

than 25% of its individuals with bands 6, 7, 9, and 11. In *P. velutina*, population sample *2227* had about 25% of its individuals with bands 7, 8, 11, and 12, and about 65% with bands 6, 7, 9, 10, and 11. On the other hand, population samples *2211* and *2204* had more than 50% of their individuals with bands 7, 8, 11, and 12 and about 30% with bands 6, 7, 10, and 11.

MDH. There were no appreciable differences between population samples either with respect to H'/H'_{max} ratios or with respect to zymogram phenotypes.

Diversity and variation between different species

The various species differed from each other in two respects: (a) frequency and electrophoretic mobility of isozyme bands and (b) levels of variation.

α-esterase. *Prosopis tamarugo* is different from all other species because it has only three isozyme bands. Although these are numbered 4, 5, and 6 in Table 2, they migrated at a slightly faster rate than the equivalent bands of other species. *Prosopis ruscifolia* differs from other species in that bands 1, 2, and 3 either occur in very low frequency (less than 10%) or are completely absent. The zymograms of *P. juliflora* lack bands 1, 5, and 7, and instead appear to be fixed for bands 2, 3, 4, 6, 8, and 9. Among the closely related South American species *P. alpataco*, *P. chilensis*, *P. caldenia*, *P. algarobilla*, *P. alba*, and *P. nigra* no appreciable differences were observed. However, among the closely related North American species *P. glandulosa* and *P. velutina* there are notable differences in the frequency of certain bands. In *P. glandulosa* bands 1 and 2 occur in low frequency (less than 25%), while in *P. velutina* they occur in high frequency (more than 50%).

In terms of levels of variation, two groups of species can be distinguished. One, comprised of *Prosopis tamarugo*, *P. juliflora*, and *P. ruscifolia*, shows very little variation. The other, involving the rest of the species, is highly variable.

LAP. Except for *Prosopis alba*, *P. nigra*, *P. glandulosa*, and *P. velutina*, which had similar zymograms, all species showed differences in the location and frequency of one or more bands. Most species were quite variable in terms of H′, with the sole exception of *P. tamarugo* (Table 2).

ADH. *Prosopis sericantha* has zymograms that are quite distinct from the remainder of the species. *Prosopis tamarugo*, which differs from all the other species investigated in the patterns of α-esterase, LAP, and MDH bands, does not differ with respect to the patterns of ADH bands. *Prosopis ruscifolia*, a species quite distinct from the others analyzed in respect to the patterns of α-esterase and LAP bands, also shows a characteristic species-specific ADH zymogram, with band 8 in almost 100% frequency

in all samples studied. In the other South American species this band, if it is present at all, occurs in very low frequency (3% or less). Exceptions are *P. caldenia* and *P. flexuosa*, where the frequency of band 8 may vary from 25% in the former to 50% in the latter. Among other closely related South American species, *P. caldenia* and *P. flexuosa* differ from the remainder in having not only band 8, but also bands 11 and 12 in relatively high frequencies (TABLE 2). Among the three closely related North American species analyzed, *P. velutina* differs from *P. glandulosa* and *P. laevigata* in having bands 6, 9, and 10 in very high frequencies (more than 50%). These bands are totally absent in the other two species.

On the basis of levels of variation, the species can be included in one of two groups. The first includes *Prosopis tamarugo*, *P. ruscifolia*, *P. chilensis*, *P. juliflora*, *P. algarobilla*, *P. nigra*, *P. alba*, *P. laevigata*, and *P. glandulosa*. All or more than 95% of the individuals have the same phenotype. The second group, containing *P. sericantha*, *P. caldenia*, *P. flexuosa*, and *P. velutina*, is more variable than the first; most of the individuals in these species are more or less evenly distributed among two or three phenotypes.

MDH. *Prosopis tamarugo* again has very distinct zymograms. These differ from other species in having bands 5 and 6, which are totally absent in all other species. *Prosopis sericantha*, with bands 1, 2, and 3, also has zymograms which appear to be species-specific. *Prosopis ruscifolia* and *P. chilensis* differ from the other South American species in lacking band 1. Along the same lines, *P. alpataco* and *P. flexuosa* can be distinguished from the rest, since they have band 1 in very low frequency. The North American species, *P. glandulosa*, *P. velutina*, and *P. laevigata*, are all alike, but they differ from the South American species in having bands 1 and 2 very faintly stained.

All species are remarkably uniform in their MDH isozyme patterns and show no differences with respect to levels of variation.

DISCUSSION

Although only four enzyme systems were analyzed, we believe the number of loci controlling the expression of various isozyme bands for the four systems to be more than ten. Thus the number of loci examined in the present study is fairly large for studies of this kind, and on the basis of data already presented, it is reasonable to suggest that the species of *Prosopis* are genetically quite diverse. The progeny of all species of *Prosopis* investigated segregated for one or more enzymatic loci, indicating the existence of heterozygous individuals. The level of genetic diversity observed in various species is higher than that of some species of inbreeding herbs, such as *Avena barbata* (Jain, 1969) and species of *Leavenworthia* (Solbrig, 1972b). This is to be expected, for although precise information about breeding systems of *Prosopis* species is lacking, the taxa

analyzed are considered to be widely outcrossed (Simpson, in preparation).

One could argue that the observed levels of variation are overestimates of the actual levels of variation in populations, since the analyzed seedlings were not subjected to selection. This might be true. However, it should be pointed out that the estimates presented here take into account not only the diversity of zymogram phenotypes, but also the number of segregating bands. The allelic diversity at a locus among the seedlings cannot arise unless such a diversity is also present in the population of adults.

In regard to differences among species with respect to isozyme variability, two points deserve attention. It should first be noted that species which belong to a different section of the genus, e.g., *Prosopis sericantha* and *P. alpataco*, have vastly different zymograms for various enzyme systems; furthermore, within a section (as already discussed), some closely related species show minor differences in zymograms. The second and perhaps more important point is that some of the species and populations showed less variation than others. Three species in particular can be singled out: *P. juliflora*, *P. tamarugo*, and *P. ruscifolia*.

Three populations of *Prosopis juliflora* were investigated, one from western Colombia and two from western Venezuela. They are remarkably similar, particularly if one considers that they are separated from each other by several hundred kilometers, and more importantly, that they are separated by areas of high mountains and tropical vegetation, where *Prosopis* does not grow. Most of the plants investigated showed a remarkably uniform pattern of several (more than three) nonsegregating bands. So, for example, all 56 plants showed the same six bands for α-esterase (bands 2, 3, 4, 6, 8, and 9), although bands 10 and 11 also appeared at low frequencies in population *4716* from Colombia. Population *4715* from Venezuela showed no variability in the LAP pattern and all plants had bands 2, 3, and 5. All plants of the Colombian population were fixed for bands 5, 6, and 8, but segregated for bands 2 and 3. For MDH both populations showed the same invariable pattern of four bands, and a similar situation was also found for ADH.

The genetics of the ADH locus were investigated in more detail, and we were able to show that *P. juliflora* is a permanent heterozygote for ADH, with the genetic constitution S^2S^2, F^2F^2/S^3S^3, F^3F^3, possibly due to gene duplication. Although the patterns for α-esterase, LAP, and MDH cannot be analyzed with the same precision as the ADH locus, the similarity in the zymograms suggests that there may be some fixed heterozygosity in these systems as well (Bawa & Solbrig, in preparation).

Prosopis juliflora grows in isolated, arid, rain-shadow valleys in Colombia and Venezuela (and in the Caribbean and Mexico). These valleys are surrounded by very high mountains (3,000 m. and higher) and are separated from each other by several hundred kilometers. There is evidence that some, if not most, of these dry pockets are post-Pleistocene in origin, and most of these populations are around 10,000 years old or

less. Given the large size of *Prosopis* seeds, gene flow between populations is a very rare event indeed. Seeds are carried in the digestive tracts of animals (Solbrig & Cantino, 1975), and there is anecdotal evidence that the species has spread in Colombia with the development of the cattle industry. This special ecological circumstance (with populations being started by one or a few seeds) subjects the species to repeated events of severe genetic depletion. Under these conditions, mechanisms such as gene duplication that can create permanent heterozygotes may be favored.

Prosopis tamarugo is a species of the very dry coastal areas of the province of Tarapacá in northern Chile. Of all the species investigated, it grows in the most extreme environment. Three population samples were investigated. They were characterized by the lowest total number of isozyme bands of any species investigated and the lowest within-sample variation. A single sample of a related species, *P. ferox* (from an equally extreme environment in the high Puna of Argentina), was analyzed and was also found to be invariable and to have very few bands. It is our contention that in extreme environments selection may favor certain particular superior genotypes, and this may help to explain the lowered variability of these species.

Finally, we would like to mention *Prosopis ruscifolia*, the "vinal" from Argentina, and *P. glandulosa*, the "honey mesquite" from Texas. Both of these species (Morello *et al.*, 1971; Fisher, 1973) have become obnoxious agricultural pests in grassland areas. In both, but particularly in *P. ruscifolia*, we detected a slightly lower degree of genetic variability than the mean for all species. This could be attributed to the fact that these are expanding populations (Morello *et al.*, 1971; Fisher, 1973).

The significance of observed differences in variation patterns among samples of *Prosopis alpataco*, *P. caldenia*, *P. algarobilla*, and *P. chilensis* for α-esterase isozymes and those of *P. chilensis* and *P. velutina* for ADH isozymes is obscured by the fact that only a few samples, consisting of a small number of trees, were analyzed. Interpopulation differences with respect to isozymes have been observed as well in some coniferous trees (Clarkson & Fairbrothers, 1970). However, because of differences in techniques of different investigators, it is not possible to say whether the differences reported here are comparable to those reported for conifers.

In summary, then, species of *Prosopis* are characterized by a high degree of genetic variability. Within the genus two species show significantly lower levels of variability. This can be attributed to severe genetic depletion because of extreme reduction of the population in one case, and to extreme directional selection in the other.

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THE BALSAMINACEAE IN THE SOUTHEASTERN UNITED STATES[1]

CARROLL E. WOOD, JR.

BALSAMINACEAE A. Richard, Dict. Class. Hist. Nat. 2: 173. 1822, "Balsamineae," nom. cons.
(TOUCH-ME-NOT FAMILY)

Annual [or perennial] herbs [sometimes epiphytic, or subshrubs] with simple, alternate [opposite or whorled] exstipulate leaves. Flowers perfect, protandrous, zygomorphic, axillary, solitary, or clustered. Sepals 3 [5], the apparent lowest or posterior one (the flowers resupinate) ± saccate and [usually] spurred, the spur nectariferous, the 2 lateral sepals free [or connate]. Petals 5 [free] or by connation of the lateral petals in pairs appearing to be 3. Stamens 5, alternate with the petals; filaments short, free or ± connate, in ours with a scalelike appendage on the inner side, the scales partly united over the gynoecium; anthers 2-locular [coherent or] connivent, opening by a slit or pore. Gynoecium [4- or] 5-carpellate, syncarpous; stigmas 5, minute, sessile [or style short, subulate, stigma 1]; ovary superior [4- or] 5-loculate, each locule with 2 to many anatropous, 2-integumented ovules, the placentation axile. Fruit a ± fleshy [4- or] 5-valved capsule, usually opening elastically, or (in *Tytonia*) drupaceous or a fleshy capsule(?). Seeds with a straight embryo and without endosperm. TYPE GENUS: *Balsamina* P. Miller, nom. illegit. = *Impatiens* L.

A family of three genera and some 500 described species. *Tytonia* G. Don (*Hydrocera* Blume ex Wight & Arnott) comprises only a single species, *T. triflora* (L.) C. E. Wood (*Hydrocera triflora* (L.) Wight &

[1] Prepared for the Generic Flora of the Southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of the National Science Foundation, currently under Grant BMS74–21469 (Carroll E. Wood, Jr., principal investigator). This treatment, the seventy-sixth in the series, follows the pattern 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 apply primarily to the plants of this area, with supplementary information in brackets. References that the author has not verified are marked with an asterisk.

A preliminary paper on the Balsaminaceae written by Dr. K. A. Wilson for the Generic Flora project has been consulted in the preparation of this treatment. Beverly Vincent has aided in the preparation of the bibliography and the typing of the manuscript. The illustration was drawn by A. D. Clapman under the direction of the author. The material for the drawing of *Impatiens pallida* was collected by R. B. Channell and H. F. L. Rock.

Arnott),[2] $2n = 16$, of marshes from India to Java. *Semeiocardium* Zoll. is also monotypic, including only *S. Arriensii* Zoll., known solely from Madura and Kangean islands off the northeast coast of Java. *Impatiens* L. comprises the remainder of the species.

The family is a distinct one, characterized by the simple, exstipulate leaves, watery sap, resupinate zygomorphic flowers with a usually spurred often saccate sepal, stamens that are coherent around the gynoecium, and (in *Impatiens* and *Semeiocardium*) elastic dehiscence of the capsule. The fruit of *Tytonia* has been variously described as a berry; or as succulent, drupaceous, 5-angled, 5-furrowed, 5-loculate, the endocarp hard and bony, the seeds solitary (Wight & Arnott, p. 140); or as a 5-pyrenous drupe, "the stones 3–4 celled; only 1–2 cells seed-containing; the other ones empty and serving as a floating apparatus" (Backer & Bakhuizen, Fl. Java); or most recently as a purplish-red capsular berry dehiscing septicidally from the top leaving the seed attached to the column (Venkateswarlu & Dutt).

In *Tytonia* the perianth consists of five sepals (one spurred) and five petals, the lowermost largest. In *Impatiens* there are usually only three sepals (one saccate and usually spurred and two smaller lateral ones), but some species (cf. Hooker) have five, the two additional ones smaller than the others. The uppermost petal is free (and is often carinate or bifid), and the four others are connate in pairs, the pairs free from each other, each usually giving the appearance of a single two-lobed petal, but in *I. Wallerana* free nearly to the base and equal in size. An earlier interpretation of the perianth as composed of four sepals (the fourth [the uppermost petal in the above interpretation] being petaloid and often notched, presumably representing two sepals) and four petals (united in pairs) seems unlikely in view of the 10 perianth segments of *Tytonia* and the five sepals of some species of *Impatiens*. The perianth of *Semeiocardium* is composed of three sepals and five petals as in *Impatiens*, but the two fused petal-pairs have become connate into a bifid two-clawed liplike structure. *Semeiocardium* differs further from *Tytonia* and *Impatiens* in the largely connate lateral sepals, the 4-locular ovary, and the short, subulate style with a single stigma. Although it was originally described by Zollinger as a member of the Balsaminaceae, first Hasskarl and then Chodat mistakenly assigned it to the Polygalaceae. However, Backer's observations on living plants show that it is closely allied with *Impatiens* (cf. Miller, Jour. Arnold Arb. **52**: 273. 1971).

[2] As Backer & Bakhuizen van den Brink (Fl. Java **1**: 251. 1963) pointed out a dozen years ago, Blume (Bijdr. Fl. Nederl. Indië 241. 1825) did not publish the generic name *Hydrocera* validly, since he gave only a family description (Hydrocereae) and neither a generic description nor a specific one that might serve as a combined generic-specific description. *Hydrocera* was first validly published by Wight & Arnott (Prodr. Fl. Penin. Indiae Orient. 140. 1834), but they cited *Tytonia* G. Don (Gen. Syst. Garden. Bot. **1**: 749. 1831) in synonymy, making *Hydrocera* superfluous and illegitimate. The single species in this genus should be known as **Tytonia triflora** (L.) C. E. Wood, comb. nov., basionym, *Impatiens triflora* L. Sp. Pl. **2**: 938. 1753.

The Balsaminaceae have been considered to be allied with the Geraniales, and they have even been included in the Geraniaceae, but neither position is supported by recent studies. Most recent students have placed the family with the Sapindales, but this association is also uncertain. Erdtman notes that "an affinity with Celastrales, Geraniaceae, Oxalidaceae, Simaroubaceae, or Violaceae has been suggested but is not supported by pollen morphology."

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1. **Impatiens** Linnaeus, Sp. Pl. **2**: 937. 1753; Gen. Pl. ed. 5. 403. 1754.

Annual [or perennial] herbs [to subshrubs, sometimes acaulescent, sometimes epiphytic], usually with succulent stems and alternate [opposite, or pseudoverticillate], simple, exstipulate leaves [but sometimes with a nectary at each side of the leaf base]. Flowers axillary, solitary, in clusters of 2 or 3 [or in panicles]. Sepals 3 [5], the two lateral ones small, the posterior one large (in ours), petaloid, [usually] saccate [or funnel-shaped] and spurred. Petals 5, appearing to be 3, each of the 2-lobed laterals representing a fused pair, the single upper petal free, often carinate and/or more or less bifid. Stamens 5, the filaments short and flat, each bearing a scalelike appendage on the inner side, the scales partly or completely united over the ovary and stigma, the filaments partly connate; anthers introrse, often connate; pollen strongly flattened [3- or] 4-colpate, reticulate [rarely spinulose]. Gynoecium of 5 united carpels; stigmas 5; style short or absent; ovary 5-locular, the septa delicate, compressed by the ovules, the placentation axile, each locule with 3 to many anatropous ovules. Fruit capsular, the 5 fleshy valves elastic, in ours coiling violently from base to apex in dehiscence, scattering the seeds. Seeds with a straight embryo; cotyledons plump, hypocotyl and epicotyl short; endosperm none. LECTOTYPE SPECIES: *I. noli-tangere* L.; see Britton & Brown, Illus. Fl. No. U. S. Canada. ed. 2. 2: 440. 1913. (Name Latin, *impatiens*, in reference to the sudden bursting of the ripe fruit when touched.) — TOUCH-ME-NOT.

A genus of about 500 described species in 14 sections (see Warburg & Reiche), primarily of tropical and subtropical Asia (about half of the species in India and Burma) and Africa (about 150 species), with a few in temperate Eurasia and North America and none in either South America or Australia. Five indigenous species, all annuals of sect. IMPATIENS (§ *Brachycentron* Warb.), and two naturalized species occur in the United States and Canada; two of the indigenous species occur in our area.

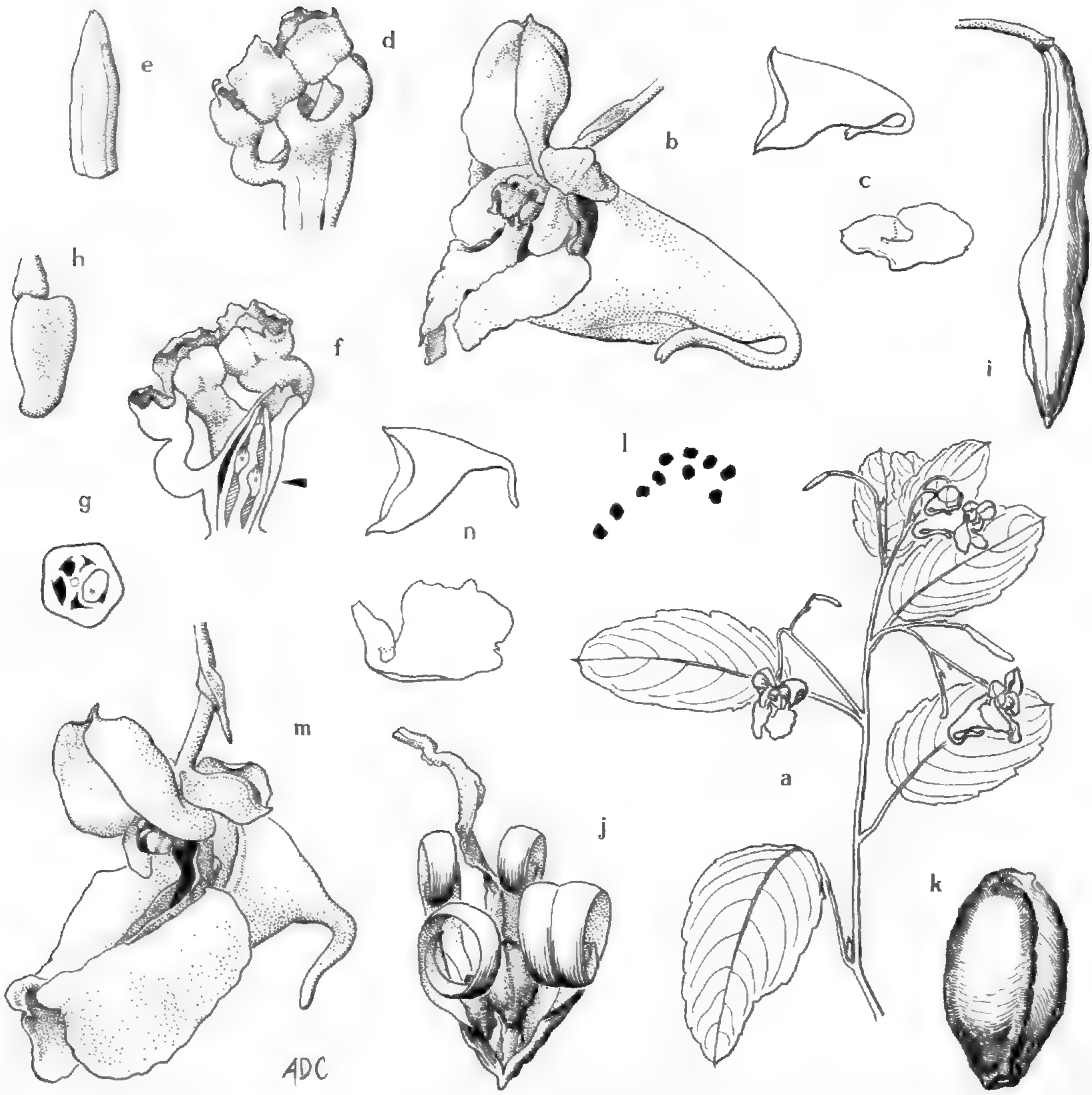

FIGURE 1. **Impatiens.** a–l, *I. capensis*: a, tip of flowering shoot, × ½; b, flower, × 2; c, spurred sepal and petal-pair (inner surface), × 1; d, androecium inclosing gynoecium, × 5; e, gynoecium, × 5; f, androecium and gynoecium in vertical section, the ovary semidiagrammatic to show central axis with two pendulous ovules in section through micropyle, septa omitted — note fused appendages of stamens covering gynoecium, × 5; g, ovary in cross section at level indicated in "f," × 10; h, pendulous ovule, micropyle at upper right, × 15; i, mature fruit before dehiscence, × 2; j, same, after dehiscence, × 2; k, seed, × 5; l, chromosomes in prometaphase of generative cell division in pollen from herbarium specimen (after Khoshoo, 1957), × 1500. m, n, *I. pallida*: m, flower, × 2; n, spurred sepal and petal-pair (inner surface), × 1.

Impatiens capensis Meerburg (*I. biflora* Walter, *I. fulva* Nutt.), jewelweed, $2n = 20$, is widely distributed in wet places, on stream banks, and in swamps from Newfoundland to Alberta, south to Florida, Alabama, Arkansas, and Oklahoma. The saccate part of the spurred sepal is longer than broad and the sepal spur is usually strongly incurved. The flower color is orange with red spotting, but it is very variable, and numerous color forms have been named (cf. Weatherby). Disjunct populations occur in northwestern Oregon and in extreme northwestern Washington and southwestern British Columbia. Ornduff, who has studied the Oregon

populations, thinks that *I. capensis* may be introduced in Oregon but indigenous in Washington and British Columbia. This species is widely naturalized in Great Britain and in France.

Impatiens pallida Nutt. (*I. aurea* Muhl.), $2n = 20$, with yellow, unspotted or sparingly spotted flowers, with the sac of the spurred sepal broader than long and the spur at a right angle to the sac, occurs in wet places or on stream banks in rich, shaded areas, most often on calcareous soils. It is distributed from Newfoundland to Saskatchewan, south through Nova Scotia and New England to Georgia, Tennessee, Missouri, and Kansas.

Impatiens pallida and *I. capensis*, vegetatively similar, often grow together, but there seems to be no evidence of hybridization anywhere in eastern North America. The chasmogamous flowers of both species are protandrous (as are those of other species of *Impatiens*), and the appendages of the filaments form a cover over the stigmas preventing pollen from falling on them. The stamens fall off as a unit, exposing the receptive stigmas. Unpollinated chasmogamous flowers of *I. pallida* and *I. capensis* do not set fruit. The effective pollinators of the two seem to be different, the rather small sepal sac and orange-and-red color of *I. capensis* favoring the ruby-throated hummingbird (*Archilochus colubris*), which seems to be the only "legitimate" visitor to the flowers both before and after the stamens fall. (Various bees collect pollen, and bees and wasps bite holes in the nectariferous spur, robbing the flowers illegitimately.) *Impatiens pallida*, with its yellow flowers and larger saccate sepal, is visited by species of *Bombus*, which Robertson noted were more constant in their visits to flowers of this species than to those of *I. capensis*. He did not see hummingbirds visiting the flowers of *I. pallida*.

A relatively small proportion of the chasmogamous flowers of either species set fruits, and the bulk of seed production appears to be from cleistogamous flowers. These are much smaller but bear all of the parts present in open ones except for the staminal appendages that cover the stigmas, pollen thus coming directly into contact with the stigmas. The floral parts never expand, but are forced off by the developing fruit. (See Bennett, Carroll, and Gray.)

Ornduff has pointed out that the center of diversity for the genus in North America is in the Pacific Northwest (Oregon, Washington, Idaho, western Montana, and southern British Columbia), where four species occur and the ranges of several overlap. In the northern extreme of its distribution in Oregon on the lower Columbia River, *Impatiens capensis* forms large hybrid swarms with *I. ecalcarata* Blankinship, which has unspotted yellow or orange spurless flowers. The Eurasian *I. noli-tangere* L. (*I. occidentalis* Rydb.), $2n = 20$, which occurs in North America from southern Alaska through British Columbia to northwestern Washington, overlaps the range of *I. ecalcarata* and that of *I. aurella* Rydb., which has relatively small, spurred, unspotted orange flowers. Puzzling plants combining in various ways the morphological features of these four species led Ornduff to hypothesize that "in the Pacific Northwest *I. capensis* was

once widespread, but subsequently the species has largely been exterminated in the region as a result of extensive and widespread hybridization with various other species. Vestiges of the floral morphology and pigment pattern of *I. capensis* still occur, but they are mostly in combination with features derived from *I. noli-tangere*, *I. ecalcarata*, or *I. aurella*. The last species in turn combines characters of *I. ecalcarata* and *I. noli-tangere* and may have originated by means of hybridization between these two species, followed by additional local hybridization with *I. capensis*."

Impatiens glandulifera Royle (*I. Roylei* Walpers) (sect. SALPINGOCHILON Warb.), $2n = 18, 20$, of the Himalayan region, is naturalized in the cooler, moister areas of Nova Scotia, New England, and Quebec, and appears to be spreading in western British Columbia, Washington, and Oregon. It is extensively naturalized in Great Britain, and is spreading in western and central Europe. It is distinctive in its opposite to pseudoverticillate leaves and clusters of large dark magenta-red to rose, pink, or white flowers.

Impatiens parviflora DC. (sect. IMPATIENS), $2n = 20, 24, 26$, a native of central Asia, is now widely naturalized in northern, central, and eastern Europe and in Great Britain, and it is introduced in Prince Edward Island and Quebec and on Vancouver Island, British Columbia. This very small-flowered species apparently is quite variable in its native area, but all of the naturalized plants apparently are descendants from a single seed lot planted in Geneva, Switzerland, about 1830, and are notably uniform. The five-sepaled flowers of *I. parviflora* apparently are largely self-pollinated. (See Coombe for a very complete account of this species in Britain.)

The very variable *Impatiens Balsamina* L. (sect. MICROCENTRON Warb.), $2n = 14$, from India, Malaya, and China, is cultivated in many parts of the world as an ornamental garden plant. This and the African *I. Wallerana* Hooker f. (*I. Sultani* Hook. f., *I. Holstii* Engler & Warb.) (sect. LONGICORNES Warb.), $2n = 16$, notable for a wide range of colors and nearly equal lobing of the paired petals, are probably the two most widely cultivated species of *Impatiens*. Their range of flower colors and ease of cultivation have made them the subject of many physiological, chemical, and genetic studies (see references). Although both are naturalized in various warmer areas, they are only occasional waifs in our region.

Embryo sac development of the Polygonum type (e.g., in *Impatiens capensis*, *I. pallida*, *I. Balsamina*) and of the Allium type (e.g., in *I. Wallerana*, *I. glandulifera*) has been reported in the genus. Species of *Impatiens* are unique in that the strongly flattened pollen is shed while the generative nucleus is in prometaphase of the division that produces the two sperm nuclei; hence the chromosome number can be determined at this stage. This nuclear stage persists in the pollen of herbarium specimens, and it has been possible to obtain chromosome counts from such material (cf. Khoshoo). Diploid chromosome numbers of 12, 14, 16, 20, 26, 32, 34, 36 (+ 2f), 40, and 66 have been recorded in various

species of the genus. These numbers fall into groups based on $x = 7, 8, 10$, and 11 (cf. Jones & Smith).

Huynh (1968), who studied the pollen of about 450 species of *Impatiens* but who apparently was unaware of the numerous relationships between the floras of North America and Asia, remarked with some surprise that the species of *Impatiens* of North America have pollen which recalls curiously that of the group of *I. noli-tangere*, which includes about 20 species of southern China.

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STUDIES IN SCHEFFLERA (ARALIACEAE): THE CEPHALOSCHEFFLERA COMPLEX

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IN RECENT YEARS there has been a renewal of interest in the morphology, anatomy, and systematics of the Araliaceae, beginning with the work of Baumann (1946) and continuing to the present (Baumann-Bodenheim, 1955; Rodríguez, 1957; Hoo & Tseng, 1965; Hutchinson, 1967; Smith & Stone, 1968; Eyde & Tseng, 1969, 1971; Grushvitzky & Skvortsova, 1970; Hladik, 1970; Philipson, 1970; Grushvitzky *et al.*, 1971; Tseng, 1973; Bamps, 1974b). This paper, a preliminary report on the complex of sect. CEPHALOSCHEFFLERA Harms and some related topics, represents the first of a series aimed at elucidating the systematics of *Schefflera* J. R. & G. Forst., the largest and geographically most widespread genus in the family, and one which is conspicuous in many tropical vegetation formations. Although there are several recent regional revisions (Backer & Bakhuizen, 1965; Bamps, 1974a, 1974b; Bernardi, 1969; Grushvitzky & Skvortsova, 1969; Hoo & Tseng, 1965; Li, 1942; Macbride, 1959; Smith, 1944; Smith & Stone, 1968; Tennant, 1968), the latest general revision on a world-wide basis is an incomplete and uncritical compilation by Viguier (1909). In addition, the limits of *Schefflera*, like those of various other genera in the Araliaceae, have been subject to many differences of opinion, which a perusal of even some of the above-cited references will show.

THE CEPHALOSCHEFFLERA COMPLEX

The first part of this paper is primarily a reconsideration of sect. CEPHALOSCHEFFLERA Harms (1894), which, for convenience, I shall here call "the *Cephaloschefflera* complex." It is a partial summary of an as yet unpublished dissertation (Frodin, 1970), which is in turn based on research toward a world-wide revision of *Schefflera* and allied genera. Associated with this question is the status of *Brassaia* Endl., included by Harms within his sect. CEPHALOSCHEFFLERA but still kept separate from *Schefflera* by a number of authors, both botanical (Burbidge, 1963; Parham, 1964; Hutchinson, 1967; Smith & Stone, 1968; Stone, 1970; Clifford & Ludlow, 1972) and horticultural (Neal, 1965). This may be in part due to tradition (*Brassaia* was recognized as distinct by Bentham (1867)) or convenience. It may be noted that the type species of *Brassaia*, *B. actinophylla* Endl. (= *S. actinophylla* (Endl.) Harms), has long been a well known staple of ornamental horticulture, both indoors and out, and in some countries or regions it is adventive or naturalized (e.g., Fiji,

Singapore, southern Queensland). The question as to whether *Brassaia* should be kept separate or should be merged with *Schefflera* in a way highlights the whole problem of the *Cephaloschefflera* complex: is it or is it not a natural grouping?

Schefflera is presently considered to have ca. 200 species (Willis, 1973). These species are found in most of the tropical and subtropical regions of the earth, but they are especially numerous in certain mountainous belts, such as the Andes and the mountains of Southeast Asia and Malesia (notably the central cordillera of New Guinea); the other main concentrations are found in the Guayana Highlands, Madagascar, and New Caledonia. The genus is typified by the single species in New Zealand, *Schefflera digitata* J. R. & G. Forst. As delimited by Harms (1894–97), *Schefflera* comprises trees, shrubs, epiphytes, hemi-epiphytes (sometimes strangling), and climbers. The genus is largely characterized by the following: a) an absence of prickles on vegetative parts; b) once palmately compound leaves with fused stipules extending into an appendage of greater or lesser length at the base of the petiole; and c) inflorescences in panicles with a main axis and a varying number of branches along which the flowers are arranged in more or less numerous, usually stalked umbellules, capitula, racemules or spicules. Less commonly, the entire inflorescence forms a compound umbel recalling those present in the vast majority of the Umbelliferae. The flowers lack an articulation at the base of the pedicel and are most often characterized by an ovary with five (or more) locules.

Associated with *Schefflera* are a number of related genera: *Crepinella* E. March., *Didymopanax* Decne. & Planchon, *Dizygotheca* N. E. Br., *Enochoria* Baker f., *Geopanax* Hemsley, *Neocussonia* (Harms) Hutchinson, *Octotheca* R. Vig., *Plerandra* A. Gray, *Schefflerophsis* Ridley, and *Tupidanthus* Hook. f. & Thomson. *Agalma* Miq. and *Brassaia* Endl. are maintained as segregates of *Schefflera* by Hutchinson (1967), while several authors, past and present, have merely segregated *Brassaia*. In the Philippines, Merrill (1923) added a further segregate, *Cephaloschefflera* (Harms) Merr. (based on sect. CEPHALOSCHEFFLERA Harms). All of these taxa are distinguished from one another by essentially small differences in inflorescence morphology and in the absolute and relative numbers of floral parts. More distantly related are *Brassaiopsis* Decne. & Planchon, *Macropanax* Miq., and *Pseudopanax* C. Koch.

Harms (1894) proposed the division of *Schefflera* (as delimited by him) into two sections:

Sect. CEPHALOSCHEFFLERA. Flowers sessile, in more or less densely aggregated capitula, these mostly pedunculate and arranged in racemes [including *Brassaia*]. (PLATE III–A.)

Sect. EUSCHEFFLERA. Flowers pedicellate, in racemes or umbels. (PLATE III–B.)

The geographical distribution of both sections was shown to be more or less pantropical, although sect. CEPHALOSCHEFFLERA was not re-

corded for the islands east of New Guinea. Harms intended his delimitation of sections and subsections to be practical; to him, attempting a natural arrangement at that time was not advisable, since available herbarium material and field data were too often imperfect. Unfortunately, he never made a new overall revision of *Schefflera* before his death in 1942, although in the intervening 48 years he described numerous new species and made various regional revisions, of which the most important was that forming part of his treatment of the Papuasian Araliaceae (Harms, 1920–21).

Harms's arrangement came into wide use, its outlines (although sometimes modified) being used for treatments of *Schefflera* and other Araliaceae in many floras and regional revisions. Initial acceptance of his arrangement may have been consolidated by the wide influence of Engler and Prantl's *Die natürlichen Pflanzenfamilien* and other German works of the pre-World War I era. Since then, the most significant modification of Harms's system has been that of Hoo and Tseng (1965), in which that part of the *Agalma* group characterized by entirely racemose inflorescences was elevated to sectional rank, along with their sect. BRASSAIA (= sect. CEPHALOSCHEFFLERA Harms) and sect. SCHEFFLERA (= sect. EUSCHEFFLERA of Harms, except for the racemosely flowered species in the *Agalma* group); this arrangement has also been adopted by Grushvitzky and Skvortsova (1969).

An alternative arrangement of *Schefflera* was proposed by Viguier (1909). In his compilation he showed that a few species were intermediate in so far as pedicel development was concerned. In other words, the flowers *appeared* to be in capitula, although in fact they were pedicellate. This interpretation cut across the primary division in Harms's scheme, thus rendering it open to question. For the sake of comparison, Viguier's scheme is given below in synoptic form (no formal nomenclature was applied to his groups):

1. Styles distinctly developed, united into a column on a more or less convex disk; flowers in racemes or in racemosely arranged umbellules (rarely capitula). [Only one capituliferous species, *Schefflera schumanniana* Harms from New Guinea, was included here; the other members are the *Agalma* group of species of sect. EUSCHEFFLERA Harms.] (PLATES I–A, I–B.)
2. Styles none and stigmata sessile on the disk, or styles free or united only at the base, radiating outward in fruit; flowers in racemosely arranged umbellules or capitula.
   a. Flowers in capitula. [Most members of sect. CEPHALOSCHEFFLERA Harms, including *Brassaia*, were listed here.] (PLATE III–A.)
   b. Flowers in umbellules. [This group included the greater part of sect. EUSCHEFFLERA, except for the *Agalma* group of species.] (PLATES II–A, III–B.)
3. Styles variously developed; flowers umbellulate, arranged in compound umbels. [This group included miscellaneous members of sect. EUSCHEFFLERA, mostly from northern South America, Madagascar, and New Caledonia.] (PLATE II–B.)

Viguier regarded the form of the inflorescence and the nature and degree of fusion of the styles as more important attributes than the presence or absence of capitula, a characteristic which was, so to speak, relegated to third place. Apparently, whether or not a given species was considered capituliferous depended, in his view, on the overall *appearance* of the cluster of radiating flowers; whereas Harms maintained a more exact outlook, basing his delimitation on the presence or absence of pedicels. (At a later date, however, Harms appears to have made the delimitation in Viguier's sense; see his treatment of Papuasian *Schefflera* (1920–21, p. 385).)

As already noted, the Philippine species of the *Cephaloschefflera* complex were the first to be elevated to generic rank (Merrill, 1923). However, Hutchinson (1967) proposed that *all* of the capituliferous species be raised to that rank, reinstating *Brassaia* to incorporate them. His distinction was based merely on the presence of capitula as opposed to umbellules, without qualification. In an appendix (1967, pp. 622–624), he listed 45 species as belonging to his expanded concept of *Brassaia*; even then, a great many more published species which should logically have been accounted for were left out. In a similar manner, Hutchinson reinstated Miquel's old genus *Agalma* to include those species of *Schefflera* with flowers racemosely arranged throughout, notwithstanding their other relationships.

Hutchinson's proposals provided the lead which stimulated my studies in the direction of the *Cephaloschefflera* complex. During field work in New Guinea and New Britain in 1965–66, there first arose the suspicion that the complex as it stood might be an artificial grouping; the relationships of the various species of *Schefflera* observed, and the groups into which they seemed to fall, appeared not to correspond to the divisions proposed in the literature for the Papuasian species (Harms, 1920–21, 1938; Philipson, 1951). A satisfactory explanation appeared to be that series of capituliferous species were, as groups, more closely related to otherwise similar series of umbelluliferous species in the Papuasian region than they were to other series of capituliferous species in that region or elsewhere. Subsequent research in herbarium and library, covering all 123 described species that should logically be assigned to the *Cephaloschefflera* complex because of their inflorescence type, has shown that this preliminary hypothesis is correct when applied on a world-wide basis.

There are examples of close relationships between umbelluliferous and capituliferous species in the Neotropics, the African region, and mainland Asia, as well as throughout Malesia. In fact, the similarity in the patterns of evolutionary radiation, both in Papuasia and the Andes, each involving umbelluliferous and capituliferous species, is especially striking and merits closer study. A detailed discussion of all observed progressions is beyond the scope of this paper and the cases enumerated below are merely representative.

In the Neotropics, the umbelluliferous species *Schefflera ternata* Cuatr. of Colombia is closely related to the capituliferous *S. herthae* Harms of

Ecuador by virtue of its 3–5-foliolate leaves, slender 2–3-branched inflorescences, capitula/umbellules with few flowers, and conical corollas. An example of a gradual transition is that from *S. sphaerocoma* (Bentham) Harms (an umbelluliferous species with moderately long pedicels growing from Costa Rica to Colombia) through *S. sciadophyllum* (Swartz) Harms (an umbelluliferous species with rather short pedicels growing in Jamaica) to the capituliferous *S. robusta* (A. C. Sm.) A. C. Sm. of Costa Rica. The common features of these three species include large leaves with many leaflets, inflorescences with many radiating branches bearing numerous racemosely arranged few-flowered capitula/umbellules, and small flowers with elevated disks and short, partially free styles.

In the African region, the capituliferous *Geopanax procumbens* Hemsley [1] of the Seychelles is more closely related to the umbelluliferous species *S. barteri* (Seem.) Harms and *S. goetzenii* Harms from mainland Africa, all three having similar leaf venation, calyptrate corollas with minute sutures, and a 5–10-locular ovary, than to the capituliferous *S. mannii* (Hooker f.) Harms, *S. stolzii* Harms, and *S. volkensii* Harms, all of which have discrete petals and a 5-locular ovary.

In Asia, the umbelluliferous species *Schefflera wallichiana* (Wight & Arnott) Harms of South India and *S. khasiana* (C. B. Cl.) Viguier of eastern India to China are very closely related to the capituliferous *S. capitata* (Wight & Arnott) Harms by virtue of their nearly identical leaflet form and venation, short stipular ligules, sutured calyptrate corollas, inflorescences with a moderate number of branches, stylar column absent or nearly so, and ovary 5–9(–10)-locular. However, *S. capitata* differs from *S. actinophylla* by the presence in the latter of four large bracts per flower (in contrast to three in *S. capitata*), a 10–12-locular ovary, elongated anthers, and much longer stipular ligules. The apparent similarity between the two (noted by earlier workers) is due to convergence and is not necessarily indicative of close relationship, although there is evidence that the group of species associated with *S. actinophylla* are more closely related to this *S. wallichiana/S. capitata* group than to any other in the Old World.

In New Guinea, the capituliferous species *Schefflera schumanniana* Harms is more closely related to the umbelluliferous *S. hellwigiana* Harms (the two species having similar habitats in the understory of damp montane forests, shrubby habits, 5-foliolate leaves with strongly reticulate leaflets, slender, few-branched inflorescences, and long-styled globose fruits) than to large, canopy-dwelling, sun-loving capituliferous species such as *S. carrii* Harms, *S. lasiosphaera* Harms, *S. stolleana* Harms, or *S. morobeana* Harms. Similarly, the capituliferous *S. chaetorrhachis* Harms is more closely related to the umbelluliferous *S. bougainvilleana* Harms, both having small green flowers in 60–100-branched inflorescences, than to the capituliferous *S. actinophylla* or the capituliferous *S. pachystyla*

[1] This taxon should be transferred to *Schefflera*. Availability of better material has enabled me to find that the characters used by Hemsley (1906) to segregate *Geopanax* do not hold.

Harms, both of which have large red or pink flowers and 5–12-branched inflorescences.

Reference should also be made to those "intermediate" species which were first noted by Viguier as not readily fitting into either the capituliferous or umbelluliferous assemblages. His list included the following Malesian species: *S. cephalotes* (C. B. Cl.) Harms, *S. tomentosa* (Bl.) Harms, *S. scortechinii* (King) Viguier, and *S. apiculata* (Miq.) Viguier. In addition, he considered the neotropical *S. heterotricha* (Planchon & Linden ex E. March.) Harms ex Viguier, placed by Harms in his sect. EUSCHEFFLERA, to be capituliferous and grouped it with *S. trianae* (Planchon & Lindley ex E. March.) Harms and *S. euryphylla* Harms, mentioning that (translated) "in this case it is impossible to trace the limit between the two sections which he [Harms] proposes." He also noted that "for example, *S. cephalotes* of Malaya, of his [Harms's] section CEPHALOSCHEFFLERA, has distinctly pedicellate flowers." Since Viguier's time, more "intermediate" species have come to light, among them *S. angiensis* Gibbs of New Guinea, *S. merrillii* Elmer of the Philippines, and *S. chinensis* (Dunn) Li of western China. In addition, it has become evident that the flowers in the immature inflorescences of many species that are umbelluliferous when mature appear to be in capitula, since evident pedicel elongation has not yet taken place. Furthermore, there are a number of examples of both capituliferous and umbelluliferous species in which further pedicel development can take place *after* anthesis; e.g., *S. cephalotes*, *S. barteri*, and *S. versteegii* Harms of New Guinea. In some species the flowers, although forming capitula, are found to be distinctly pedicellate when the capitula are bisected; this is seen in *S. cephalotes*, as noted by Viguier, and in *S. lasiosphaera* of New Guinea. A further list of "intermediate" species has been given by Jacques-Felix (1970).

While recognizing that the existence of these "intermediates" cast doubt on the validity of Harms's primary divisions in *Schefflera*, Viguier did not attempt a more thorough analysis of relationships at the species level. However, the evidence now available has made possible the "linking" of most of the intermediates with other species. *Schefflera cephalotes* is in leaf, inflorescence, and fruit characters most closely linked with the umbelluliferous *S. havilandii* Merr. of Borneo and *S. latifoliolata* (King) Viguier of Malaya; *S. tomentosa* appears to be close to the umbelluliferous *S. yatesii* Merr. of Sumatra and Malaya and *S. petiolosa* (Miq.) Viguier of Borneo in leaflet, inflorescence, and fruit characters; *S. apiculata* seems quite close to the umbelluliferous Moluccan species of *Schefflera* now known as *Brassaia littorea* Seem.; and *S. scortechinii* is but a phase of the umbelluliferous *S. hullettii* (King) Viguier of Malaya and Sumatra, with immature inflorescences. These umbelluliferous species do not on any account belong to the same series or even the same section. The affinities of *S. heterotricha* are more obscure. Related taxa may include *Didymopanax allocotanthus* Harms of Bolivia and *Schefflera rubiginosa* (Decne. & Planchon ex Harms) Steyerm. [non

Ridley] of Colombia and Venezuela; all have elongated styles with five (or two) radiating stigmata and a 5-toothed calyx. *Schefflera chinensis* is closer to the umbelluliferous *S. hypoleucoides* Harms of northern Viet Nam and *S. hypoleuca* (Kurz) Harms of eastern India to China than to any other capituliferous species, the three taxa having relatively similar leaf form, inflorescence, and fruit; collectively, however, the three are amply distinct from species such as *S. cephalotes*, with which Hoo and Tseng (1965) tried to link *S. chinensis*.

Section CEPHALOSCHEFFLERA (including *Brassaia*), as proposed by Harms and more or less modified by him and later authors, is thus manifestly an evolutionary grade (Huxley, 1958; Simpson, 1961). The probable direction of evolution has been in the gradual reduction and suppression of pedicels in different series of species, perhaps by successive retardations of pedicel growth during development of the inflorescence before and after anthesis. Whether or not this is associated with changes in pollination and/or dispersal mechanisms and, if so, what kinds of mechanisms are involved, I am unable to determine at present.[2] It may be noted here that the occurrence of capitula in the Araliaceae (apart from *Schefflera*) is generally relatively uncommon. Only the neotropical *Oreopanax*, the Pacific-insular *Meryta*, and the essentially eastern Malesian/Melanesian *Boerlagiodendron* and *Osmoxylon* are wholly or partially made up of species with capituliferous inflorescences.

Within *Schefflera* the only series of capituliferous species without close relatives amongst umbelluliferous species is the *Brassaia* group (in the strict sense), the type species of which is *S. actinophylla*. The geographical range of these species is centered in Papuasia. As a group, the species are very distinctive, with fruits black at maturity and brilliantly-hued red or pink flowers and young fruits. (An exception is *S. kraemeri* Harms, which has fruits green when unripe and white flowers.) However, the only important "attribute state" (cf. Jardine & Sibson, 1971, pp. 3, 4) characterizing the *Brassaia* group and not appearing elsewhere in *Schefflera* is the presence of four large, winglike, imbricated basal floral bracts. (In other *Schefflera* species such bracts are absent or only one to three in number and are virtually always otherwise shaped.) In addition, some species have an exceptionally large number of carpels (ovary-locules), reaching 25 to 30 in *S. thaumasiantha* Harms of southeastern New Guinea. However, in habit, gross morphology, overall inflorescence structure,

[2] Recently I have learned that the inflorescences in at least some of the capituliferous species in New Guinea act as "perches" for some birds of paradise feeding on the flowers or fruit (but not necessarily as display trees). *Paradisaea raggiana* (the Raggiana Bird of Paradise) has been seen on *Schefflera thaumasiantha* Harms in the Sogeri Plateau (C. Nicholson, pers. comm.), while *Astrapia stephaniae* (the Princess Stephanie Bird of Paradise) has been seen on *S. lasiosphaera* near Mt. Giluwe (J. Croft, pers. comm.). On a 1973 issue of Papua New Guinea postage stamps depicting birds of paradise, the 21-cent stamp illustrates the Ribbontail Bird of Paradise, *Astrapia mayeri*, perching on a yet-to-be-described species of *Schefflera* found in the Mt. Giluwe area. All these birds of paradise are at least sometimes frugivorous (Gilliard, 1969).

flowers, and fruits, the *Brassaia* group is very similar to the rest of the pantropical "central nexus" of *Schefflera* (as exemplified by such species as *S. sciadophyllum* (Swartz) Harms of Jamaica, *S. tomentosa* (Bl.) Harms of West Malesia, *S. venulosa* (Wight & Arnott) Harms of South India, and *S. volkensii* Harms of East Africa). I do not consider differences such as the presence of four large floral bracts (in contrast to three or fewer smaller bracts in other *Schefflera* species) and a relatively large carpel number (8 to 30) to be sufficient grounds for separation at the generic level, particularly when the strong overall resemblances with other groups of *Schefflera*, both in the field and on closer examination in the herbarium, are considered.

The *Brassaia* group seems best regarded as a section of *Schefflera* in a wider sense, although it is perhaps somewhat isolated. The series of species within *Schefflera* most closely related to the *Brassaia* group is that centering on *S. wallichiana* (Wight & Arnott) Harms, *S. capitata*, and *S. khasiana*, all of which are in mainland Asia; other sections of *Schefflera* within Papuasia are not as closely related to the *Brassaia* group. Together with the unusual features of the high average carpel number (considered a "primitive" feature by Eyde and Tseng (1971)) and the presence of the large floral bracteoles (which I believe also to be a "primitive" feature), the geographical isolation of the *Brassaia* group from its nearest relatives suggests that it is relictual in the Papuasian context. The very close, partly reticulate relationships of the known species also suggest that the group is presently undergoing a secondary evolutionary cycle.

In the second part of this paper I have given an annotated list of published taxa which are correctly referable to the *Brassaia* group. This excludes the great majority of the *Brassaia* combinations proposed by Hutchinson (1967). Some other *Brassaia* combinations of longer standing must also be excluded from the group, i.e. *B. capitata* (Wight & Arnott) C. B. Cl. (= *Schefflera capitata* (Wight & Arnott) Harms); *B. sessilis* (Miq.) Seem. (= *S. sessilis* (Miq.) Harms); and *B. littorea* Seem. (= *S. littorea* (Seem.) comb. nov.).[3]

As I propose to regard the group as circumscribed here at the sectional level, the correct formal name appears to be *Schefflera* sect. BRASSAIA (Endl.) Tseng & Hoo. When Hoo and Tseng (1965) recognized sect. BRASSAIA (Endl.) Tseng & Hoo, they included two subsections, subsect. CEPHALOSCHEFFLERA (Harms) Tseng & Hoo and subsect. ACTINOPHYLLAE (Endl.) Tseng & Hoo, the former being lectotypified by *S. cephalotes* (C. B. Cl.) Harms. This was the first lectotypification of the name *Cephaloschefflera*; Harms did not designate a type for his section CEPHALOSCHEFFLERA, and when Merrill (1923) raised section CEPHALOSCHEFFLERA to generic rank, he did not transfer any species which Harms had originally included in that section. Although Viguier (1909) indicated that the flowers of *S. cephalotes* were shortly pedicellate, they

[3] Basionym: *Brassaia littorea* Seem. Jour. Bot. London **2**: 244. 1864 (*Papaja litorea* Rumph. Herb. Amb. **1**: 151. *t. 52.* 1741). The species has an involved synonymy, which will be dealt with elsewhere.

are clearly aggregated into capitula, agreeing with the original description of the section, and hence *S. cephalotes* is a not unreasonable lectotype for section CEPHALOSCHEFFLERA. Although Hoo and Tseng (1965) should have used the sectional name CEPHALOSCHEFFLERA for a section including both *S. cephalotes* and *S. actinophylla* (Article 63 of the *International Code*, Stafleu *et al.*, 1972), BRASSAIA (Endl.) Tseng & Hoo is now the correct name to use for a section which includes *S. actinophylla*, but not *S. cephalotes*. The name *Brassaia* has been widely used in various contexts for *S. actinophylla* and its allies, and it is fortunate that it can continue to be used for these plants.

What of the name *Cephaloschefflera*? As presently typified, it appears that it will become synonymous with Blume's *Aralia* sect. PARATROPIA (1826), based partly on the umbelluliferous *A. rigida* Bl. (= *Schefflera rigida* (Bl.) Harms, presently included in *S. lucescens* (Bl.) Viguier), to which *S. cephalotes* is closely related, along with *S. havilandii*, *S. latifoliolata*, and *S. hullettii*. This question will be considered more fully elsewhere.

The necessary break-up of the *Cephaloschefflera* complex has led to preliminary research toward a revision of the whole of *Schefflera*, together with the several segregates and closely related taxa listed elsewhere in this paper. A detailed discussion of this work is outside the scope of the present contribution. However, it is my opinion that most of the attributes used to distinguish these taxa appear to be as trivial as those indicated as distinguishing the *Brassaia* group from the main nexus of *Schefflera*, particularly when the whole assemblage of some 450 described and undescribed species is viewed. The worth of some of these attributes has already been discussed (Baumann, 1946; Philipson, 1970; Eyde & Tseng, 1971). I believe, therefore, that the best course is to reduce all of these segregates to *Schefflera*, except for *Enochoria* (which will be discussed in the third part of this paper). In subsequent papers, further details will be given concerning the 17 sections (in six subgenera) which are presently being considered for recognition. Of these sections, five (all in one subgenus) incorporate nearly all of the species formerly in the *Cephaloschefflera* complex, together with a large number of umbelluliferous species.

PRELIMINARY SYNOPSIS OF SCHEFFLERA SECT. BRASSAIA (AS EMENDED)

Schefflera sect. **Brassaia** (Endl.) Tseng & Hoo, Acta Phytotax. Sinica, Addit. 1: 133. 1965, *quoad* subsect. *Actinophyllae*; Grushvitzky & Skvortsova, Adansonia (n. s.) 9: 386. 1969. BASIONYM: *Brassaia* Endl. Nov. Stirp. Dec. 89. 1839; Bentham, Fl. Austral. 3: 385. 1866; Bailey, Queensl. Fl. 2: 735. 1900; Hutchinson, Gen. Fl. Pl. 2: 73. 1967, *sensu lato*; Smith & Stone, Jour. Arnold Arb. 49: 489. 1968. TYPE SPECIES: *S. actinophylla* (Endl.) Harms (*B. actinophylla* Endl.).

Schefflera sect. *Cephaloschefflera* Harms in Engler & Prantl, Nat. Pflanzenfam. III. 8: 36. 1894, *p.p. quoad spp. actinophylla et macrostachya*; Bot. Jahrb. **56**: 385. 1920; Philipson, Bull. Brit. Mus. Nat. Hist. Bot. **1**: 14, 15. 1951; Hutchinson, Gen. Fl. Pl. **2**: 73. 1967, *ut syn. Brassaiae*.

DISTRIBUTION. Aru Islands; New Guinea (mainland) and Geelvink Bay Islands (except Biak); Bismarck Archipelago (except the Admiralty Islands); Solomon Islands (including Rennell); Torres Strait Islands; northern and northeastern Australia. Also in the Caroline Islands (Truk group).

ENUMERATION OF SPECIES

Studies to date have shown that some of the species assigned to the section must or are likely to be relegated to synonymy. As far as is practicable, these reductions are indicated below. In addition, one or two additional species have yet to be described, but consideration of these is deferred until a later paper.

1. **Schefflera actinophylla** (Endl.) Harms in Engler & Prantl, Nat. Pflanzenfam. III. 8: 36. 1894. PLATE IV–A.

Brassaia actinophylla Endl. Nov. Stirp. Dec. 89. 1839.
Brassaia singaporensis Ridley, Jour. Asiatic Soc. Straits Settlements **75**: 38. 1917.

DISTRIBUTION. Australia: northeastern Queensland and northern Northern Territory; Aru Islands; New Guinea: southern and southeastern parts south of the central cordillera; Torres Strait Islands. Now escaped and naturalized in several other parts of the tropics (and subtropics).

Widely cultivated as an ornamental and street tree or as a pot plant, both indoors and out. The species is not native to the Hawaiian Islands, although otherwise indicated by Hutchinson (1967, p. 73). *Brassaia singaporensis* was based on escaped plants occurring on Singapore Island.

2. **Schefflera brassaiella** Ridley, Trans. Linn. Soc. II. Bot. **9**: 65. 1916.

Schefflera pullei Harms, Bot. Jahrb. **56**: 388. 1920.
Brassaia brassaiella (Ridley) Hutchinson, Gen. Fl. Pl. **2**: 622. 1967.
Brassaia pullei (Harms) Hutchinson, *Ibid.* 623.

DISTRIBUTION. New Guinea: Carstensz Range east to the Hindenburg Range near Telefolmin.

The stamens of *Schefflera brassaiella* usually exceed the ovary-locules in number.

3. **Schefflera corallinocarpa** Harms, Bot. Jahrb. **56**: 388. 1920.

Brassaia corallinocarpa (Harms) Hutchinson, Gen. Fl. Pl. **2**: 622. 1967.

DISTRIBUTION. New Guinea: lowlands of the middle Sepik valley, near the junction of the Sepik and May rivers.

The type (*Ledermann 7211*) was destroyed at Berlin and no isotypes have yet been located. However, from the description it appears that the plant may be only a form of *S. macrostachya.*

4. **Schefflera kraemeri** Harms, Notizbl. Königl. Bot. Gart. Berlin **5**: 73. 1908; Kanehira, Jour. Coll. Agric. Kyushu Imp. Univ. 4(6): 434. 1935.

Schefflera pachyclada Kanehira, Bot. Mag. Tokyo **46**: 670. 1932; Fl. Micrones. 294, *fig. 148.* 1933.

DISTRIBUTION. Caroline Islands: Truk group.

Distinctive in the section for its white flowers and green (in unripe stage) fruits; otherwise closely related to *Schefflera waterhousei* of the Bismarck Archipelago and the Solomon Islands. *S. pachyclada* was reduced by its author a few years after being described.

5. **Schefflera macrostachya** (Bentham) Harms in Engler & Prantl, Nat. Pflanzenfam. III. **8**: 36. 1894.

Sciadophyllum macrostachyum Bentham, London Jour. Bot. **2**: 222. 1843. (As "*Sciodaphyllum.*")
Paratropia macrostachya (Bentham) Miq. Fl. Ind. Bat. **1**(1): 760. 1856.
Brassaia macrostachya (Bentham) Seem. Jour. Bot. **2**: 244. 1864; Hutchinson, Gen. Fl. Pl. **2**: 623. 1967.

DISTRIBUTION. New Guinea: Japen Island in Geelvink Bay and the mainland lowlands north of the central cordillera from the Meervlakte east to the Markham-Ramu Valley near Dumpu, including the foothills of the Adalbert, Prince Alexander, Torricelli, and Van Rees ranges (so far as known). A variant form with sutures extending only part way from the apex of the corolla occurs in the Vogelkop, where it apparently replaces the more easterly form.

Schefflera macrostachya is closely related to *S. actinophylla,* and the two species may be considered as a vicariant pair with mutually exclusive ranges largely separated by the central cordillera. The inflorescences of the two are very similar in gross structure, but on the other hand there are some more or less constant differences in leaflet shape and venation. The status of the Vogelkop variants remains to be determined.

6. **Schefflera megalantha** Harms, Bot. Jahrb. **56**: 386. 1920.

Brassaia megalantha (Harms) Hutchinson, Gen. Fl. Pl. **2**: 623. 1967.

DISTRIBUTION. New Guinea: in the central cordillera from the Baliem-Meervlakte divide east to the Krätke Range, and on the Ramu-Astrolabe Bay dividing range west of the Finisterre Range.

The flower buds of *Schefflera megalantha* are distinctly cone-shaped. The species is occasionally cultivated locally (Mt. Hagen).

7. **Schefflera ovalis** J. J. Sm. ex Dakkus, Bull. Jard. Bot. Buitenzorg III. Suppl. **1**: 262. 1930, *nomen nudum.*

DISTRIBUTION. Aru Islands; New Guinea: southwestern coast along the Arafura Sea from the Lorentz River to the Uta River below the Carstensz Range. Cultivated in Hortus Bogoriensis.

The name *Schefflera ovalis* first appears in print in Dakkus's alphabetical list of plants cultivated in Hortus Bogoriensis. It also appears on a few herbarium specimens distributed from Bogor. No description has ever been published. The plants concerned represent a form of *S. actinophylla* differing in its leaflets, which are coarsely toothed at the apex, and in its flower buds, which are more elongated. In addition, the leaflet venation is suggestive of *S. macrostachya.* The distribution of this form, as far as it is known, is just west of that of *S. actinophylla* in New Guinea.

8. **Schefflera pachystyla** Harms, Bot. Jahrb. 72: 205. 1942.
PLATE IV–B.

Schefflera gigantea Philipson, Bull. Brit. Mus. Nat. Hist. Bot. **1**: 14. 1951.

DISTRIBUTION. New Guinea: central cordillera from just east of Wau through the Bulolo-Watut basin to the Krätke Range, as well as in the mountains of the Huon Peninsula and the Saruwaged Range.

Both *Schefflera pachystyla* and *S. gigantea* were based on the same collection (*Clemens 5386*). The species is intermediate between *S. megalantha* and *S. thaumasiantha.*

9. **Schefflera pseudobrassaia** Harms, Bot. Jahrb. **56**: 388. 1920.

Brassaia pseudobrassaia (Harms) Hutchinson, Gen. Fl. Pl. **2**: 623. 1967.

DISTRIBUTION. New Guinea: foothills of the central cordillera in the upper April River watershed, southwest of Ambunti (middle Sepik region).

The type (*Ledermann 9977*) was destroyed at Berlin and no isotypes have yet been located. However, the difference between the numbers of stamens and ovary-locules as described is also found in *Schefflera brassaiella,* as are the relatively small leaflets and short inflorescence-branches. Harms himself noted that this taxon was very close to his *S. pullei,* here united with *S. brassaiella.* It is probable that the differences given are insufficient to maintain *S. pseudobrassaia* as a species distinct from *S. brassaiella.*

10. **Schefflera secunda** Philipson, Bull. Brit. Mus. Nat. Hist. Bot. **1**: 14. 1951.

DISTRIBUTION. New Guinea: mountains of the Vogelkop.

The inflorescences of this very distinct species consist of a few spreading branches which bear numerous very small, few-flowered heads on long peduncles, all oriented upward. Another striking character is that the fruit at maturity may be as much as two-thirds superior (cf. Eyde & Tseng, 1969).

11. **Schefflera stenopetala** Harms, Bot. Jahrb. **56**: 390. 1920.

Brassaia stenopetala (Harms) Hutchinson, Gen. Fl. Pl. **2**: 623. 1967.

DISTRIBUTION. New Guinea: lowlands of the middle Sepik valley near Ambunti.

The type (*Ledermann 8146*) was destroyed at Berlin and no isotypes have yet been located. However, the differences indicated by Harms appear to fall within the range of variation of *Schefflera macrostachya*; in addition, a recent collection from the Ambunti region agrees well with the description of this latter species. Consequently, it is unlikely that *S. stenopetala* can be maintained as distinct.

12. **Schefflera thaumasiantha** Harms, Bot. Jahrb. **69**: 278. 1938.
PLATE V–A.

DISTRIBUTION. New Guinea: in the foothill and lower montane zones of the Wharton and Owen Stanley Ranges from Tapini (north of Port Moresby) through the Sogeri Plateau to Nowata (northwest of Amazon Bay).

This spectacular species is characterized by its fruits, which have 25 to 30 or more locules, and by its inflorescence-branches, which are up to a meter or more long. It is sometimes cultivated locally (Sogeri, Brown River, Port Moresby).

13. **Schefflera waterhousei** Harms, Notizbl. Bot. Gart. Berlin **15**: 678. 1942.
PLATE V–B.

DISTRIBUTION. Bismarck Archipelago: Mussau (St. Matthias) I., New Ireland, New Britain; Solomon Islands: Bougainville to Guadalcanal and Rennell.

Schefflera waterhousei is fairly closely related to *S. actinophylla*, but the smaller leaflets and few-flowered heads are distinctive. The species is rather variable, although most collections fall into one of two distinct groups, of which the ranges are almost mutually exclusive. The "typical" form occurs in the northern Solomon Islands and the Bismarck Archipelago, while the other form is limited to the southern Solomon Islands. The differences may be sufficient to warrant separation at the species level, but further study is required.

A RECONSIDERATION OF THE STATUS OF ENOCHORIA

Enochoria Baker f., a rather enigmatic araliaceous genus with one species, *E. sylvicola* Baker f. (1921), was originally described from one collection (*Compton 1336*) gathered from near Canala on the north coast of New Caledonia in 1914 and preserved in the British Museum of Natural History. This holotype collection consists of single fragments respectively of a leaf and an inflorescence. No isotypes have come to light, and to the best of my knowledge no further collections have been made. The genus was accepted without comment by Guillaumin (1948) for his *Flore analytique et synoptique,* as well as by Hutchinson (1967). Because of the presence of digitately compound leaves and capituliferous inflorescences, the genus was placed near *Schefflera* in Hutchinson's system of the family Araliaceae.

In connection with the studies of the group of genera associated with *Schefflera,* I have re-examined the type specimen of *E. sylvicola.* The only conclusion that can be drawn is that the specimen is an artifact. The leaf fragment is from a species of *Schefflera,* probably *S. affinis* Baillon, while the inflorescence fragment, with flowers all carpellate, represents *Meryta macrocarpa* Baillon. Although both parts of the specimen carry tags with the same number, it is possible that it was not actually collected by Compton himself, but brought into camp by field workers or local residents. If the identifications of the two elements are correct, they both belong to taxa described well before 1921 and for which generic segregation is not warranted. It is therefore not possible to retain either name for any part of the specimen. The genus *Enochoria,* and its sole species *E. sylvicola,* should therefore be rejected under Article 70 of the *International Code* (Stafleu *et al.,* 1972).

SUMMARY

The long accepted division of the araliaceous genus *Schefflera* J. R. & G. Forst. *sensu lato* (including *Brassaia* Endl.) into two pantropical sections, CEPHALOSCHEFFLERA Harms (with flowers sessile, in capitula) and EUSCHEFFLERA (with flowers pedicellate) has been shown to be untenable. The species of the *Cephaloschefflera* complex represent an evolutionary grade (probably resulting from parallel retardation of pedicel growth) derived from various groups of umbelluliferous species throughout the geographical range of the complex. Special attention has been given to the status of *Brassaia sensu stricto,* since it has continued to be segregated from *Schefflera* by a number of authors, and the conclusion is reached that only sectional rank within the latter genus is warranted. Finally, an argument has been made for the reduction to *Schefflera* of a number of other segregate and allied genera on the grounds that the differences between most of the "attribute states" which have been used to distinguish these taxa are essentially as trivial as those used in the past to separate *Brassaia.* One of the segregates, *Enochoria,* has been shown

to have been based on an artifact. The question of the use of the name *Cephaloschefflera* for some infrageneric taxon of more restricted extent within *Schefflera* has also been discussed, with the conclusion that it could not be applied to the *Brassaia* group as presently lectotypified and is likely to become united with Blume's *Aralia* sect. PARATROPIA. An enumeration of species properly referable to sect. BRASSAIA (Endl.) Tseng & Hoo is given in the second part of this paper.

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EXPLANATION OF PLATES *

PLATE I

A (left). Diagram of inflorescence, *Schefflera hoi* (Dunn) Viguier (Burma, southwestern China). B (right). Diagram of inflorescence, *S. capuroniana* (Bernardi) Bernardi (Madagascar).

PLATE II

A (left). Diagram of inflorescence, *Schefflera barteri* (Seem.) Harms (West tropical Africa). B (right). Diagram of inflorescence, *S. japurensis* (Mart. & Zucc. ex E. March.) Harms (northern South America).

PLATE III

A (above). Inflorescence of *Schefflera* sp., near Kaibola, Kiriwina I., Trobriand group, New Guinea, ± 40 m. (1972). B (below). Inflorescence of *S. versteegii* Harms, along upper Musgrave River, east of Sogeri Plateau, New Guinea, 200–300 m. (1971).

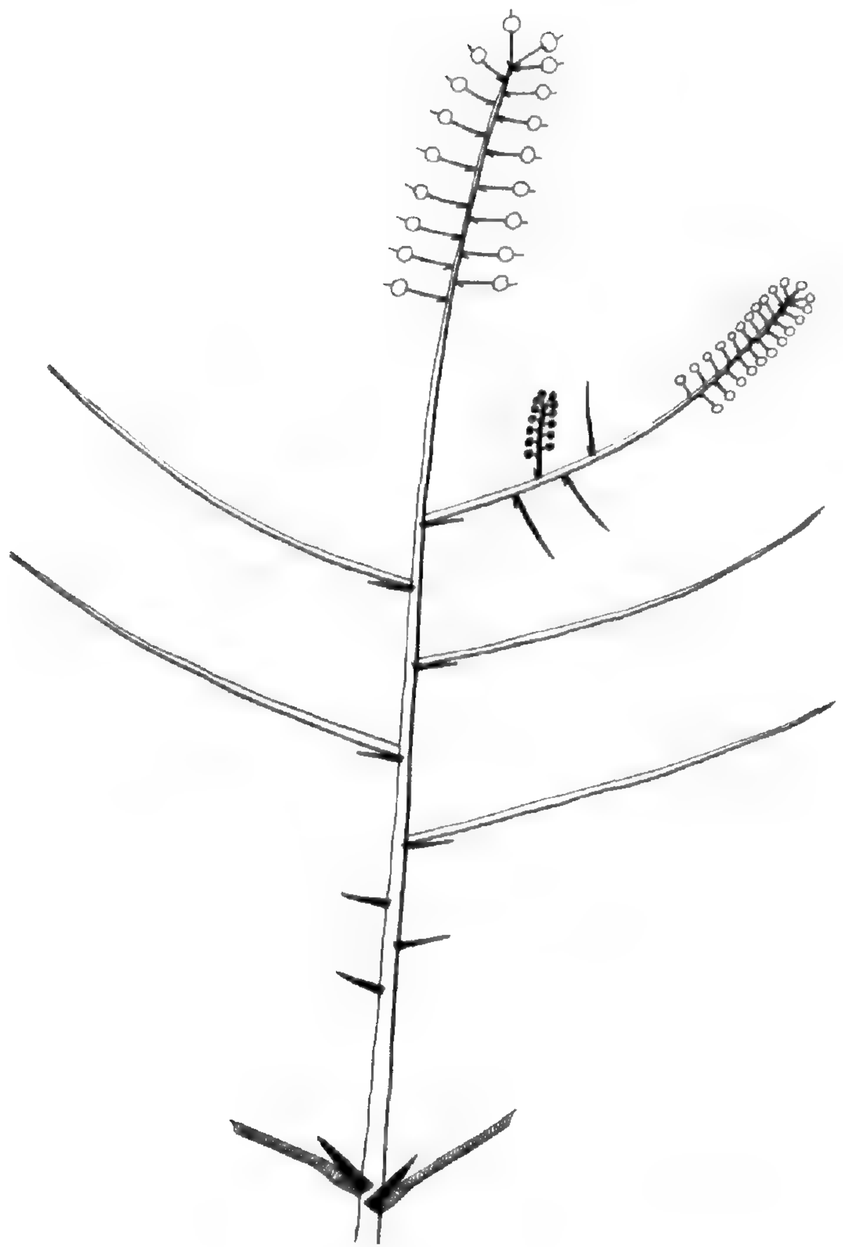
PLATE IV

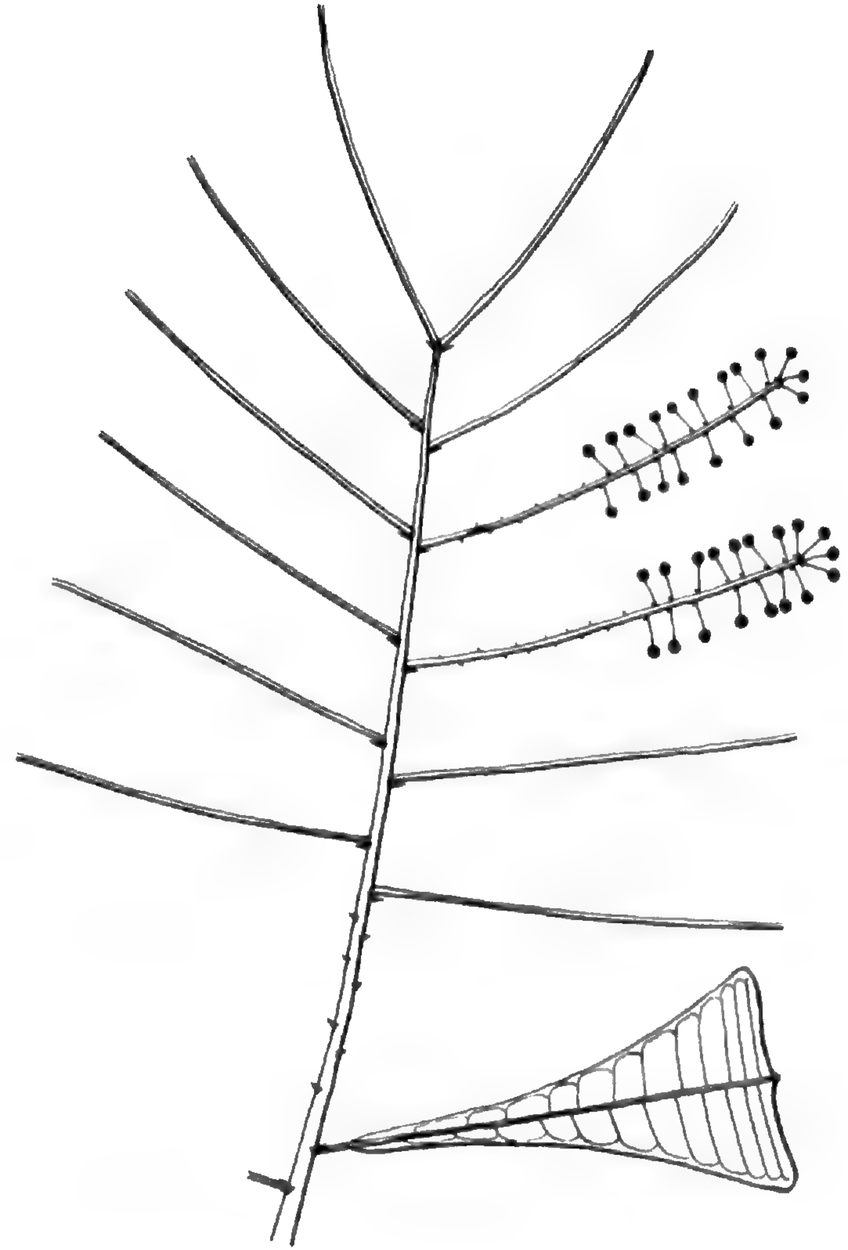
A (left). *Schefflera actinophylla* (Endl.) Harms, Royal Botanic Gardens, Sydney, Australia, ± 10 m. (1967). B (right). *S. pachystyla* Harms, near Zenag, along Lae-Bulolo Road, New Guinea, ± 1300 m. (1972).

PLATE V

A (left). *Schefflera thaumasiantha* Harms, Sogeri Plateau, New Guinea, 500–600 m. (1974; courtesy of Mr. J. Dodd). B (right). *S. waterhousei* Harms, track to Lelet Plateau, New Ireland, 500–600 m. (1973).

* In the inflorescence diagrams, the cross-hatched axes near the base represent leaf bases together with their stipules (in black).





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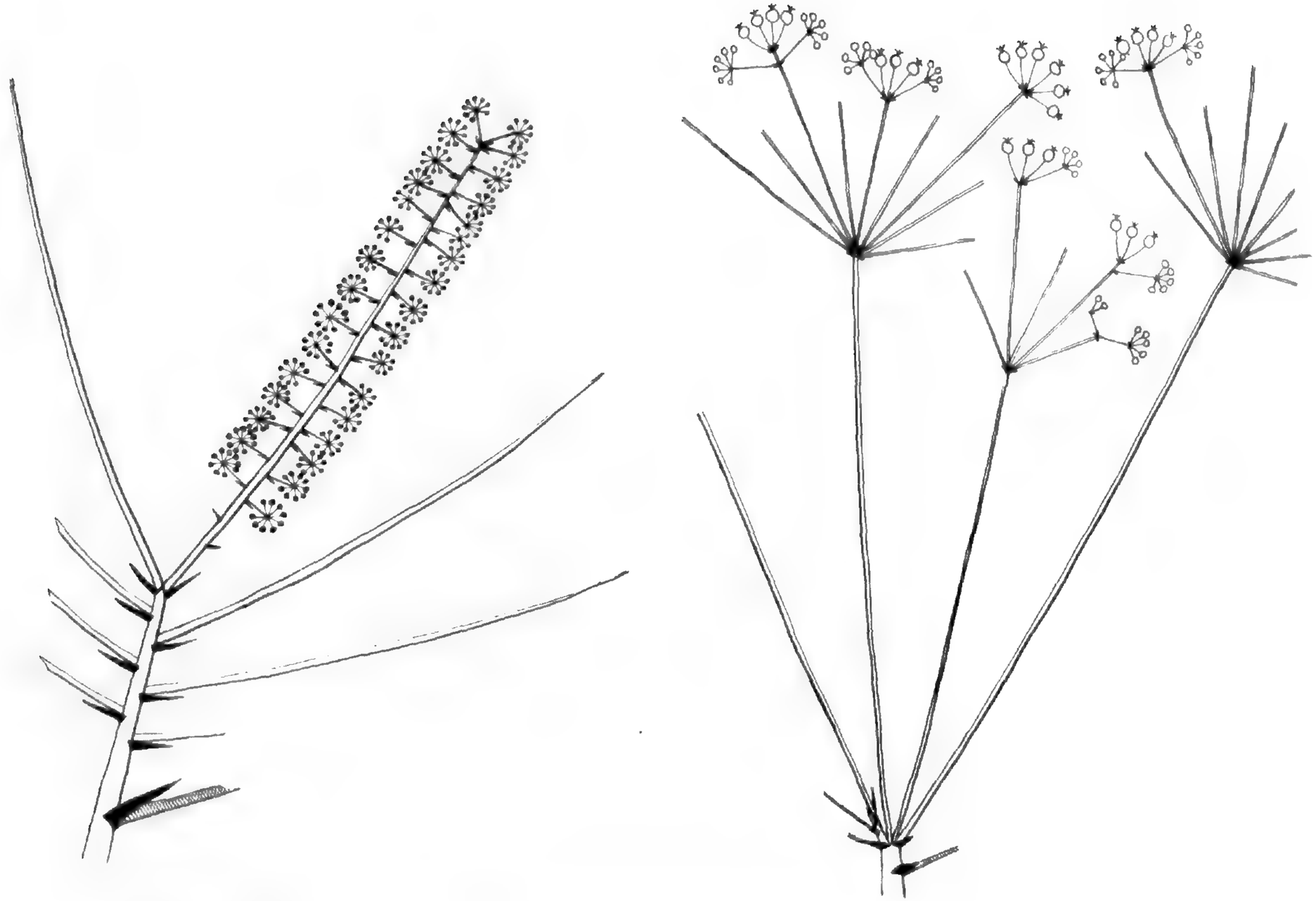

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LINDERNIA BRUCEI, A NEW WEST INDIAN SPECIES OF THE ASIAN SECTION TITTMANNIA

RICHARD A. HOWARD

IN 1950 I COLLECTED an unusual herbaceous plant while making general collections on a fragment of an old volcano above the Soufrière on the island of St. Vincent in the Lesser Antilles. The specimen appeared to be a member of the Gesneriaceae and was sent to the late C. V. Morton, who stated that it was a new genus but that the material was inadequate for description. Subsequently, botanists visiting St. Vincent were asked to seek that plant, but no one was able to locate the population. In March of 1971 I returned to St. Vincent again and made several attempts to find the plant, but without success. Although the ascent of the Soufrière volcano to the edge of the crater at 3300 feet is relatively easy, the Soma to the north of the present crater lake and the dry crater of the 1912 eruption must be climbed by the only directly ascending ridge, which I had used previously. With the frequent cloud cover, this approach to the Soma is not always visible.

In November of 1971 the crater lake of the Soufrière was observed in an agitated condition. The lake level had begun to rise, gases were being emitted, and the temperature was considerably elevated. It was apparent that the volcano was in a stage preliminary to an eruption. Eventually a cinder cone was formed from the bottom of the crater, exceeding the elevated water level by nearly 600 feet (W. P. Aspinall, H. Sigurdsson, & J. B. Shepherd, Science **181**: 117–124. 1973).

When word of this potential eruption was received, a trip was planned to photograph the vegetation around the crater in the event that an eruption occurred or lava or cinders overflowed the rim and destroyed the vegetation, as had happened in the past. (See bibliography *in* R. A. Howard, Volcanism and vegetation in the Lesser Antilles, Jour. Arnold Arb. **43**: 279–311. 1962). It also seemed that this might be a last chance to locate and collect additional material of the undescribed "new genus." On this trip in February, 1972, the summit was again cloud-covered, a condition possibly accentuated by the heat of the volcanic ejecta and the 80° C water of the crater lake. The field work was exciting at the time and remains so in retrospect. Although the summit of the Soma was obscured by clouds and visibility was limited, on our final trip occasional strong winds lifted the clouds and permitted some safe progress over the cinder slopes and crevasses. By early afternoon we had approached the Soma cliff. It was apparent that we would not see the upper levels of any of the ridges, for although they were directly in front of us, they ended in clouds. After we had climbed a bit on several

FIGURE 1. Above: Soufrière crater in February, 1971. Foreground vegetation is *Baccharis pedunculata* and *Freziera undulata*. Photo taken with a 50 m. lens. Below: Soufrière crater in February, 1972, while mound of ejecta was still increasing. Photo taken with a wide-angle lens. Arrows in the two pictures mark comparable positions; in the lower photograph, points of arrows mark the upper limit of hot water damage to the vegetation.

of the ridges, however, fortune favored us and the plant we sought was finally relocated. Field observations were made and a sizeable set of specimens was obtained.

Living plants were returned to the Botanic Garden in Kingstown but did not survive at the lower elevation. Specimens returned to the greenhouses of the Arnold Arboretum also progressively declined until, after six months, all were dead. Various methods of maintenance had failed. The plant appeared to be strongly rhizomatous and cuttings of these horizontal stems rooted readily, yet the shoots produced small leaves and failed to elongate. The thick, fleshy, pubescent leaves, reminding one of the leaves of *Saintpaulia* in texture, also proved capable of developing good masses of roots in a propagation bed; however, as they did not develop shoots, eventually these rooted leaves also failed. In retrospect, we can only surmise that the plant may be an annual.

After the death of Dr. Morton, specimens of the new collection were sent to Mr. Hans Weihler, a current student of the Gesneriaceae, who reported that the plant was different from anything known in the family from tropical America. He suggested that this material might be associated with the poorly known genus *Anetanthus* reported from Central America. This suggestion led to the study of the species of *Anetanthus* and the eventual rejection of an association with them. Advice was also sought from Dr. Harold Moore, Dr. B. L. Burtt, and Dr. John Thieret for means of distinguishing between the Gesneriaceae and Scrophulariaceae. Dr. Burtt, in a thoughtful and very helpful consideration of the problem, concluded that the plant was most likely a member of the Scrophulariaceae, and both he and Dr. Thieret suggested an association near *Lindernia* of this family.

The specimen from St. Vincent fits section TITTMANNIA according to the recent monograph of the Malaysian species of *Lindernia* by David Philcox (Kew Bull. 22: 1–72. 1968), who included a key to the sections of the genus in that area. The stamens in our material are four, are associated in pairs, and all bear fertile anthers. The nonparallel anther sacs are divergent and open by slits. In bud both the posterior pair of stamens and the anterior pair are adherent by their anthers. The filaments of the anterior pair are geniculate at the base. The calyx is deeply divided into equal segments to the base. The capsule, clearly superior, is ellipsoidal and shorter than the calyx. The stigma is bilobed.

Although Philcox did not supply a complete list of the species within section TITTMANNIA or geographic ranges, he subsequently stated that all species occur in South East Asia and that all entries in *Index Kewensis* under the name *Tittmannia* are from tropical Asia. The assignment of a West Indian specimen, clearly not an introduced plant, to this section requires serious consideration.

The genus *Tittmannia* Reichenbach (Scrophulariaceae), although long considered synonymous with *Vandellia* L., has been rejected in favor of *Tittmannia* Brongniart (Bruniaceae #3285, ICBN). *Vandellia* L. is considered a synonym of *Lindernia* Allioni by Philcox, who follows Pennell

in this treatment. Thieret did likewise in the treatment of the Scrophulariaceae for the *Flora of Peru* (Field Mus. Bot. **13**: 685. 1971), although Standley and Williams, in a later treatment of the family for the *Flora of Guatemala* (Fieldiana Bot. **24**: 374. 1973) stated, "We have followed Thieret in placing *Vandellia* L. as a synonym of *Lindernia*, but with misgivings." Yamazaki (Jour. Jap. Bot. **29**: 299–305. 1954) recognized both *Lindernia* and *Vandellia* in his treatment of the plants of eastern Asia, with the latter genus including *Tittmannia*. The species of *Vandellia* listed in *Index Kewensis* are all from Asia except *V. diffusa* L. of the New World and *V. racemosa* Sprengel, said to be from Brazil. *Vandellia diffusa* L., currently called *Lindernia diffusa* (L.) Wettst., is clearly distinct from the St. Vincent material. *Vandellia racemosa* Sprengel (Neue Entdeck. 1: 262. 1820) is described as having alternate leaves, and I can find no modern use of this binomial or any description in the many recent floras of Brazil.

A glabrous, fleshy, and quite conspicuous glandular process at the base of the ovary of the St. Vincent material, associated with the fleshy opposite leaves and the adherent anthers, directed my original search for the identity of this material with the Gesneriaceae. Neither Pennell in his many papers nor Philcox in his treatment of the Malaysian species of *Lindernia* nor any other modern floristic treatment has described this basal gland, although Philcox illustrated it indistinctly in his *figures 2–3, 3–3*, and *4–3* (Kew Bull. **22**: 14, 16, 22. 1968). However, the gland was described and illustrated by Yamazaki (Jour. Jap. Bot. **29**: 303. 1954), who in *figure 4* showed the variations in this basal glandular process for *Lindernia pyxidaria*, *Vandellia angustifolia*, *V. crustacea*, and *Torrenia violacea*. The St. Vincent material has a gland similar to that illustrated by Yamazaki for *Vandellia angustifolia*, a species Philcox calls *Lindernia anagallis* (Burm. f.) Pennell. I have examined material which Philcox cited and assigned to sect. TITTMANNIA and have found a comparable gland. Other species of other sections examined at random do show variation in the shape of the gland, so that it is possible that a character of taxonomic value may exist in the basal gland. The St. Vincent material appears to conform to the limits of the genus *Lindernia* and does not represent a new genus.

The copious pubescence of simple unicellular hairs present on all parts of this *Lindernia* from St. Vincent is distinct from the multicellular uniseriate hairs of *Anetanthus* and other genera of the Gesneriaceae. Comparable hairs are found on specimens of *Lindernia viscosa*, *L. montana*, and *L. stemodioides* cited by Philcox.

The following description of the pollen grains and the photograph (FIGURE 2) were supplied by Dr. Umesh Banerjee: pollen grains prolate, tricolpate, colpi long tapering, membrane in the colpus region consisting of warty structure, no well defined pores present, exine reticulate, thickness 1.0 μm. Superficially, the pollen grains resemble those of *Anetanthus* and *Goyazia* of the Gesneriaceae and are unlike those of *Stemodia peduncularis* Benth. of the Scrophulariaceae (Howard, Jour. Arnold Arb.

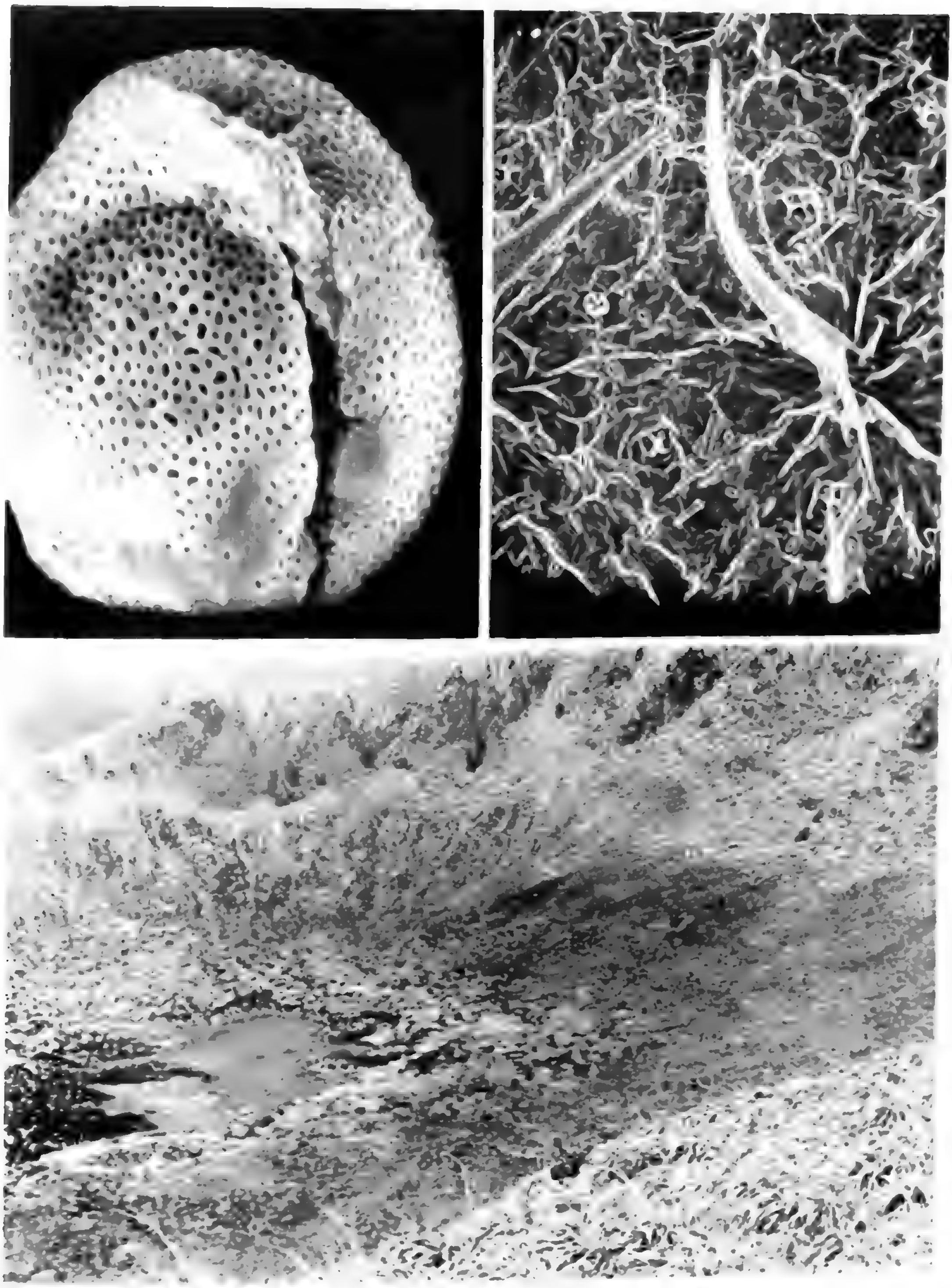

FIGURE 2. Above (left): **Lindernia brucei,** pollen grain. × 5,000. Above (right): **L. brucei,** SEM photograph of unicellular hair and a reticulated pattern of the epidermis. × 150. Below: "Dry Crater" from the 1812 eruption north of the Soufrière crater lake. Foreground vegetation is mostly *Lobelia* spp. and *Pitcairnia* spp. Slopes of the Soma are visible in the background.

56: 364–368. 1975). I have been unable to find other published SEM photographs of the Scrophulariaceae or Gesneriaceae for further comparison.

Dr. Philcox has examined material of this St. Vincent plant and agrees that the new *Lindernia* should be assigned to sect. TITTMANNIA, for which

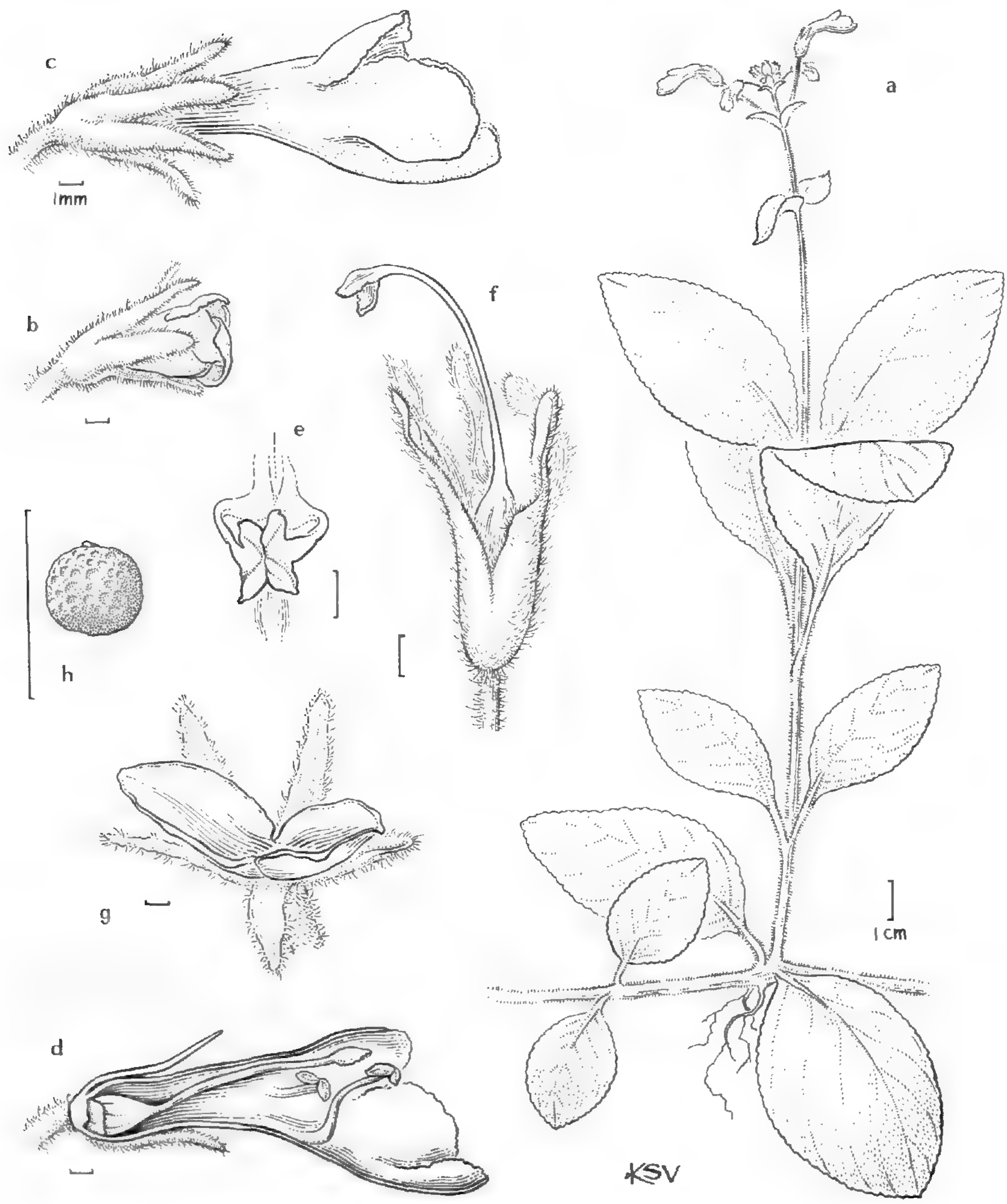

FIGURE 3. **Lindernia brucei** Howard: a, habit; b, flower in bud; c, open flower; d, longitudinal section showing basal ovarian disc and geniculate filament; e, pair of geniculate stamens with fused anthers; f, flower after corolla has fallen, stigmatic lobes flat; g, open fruit; h, reticulate seed.

it comprises a major range extension. He has suggested *L. latifolia* (Bl.) Koord. as the closest related species. I am grateful to the several people cited for their help in this problem.

Lindernia brucei Howard, sp. nov.

Herba, rhizomatibus vel caulibus serpentibus copiose radicantibus, ramis floriferis erectis usque 30 cm. altis. Lamina elliptica vel oblonga,

4 × 2.5 ad 5.5 × 3 cm., apice rotundata vel obtusa, basi rotundata vel cuneata, margine obtuse crenata, nerviis primariis 4–5, utrinque copiose pubescentia, pilis simplicis unicellularibus. Petioli 5–15 mm. longi. Inflorescentia ad medium bibracteata, bracteis ambitu deltoideis, basi truncatis, apice acutis, 1.3 × 1.1 ad 3.5 × 2.5 cm., bracteis floralibus multo deminutis, ovato-deltoideis, 5 × 3.4 mm. Pedicelli ca. 1.5 cm. longi pubescentes. Sepala 5 libera, aequalia, lanceolata 5 × 2.5 mm. longa lataque, extus copiose pubescentia. Corolla purpureo-rosea, tubo 1 cm. longo, in alabastro labio inferiore superiorem includente; labio superiore bifido, lobis rotundatis, 3.0–3.5 mm. labio inferiore majore tripartito, lobis centralis 5.5 × 6.5 mm., lobis lateralis 4.0 × 4.8 mm. Stamina didynama, glabra; filamentis duobus superioribus basi geniculatis, 3 mm. longis, inferioribus rectis 2 mm. longis. Pistillum glabrum, glandula carnosa glabra 0.8 mm. alta dimidio basi ovarii cingente; stylo 1 cm. longo, supra complanato; stigmatibus 2 planis, marginibus erosis; ovario 2 mm. longo, ellipsoideo leviter complanato. Fructus ellipsoideus 2.5 mm. longus, calyce fructifero brevior; seminibus globosis 0.4–0.45 mm. diametro, brunneis, testa reticulata.

Distribution. St. Vincent, Lesser Antilles, West Indies. Ridges at the base of the Soma, north of the crater lake on the Soufrière mountain at an altitude of 3600 ft. Flowering in February with flowers and fruit in April.

Specimens examined. *R. A. Howard 11912* (GH, US); *R. A. & B. R. Howard 18060* (holotype, A), Feb. 26, 1972.

I take pleasure in naming this species for my son, Bruce Howard, a companion on the trip on which I re-collected the material and my assistant in earlier field work on Pico del Oeste in Puerto Rico.

I am grateful to Ms. Karen Velmure and Dr. L. M. Perry for assistance in the preparation of this paper.

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THE PODOSTEMACEAE IN THE SOUTHEASTERN UNITED STATES [1]

S. A. GRAHAM AND C. E. WOOD, JR.

PODOSTEMACEAE L. C. Richard ex C. A. Agardh, Aphor. Bot. 125. 1822, "Podostemeae," nom. cons.

(RIVERWEED FAMILY)

Moss- or alga-like, submerged aquatics, generally restricted to sunny, clear, swiftly flowing streams and waterfalls of the tropics and subtropics. Plant body often reduced to a "thallus" and anchored to the rock substrate by cement-secreting root hairs and haptera (specialized rootlike organs that act as holdfasts). Stems present [or lacking]. Leaves alternate, simple to much divided. Inflorescences diverse, the flowers solitary [or fasciculate or in a 2-sided spiciform monochasium], [enveloped by a few leaves or] entirely inclosed within a membranaceous spathella (or "spathe") that ruptures irregularly as the pedicel elongates before anthesis. Flowers [actinomorphic to] zygomorphic, perfect. Perianth of 2 or 3 [or 5 to many] tepals (staminodes?), [petaloid to] reduced and scalelike. Stamens [1 or] 2 [to many]; anthers 4-loculate; pollen commonly in dyads [monads or polyads]. Gynoecium [1-], 2- [or 3-] carpellate, syncarpous; ovary superior, [1-], 2- [or 3-] loculate; ovules [2 to] many, on an axile placenta. Fruit a septifragal [or septicidal] capsule; seeds many, without endosperm; embryo straight. TYPE GENUS: *Podostemum* Michx.

[1] Prepared for the Generic Flora of the Southeastern United States, a joint endeavor of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of the National Science Foundation. This treatment, the seventy-seventh to be published, follows the format established in the first paper in the series (Jour. Arnold Arb. **39**: 296–346. 1958). The area covered 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 additional material in brackets [ ]. References that we have not seen are marked by an asterisk.

The manuscript for this account was originally prepared when the first author was a member of the Generic Flora project in Cambridge in 1963–64 (NSF Grant GB-171, C. E. Wood, Jr., principal investigator). Since only a single species was involved, and the New World members of the family had been recently revised, publication was delayed pending the addition of other material and the preparation of a suitable illustration. The manuscript has been revised and updated by the second author (under NSF Grant BMS 74–21469). Since the family is one of great biological interest and since the numerous references are rather widely scattered, an unusually large number of references (out of all proportion to the representation of the family in our flora) are presented here. The illustration was drawn in April, 1975, by Karen S. Velmure under the supervision of Kenneth R. Robertson, who also prepared the dissections. The liquid-preserved material from which figures *a* to *h* were drawn was collected in North Carolina by S. W. Leonard and William Waterfield and came to us through the kindness of S. A. Spongberg and R. E. Weaver, respectively.

A remarkable pantropical family of highly modified submerged aquatics, including about 45 genera and 200 species, many of these narrow endemics, a few widely distributed. Almost all are restricted to rocky substrates in clear, sunlit, swift-running streams and rivers, where they occur especially in waterfalls and rapids. About 140 species are known from the Americas, 40 from Africa, and 20 from Asia (northward to southern Kyushu, Japan) and Australia (Queensland). *Podostemum ceratophyllum* Michx., one of the few representatives of the family in temperate regions, occurs in the southeastern United States.

The unique habitat of these plants is shared by hardly any others, except Hydrostachyaceae. The family is notable for a high degree of speciation and endemism, with several species and some genera known only from a single rapids or cataract, and with some closely related species occupying adjacent tributaries of the same river or nearby rivers (Van Royen, 1951, p. 13). A few exceptional species, including *Podostemum ceratophyllum*, are widely distributed. *Tristicha trifaria* (Bory ex Willd.) Sprengel is noteworthy, extending as it does from Cuba to Mexico, southward to Uruguay and Argentina, and over a large part of Africa to Madagascar.

The plants flower as the water level recedes (usually with the onset of a dry season) and as they become exposed to the air. Pollination is usually by insects or wind and is followed by very rapid fruit development, in some cases the fruit maturing in as little as 24 hours (e.g., in *Apinagia*; see Went, 1926, 1929). The seed coat is mucilaginous when moistened and adheres to the substrate, where the seed germinates if it is not washed away as the water level rises (cf. *Podostemum*). *Polypleurum submersum* J. B. Hall is a rare exception in the family in that it grows in still rock pools in the River Asuboni, Ghana, prospering "even in pools that are stagnant and separated from the flowing water. Spathellae open under the surface and flowers are pollinated by the current." The fruits dry and dehisce, however, only when exposed to the air.

Podostemaceae are so variable morphologically that it has proved difficult to devise a satisfactory subfamilial classification, although several have been proposed. Most recently, Van Royen (1951) has recognized two subfamilies: Tristichoideae Engler emend. Royen, with flowers enveloped by a few leaves and with a 3- or 5-lobed perianth, and Podostemoideae, with flowers inclosed in a "spathella" and with the tepals reduced to scales. The four tribes (Tristicheae, Weddelineae; Mourereae, Podostemeae), two in each subfamily, are based mainly on characters of the inflorescence, perianth, and stamens.

The relationships of the family Podostemaceae to other families have been the subject of much discussion, leading to its placement near such diverse families as the Piperaceae, Polygonaceae, Caryophyllaceae, Crassulaceae, Nepenthaceae, and Scrophulariaceae. Embryogeny provides strong evidence of its relationships to Crassulaceae and to Hydrostachyaceae, a small family once united with the Podostemaceae. Among the characteristic features of the embryology of the Podostemaceae are the

tetranucleate megagametophyte (embryo sac) that lacks antipodal cells or has only a single one; the absence of endosperm; the growth of the top of the megasporangium (nucellus) beyond the inner integument into the endostomium; the restriction of the megagametophyte (embryo sac) to the upper part of the megasporangium (nucellus), while the lower part elongates to form a pseudo-embryo sac; and the appearance of the outer integument to form the micropyle before development of the inner integument. Maheshwari, drawing support from the earlier embryological studies and conclusions of Mauritzon, has suggested that the Podostemaceae (and Hydrostachyaceae) are derived by reduction from the Crassulaceae, a theory based mainly on the highly developed suspensor haustoria found in both families and the similarities in embryogeny between some aquatic Crassulaceae (e.g., *Tillaea aquatica*) and the Podostemaceae.

In floral morphology the evolutionary trend appears to have been from actinomorphic to zygomorphic flowers, accompanied by a change from entomophily to anemophily or autogamy. A high degree of ovule abortion, of unknown cause, has been reported.

The only chromosome numbers reported are those of *Terniola ceylanica* (Gardner) Tulasne (as *Lawia zeylanica*), $2n = 20$; *Podostemum subulatum* Gardner, $2n = 40$?; and *Weddelina squamulosa* Tulasne, $2n = 40$.

Van Royen notes that plants of this family throw off part of the outer tissues after the water level subsides, producing great changes in appearance and making it difficult to judge herbarium material, in which these same changes can occur during the process of pressing and drying. The best way of preserving specimens is in 60–70 per cent alcohol, in 4 per cent formalin, or in a mixture of the two.

The Podostemaceae are of great biological interest but of no economic importance.

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Subfam. PODOSTEMOIDEAE

Tribe PODOSTEMEAE

1. **Podostemum** Michaux, Fl. Bor. Am. **2**: 164. *pl. 44.* 1803.

Gregarious, dark green to reddish herbaceous perennials of shallow, rushing streams or rapids, firmly attached to rocks or gravel by means of cement-secreting root hairs and fleshy disclike haptera arising from the lower surface of ± dorsiventral, photosynthetic, horizontal (plagiotropic), creeping, branched roots. Stems present [or lacking], originating in pairs along the sides of the roots, without a growing point, the leaves alternating in two ranks, each leaf arising from the base of the next older leaf in its rank; lateral shoots arising at the base of the leaf on its outer (abaxial) side, not in the axil of the leaf. Leaves distichous, repeatedly forked [or entire], spathulate to mainly filiform, with the exception of the lower leaves with an intrapetiolar stipule. Flowers axillary, solitary on short pedicels, the spathella rupturing at the distal end, the tepals and stamens restricted to the adaxial side of the flower. Tepals (the "staminodes" of some authors) 2 or 3, filiform, acute, one on each side

FIGURE 1. **Podostemum.** a–n, *P. ceratophyllum.* a, part of horizontal root with several opposite branches (some removed for clarity), anchoring haptera produced on root below branches, the leaves repeatedly forked, × 2; b, detail of hapteron, × 3; c, detail of branch, showing bases of leaves with intrapetiolar stipules, each flower solitary in a spathella in axil of leaf, × 3; d, young flower emerging from spathella, × 6; e, same flower from behind (removed from spathella), a tepal to each side of androphore and a third inserted on androphore

of the androecium (partially fused filaments, androphore, andropodium), the third (the "scale" of some authors), when present, in the fork between the filaments of the two stamens. Androecium of (1), 2 (or 3) stamens, borne by an andropodium or androphore (or this interpreted as the staminal filaments fused for about one-half their length); anthers introrse, 4-locular, longitudinally dehiscent; pollen grains in dyads. Gynoecium 2-carpellate, syncarpous; styles 2, simple, equal, free, the stigmata indistinct; ovary superior, 2-loculate, the abaxial locule larger; ovules many, anatropous on a thick, fleshy, axile placenta. Fruit a [6- or] 8-ribbed, septifragal, 2-valved capsule, the smaller, adaxial valve caducous, the larger, abaxial valve persistent, the enlarged placenta and seeds becoming detached; seeds numerous, minute, with an outer mucilaginous layer (when moistened). TYPE SPECIES: *P. ceratophyllum* Michx. (Name from Greek, *pous*, *podos*, foot, and *stemon*, stamen, in reference to the stamens apparently supported by a pedicel: "stemonia pedicello suffulta.") — RIVERWEED.

A primarily tropical genus of 17 or more species of North and South America, and perhaps India and Ceylon: *Podostemum ceratophyllum* in eastern North America, Hispaniola, and Honduras; *P. ricciiforme* (Liebm.) Royen in Mexico and Costa Rica; and 15 species distributed from central Brazil to Uruguay, Paraguay, and northern Argentina. Species attributed to this genus have been described from Africa, Madagascar, India, and Ceylon, but all except two, *P. subulatum* Gardner (Ceylon and southern India) and *P. Barberi* Willis (southern India), have been excluded (cf. Engler, 1915; Willis 1902b, c; Hall). The taxonomic disposition of these two species appears to be unresolved, but it may be worth noting that their leaves are spirally, rather than distichously, arranged and lack stipules.

Podostemum ceratophyllum, the only species of the family in eastern North America, has an unusually broad distribution, extending northward to New Brunswick, Quebec, and Ontario, and southward to Georgia, Alabama, Mississippi, Louisiana, southeastern Oklahoma, and western Arkansas, and with disjunct localities in the Dominican Republic and (as var. *circumvallatum* Royen) in Honduras. It is of local occurrence and is extremely variable in habit, especially in size and dissection of the leaves. One extreme with lax, elongate leaves has been named f. *abrotanoides* (Nutt.) Fassett, and the opposite extreme with coarse, rigid leaves is f. *chondroides* Fassett, the author of the combinations acknowledging that the two are not geographically distinct and are connected by a series of

between filaments, × 6; f, flower immediately before anthesis, × 6; g, flower at anthesis, × 6; h, cross section of ovary to show unequal locules and axile placentation, × 12; i, part of stem with nearly mature fruit to upper left (spathella mostly broken away), immature fruit with withered, persistent anthers to upper right, leaf base and young leaf to lower right, × 6; j, mature fruit before dehiscence, × 12; k, fruit after dehiscence, larger valve of capsule persistent on pedicel, × 12; l, placenta removed from fruit, × 12; m, seed, moistened to show mucilaginous seed coat, × 25; n, dry seed, × 25.

intermediates. Whether this variation is genetic or ecological is largely unstudied. Hammond found, however, that at Difficult Run, Virginia, three forms grew side by side, forming colonies of various sizes, the plants of a colony being usually uniform in size and structure. When plants of the two extremes were transplanted to two localities in Maryland, they grew well and retained their original characteristics during an observation period of several weeks.

The extraordinary life history of *Podostemum ceratophyllum* was studied by Hammond, who observed the entire cycle in Maryland and Virginia, with the exception of seed germination. Growth of roots and shoots begins in the spring from the bases of plants of the previous season; by June flower buds are formed in the axils of leaves, where they remain inclosed in the spathella as long as the plants are submerged. If the water level subsides, exposing the plants, the pedicel promptly elongates and the spathella ruptures, revealing the flower. Self- or perhaps wind-pollination occurs, and within a few days the seeds are mature and shed from the open capsule, where they adhere to the surrounding dry rocks by means of mucilaginous seed coats. In our area, where wet and dry seasons are indistinct, the plants may remain submerged through an entire summer, never flowering, but growing vegetatively and propagating by regeneration from pieces of roots, stems, or leaves that have broken from the parent plant.

Seed germination apparently has not been observed in *Podostemum ceratophyllum* but is probably like that of *P. subulatum* (cf. Willis, 1902c, p. 329) and many other genera of the family. With the rise in water level the hypocotyl emerges from the seed, bends downward, attaches itself to the substrate by root-hair-like rhizoids and expands to form a larger area of attachment. The seedling becomes erect, cotyledons and primary leaves appear in two ranks, and the primary axis then stops growing. No developed primary root has been reported for any member of the family, and the secondary root is adventitious from the base of the hypocotyl. The root is dorsiventral, and in *P. ceratophyllum* there are only two rows of lateral roots, all of which retain this symmetry. Branches are produced in pairs a short distance behind the root growing point. The roots attach themselves by root hairs and by disclike or fingerlike haptera that arise exogenously from the underside of the root, usually under the base of each shoot. The haptera are entirely parenchymatous, have a terminal growing point, and lack vascular tissue. They are believed by some to be derived phylogenetically from the root, by others to be similar to tendrils in origin. The shoots grow out transversely to the root and more or less erectly from the substrate.

There is no stem growing point, each of the two-ranked leaves arising from the base of the next older leaf in its rank. Each leaf has an intrapetiolar stipule. Lateral branches of the shoot are not axillary within these stipules but arise at the base of the abaxial side of the leaf (i.e., on the side opposite the stipules) and are covered by a stipulelike structure formed on this same side of the leaf. Stomata are completely absent,

and the epidermal cells of the root, as well as of the leaves, contain chlorophyll.

The only chromosome number reported for the genus is $2n = 40?$ in the Ceylonese and southern Indian *Podostemum subulatum*.

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ADDENDA

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